Hultsch, Henrike; Todt, Dietmar

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HENRIKE HULTSCH and DIETMAR TODT

Institute of Biology, Department of Behavioural Biology, Free University of Berlin
Haderslebener Str. 9, 12163 Berlin, Germany

ABSTRACT

There is growing evidence that, during song learning, birds do not only acquire 'what to sing' (the inventory of behavior), but also 'how to sing' (the singing program), including order-features of song sequencing. Common Nightingales *Luscinia megarhynchos* acquire such serial information by segmenting long strings of heard songs into smaller subsets or packages, by a process reminiscent of the chunking of information as a coding mechanism in short term memory. Here we report three tutoring experiments on nightingales that examined whether such 'chunking' was susceptible to experimental cueing. The experiments tested whether (1) 'temporal phrasing' (silent intersong intervals spaced out at particular positions of a tutored string), or (2) 'stimulus novelty' (groups of novel song-types added to a basic string), or (3) 'pattern similarity' in the phonetic structure of songs (here: sharing of song initials) would induce package boundaries (or chunking) at the manipulated sequential positions. The results revealed cueing effects in experiments (1) and (2) but not in experiment (3). The finding that birds used temporal variables as cues for chunking does not require the assumption that package formation is a cognitive strategy. Rather, it points towards a mechanism of procedural memory operating in the song acquisition of birds.

Key words: song learning, procedural memory, song sequencing, short-term memory, chunking.

INTRODUCTION

When humans have to memorize a larger body of learning material, they use a strategy that Bower (1970) termed 'divide and conquer', better known as chunking. The chunking of information has been extensively studied in human list learning paradigms, but it also turned out as an organizing principle in the serial learning of non-human vertebrates, including birds (for review see Terrace 1991, Hultsch et al. 1999). Thus chunking seems to be a rather basic mechanism of processes involved in memory formation.

Correspondence to: Henrike Hultsch
E-mail: hultsch@zedat.fu-berlin.de
Dedicated to the memory of Dagmar von Helversen

We have addressed the role of chunking in memory formation in the song acquisition of birds, which provides an ideal model for a number of reasons. (1) Like humans, songbirds are predisposed for the acquisition of the species specific vocal patterns (for review see Marler 1987). This enables the use of natural stimuli of high biological salience in the learning situation. (2) In many species, perceptual and motor learning do not overlap in time. Hence, memorization and storage of information during instruction can be distinguished from the retrieval of information during performance. (3) Many songbirds readily acquire a large repertoire of diverse and structurally distinct vocal signals through

learning, permitting the use of large sets of alternative model song patterns, similar to the list learning paradigms used in studies on human serial learning. (4) Singing is serial in time. Therefore the sequencing of acquired songs can be compared to the sequence presented during the tutoring.

In studying the mechanisms of how auditory information is stored and retrieved in the bird's brain, we have shown that Common Nightingales *Luscinia megarhynchos* (hereafter named nightingale) learn not only 'what to sing' (i.e. an inventory of behavior, here the tutored song-types), but also 'how to sing' (i.e. a singing program, here song sequencing; review in Todt and Hultsch 1996). The way males imitated order-features of a tutored song string suggested that they segmented that string into smaller subsets and stored them as clusters or 'packages' of sequentially associated songs ('package formation', Hultsch and Todt 1989). By presenting song strings the experimental design eliminated any cues that might induce the grouping of song models by the subjects. These design features included random selection and arrangement of song-types, regular spacing (4s) of successive songs, and playback in standardized tutoring sessions. Therefore, any string segmentation was induced by the system itself, suggesting that it results from constraints in the information processing machinery (e.g. working memory).

In the study reported here we set out to examine this question from the opposite point of view. That is, we asked whether package formation could be influenced by phrasing cues or 'tags' experimentally introduced into a string of song models. If birds responded to cueing by developing package boundaries at manipulated sequence positions, package formation could be interpreted as a cognitive coding strategy in the song acquisition of birds. In addition, this would allow us to make comparisons with the concepts of memory formation put forward in the area of cognitive research (for review see Terrace 1991, Cowan 2001).

In our experiments we used three kinds of cues to tag particular song-types of a master string: (1)

in the 'time cueing' experiments, particular master song-types in a string were spaced out by a silent intersong interval longer than those between other song-types (duration: 20s versus 4s); (2) in the 'novelty cueing' experiment, a basic song string was progressively enlarged upon subsequent presentations by the addition of song-types to which the subjects had not been exposed before; and (3) in the 'pattern cueing' experiment, particular master song-types were similar in phonetic structure, i.e. they shared initial element-types.
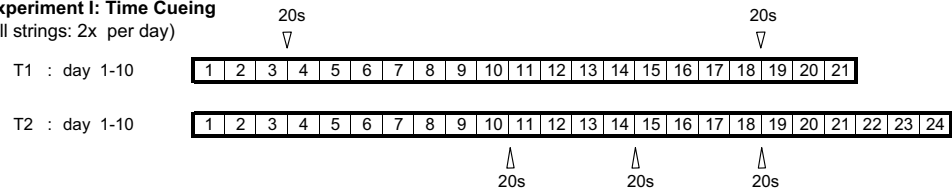
MATERIALS AND METHODS

Subjects. The study was conducted on 18 male nightingales, which were taken from the field as nestlings (last May to first June decade; age: 3-8 days) and hand-raised as four groups. Subjects were transferred to separate cages at day 15 after leaving the nest (age: ca. 28 days). From then on they had visual contact only with the human caregiver (tutor) who did the hand-raising and later presented the tutoring programs. Subjects were shielded from auditory contact with other birds, and when their own song production began (ca. 20 weeks after hatching), they were housed in separate rooms.
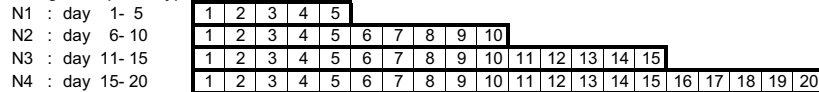
Tutoring. The song-types which were used as master song-types were selected at random from a catalogue of nightingale song-types which, in earlier studies, had proven to be equally 'attractive' for acquisition and to which occurred in a subject's repertoire only if they had been presented as model song-types. The songs were successively recorded on tape with silent intersong intervals of 4s, which is their typical duration. Several tapes were generated each containing a particular string of master song-types. Each successive song in a given string was a different song-type ('pattern-type labeled tutoring', Hultsch et al. 1984). The details of string composition and modification of this basic design are illustrated in figure 1 and further specified in the description of the experiments.

The playback of master song strings was done through a loudspeaker positioned close to the human

Exposure Schedule   Song Strings and Succession of Master Song-types

Experiment I: Time Cueing
(all strings: 2x per day)

T1 : day 1-10

| 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 |

T2 : day 1-10

| 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 |

Experiment II: Novelty Cueing
(all strings: 1x per day)

N1 : day 1- 5 | 1 | 2 | 3 | 4 | 5 |
N2 : day 6- 10 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
N3 : day 11- 15 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 |
N4 : day 15- 20 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 |

Experiment III: Pattern Cueing
(2x per day)

P1 : day 1- 10

| 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 |

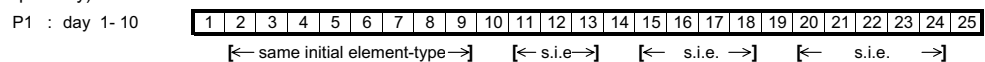[← same initial element-type →]   [← s.i.e →]   [← s.i.e. →]   [← s.i.e. →]

Fig. 1 – Design and presentation schedule of song-type strings used in the experiments I (top: T1; T2: time cueing), II (middle: N1-N4: novelty cueing) and III (bottom: P: pattern cueing). The succession of master song-types in a string is given by numbered cells. Top: Arrows indicate the sequential location where intersong intervals of 20s were introduced in the song succession (intersong spacing otherwise: 4s). Bottom: Groups of song-types which had identical initial song sections are within parenthesis. Interspersed between these different groups were 'single' song-types with an initial song section that differed from both the preceding and the following group.

tutor who was sitting in front of the cages. The presence of a socially familiar individual (here: caregiver) enhances early song acquisition in nightingales (for review see Todt and Hultsch 1996). Playback sessions were conducted between 9 and 11 a.m. Tutoring began when the birds had reached an age of about 4 weeks and ended during their 7th week of life. So, it was conducted within the first sensitive period of song acquisition in nightingales (Hultsch and Kopp 1989). During that time and until approximately the end of November, fledgling nightingales do not, as a rule, vocalize patterned song.

Data sampling and analysis. The singing of males was automatically recorded by a computer controlled, voice activated registration (R. Specht, Berlin) using Panasonic Hi-Fi F55 stereo video recorders and Sennheiser ME 80 microphones. Recordings were analyzed by sound spectrography using a 'Nicolet UA 500A' spectrum analyzer connected to a 'Tönnies' film camera for hard copy production of spectrograms. In addition, songs were sampled and printed as spectrograms using the commercial program 'Avisoft' (R. Specht, Berlin).

The data for the present study are based on 'crystallyzed' singing, recorded at about 44 weeks of age (criteria: songs were delivered in their final structure – i.e. song patterns were stereotyped in their phonetic structure and syntax – and successive songs were segregated by silent intersong intervals of $> 0.5s$). Long records of singing behaviors (at least 30min of continuous performance) were selected and analyzed by sound spectrography.

Spectrographic displays of the birds' songs

were compared by eye to the presented master song-types. A given song was accepted as an imitation of a model song-type, if it contained the complete trill section (γ-section) of the respective master song-type plus at least 3 successive syllables from the note complex (β-section) preceding the trill section (Hultsch 1980). Vocal patterns that could not be identified as an imitation were pooled in a remainder class ''R''.

For the sequential analysis of song-type successions, transitions between successively produced imitations were examined by matrices (first order) with both row and column categories following the serial order of master song-types in a tutored string (Fig. 2). The distribution of entries in matrix cells served as a basis for the detection of song-type packages. For an examination of cells located around the major diagonal we used the coefficient of directed transitions (CDT) which compares the frequencies of 'forward' and 'backward' transitions (for details see Hultsch and Todt 1989). Statistics on the identified packages were conducted on partitioned contingency tables (Castellan 1965) which examined whether a package was a significant category in a bird's performance (chi-square test).

RESULTS

EXPERIMENT I: TIME CUEING

In this experiment we examined whether package formation would be influenced by temporal phrasing cues occurring within a presented item list (string of master song-types). The time structure of string presentation was manipulated by modifying the duration of intersong intervals between successive master song-types (normal duration: 4s) at particular positions of a master string (prolongation to 20s). If package formation of birds was cued by the longer intersong intervals, package boundaries should be preferentially located at those serial positions of the string where the master song-types had been spaced out. In addition, as there is evidence that package formation is controlled through a time-constrained gating process upon exposure (Hultsch 1992), we

expected a relationship between the size of packages and the particular string segment from which they had been developed.

To prepare for this experiment, two tapes (T1, T2) were generated that differed in the sequential location at which intersong spacing was modified. Tape composition and the schedule of presentation are given in figure 1. T1 was presented to 5 males (A, B, C, D, E) and T2 was presented to 4 males (F, G, H, I). The strings were played twice in a row (interval between subsequent renditions: 2min) on 10 successive days, yielding a 20 times total exposure.

The sequential analysis of transitions occurring in imitations (cf. Materials and methods) revealed that subjects reproduced master song-types as packages of sequentially associated song-types. As found previously (Hultsch and Todt 1989): (1) packages comprised only imitations from sequentially adjacent master song-types, (2) the mean package size was around 4 song-types, and (3) acquisition failures did not occur within song-type packages.

Figure 3 illustrates the distribution of song-type packages with reference to the succession of song models in the master strings. Subjects shared most boundaries at those sequential position where a longer intersong interval (20s) separated successive master song-types, whereas at the other positions most boundaries were particular to the individual (mean number of males sharing boundaries at spaced-out positions: 2.2 versus 1.2 at the remaining positions). 73% of the packages around spaced-out positions had a boundary related to these positions, while only 27% were made up by imitations of master songs heard both before and after a temporal gap. This effect was most prominent when 20s interval had separated the first three master song-types from the rest of the string (T1), but was less marked when the 20s interval had been introduced later in the string (T1, T2).

The mean package size was slightly but not significantly smaller for those packages which spanned a temporal gap as compared to packages developed from the temporally 'coherent' parts of the strings
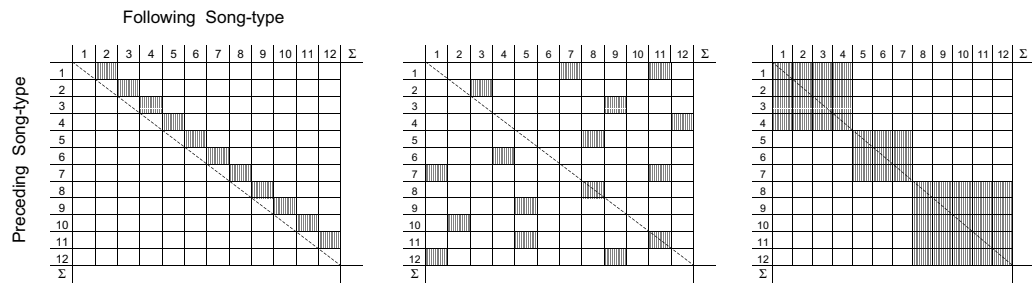
Fig. 2 – Schematic illustration of three possible relationships between the serial succession of master song-types and that of imitations developed by the subjects. The succession of master song-types in a given string is represented in the row and column categories of the transition matrices. Sequential transitions between imitations from that string are illustrated by hatched areas in the cells of the matrix body. Left: the sequential succession of imitations matches that of master song-types: all transitions are in the cells next to the major diagonal. Middle: transitions between imitations are random with respect to the sequencing of the master song-types. Right: the sequential succession of master song-types is reflected in the subjects singing. Transitions between imitations are centered around the major diagonal, but this holds only for a limited number of imitations developed from successively presented master song-types. Imitations which form a cluster of transitions are the constituents of a given 'song-type package'.
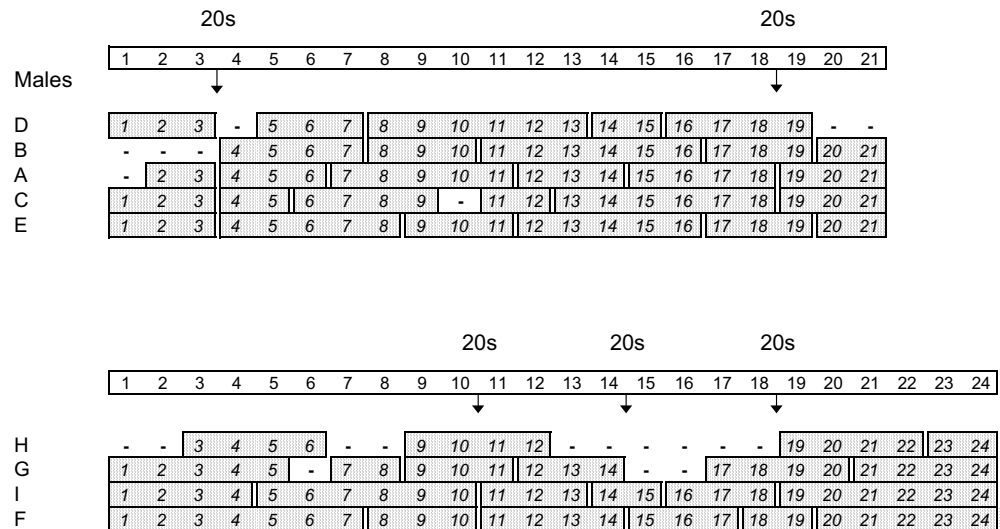

Fig. 3 – Imitations (italic numbers) and their sequential associations (song-packages, stippled areas) developed by the birds A-E and F-I from the strings T1 and T2 presented in the experiment 'time cueing'. Arrows indicate the sequential locations where two successive songs were segregated by 20s (instead of 4s) and where package boundaries were expected if cueing occurred. Acquisition failures are given by '–'.

(M ± SD: 3.1 ± 0.8 versus 3.9 ± 1.6; Fig. 4). However, in the former sample, the maximal number of song-types associated in a package was four, whereas package sizes of up to seven song-types were found in the latter sample.
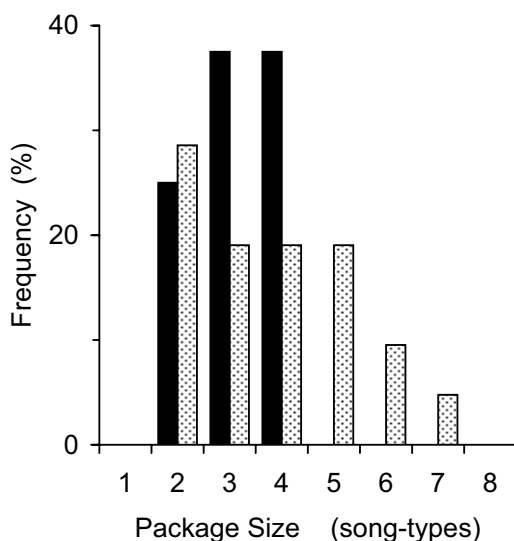

Fig. 4 – Frequency distribution of package sizes (given as number of song-types) assessed in packages that spanned a longer temporal interval between master song-types (20s interval; black columns) or in packages developed from temporally 'coherent' string portions (4s interval; stippled columns). The latter sample does not include packages that had a boundary at the spaced out string positions.

With regard to the question of whether a temporal gap (20s) between otherwise evenly spaced (4s) items would act as a cue for package formation the results were equivocal: cueing was effective when a gap was introduced into the first quarter of the master string (T1), but the relationship between package boundaries and spaced-out master song-types for the other positions was less clear. The latter finding substantiates the notion that song-type packages are the result of a segmentation process, which is controlled through a time constrained gating mechanism during the acquisition process (Hultsch 1992). Within a time window, the elapsed time between state 'on' and state 'off' determines how much song-type data

is processed and memorized as a package of information. In the study of Hultsch (1992), the duration of the time window was empirically assessed as 35s on average (max. around 55s). A similar duration limit was evident in the findings of the present study: none of the packages that spanned a temporal gap comprised more than four song-types. Translated to the segmental time, span encompassed by a segment of that size is equivalent to around 48s.

From this model, a testable prediction can be derived: a further prolongation of temporal intervals (e.g. to 30 or 40s) should significantly raise the probability for package boundaries at the spaced-out master songs. Implicit in this interpretation is the assumption that temporal phrasing as such was not recognized as a cue for package 'closure'. Rather, it is more parsimonious to interpret preferred package boundaries at the spaced-out positions as being generated by time constraints in the gating process, switching from state 'on' to state 'off'. It remains an open question then, why package formation had been perfectly cued by the first 20s gap in string T1.

Experiment II: Novelty Cueing

This experiment examined whether package formation would be cued through groups of novel song-types (substrings) subsequently added to groups of songs which, due to prior exposure, could be regarded as having been 'experienced'. If cueing was effective, package boundaries should be frequent at locations where a novel substring had been added to the basic string. The experiment also referred to the hypothesis that a given package is a stable unit of processing during memorization and/or storage and that package formation occurs upon the first exposure to a song-type string (Hultsch and Todt 1989). As a prediction from this hypothesis, the developed song-type packages should not be larger than the size of the presented substrings, i.e. package boundaries should not span the boundaries of substrings.

To prepare this experiment, four tapes (S1-S4) were generated holding 5, 10, 15, or 20 songs. Their composition and the schedule of presentation is given in figure 1. Total exposure was 20 times
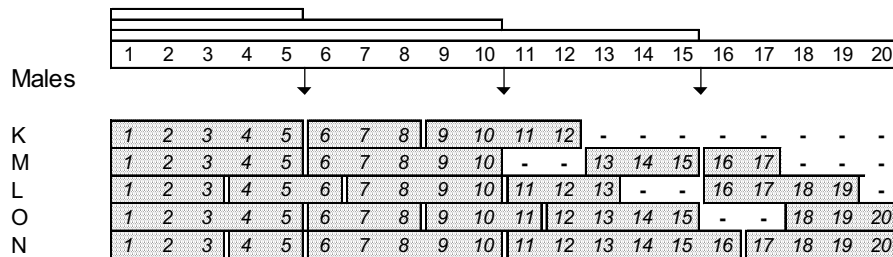
Novelty cueing

Fig. 5 – Imitations (italic numbers) and their sequential associations (song-packages, stippled areas) developed by the birds K-O from strings presented in the experiment 'novelty cueing'. Symbols of master song-types are given on top. Arrows indicate the sequential locations where new substrings were added and where package boundaries were expected if cueing occurred. Acquisition failures are given by '–'.

(song-types 1-5), 15 times (song-types 6-10), 10 times (song-types 11-15) or 5 times (song-types 16-20). Compared to a simple addition of different substrings to only one basic string, this design allowed for the examination of different 'degrees' of novelty through differences in exposure frequency. The tapes were played to 5 birds (males K, L, M, N, O) on 20 successive days.

Birds differed in the number of master song-types they had acquired from the tutoring, and only one subject (male N) imitated all song-types to which he had been exposed (Fig. 5). The acquisition success for the other males showed a relationship to the frequency of exposure to master song-types: while they imitated all master song-types which they had heard 20 or 15 times, they showed acquisition failures with fewer exposures. Thus, exposure frequencies of five or ten times were liable to constrain the acquisition of master songs. The difference in acquisition success for master song-types heard 10 or 5 times (in total: 7 versus 11 acquisition failures) invites further experiments on a relationship between acquisition success and presentation frequency.

The examination of package distribution yielded the following results (Fig. 5). The size of song-type packages developed from this experiment (M ± SD: 3.72 ± 1.1) differed from the size of the added substrings (i.e. 5 song-types). The assumption that package formation might have been cued by substring boundaries (experienced five times for any substring) was, however, supported by the location of package boundaries: these were clearly related to the sequential locations at which new substrings were introduced. In total only four packages (out of 22) held songs from two different substrings.

The results obtained from this experiment do not allow us to conclude that birds developed packages by referring to the size of the presented substrings. Concurrently, however, package boundaries were clearly related to substring boundaries. That is, the findings suggest that the offset (or continuation, respectively) of a string of master songs during exposure is an effective cue for the 'closure' (or opening, respectively) of a data segment that is transferred to memory and later evident as a package of imitations. This was indicated by the rare occurrence (n=4) of packages that spanned the boundaries of a substring. Referring to the hypothesis that package formation is as an early acquisition process (i.e. 'seeded' already during the first exposure to a string, Hultsch and Todt 1996), a recoding of already formed packages has to be taken into account in these four cases. If such recoding at the transitions from the experienced to the enlarged string was facilitated by the total exposure frequency to the enlarged string, its
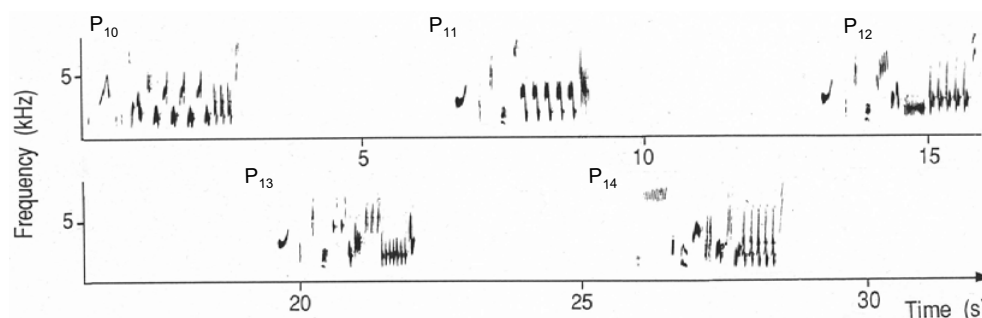
Fig. 6 – Spectographic display of a section of the song string P (pattern cueing), showing the master song-types P10 through P14. Songs 11, 12 and 13 have the same initial song section (here a succession of four identical element-types), whereas the initials of song 10 or 14 are different.

probability should be highest at the boundary from the first to the second list (tape 2: 15 times exposure) and decrease with the addition of the third list (tape 3: 10 times exposure) and the fourth list (tape 4: 5 times exposure). The data do not support this assumption. To conclude, as with the experiment I, variables in the time domain (offset or continuation of the list) may explain the results of this experiment.

EXPERIMENT III: PATTERN CUEING

The objective of this experiment was to examine whether structural similarity between master songs would influence package formation. In particular we tested whether successive master song-types that shared particular element types would be perceived as members of the same category and later occur as imitations associated in a song-type package. For both analytical and biological reasons, pattern sharing was experimentally confined to the initial elements of master song-types (Fig. 6). Imitations should be reliably distinguishable and identifiable as acquired from a particular master song-type presented during the tutoring. In their natural song delivery, nightingales tend to sing several successive songs holding the same initial element-types before they switch to songs starting with other initial element-types (schema: α_1A, α_1B, α_1C, α_1D, α_2E, α_2F, α_2G . . . ; α plus subscript = initial element-types, capitals = rest of song pattern). In this respect, the string composition used here was quite similar

to a natural performance and we expected that such syntactical conformity would produce a category effect for package formation. The group size of master song-types holding same initial element-types was 3, 4, 5, or 8 song-types. While the smaller same-initial groups (3, 4, 5) were within one standard deviation of the distribution of package sizes under control conditions (ungrouped string structure), the larger one (8) also tested whether grouping would drive package size beyond its normal limits (cf. stippled area in Fig. 8).

In preparing for this experiment we generated one tape holding a string of 25 master song-types (see Fig. 1 for string composition and presentation). The string segments holding the same initial element-types were segregated from each other by a single song holding an initial particular to this song-type only. The string was played twice in a row (interval between subsequent renditions: 2min) on 10 successive days, yielding a 20 times total presentation to the four males (P, Q, R, S).

The results with respect to a cueing of package formation through the particular pattern structure of master song-types were negative (Fig. 7). There was no indication that a switch from a bout of 'same-initial' master songs to a master song holding a different initial element-type induced package boundaries: only two (out of 20) packages had boundaries with reference to these positions.

In contrast to results obtained from ex-

Pattern cueing

| | i-1 (| | | i-2 | | | | |) i-3 (| | | i-4 |) i-5 (| | | i-6 |) i-7 (| | | i-8 | |) i-9 |

| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 |

Males

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
R	1	2	3	4	5	6	7	8	9	10	-	-	13	-	-	-	-	18	19	20	-	-	-	-	-
P	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	-	-
S	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	-	-	19	20	21	22	23	24	25
Q	1	2	3	4	5	6	7	8	9	10	11	-	13	14	15	16	17	18	19	20	21	22	23	24	25

Fig. 7 – Imitations (italic numbers) and their sequential associations (song-packages, stippled areas) developed by the birds P-S from strings presented in the experiment 'pattern cueing'. Symbols of master song-types are given on top. The arrows indicate the sequential locations where a group of song-types which shared initial song sections ended, and where package boundaries were expected if cueing occurred. Acquisition failures are given by '–'.

periments I or II, birds did not chunk song-type sequences on the basis of experimental string organization. It is not possible to decide whether males did not perceive pattern similarity as a categorical cue or whether pattern similarity was irrelevant for cueing package formation.

From a biological perspective, these results raise interesting questions about the significance of early acquisition processes for performance organization. In their normal singing nightingales tend to initiate several successive songs by identical element-types, and this is a common principle of song organization also in other thrush species (Todt 1970, Thimm et al. 1974, Hultsch 1980). Analyses of the motor development of singing in juveniles revealed that this trait develops only late in ontogeny (Hultsch, unpubl. data) and often includes 'inventions' of new initials that had not been present as constituents of the presented master songs (Fischer 1990). The fact that string composition in experiment III did not produce a category effect for package formation can be taken as circumstantial evidence for the independence of basic programs underlying song delivery from early acquisition processes.

DISCUSSION

The effects on the cueing of package formation revealed in this study can be ranked as follows: (1) 'novelty' and (2) 'time'. While the findings of
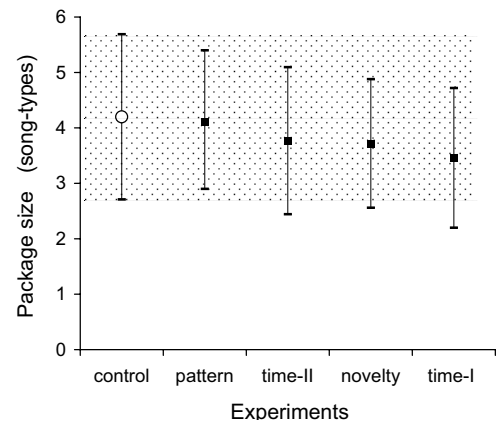
Fig. 8 – Mean ($\pm$SD) size (given as number of song-types) of packages developed from the song strings to which subjects were exposed in this study. In addition, the respective measure pooled from control experiments (homogeneous string structure; n = 75 packages, see Hultsch and Todt 1989) is given for comparison.

the first two experiments suggest that subjects responded to the organization of stimulus succession, no such indication was obtained from the pattern cueing experiment. This notion is substantiated by a comparison of package sizes developed under 'control' conditions (ungrouped string structure, Hultsch and Todt 1989) with those assessed in the present study (Fig. 8). Although these distributions did not differ from each other (ANOVA, one-way, $P > 0.05$), the packages developed from the third experiment were clearly most similar to

packages developed under control conditions.

Experiment III was the only one where experimental string organization concerning a syntactical variable was manipulated in the presented songs. The findings indicate that in song acquisition the chunking of serial information may not be based on an acoustic or syntactical analysis of the perceptual input.

The evidence from both the novelty and the time cueing experiments suggests that temporal proximity of learning stimuli is a crucial variable that influences package formation. The findings on (a) the rare incidents of package recoding after substring addition, and (b) the relatively small size of packages that spanned a temporal gap are compatible with the assumptions of a model put forward by Hultsch and Todt (1989, 1996, Hultsch 1992). It assumes that package formation is 'seeded' upon the first exposure to a song string through a time controlled gating process. Subsequently, stored information on both item structure and item association within string segments may act as expectancy based reference memories during further exposures to that string.

With these conclusions in mind, package formation can be interpreted as a consequence of a short term memory process that influences further data processing and eventually memory organization. Why, then, should package formation be discussed at all as a paradigm for chunking as it is conceived of in cognitive research? In this field, chunking is interpreted as a functional coding strategy, where smaller units are grouped or reorganized into larger, 'meaningful' ones. Thus chunking is viewed as mediated through a higher order cognitive process that reduces the actual load of working memory. The evidence on the facilitation of both acquisition and performance suggests that subjects are 'seeking' for a rule based organization of a serial task, be it in sequence discrimination, sequence production or stimulus tracking paradigms (Hulse 1978, D'Amato and Colombo 1988, Dallal and Meck 1990, Fountain and Annau 1990, Terrace 1991). During song learning the success of pattern acquisition seems not to be based on such rule based coding: subjects did not imitate more songs from the strings which they had chunked according to experimental structure than from the string where cueing was not successful (experiment III). In addition, low or high acquisition rate was determined in the first place by the individuality of a songster. Therefore, measures like acquisition rate or acquisition speed are not appropriate tools for considering the issue of chunking in the song acquisition system.

Our findings on the cueing of package formation show that there is no need to presuppose a cognitive, rule based perception of serial stimuli. Songbirds are renowned for their ability to exactly reproduce song patterns which they had heard only a few times early in life and they acquire a vocal signal system whose structural complexity is unrivalled in animals (review in Todt and Hultsch 1996, Todt and Geberzahn 2003). For example, a single nightingale song (duration ca. 3s) is composed of around 9 discretely different structural units or note-types (mean: 8.6 ± 1.4) (Hultsch 1980; cf. Fig. 6). In a natural setting a male is exposed to around 80 of these different units within one minute, which he memorizes and finally stores in long term memory. Thus the chunking of extended trains of song stimuli to which young birds are exposed may be one component in a network of adaptations for coping with the high informational density of song patterns.

CONCLUSION

To summarize, the finding that nightingales used temporal variables as cues for chunking does not require the assumption that package formation is a cognitive coding strategy. Rather it points towards a mechanism of procedural memory in the song acquisition of birds. It remains open, however, whether song is represented by other kinds of memory as well, e.g. of the declarative type. Such memory could be particularly significant for the actual use of birdsong as a communicative signal and it is a matter of forthcoming research to deal with this question.

RESUMO

Há evidências crescentes de que, durante a aprendizagem do canto, as aves adquirem não somente ''o que cantar'' (o repertório comportamental), mas também ''como cantar'' (o programa do canto), incluindo regras de seqüência do canto. O Rouxinol-comum *Luscinia megarhynchos* adquire essas informações seriadas dividindo as longas cadeias de cantos ouvidos em segmentos ou pacotes menores através de um processo lembrando o corte (''chunking'') de informação como mecanismo codificador na memória de curto prazo. Aqui relatamos três experimentos de aprendizagem pelo rouxinol para ver se tal ''chunking'' é suscetível de marcação experimental. Os experimentos testaram se (1) a ''articulação temporal'' (intervalos de silêncio entre cantos repartidos em determinadas posições na série aprendida), ou (2) a ''novidade do estímulo'' (grupos de novos tipos de canto acrescidos a uma série básica), ou (3) a ''similaridade de padrão'' na estrutura fonética do canto (aqui o mesmo início dos cantos) induziria os limites dos pacotes (ou seja o ''chunking'') nas posições seqüenciais definidas experimentalmente. Os resultados mostram efeitos de marcação nos experimentos (1) e (2), mas não no (3). A descoberta de que as aves usam variáveis temporais como marcas para o ''chunking'' não exige assumir que a formação dos pacotes seja uma estratégia cognitiva. Isto melhor indica que um mecanismo de memória procedural opera na aquisição do canto das aves.

Palavras-chave: aprendizagem do canto, memória procedural, seqüenciamento do canto, memória de curto prazo, ''chunking''.

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