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MOTOR THEORY OF AUDITORY PERCEPTION(U) ROCKEFELLER UNIV

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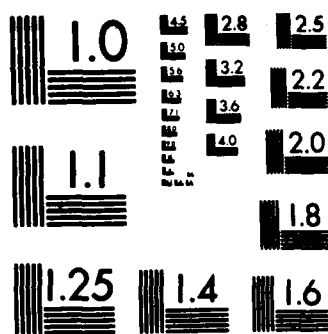
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The behavioral and neural substrate for motor processing of vocalizations exists in an animal model (the zebra finch). What had been considered a simple vocalization, learned from one model and carrying one message, proves to consist of compound sound units (syllables) arranged in a complex structure. The syllables in each vocalization are learned from several different sources or improvised, and are assembled to form a new vocalization. The vocal motor neurons have an auditory function (the muscles of the vocal organ contract slightly when the animal is presented with an auditory stimulus), the vocal motor neurons are spatially ordered according to their target muscle (and hence their vocal function), and vocal motor neurons in different pools have different auditory responses. Behavioral experiments to test whether the vocal motor system is involved in perception have been initiated. A new method for visual analysis of sounds is being tested. Key words: 152

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1 Sep 86 - 31 Aug 87

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Progress has been made on a number of fronts.

Dr. David Vicario, working in the same laboratory as the P.I., has mapped the locations of the motor neuron pools within the tracheosyringeal motor nucleus (nXIIts) which innervate the muscles of the syrinx (the avian vocal organ). He then replicated the P.I.'s results, showing that acoustic stimuli, including bird song, excite the motor neurons, and then extended this finding to show that the muscles of the syrinx have different patterns of contraction during the production of different song syllables, as well as differential responsiveness to sound stimuli (the syringeal muscles themselves contract when an acoustic stimulus is presented to the bird, although, in the absence of a pressure head in the airway, no sounds are produced). Dr. Vicario also confirmed the P.I.'s finding that the conspecific song is the best stimulus for exciting the tracheosyringeal motor neurons of the awake bird.

Dr. Vicario has also performed lesions of a few of the various muscle pairs that control the articulatory position of the syrinx. He has shown that, for at least one class of syllables, one set of muscles predominates in defining the frequency structure of the sound. Lesioning the other muscles does not affect that particular syllable within the bird's song.

These experiments were inspired by the P.I.'s work and were carried out with frequent input and design assistance from the P.I. The results serve to confirm some of the hypotheses arising from the motor theory of perception as applied to birdsong, which in turn resulted from the P.I.'s discovery of auditory responses in the vocal motor neurons:

- a) the motor neurons in the nXIIts are arranged in distinct spatial subsets, each of which can be mapped onto a muscle in the syrinx
- b) certain syringeal muscles have different firing patterns during the production of different song syllables
- c) the motor neurons innervating different syringeal muscles have different response patterns to song syllables delivered as acoustic stimuli.

These findings show that an appropriate neural substrate for motor processing of vocalizations exists, and that it is a close match to the format anticipated by the motor theory of auditory perception.

The methodologies for the use of fluorogold and rhodamine-fluorescent latex beads as retrograde tracers have been perfected, with the ability to inject precisely controlled nanoliter amounts to obtain injection sites of calibrated size. This step was necessary before completing the anatomical studies because of the problem of

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tracer spread within the thalamus. The attempt to find the putative link between the telencephalic auditory areas that respond with a very long latency and the motor nucleus auditory activity can now proceed.

Significant progress has also been made on the behavioral front, although there are as yet no definitive results.

The songs of 37 adult male zebra finches were recorded, sonographed, and analyzed to obtain a library of zebra finch sounds, separated into categories that may roughly correspond to phonemes. The vast majority of syllables could be sorted into relatively few categories, defined by the temporal and frequency structure of the sounds. Many syllables are relatively simple, with little or no frequency modulation and little or no difference in emphasis of the harmonics. However, some complex syllables appeared to be "co-articulated" in the same way that phonemes are in human speech: that is, a syllable starts as one type and then merges into and ends as another type without a break in sound production (Fig. 1a). Likewise, the unmodulated harmonic series that make up some zebra finch notes could be seen, on closer examination, to have complex patterns of harmonic emphasis or attenuation, with occasional "missing harmonics" (Fig. 1b). These patterns were repeated consistently for a single syllable within the song of an individual bird, but varied among the syllables of a bird's song and between birds. They patterns of harmonic emphasis are also learned; in copying an adult's song, a young bird might also copy the pattern of harmonic emphasis for a syllable or might copy the pattern from another adult male (see Fig. 1b). Females' calls do not seem to show this variability in patterns of harmonic emphasis. The differing patterns of harmonic emphasis bear a resemblance to the manner in which vowels are formed in human speech, although, because of the lower fundamental frequency of laryngeal phonation, the zebra finch's patterns of harmonic emphasis are not directly comparable to the formants seen in human vowels.

A further complexity in the structure of zebra finch song was revealed by an aviary study of song learning (see Appendix I). Males had been thought to learn their songs from their fathers (Bohner, 1983), but previous studies had restricted physical contact between young and adults by means of wire screens. Free-living aviary birds with unrestricted contact between individuals do not learn their songs from their fathers, but pick and choose pieces of songs from among the adult male population, rearrange these pieces, and add bits of their own improvisations. The adult males that are prominent song models are also prominent in giving care to fledglings; the young males may thus be picking and choosing which messages to send through their song in a much more complex manner than had been hitherto imagined. Thus, the songs of the males may encode more information than was expected when the "sons sing their fathers' songs" model obtained.

The outcome of these last two studies is important because they address a bothersome property of zebra finch song that arises when



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considering the rationale for motor processing. If the sound structures and the messages in zebra finch song were simple (such as simple harmonic series and downsweeps encoding "I am the son of my father"), the need for a sophisticated system for processing these sounds is hard to understand. Since the songs of zebra finches are far more complicated than had been believed, the existence of a neural structure underlying the motor processing of song becomes evolutionarily plausible.

In collaboration with Dr. Jeffrey Cynx, also of the Nottebohm laboratory and the Rockefeller University, the ability of zebra finches to discriminate between syllables consisting of harmonic series that differ only in the energy present in certain harmonics was tested. The birds were taught to hop to a perch for a food reward when they heard one syllable and remain on a central perch when another syllable was presented in a "go - no go" paradigm. The zebra finches were able to acquire this discrimination in a few thousand trials. However, the ability to discriminate the two syllables was not lost when HVC, a forebrain song nucleus high in the chain that projects to the motor neurons, was lesioned, and it seems likely that, at least for the time being, the operant conditioning paradigms are too foreign to naturalistic conditions to contribute directly to answering some of the behavioral questions arising from the motor theory of auditory perception.

An alternative, more naturalistic method for assessing the behavioral importance of sound stimuli is the playback paradigm. After some preliminary pilot work, Dr. Stephen Clark and I have decided upon a method which we believe will prove successful in evaluating zebra finches' differential responsivity to conspecific songs (or edited sounds consisting of altered or degraded song). A soundproof observation chamber outfitted with balanced speakers and recording facilities has been designed and built, and editing of a catalog of males' songs into usable, uncontaminated (by outside noise or other birds' calls) segments has been completed. The females to be tested with the males' songs have been primed by implantation of silastics containing estradiol. The test procedure is as follows: The female is habituated to the chamber over a period of several days. After the habituation period is complete, a tape consisting of introductory notes followed by five songs is played, repeating for 30 seconds, followed by 30 seconds of silence. The cycle is repeated for 3 minutes, and followed by a 3-minute silent period before presenting another test song. Solicitation displays are noted and their duration and intensity recorded (see Searcy and Marler, 1981). This data is supplemented (and perhaps supplanted) by recordings of female vocal activity during the playback. I have found that females give three calls in response to male song: 1) long contact calls, either singly or multiply, and sometimes synchronized to a particular

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note within the male's song; 2) short calls; and 3) a "churr" or aggressive call. Females repeatedly (trials separated by 1 or more weeks) presented with the same series of singing live males consistently responded with same calling pattern to the same singing male, and gave solicitation displays repeatedly to the same males even after a long interval of separation. This data indicates that the females' behavioral responses are both consistent and diverse enough to serve as a test for song preferences and discriminability. Males do not give solicitation displays, but respond to the song of another male by approaching or avoiding the song source, giving calls similar to the females', or singing in response.

These preliminary behavioral studies are now completed, and, once behavioral profiles of song responses are obtained, the lesions of the stations in the motor pathway for song production that are believed to be implicated by the motor theory of auditory perception will be undertaken.

Drs. Clark, Cynx and I have also undertaken a project dealing with the methodology of sound analysis. The standard method of sound analysis in use in the fields of speech and song research is the sonogram, a visual plot of frequency vs time. Consider the potential problem that arises from relying so heavily on the human eye and brain in analyzing sounds: might we be overlooking valuable information because the human mechanisms for processing visual patterns highlight some sound characteristics at the expense of others, others which may in fact be more salient to the auditory system? Inspired by the work of Clifford Pickover (1986), we are attempting to calibrate the use of "snowflakes", a form of visual plot that uses the auto-correlation function of a digitized sound to generate a radial plot with 6-fold symmetry. This method of plotting sound is believed to emphasize the intensity and frequency characteristics of the sound, and has been shown to differentiate among sounds that seem similar using other methodologies. I have written a program that generates snowflake plots, and we are performing comparisons of 25 snowflakes generated from digitizations of zebra finch syllables, sonograms of the same sounds, and the sounds themselves (see Fig. 2). Initial results are encouraging, and Dr. Cynx will be testing zebra finches with the same set of syllables in an attempt to correlate zebra finches' ratings of the syllables to all three human analytical methods.

Work on the problem of gating of the auditory and motor functions of the neural pathways for vocalization has also continued. The thalamic nucleus Uva, which was earlier discovered to control the responsiveness of neurons in the vocal "motor" pathway to auditory stimuli, was lesioned in young and adult animals. Lesions to young animals produced deficits in song production similar to those described by Price (1979) after deafening. Lesioning the Uva of adult birds induced a systematic problem in song production - the time/frequency structure of syllables was unimpaired, but the order and rate of delivery (syntax) was grossly abnormal, with multiple

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repeats of syllables in a variable order, unlike the stereotypical delivery of a normal animal (Fig. 3). These findings suggest a dual role for nucleus Uva: in young animals, Uva may control or modulate the auditory feedback against which the vocalizations are measured to converge on the learned song model, while in adults, when song is crystallized and is no longer affected by auditory feedback, lesions unmask Uva's role in song production. These findings suggest that manipulation of Uva's activity through chronic stimulation or lesioning may affect which auditory signals reach the forebrain vocal nuclei (HVC, RA) and thence the motor neurons, and that this modulation may provide a convenient aid in assessing the importance of motor processing of auditory stimuli.

References:

- Bohner, J. (1983) "Song learning in the zebra finch (Taenopygia guttata): Selectivity in the choice of a tutor and accuracy of song copies" Anim. Behav., 31: 231-237.
- Pickover, C.A. (1986) On the use of symmetrized dot patterns for the visual characterization of speech waveforms and other sampled data. J. Acoust. Soc. Amer., 80: 955-960.
- Price, P. (1979) "Developmental determinants of structure in zebra finch song" J. Comp. Physiol. Psych., 93: 260-277.
- Searcy, W.A., & P. Marler (1981) A test for responsiveness to song structure and programming in female sparrows. Science, 213: 926-928.
- Vicario, D.S. (1986) Inputs to syringeal muscles in the zebra finch. Neurosci. Abstr., 12: 1538.

The above report summarizes the studies conducted during the period between 1 September 1986 and 31 August 1987.

The goals of the research supported under this grant remain the same as described in the original proposal.

Specific objectives for the coming year are:

- a) Use neuroanatomical methods to define the connections of the thalamic nuclei linking lower brain auditory centers to forebrain song centers (specifically nuclei DLM, DM, and Uva).
- b) Record from individual units responding to auditory stimuli in the nuclei MAN and DLM, and characterize the selectivity of these responses.
- c) Perform behavioral tests defining the responses of female and male zebra finches to playbacks of normal vocalizations.
- d) Repeat the behavioral tests with edited vocalizations containing altered syllables, high- or low-pass filtered elements, or abnormal syntax (syllable order), using both males and females.

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- e) Lesion the vocal "motor" nuclei HVc, RA, and nXIIIts (in different animals) and compare the performances on behavioral tests of discriminations of vocalizations before and after lesions.
- f) Explore the feasibility of controlling the modality of the forebrain vocalization nuclei through stimulation (to inhibit auditory responses) or removal (to increase auditory responsiveness) of the thalamic nucleus Uva.

Publications:

Nottebohm, F., and H. Williams (in press) Fifteen million neurons mediate the memory of a circle and a star. Or do they? Science.

Williams, H. (1986) Modulation of the auditory and motor modes in the avian song system nucleus HVc. Soc. Neurosci. Abstr., 12: 315.

Williams, H. (in prep.) A small thalamic nucleus coordinates song-related neural activity in the left and right hemispheres.

Williams, H. (in prep.) The neural mechanism for the inhibition of auditory activity in the song system nuclei of singing birds.

Williams, H. (in prep.) Song learning in the zebra finch: Do fathers supply the models for their sons' songs?

A preprint of the latter manuscript is included with this technical report as Appendix I.

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Summary of expenditures under the current budget period.

From 01 Sep 86 through 31 Aug 87.

	Approved Budget	Expenditures thru 8/31/87	Outstanding Commitments	Balance
Direct Costs	43,012	42,394	618	0
Indirect costs	27,042	27,042	0	0
Totals	70,054	69,436	618	0

Next budget period.

Costs and budget remain as anticipated in the original application.

Personnel engaged on project.

Principal Investigator:

Dr. Heather Williams

Assistant Professor

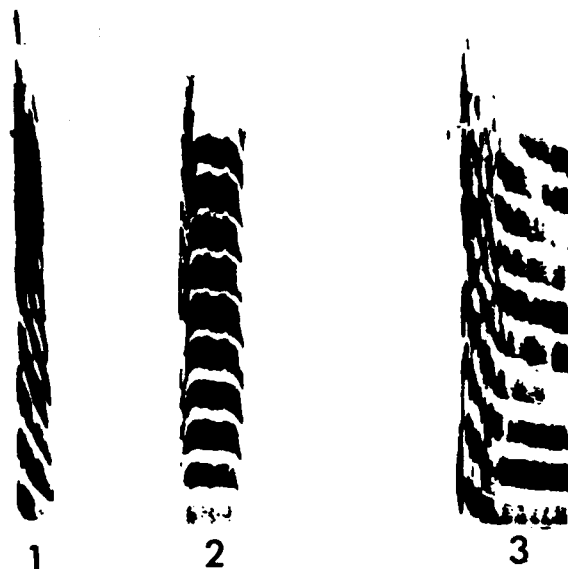
Colleagues in the Nottebohm laboratory at Rockefeller University with whom collaborative projects have been undertaken:

Dr. David Vicario
Dr. Jeffrey Cynx
Dr. Stephen Clark
Robert MorrisonAssistant Professor
Postdoctoral Fellow
Postdoctoral Fellow
Doctoral StudentVertebrate animals involved: Zebra finch (Poephila guttata)

I certify that the statements herein are true and complete to the best of my knowledge.

*Heather Williams**24 Sep 87*

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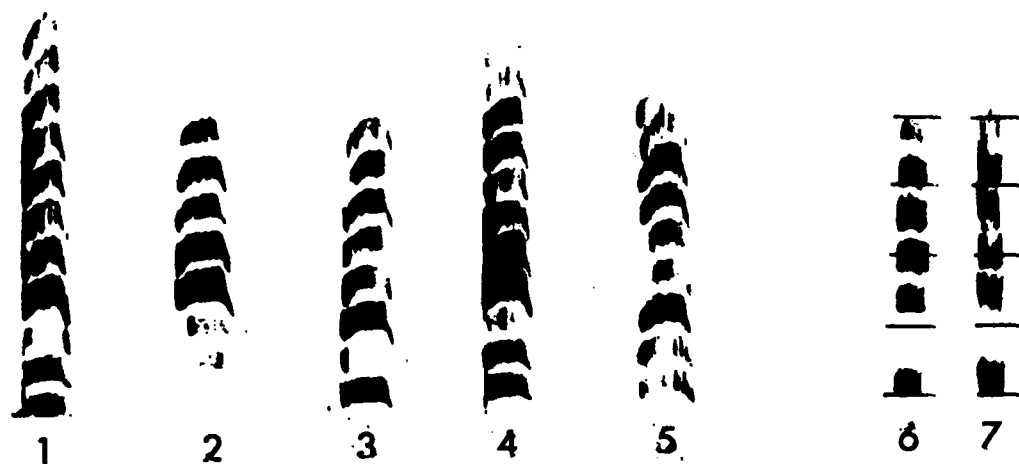


Figure 1. Complex characteristics of zebra finch vocalizations.
 a. Syllables consisting of a simple downsweep (1), an unmodulated harmonic series (2), and a combination of the two types showing some evidence of possible coarticulation (3).
 b. Several syllables consisting of relatively unmodulated harmonic series, showing different patterns of harmonic emphasis. One bird can produce several different patterns of harmonic emphasis (e.g., syllables 2 and 4 were produced by the same bird), and the patterns of emphasis are learned (syllable 7 was sung by a bird that copied the song which contained syllable 6).

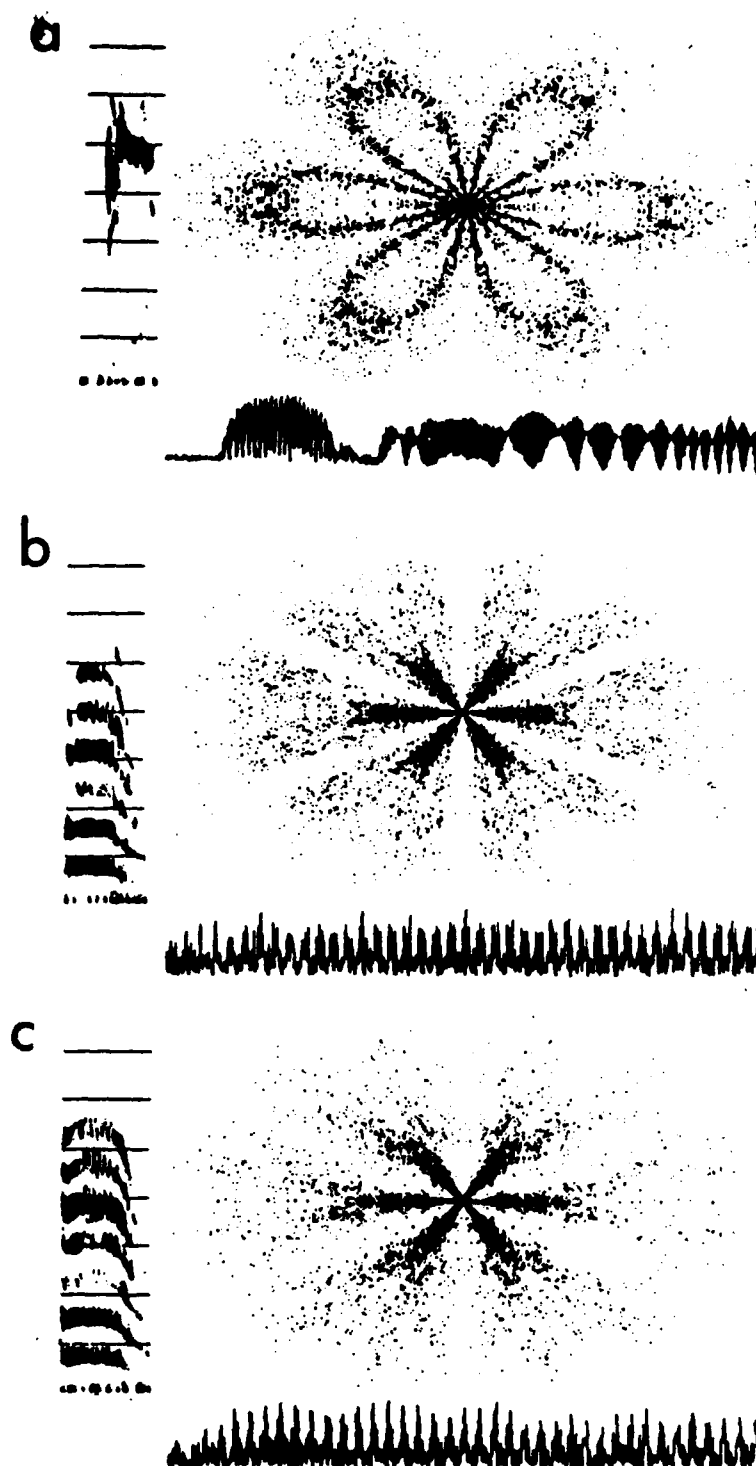
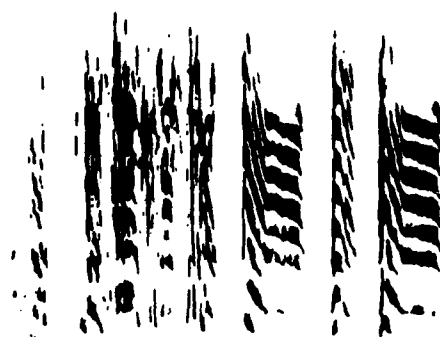


Figure 2. The "snowflake" plot as a visual representation of sound. The sonogram, the digitized and rectified oscillogram, and the snowflake plot of three different syllables are shown in a, b, and c. The snowflake plot is derived from the digitized sound, with values scaled to lie in the range of 0 to 30. Each point in the digitized sound is used to define an angle relative to the origin, and the next point in the digitized sample determines distance from the origin. Multiple reflections of the plot give the snowflake its symmetry. See Pickover (1986) for more on the snowflake plot.

a



b

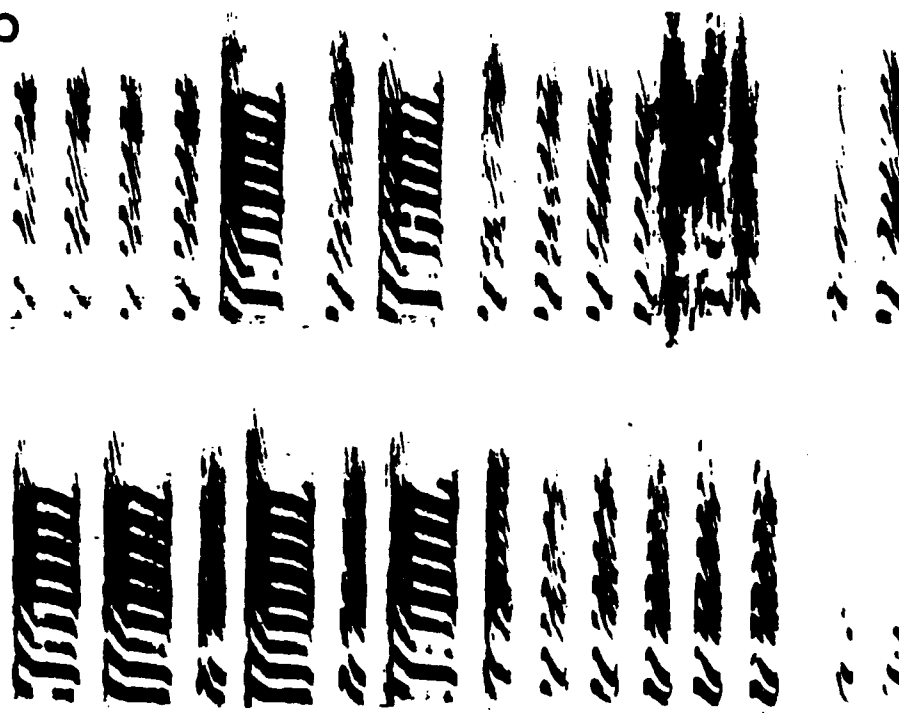


Figure 3. Effects of Uva lesions upon vocalizations.

a) Stereotyped song delivered by an adult male before lesioning Uva.
 b) After lesioning, the time/frequency structure of each individual syllables is delivered as in the intact bird's song, but the order of delivery is abnormal and variable.

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APPENDIX I

**Song learning in the zebra finch:
Do fathers supply the models for their son's songs?**

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Abstract

The zebra finch, a small colony-nesting bird, has been used extensively as the subject of behavioral and neural studies of imprinting and song learning. Previous research with individually caged pairs led to the conclusion that young zebra finch males imprint upon their fathers at an early age, and model their songs upon his song. In this study, an aviary containing 10 breeding pairs of zebra finches and 2 non-breeding males was observed while the F1 generation was raised young to independence. The young then remained in the colony until sexual maturity, when song learning is complete.

The songs of young males and their fathers were then analyzed and compared. The mean number of syllables in the sons' songs was greater than the number in their fathers' songs. Each adult's song was copied by at least one young male, but sons did not preferentially copy their fathers' songs. The majority of the F1 males copied syllables from at least two of the adult males in the parental population. Two adult males were preferentially chosen as song tutors by the population of young males; these two males had a greater number of interactions with fledglings and gave a greater amount of parental care to fledglings (including those not their own) than the other adult males in the colony.

The dynamics of tutor choice and song learning in the zebra finch are not as simple as has been assumed; young males may be making complex choices about which adult males to copy and how to represent themselves in their songs.

Acknowledgements

I wish to thank Fernando Nottebohm for valuable comments on the manuscript, and Stephen J. Clark for advice on statistical methods. This study was supported by grant 86-0336 from the Air Force Office for Scientific Research.

Introduction

Zebra finches have been the subject of many anatomical, physiological, and hormonal studies that relate their results to song learning (e.g., Arnold and Saltiel, 1979, Bottjer et al., 1984, Gurney and Konishi, 1980, Nottebohm and Arnold, 1975). There have also been numerous studies on imprinting (Immelmann, 1972, Ten Cate, 1987), mate choice (Miller, 1979a) and pair bond formation (Silcox and Evans, 1982) that discuss song learning and its implications with respect to their data and conclusions. These discussions are based upon laboratory studies of song learning, which state that zebra finch males learn their songs only from their father (Böhner, 1981) or, if the males are separated at an early age from their fathers, from males whose song resembles those of their fathers (Clayton, 1987). Conclusions based upon these findings are often further extrapolated to make statements about the behavioral ecology of wild zebra finches (Miller, 1979b, Slater and Clements, 1981).

Since zebra finches fledge at day 21 (Immelmann, 1965, 1969) and the sensitive period for song learning in the zebra finch can extend past 40 days (Eales, 1986, Clayton, 1987), it seems well within the realm of possibility that young zebra finches, living in the social environment of the breeding colony, may acquire song models from adults other than their father. In the two past studies which address the zebra finch's choice of song models, this was not the case. Böhner (1983) found that zebra finches given a choice between their father and another male as song models learned only the elements of their father's song. However, in Böhner's study the young zebra finches were separated from their fathers after fledging and then housed in a separate (though adjacent) cage, with a wire mesh preventing contact with either of the two adult male zebra finches; the only physical contact with an adult male was with their fathers before fledging. A recent study by Clayton (1987) found that young males preferred a song similar to their father's over a dissimilar one but again restricted contact between the young males and the adults. Zebra finches are highly social, colonial breeders; these conditions of restricted physical access to conspecifics are extremely unnatural and may influence song learning.

Methods

Aviary conditions

In an attempt to provide a naturalistic zebra finch environment, 12 color-banded adult males whose songs had been previously recorded and 11 color-banded adult female zebra finches were introduced simultaneously (to simulate the onset of the breeding season) into an indoor aviary provided with 12 nest boxes, a multiplicity of perches, nesting material, and water and seed ad lib. Pairings, nest sites, and the dates of egg-laying, hatching, and fledging were recorded. Each brood of young was banded with a distinctive color band while nestlings, and interactions between adults and fledglings of known nest identity were recorded during a daily 30-minute observation period. Since the sensitive period of normally reared zebra finches is thought to span the interval between 21 and 40 days of age - the fledgling period - (Immelmann, 1969, Price, 1979, Eales, 1985), behavioral observations were taken during that period. The young remained in the colony until they reached 90 days of age, when they reach sexual maturity and the males' songs are crystallized (Immelmann, 1959; Price, 1979). The young birds were removed from the aviary and the males' songs were recorded. This aviary environment allowed the zebra finches to interact freely, as would be the case in a wild population, and contact between young males, their siblings, and adults was not restricted by wire, sound isolation, or separation before maturity.

Song analysis

All analyses of song syllables were performed blind. A Kay digital Sonograph was used to obtain sonograms of the songs of the 28 male zebra finches used in the study. The identities of the singers were not retrieved until the analysis was complete.

In order to quantify the amount of song learning from each adult male and by each young male, each of the syllables in the songs of the 16 young males were scored on a 0-4 (0 = no similarity, 1 = slight similarity, 2 = some similarity, 3 = very similar, 4 = identical) point scale for similarity with each of the syllables in the 12 adult males' songs.

Each syllable received two scores: the first for the time/frequency structure of the sound, and a second score for the context of the note within the song (i.e., the similarity of the immediately preceding and following notes in the two songs being compared).

Since these similarity rankings are an ordinal scale and the intervals between scores cannot be assumed to be constant, averaged similarity scores cannot be used for comparisons. The number of syllables scoring 3 or 4 ("very similar" or "identical") for time/frequency structure and 2, 3, or 4 for sequence (with at least one adjacent syllable in common) were summed for each comparison between songs and these scores were divided by the number of syllables in the longer of the two songs being compared (to adjust for differences in song length between two otherwise similar songs). This procedure yields two song similarity measures, one for the time/frequency structure of individual syllables and the second for the syllable order within the song. These two measures were computed and then summed (weighted equally) to give an overall song similarity score for every possible comparison of the 28 (12 fathers, 16 sons) males' songs. This overall measure, though derived from an ordinal measure, is linear.

As a further measure of song copying, the best-matching adult syllable, for both structure and context, was determined for each syllable in each young male's song. Any syllable scoring less than a 3 for time/frequency structure or a 2 for sequence (as above) was scored as improvised, and the sources of the notes for each young male's song were tabulated.

Results

Number of syllables.

As a population, the sons' songs contain more syllables than those of their fathers (Table 1). The sons' songs also contain more unique syllables; the increase in number of syllables is not due to adding repeated syllables to the song. The young males are adding new syllables, and thus complexity, to the songs they hear.

This trend towards longer, more complex songs in the young males brings to mind Immelmann's (1969) and Böhner's (1983) observations that wild zebra finches have longer, "more complex" songs than domesticated birds. It may be that the domesticated birds, bred in single cages with physical access to only one tutor, learn their songs in an impoverished social environment and gradually, over the generations, develop shorter songs.

Comparison of fathers' and sons' songs

When sonograms of the fathers' and sons' songs are examined, it is clear that there is no strict father-to-son transmission of song. Figure 1 shows the song of a father, RW/B, and those of his three sons. Examination of these sonograms reveals little similarity between the sons' songs and those of their father. However, the sons' songs did strongly resemble those of other adult males; one sang an exact copy of adult male O/W's song.

In contrast, Figure 2 shows the songs of adult male LG and 3 young males, not his sons, all deriving from different broods. A strong resemblance can be seen between the songs of these young males and that of LG, who did not fledge any of his own young.

The number of syllables that would be expected to be derived from the father's song if the young male zebra finches learned their songs at random from the population of syllables sung in the aviary was calculated, and compared (using a Wilcoxon matched-pairs test) to the number of copied syllables in the son's song whose best match was in their father's song. Sons did not show significant copying of their

fathers' notes, sequence, or combined song measures (Wilcoxon $T = 64$ (note), 58 (sequence), 49 (combined), $N = 16$, $p \gg 0.05$).

The song similarity measure (see methods) was computed for every possible comparison between the 12 adults and the 16 young males' songs. These measures were grouped into five categories: 1) comparisons between fathers' and sons' songs, 2) between brothers' songs, 3) between unrelated adult males' songs, 4) between unrelated young males' songs, and 5) between young males' songs and unrelated adult males' songs (Table 2). Unrelated males have slightly less similar songs than fathers and sons or brothers, and an analysis of variance shows this trend to be significant. Brothers' songs showed the greatest similarity according to this measure.

The song similarity scores were also used to map the relationships between songs in three-dimensional space (Figure 3, the plot coordinates were determined by ALSCAL, the multi-dimensional scaling routine found in SPSSx). It can be seen that, although there exists a slight overall tendency for sons' and fathers' and brothers' to be similar and lie near each other in this spatial plot, there are also outliers whose songs bear no similarity to those of their close kin. The same data are also represented in Figure 4 as a cluster analysis, showing the hierarchy of similarities among the songs of the entire population. Again, many related males are to be found in clusters that join only very distally in the hierarchy, indicating that their songs most closely resemble those of unrelated males.

The question then arises as to whether the young males were learning syllables (or songs) randomly chosen from the population of songs or syllables to be heard in the aviary. A total of 80 different syllables were represented in the songs of the adult males; these can be broken down into five categories according to the number of times the syllable was represented in the songs of the 12 adult males (Table 3).

If the young male zebra finches are learning syllables randomly, they should learn and sing syllables in proportion to the syllables' frequency of occurrence within the adults' songs. As Table 3 shows, syllables are not learned out of proportion to the number of times they occur in the adult males' songs ($\chi^2 = 4.66$, $0.3 > p > 0.5$).

The results described above would seem to indicate that no single male is preferred as a tutor. However, when the results of the analysis of which adult syllables best matched those sung by young males are

plotted (Figure 5), it can be seen that two males, LG and LB/Y, were preferentially copied by the young zebra finch males, and that some males were shunned as song tutors while others were imitated by at least a few young males.

What factors influence the choice of a song model?

It seemed possible that young male zebra finches learned the songs of adult males occupying the nearby nest boxes. Figure 6 maps the songs learned by the young and the nest box locations of the young and their adult tutors. The similarity between an adult and a young male's songs was only very weakly correlated to the distance between their nest boxes ($r = .15$ (note type), $r = .14$ (sequence), $r = .13$ (combined song)). However, there may be a brood-dependent effect for the young of RW/DB - this male sequestered his young near their nest box (top right box of Fig. 6) after fledging and kept them separate from the crèche which the other fledglings formed at the opposite end of the aviary (see Immelmann, 1965). RW/DB's three sons' songs consisted mostly of syllables copied from the three nearest neighbor males.

The results of a multiple regression performed on the number of a males' syllables that best matched a syllable in the young males' songs and 14 behavioral, physical, and song measures are shown in Table 4. Only a few of these measures showed strong correlations with song learning. The only significant correlations between song tutor prominence and male characteristics were with the male's total number of interactions with all fledglings and the amount of parental care a male delivered to all fledglings. A large proportion (83%) of the adult males' total interactions with fledglings were parental care.

In this study, parental care given to fledglings can roughly be equated with paternal care given to fledglings (Figure 7). The males provided 91% of the feeding, preening and clumping behaviors the fledglings received from adults. They provided this care indiscriminately; only 10% of these male adult-fledgling interactions took place between fathers and sons, which does not differ from what would be expected were interactions to be randomly distributed among the young ($\chi^2 = 15.46$, $df = 11$, $0.20 > p > 0.10$). The few instances of parental care provided by the mothers, on the other hand, were invariably received by their own fledglings (Figure 7b).

Do young zebra finches learn from more than one tutor?

In the free-living aviary environment, young zebra finches hear and interact with several adult males. It is possible that, rather than imitating one song tutor, the young males may model their songs on more than one adult male. Figure 8 shows the number of adult males' songs represented in the set of syllables that best match the young males' songs. Since any young male's syllable without a matching syllable among the adult population scoring 3 or higher (for the time/frequency structure of the syllable) or 2 or higher (for the sequence or context of the syllable) is scored as an improvisation rather than a copied syllable, Figure 8a shows the number of sources (including improvisation as one source) represented in the young males' songs, while figure 8b shows the number of tutors contributing to each song. The peak of the distribution lies at 2 tutors or 3 sources contributing to each young male's song, even when sources contributing to less than 10% of the song are omitted, and a few birds derive material included in their songs from as many as 6 tutors.

The proportion of syllables in each song deriving from sources other than the primary tutor and improvisation make up a substantial portion of the young males' songs. On the average, approximately 30% of the syllables in a young male's song are copied from secondary and other song models (Figure 9), although there is a rapid decrease in the importance of the contribution as the number of sources increases.

Discussion

When zebra finches are raised in group aviaries, which more closely approximate natural conditions by allowing physical interactions among all the birds, the young males do not specifically learn their songs from their fathers, but from the adult males that interact most with the fledgling population. The main types of interaction between adult males and fledglings were feeding, preening, and clumping, parental care that is known to be given by zebra finch males, and to vary in its quality between different individuals (Delesalle, 1986; Immelmann 1965; Ten Cate, 1982). Similarly, Immelmann (1969) observed that young zebra finches raised by Bengalese finch foster parents in aviary containing a pair of zebra finches learned zebra finch song (as opposed to Bengalese finch song) only if the adult zebra finches fed the young that had been fostered out. This correlation of parental care to song model potency differs from the studies showing a correlation between aggression and song model potency in indigo buntings (Payne, 1981) and the suggestion that a similar mechanism is at work in zebra finches (Clayton, 1987).

The apparent conflict between these sets of results may have to do with differences between colonial and territorial species, or perhaps with differences in the housing conditions; the aviary is a more naturalistic environment than small wire cages housing unisexual groups. Females' responses to songs are known to affect song learning in male cowbirds (King and West, 1983; West et al., 1981), and restricting fledglings' interactions to just males may deprive them of a needed behavioral stimulus necessary for normal song learning.

The adult males, who were seen here to provide more than 90% of the parental care given to fledglings, were also indiscriminate in their feeding of fledglings (see Fig. 7). Upon landing with a full crop in the crèche, an adult male was immediately surrounded by begging fledglings and seemingly had no chance to discriminate among the scrambling mass of gapes. It is possible that this indiscriminate feeding is an artifact of the restricted size of the aviary and the unlimited food supply. In the absence of detailed field studies with color-banded wild populations of zebra finches, it cannot be said whether feeding of fledglings by adult males who are not their fathers occurs in the wild. However, Immelmann (1965) described the formation of crèches in the social area of the colony; it is known that the breeding season of wild zebra finches in Australia is triggered by the rainy season and is thus is synchronized

within the colony (Farner and Serrenty, 1960), and that there are specific times of day during which the adults feed before returning to the colony (Zann, 1984). This combination of factors would seem likely to produce a mob feeding atmosphere similar to that seen in the aviary and might promote indiscriminate feeding of fledglings.

This study seems to indicate that potency as a song model and thus cultural fitness is independent of genetic fitness, or the ability to produce viable young. However, the exact genetic relationship of the males in the aviary is unknown: I have used the term "father" to refer to the male who defended a nest box, incubated the eggs, associated with the female who inhabited the nest box; "son" in speaking of the males hatched and raised in their "father's" nest box; and "brother" in referring to nest box mates. It is entirely possible that these terms do not reflect genetic reality, as a low level of extra-pair matings is known to occur among zebra finches in an aviary/colony environment (Oliva-Purdy, pers. comm.). Until the blood relationships of all the members of the colony can be determined, it is impossible to know what the true father-son-brother relationships are, and whether adult males do or do not adjust their levels of parental care giving to the number of extra-pair matings they have achieved - which would, in turn, adjust cultural fitness to match genetic fitness. If the extra-pair matings are not significant, zebra finches would seem to provide an example of a species in which cultural and genetic fitness are not coupled.

The young males learned to sing a song that is a composite consisting of portions of several adults' songs added to their own improvised notes. They did not restrict themselves to one song model. This increases the diversity of song types within the population and may contribute to the high level of song complexity and diversity that exists in wild populations (Immelmann, 1969).

Thus zebra finches, like white-crowned sparrows (Baptista and Morton, in press) and marsh wrens (Kroodsma and Pickert, 1980) do not necessarily learn their songs from their fathers, but may instead evaluate the conspecific song environment before choosing a tutor(s) or a song model(s). Given the social environment of the zebra finch, this result has important implications for the studies concerning and conclusions about imprinting, the sensitive period, and mate choice in the zebra finch. If, as has been suggested, zebra finches imprint upon their parents at an early age, there must then be two different types of imprinting, as the song tutor(s) are only determined after fledging.

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Table 1. Number of song syllables by generation.

	Fathers	Sons	T	p
Mean # of syllables	9.75	11.75	24.86	<<.001
standard deviation	3.14	2.69		
Mean # of unique syllables	8.67	10.69	26.39	<<.001
standard deviation	2.49	1.99		

Table 2. Song similarity, age, and kinship.

Comparison	Song Similarity		
	Mean	S. D.	# of comparisons
Adults/Adults	.138	.173	66
Adults/Young	.160	.205	176
Young/Young	.179	.188	105
Fathers/Sons	.306	.253	16
Brothers/Brothers	.333	.243	15

ANOVA: $SSB = .777$, $SSW = 14.769$, $F = 4.908$, $p < 0.025$ (2-tailed).

Table 3. Frequency of syllables in adult and young males' songs.

Frequency of syllable occurrence in the adult male population	Number of adult males' syllables	Young males' copies	
		Note	Sequence
1	59	89	104
2	15	39	36
3	3	10	12
4	2	5	7
7	1	10	12

Table 4. Adult male characteristics and prominence as a song model.

	Syllables learned by young males		
	Note type	Sequence	Song (combined)
	r	r	r
Tutor Characteristic			
total interactions with fledglings	.53	.79	.68
parental care	.45	.72	.61
# syllables in song	.57	.56	.58
band color	-.48	-.42	-.46
# unique syllables in song	.40	.45	.44
% pop. syllables in song	.38	.44	.42
% unique syllables in song	.50	.24	.37
# males fledged	.34	.34	.35
% shared syllables in song	.37	.25	.32
date of 1st egg	.32	.26	.29
aggression	.29	.24	.27
date of 1st hatch	.27	.20	.24
# shared syllables in song	.16	.04	.10
# young fledged	.03	.14	.06

Figure legends

- Figure 1. The songs of RW/DB and his three sons.
- Figure 2. The songs of adult male LG and three young males from different broods. LG fledged no young.
- Figure 3. Multi-dimensional scaling plot representing the similarities of the songs of the 28 males used in this study as a three-dimensional map. The size of the circle represents the value of the third-dimension coordinate. Fathers are black dots, sons are gray dots, and sons are connected to their fathers by black lines. The axes do not represent a known variable or characteristic of the song, but are chosen by the computer program in order to maximize the dispersion of the coordinates. Variance in the data accounted for by the three-dimensional plot: 78.6%.
- Figure 4. Cluster analysis of the song similarities of the 28 males included in the study. Adults are in upper-case letters, and sons are indicated by lower case letters of their fathers' designations and a number. The length a song's line travels before being connected to another song's line represents the dissimilarity between those two songs (or those two clusters of songs). For example, the songs of O/W and rwb 1 are identical, while the song of R does not closely resemble any other song, though it is most similar to the cluster including O's song.
- Figure 5. Number of copies of adult males' syllables in the songs of the young males. The best-matching syllable among the adult population was determined for each syllable copied by a young male for both the frequency/time structure (black bars) and the context, or sequence (white portion of the bars).

Figure 6. Locations of the nest boxes of young males and of the adult males they copied their songs from. Squares are nest boxes occupied by adult males (two boxes were used by two males and are shown as double rectangles). Young males are shown as circles under the nest boxes they were hatched in, and lines are drawn to boxes of the adult males whose songs they copied. The thickness of the line indicates the amount of song copied from the adult male, and the thickness of the young males' symbols indicate the amount of improvisation in the song.

Figure 7. Parental care given to fledglings.

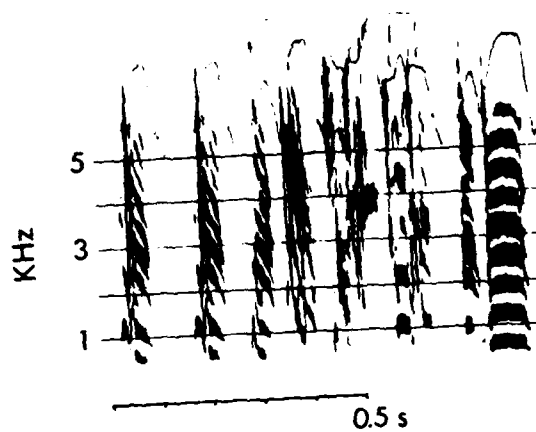
- A. Percent of adult fledgling interactions involving adult males and adult females.
- B. Percent of males' and females' interactions with known fledglings directed at the adult's own offspring.

Figure 8. Sources and tutors contributing to the songs of young males.

- A. Total number of sources (tutors + improvisation) contributing to the young males' songs. Black bars: all sources; white bars: only those sources contributing to more than 10% of a song.
- B. Number of tutors contributing to the young males' songs. Black bars: all sources; white bars: only those sources contributing to more than 10% of a song.

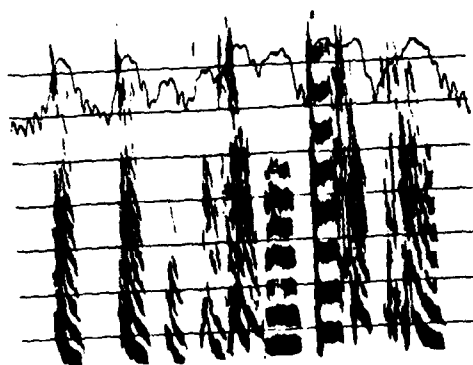
Figure 9. Relative importance of the sources contributing to the young males' songs, expressed as a percent of the young males' song.

Song of RW/DB (adult male)

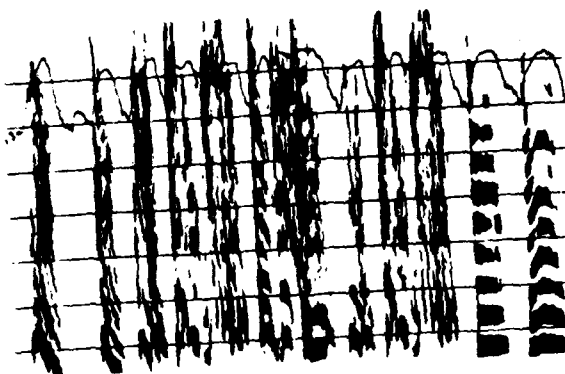


Songs of RW/DB's sons

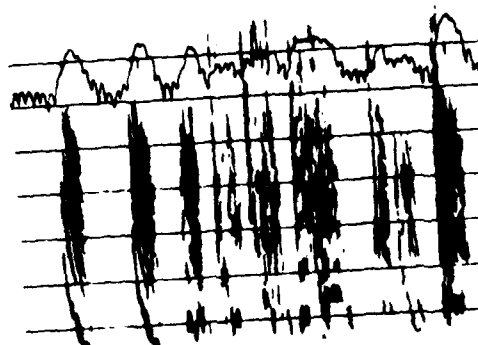
LB 91



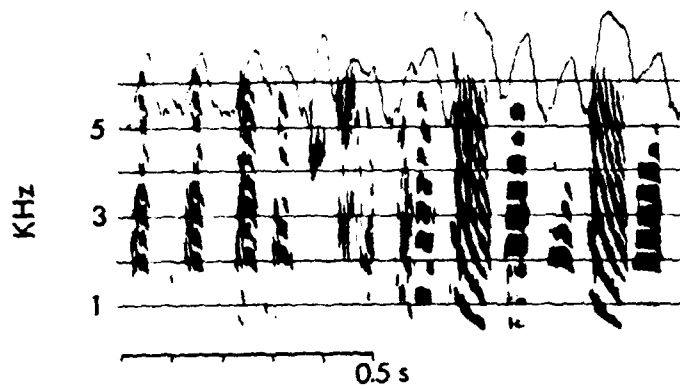
LB 93



LB 95

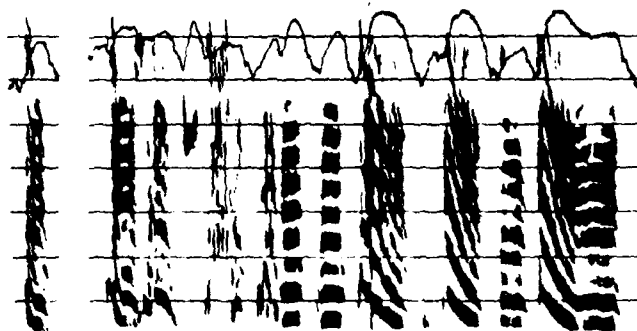


Song of LG (adult male)

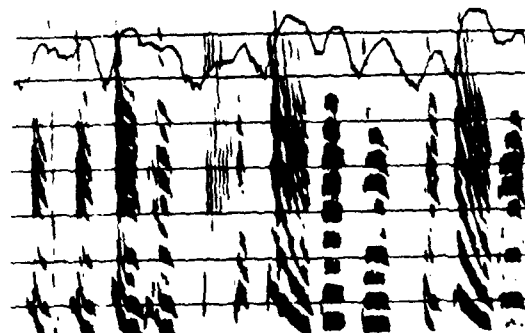


Songs of young males unrelated to LG (he fledged no young)

R 61



DB 2



R 49

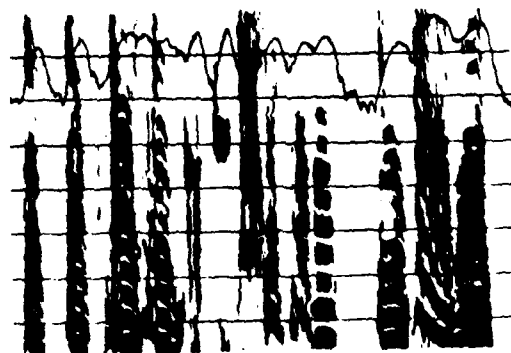


Figure 3.

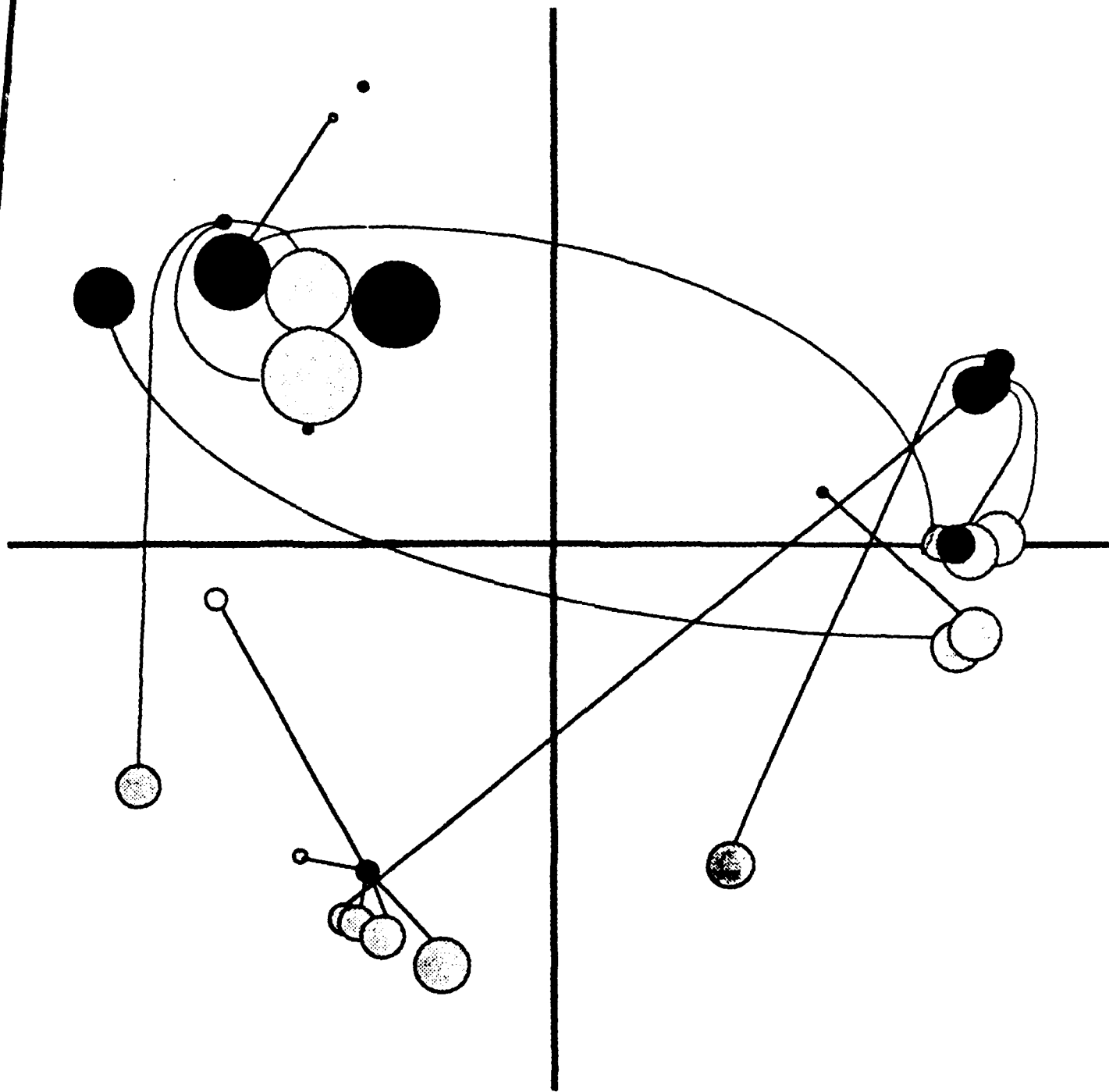
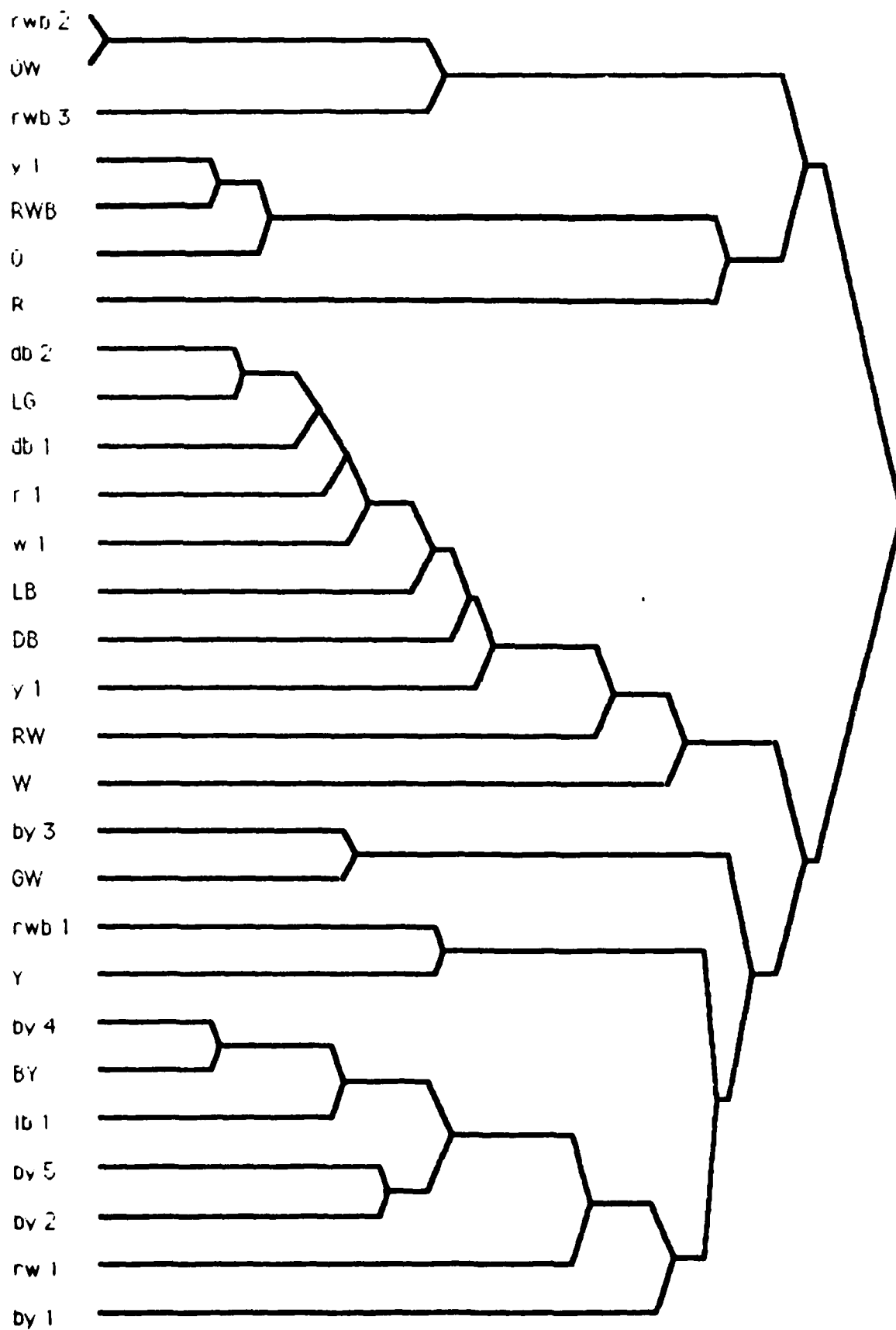


Figure 4.



Young males prefer certain adult males as song tutors

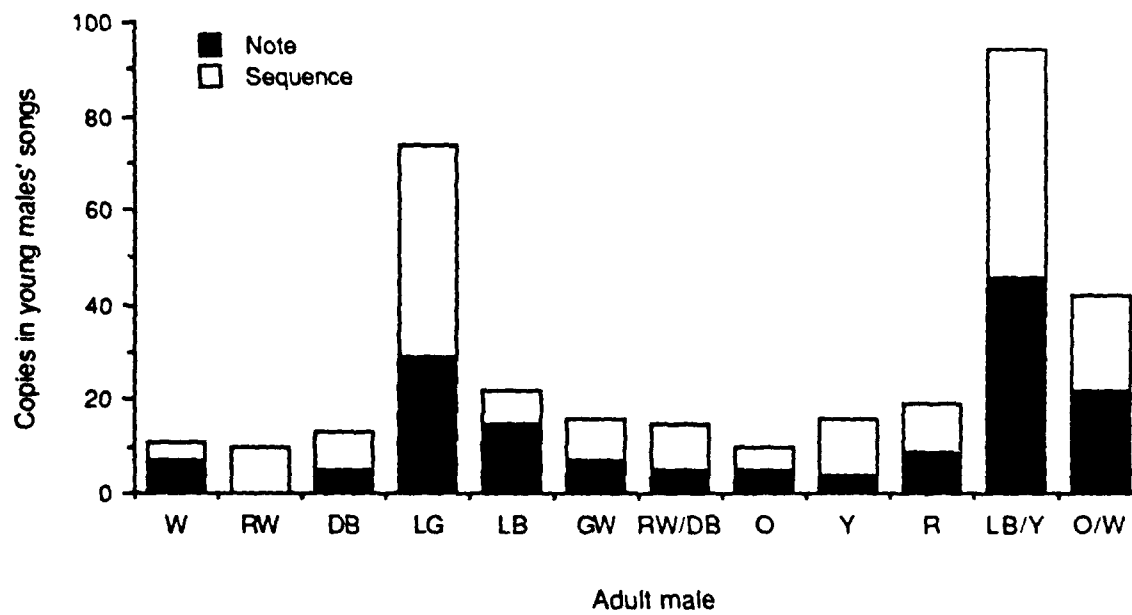
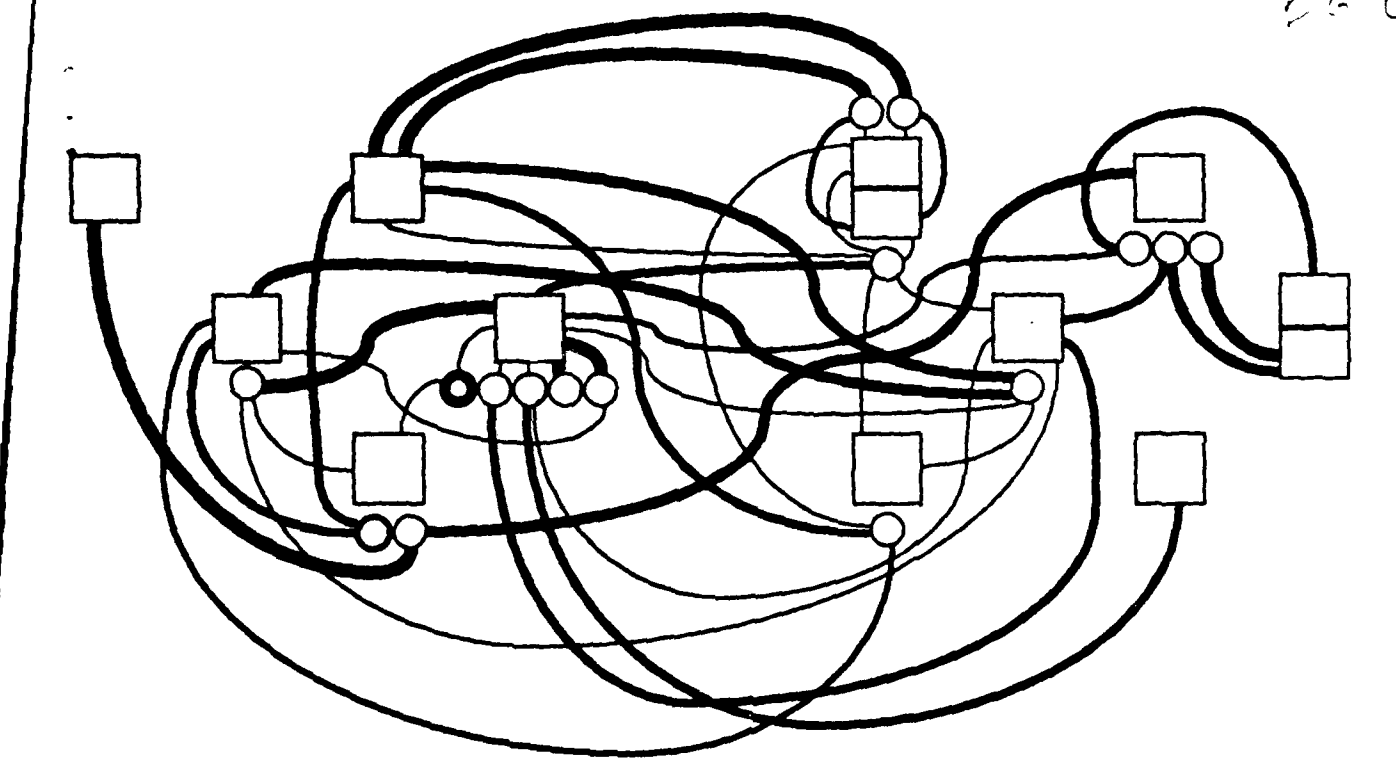


Figure 6



50 cm

-  Nest box occupied by an adult male - locations are drawn to scale.
-  Sons of the male occupying the nest box.
-  Line connecting a young male zebra finch to one of the sources of his song.
(Line thickness indicates the importance of the source)
- Thickness of the son's symbol indicates degree of improvisation in the song.

$r = 0.128$ for the correlation between song sources and the distances separating adult and young males' nest boxes.

Figure 7



Figure 8

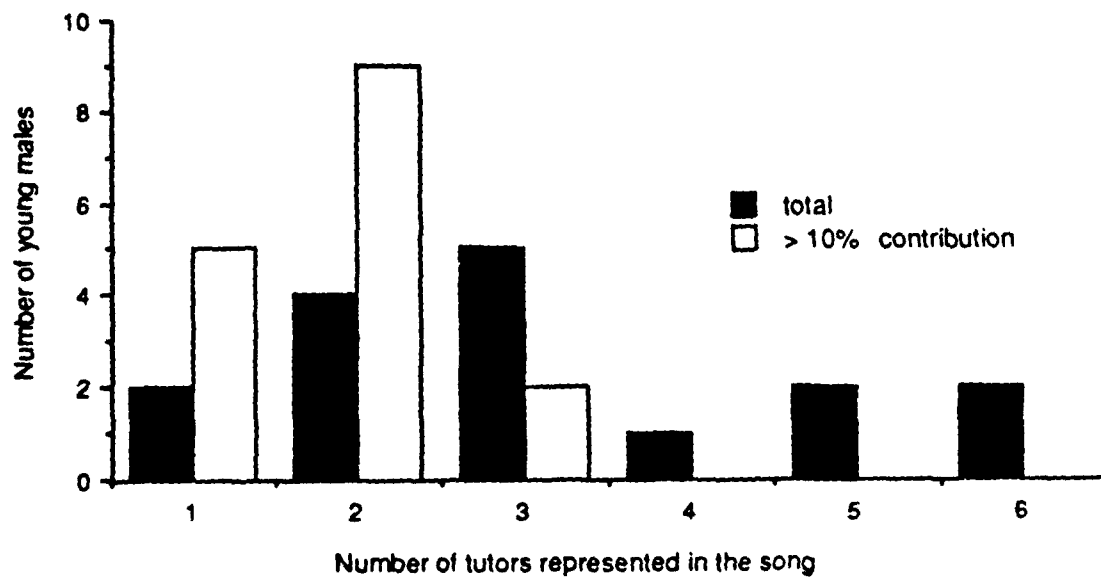
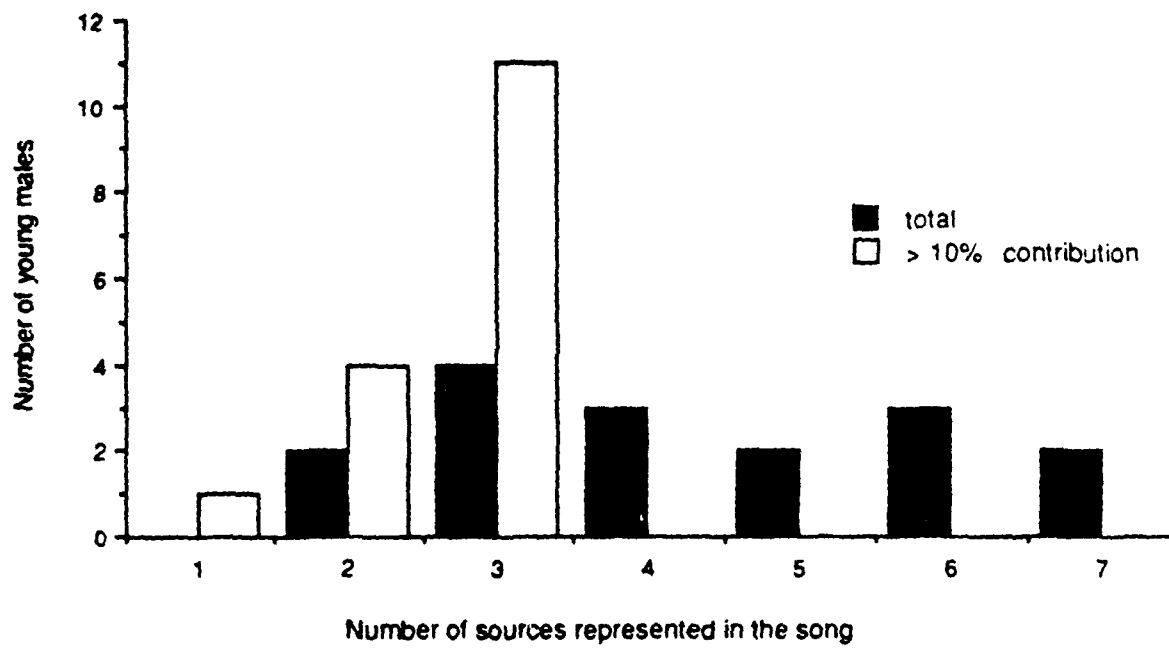
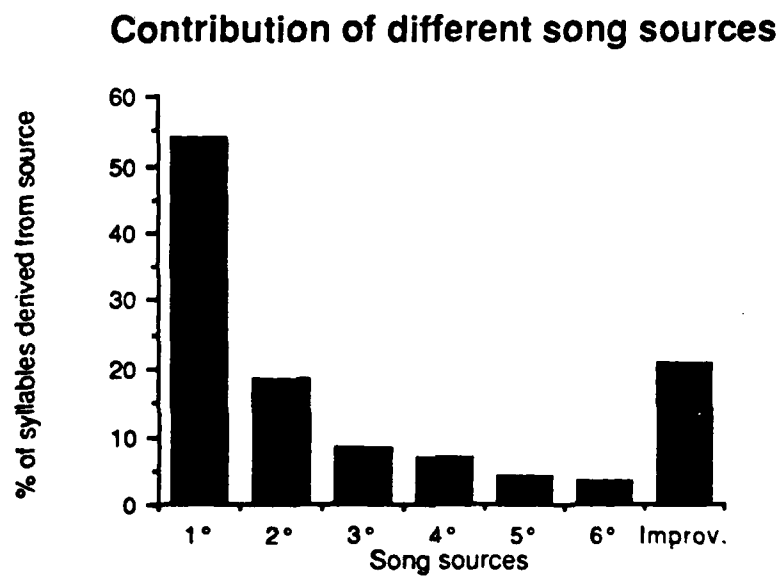


Figure 9



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