A Longitudinal Study of Syllable Usage in the Orcadian Population of the Chaffinch, *Fringilla coelebs*

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M.Phil

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Abstract

The chaffinch, *Fringilla coelebs*, population of the Orkney Islands, United Kingdom was studied to determine how syllable usage in their song repertoires has changed in the 25 years between 1977 and 2002. The constituent syllables of recordings made during 1977, 1997, and 2002 were compared for conservation of syllabic structure with respect to location, song type, and time. The results show that the overall spectral structure of a specific syllable type is maintained across all three variables, but that slight modifications in syllabic structure do occur as a function of recording location and time. These local traditions in syllable types suggest that an unlearned template for each syllable exists in this species, and that this template prevents large-scale modifications in syllable structure from taking place. This is beneficial to young male chaffinches involved in song acquisition because it simplifies the learning process. Because syllabic structure is unlearned, young males only have to refine that structure and learn the proper syllable sequences in their first spring.

Declarations

(i) I, Melville Joseph Wohlgemuth III, hereby certify that this thesis, which is approximately 10091 words in length, has been written by me, that it is the record of work carried out by me and that it has not been submitted in any previous application for a higher degree.

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(ii) I was admitted as a research student in March, 2001 and as a candidate for the degree of Master of Philosophy in Animal Behaviour in March, 2001; the higher study for this is a record was carried out in the University of St. Andrews between September, 2001 and July, 2002.

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(iii) I hereby certify that the candidate has fulfilled the conditions of the Resolution and Regulations appropriate for the degree of Master of Philosophy in Animal Behaviour in the University of St. Andrews and that the candidate is qualified to submit this thesis in application for that degree.

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Chapter 1: Introduction

The maintenance of a social system requires communication between its constituents. Avian societies are no exception, but they are distinctive from many others in that some forms of communication are learned. The chaffinch, *Fringilla coelebs*, was the first species studied to understand the capacity of vocal learning in birds. W.H. Thorpe (1958) raised young male chaffinches in acoustic isolation, and showed that auditory experience was necessary for a chaffinch to sing "typical" adult songs. Many subsequent experiments, both in the laboratory and in the field, have been aimed at understanding more about the process of song acquisition in young birds. In an approach similar to genetics, songs can be broken down into inheritable segments, and the biological worth of these segments judged by their prevalence in future generations. These segments are termed "memes," (Dawkins, 1976) and many of the same rules that govern the process of genetic inheritance also apply to memetic inheritance. Longer sections of genetic material are more susceptible to mutations and recombination, and the inheritance of multi-syllable memes is similarly affected by such alterations. It is therefore hypothesized that a high degree of fidelity exists during the inheritance of single syllable memes, which may in the extreme result in a static syllable pool from which all songs are derived. In order to test this hypothesis, chaffinch songs recorded in the Orkney Islands were examined for the conservation of syllabic structure over a 25-year time span.

1.1: Longevity of Single Memes Across Populations

Previous research on chaffinch song has investigated the inheritance patterns of song types, but not the inheritance of single syllables. One difficulty in studying the evolution of song types is determining the contribution of immigrating individuals on the meme pool. The effects of immigration can be minimized, however, by limiting the study to island and island-like populations. The chaffinches of New Zealand are one such an island-like community where the inheritance patterns of bird song have been studied. The New Zealand chaffinches were serially introduced between 1862 and 1877, with 400 individuals being released in total. Because the chaffinches released were collected from one area in England, divergence from a small collection of song types can be studied. Lynch et al (1989) quantified the amount of memetic divergence in the New Zealand population of chaffinches by comparing songs recorded over a 200-kilometer tract of the mainland. Memes of varying lengths (i.e. 1, 2, and 3 syllable inheritable units of song) were compared to the amount of meme sharing between different localities. The results show that memetic similarity is inversely proportional to both geographic distance and meme length. Memes of a single syllable were much more prevalent than memes of any other length. More than 60% of single syllables are shared by at least two populations; whereas three syllable memes are shared only 10% of the time, and memes greater than six syllables are almost never found in two different localities. The similarities between memetic and genetic inheritance provide an explanation for this phenomenon. Because mutations and recombinations are less likely to occur on smaller units of inheritance, single genes and single memes have a better chance of being

accurately copied than longer inherited units. In light of this fact, the longevity of single memes in a population should be greater than multi-syllable memes. The same syllable types were recorded over the entire 200-kilometer study site, suggesting that syllabic structure persisted after immigration spread single memes throughout New Zealand.

The longevity of single syllable memes was further substantiated through the Chatham Island population of chaffinches. Chatham Island is part of the New Zealand archipelago, and was colonized by chaffinches around 1900. The colonizers were all descendants of the original 400 individuals released in New Zealand. Songs from the Chatham and New Zealand populations have been compared in order to measure the amount of memetic change since colonization (Baker and Jenkins, 1987). Thirteen different variables (song length, trill length, syllable variants[1], etc.) were used to assess song similarity between the two communities. There was no statistical difference for any of the variables addressed, equating to a negligible divergence in song organization on Chatham Island since colonization. The syllable pool of Chatham was depauperate with respect to New Zealand, but eighteen of twenty different syllable types identified in Chatham Island were also found in New Zealand. Considering the time lag between chaffinch colonization and Baker and Jenkins' study (85 years), the high degree of similarity between the syllable types of Chatham and its ancestral community is quite remarkable.

Although few differences in song structure were observed between Chatham Island and New Zealand chaffinches, songs of New Zealand individuals are different from English birds. New Zealand chaffinch songs were compared with those recorded in

[1] Syllable Variants are syllables that are not different enough to be deemed separate types, but that show consistent modifications in their structure.

the vicinity of their ancestral population in England (Jenkins and Baker, 1984). During the century separating colonization of New Zealand and completion of Jenkins and Baker's study, noticeable changes in song organization and syllable structure developed. Less emphasis is placed upon the trill phrase in the songs of New Zealand, and much more elaborate end phrases have resulted. Jenkins and Baker speculated that the habitat acoustics in New Zealand have caused the differences seen in song organization. Chaffinches typically live in open, deciduous forests in England, while New Zealand chaffinches have colonized dense, coniferous forests. In tightly packed environments, song syllables with less temporal space between them are more distorted than syllables sung at a slower rate (Richards and Wiley, 1980). Jenkins and Baker suggest that the trill phrase, with its fast delivery, has been de-emphasized to compensate for the acoustic properties of New Zealand. The end phrase has concurrently grown in prominence because of the slower rate with which it is sung.

Even though a peculiar organizational structure of chaffinch song has developed in New Zealand, song learning follows the species-typical approach of recombination (Jenkins and Baker, 1984). Syllable structure is maintained throughout the learning process, but the ordering of syllables within the trill phrase is sometimes changed. In this type of learning paradigm, many different songs variants result, but are all related because the constituent syllables are from the same pool. The songs recorded in New Zealand show this type of relationship, and give further evidence for the longitudinal conservation of syllable structure hypothesis.

1.2: Similarities with the Indigo Bunting and the Neutral Meme Concept

The chaffinch is not the only species to show a high fidelity of syllabic structure during song acquisition. It is speculated that some species have a finite collection of syllables from which all songs are derived. One such species is the indigo bunting, *Passerina cyanea*, where it has been argued that 127 distinct syllable variants are used to construct all of the songs of the species (Baker and Boylan, 1995). Song learning occurs in a fashion similar to the chaffinch in that young males learn the songs of neighboring males during territory establishment in their first spring (Payne, 1981; and Thorpe, 1958). Not everything is learned in the first spring, however. Immature males raised in acoustic isolation from adult tutors develop abnormal songs, but the syllable structure is strikingly similar to normal song (Rice and Thompson, 1968). First-year males apparently know correct syllable structure before territory establishment, and learn only the proper ordering and finer structures of adult song in the spring. The chaffinch employs a song-learning paradigm similar to this. In laboratory-raised chaffinches, young males deafened late in the summer of their first year still crystallized species-typical songs in the spring (Nottebohm, 1968). The finer structures of adult song were missing, but the overall pattern of the song and structure of the syllables resembled normal, adult song. Chaffinches differ from the indigo bunting in that they can learn some aspects of their song in their first summer (Thorpe, 1958); but in the wild, they typically learn their songs from adjacent males during territory establishment the following year (Slater and Ince, 1980).

Young male indigo buntings benefit from learning the songs of neighbors in terms of reproductivity: first-year males singing the local song types are more successful at courtship than those who sing alien songs (Payne et al, 1981). For adults, however, there does not seem to be any relationship between particular song variants and reproductive success. A "neutral meme hypothesis" describes the situation where different song types carry equal worth in terms of biological fitness. Variations in indigo bunting song are equivalent because all songs are derived from the same finite set of syllables.

Song learning in the chaffinch has also been described as following a neutral meme model. The chaffinches colonizing the Atlantic Islands have been studied to better understand the inheritance pattern of song types, and specifically, how the neutral meme model of inheritance affects song learning. Chaffinch songs recorded on the Azores, Madeira, Canary Islands, Iberian Peninsula, and Morocco were compared to test the memetic variation within each population (Lynch and Baker, 1993). Mutation rates for memes of varying lengths were computed, and showed a similar pattern to that described earlier by Lynch et al (1989). On the Atlantic Islands, one syllable memes are subject to very little modification, and the rate of mutation increases with meme size. The number of syllable types was consistent across all populations studied except for the Azores. The Azores chaffinches live in a much higher density than the other communities studied, and more variation at the syllable level has resulted. This is expected in a neutral meme system because trait diversity should increase with population size (Lynch and Baker, 1993). Song variability did not follow the same pattern of syllable variability, however. The peripheral populations of this study: the Azores, Canaries, Madeira, and Morocco, have higher levels of song type variation than the Iberian population. The "loss of

contrast hypothesis" offers an explanation (Thieckle, 1969). Although the peripheral communities (especially those of the Azores) have greater population densities, the species diversity is markedly less than it is in Spain. Iberian chaffinches must therefore compete with more birds for the same acoustic space, resulting in less flexibility of their species-specific vocalizations as an assurance that they are both heard and understood by other individuals (Lynch and Baker, 1993). The songs of Iberian chaffinches are constrained by this phenomenon; but the Azores, Madeira, and Canary Island chaffinches can be more permissive during song learning because there are fewer acoustic competitors with which to be confused.

The Azores chaffinches are interesting because two different factors seem to be affecting song variability. The number of syllable types has increased because of a greater density of chaffinches, while song variability has increased because of a lack of inter-specific competitors (Lynch and Baker, 1993). Both of these phenomena are typical of a neutral meme model of inheritance. Parallels between chaffinch and indigo bunting song could extend beyond the neutral meme hypothesis. Neutral meme situations can result when all songs have the same basic structural units or, in other words, when all songs are constructed from the same set of syllables. This is the case for the indigo bunting, and may be true for the chaffinch as well.

1.3: The Function of Adult Song

Considering the function of adult chaffinch song may provide an explanation for the benefits of a conserved set of song syllables. Recordings of chaffinch songs made in Sussex, England, and the Orkney Islands, Scotland, suggest that song functions primarily

as a means of territory establishment and maintenance, and it's role in mate acquisition is secondary (Slater, 1981). In a breeding scheme like that of the chaffinch, females are attracted to males based upon territory quality. Because song is utilized to maintain territories, song quality has a more indirect effect upon breeding success than it would if its primary function was to attract mates. During playback studies, chaffinches respond to the songs heard by singing those in their own repertoires that are the most similar (Slater, 1981). These two findings suggest that song matching is important for territorial defense in the chaffinch. Limiting the syllables available for song learning to a fixed set increases the likelihood of two songs being similar and, in turn, the chance that a male is able to match the songs of a neighbor. This is further supported by evidence that males sing a particular song type more often when it is also in the repertoire of a neighboring male (Slater, 1981). The probability that an individual is able to match a song heard is increased when all songs are constructed of the same syllables. The function of chaffinch song therefore supports a song-learning scheme where syllable structure is conserved across the population.

1.4: The Current Project

Many studies have hinted at the fact that syllable structure is conserved in songs of the chaffinch (Lynch et al, 1989; Baker and Jenkins, 1987), but no study has specifically addressed the issue. Answering this question requires multiple years' worth of recordings, which were fortunately available for the Orkney Island population of chaffinches. Songs are available from the years of 1977 (Slater and Ince, 1979) and 1997

(Lachlan, 1999), and song types for 2002 were collected to establish three data points at interesting time intervals. The conservation of syllable structure over longer periods was studied using comparison with the 1977 recordings, as well as the short-term changes in chaffinch songs from 1997 to 2002. It was hypothesized that syllabic structure would be conserved through all years indicating that there is a finite collection of syllables that are common to all song types recorded.

Chapter 2: Methods

2.1: Slater 1977 Recordings

Peter Slater recorded songs of the chaffinches populating the Orkney Islands, United Kingdom during the spring of 1977 (Slater and Ince, 1979). Surveys were conducted on three of the islands: Mainland, Shapinsay, and Rousay. On the Mainland, songs were recorded at Binscarth, Finstown Village, Gyre House, Woodwick House, and Berstane House; on Shapinsay at Balfour Castle; and on Rousay at Trumland Woods. Recordings were made using a Uher 4200 IC tape recorder and a Grampian DP4X microphone mounted on a 50 cm parabolic reflector. The tape speed was 9.5 cm/second.

2.2: Lachlan 1997 Recordings

Robert Lachlan recorded the songs of the chaffinches in the Orkney Islands, United Kingdom during the spring of 1997 (Lachlan, 1999). Surveys were conducted on three of the Islands: Mainland, Shapinsay, and Rousay. On the Mainland, songs were recorded at Finstown Village, Binscarth, and Woodwick House; on Shapinsay at Balfour Castle; and on Rousay at Trumland House. Recordings were made using a Telinga Pro 5 microphone and a Marantz CP430 cassette recorder. The tape speed was 4.75 cm per second.

2.3: Wohlgemuth 2002 Recordings

Research was conducted from April 4, 2002 until May 8, 2002 on the Orkney Islands, Scotland. Surveys were conducted on five of the Islands: Hoy, Mainland, South Ronaldsay, Shapinsay, and Rousay. On Hoy, chaffinch songs were recorded at Bu Farm,

and Moness; on the Mainland at Binscarth and Finstown Village; on Shapinsay at Balfour Castle; and on Rousay at Trumland Woods, and Westness House. Other sites on mainland Orkney, Hoy, and South Ronaldsay were surveyed, but no chaffinches were found. Recordings were made using a Sennheiser K6 Modular gun microphone and a Marantz CP430 cassette recorder. The tape speed was 4.75 cm/second. Map 1 gives the location for all of the recording sites.

Map 1: The Orkney Islands, island names are in caps and black dots mark each recording site.

The size and density of the habitats available for Orcadian chaffinches increases the likelihood of pseudoreplication in the recordings. Most suitable places for chaffinches to nest are small and rather isolated, keeping the overall number of birds living on the islands low. On one hand, this is beneficial because it is feasible to record a

vast majority of the total songs over a relatively short time period; but, this also increases the probability that a single bird will be recorded at the same site multiple times. It was impossible to ensure that recordings made on different days at the same location were from different males, but the nature of the analyses minimizes the influences of pseudoreplication on the conclusions. The goal of the field research was to record all of the song types of each location in order to make comparisons between locations. In this system, song type abundance over all the recording sites is more important than within a location, and each site is therefore treated as a single data point. It does not matter how many songs a single male contributes to recording location's song "pool," because it will still only be considered one replicate during the analysis.

2.4: Digitization and Selection

The recordings were digitized using Goldwave version 4.25 at 44100 kHz. A spectrogram for each song was made using the Song Analysis II program (Tchernichovski, 2000). Song types were visually determined for every recording site by examination of the constituent syllables. A song type was deemed unique if either the syllable types and/or their sequencing did not match any of the other identified types of songs. Appendices A, B, and C show the song types for each year recordings were made, and the numbers under each song type correspond with the defined syllable types. If the same, visually identified syllable was found at more than one location, then these were deemed syllable variants rather than different syllable types. The nomenclature was purely semantic, however, because syllable variants were still treated separately during

analysis. The ten best examples of each song type (i.e. favorable signal to noise ratio) were chosen for further investigation.

The syllable variations constituting the trill phrase of the best versions of each song type were identified, and the ten examples with the highest signal to noise ratio were selected using Matlab version 5.3. Typical chaffinch songs contain both a trill phrase and an end flourish. The end flourish was not included in analyses because its structure is not conserved in the same manner as the trill. The inheritance patterns of syllables constituting the trill phrase can be easily determined through comparisons of neighboring males, whereas the specific structure of the end phrase follows a more random assignment (Jenkins and Baker 1984). As a result, the syllables of the trill phrase have traditionally been used for researching song learning in the chaffinch while the end phrase has not (Slater 1979; Slater and Ince 1980; Lynch and Baker 1993); this tradition has been maintained for the current research. In cases were the same syllable was found in more than one song type, ten syllables from each song type were used during analyses.

2.5: Analyses

The autocorrelation function of Avi-Soft SASLab Pro was used to compute similarity scores for each pair of syllables. Correlation coefficients between each variation of a single syllable were first computed. Histograms of the correlation coefficients were drawn using Matlab 5.3, and those with non-normal or bimodal distributions were noted for future consideration.

Dendrograms for each intra-syllable correlation matrix were constructed using the cluster analysis function of SPSS version 11.0. The clustering method employed was the

nearest neighbor technique, and squared-euclidean distances were used for interval measurements. Each dendrogram was compared with the corresponding histogram of correlation values, and clustering patterns were noted with regards to normal and bimodal distributions: in syllable sets where bimodal distributions of their correlation coefficients resulted, the grouping pattern seen in its dendrogram was related to this bimodality.

For each syllable type, one example was chosen for an autocorrelation of all syllable types within a single year and between years. Once again, Avi-Soft was used to compute the correlation matrix, and a histogram of the distribution of coefficient values was generated using Matlab version 5.3. The correlation matrix was inputted into SPSS, and the cluster analysis function (method: nearest neighbor, interval: squared-euclidian distances) was used to construct a dendrogram for the entire syllable set. The dendrogram was then used to qualitatively assess the relationship spectrograms of each syllable to their appropriate groupings. This was accomplished by comparing the recording locations of each structurally similar group of syllables to their respective histogram of correlation coefficients. The histograms were visually analyzed, and those identified as having bimodal distributions were compared to their corresponding dendrograms to determine the basis of this bimodality. A bimodal distribution of correlation coefficients infers that a subset of syllables are more similar to one another, but dissimilar to the group as a whole. This dissimilarity could be a result of differences in recording quality, or it could be a function of a more important variable such as location. Relating the bimodality of the histograms to the clustering patterns of the dendrograms, illuminates whether the basis of the structurally similar groups is a result of noise in the recordings or something more significant like location.

Syllables types found at the same recording site in all three years were used for further analyses on the longevity of specific syllable structures. Four examples of each syllable type for each year were compared using the autocorrelation function of AviSoft SASLab Pro. The resulting correlation matrix was used to construct a dendrogram for each syllable type, as well as box plots for the correlation coefficients of syllables recorded in the same year and between years. One-way ANOVA statistics were employed to determine if the values for each category were significantly different from each other, and the Tukey post-hoc test was used to calculate which sets of correlation coefficients were on average higher or lower. Equal variances were assumed for each test, and this was supported through homogeneity of variance tests.

Chapter 3: Results

3.1: Slater 1977 Data

3.1.1: Song Types and Syllable Selection

Fourteen different song types were identified in the recordings made during 1977. Not all song types were well represented in the data, and for statistical purposes, the set was further reduced to seven song types (see Appendix A for spectrograms of each song type). Effort was made to ensure that the final set of song types included all of the relevant syllables in the data. Fifteen distinct syllable types and one transition syllable (see Appendix A for spectrograms of each syllable type) were visually identified; with 7 to 20 examples of each syllable selected for analysis. Eight of these syllables were found at more than one location, and seven syllables were found in multiple song types. Table 1 summarizes general information regarding each syllable.

	Examples	Song Type	Histogram	Location
Syllable 1	10	Type 1	Uniform	Finstown
Syllable 3	20	Type 2 and 7	**Bimodal**	Finstown, Binscarth, and Trumland
Syllable 4	20	Type 2 and 7	Uniform	Finstown, Binscarth, and Trumland
Syllable 5	20	Type 2 and 7	**Bimodal**	Finstown, Binscarth, and Trumland
Syllable 6	10	Type 1	Uniform	Finstown
Syllable 7	10	Type 1	Uniform	Finstown
Syllable 8	10	Type 3	Uniform	Finstown and Binscarth
Syllable 9	10	Type 3	**Bimodal**	Finstown and Binscarth
Syllable 10	10	Type 3	Uniform	Finstown and Binscarth
Syllable 12	20	Type 4 and 5	Uniform	Balfour and Berstane
Syllable 14	10	Type 5 and 6	**Bimodal**	Trumland
Syllable 15	20	Type 4 and 5	Uniform	Balfour and Berstane
Syllable 16	18	Type 4 and 5	**Bimodal**	Balfour
Syllable 18	7	Type 6	Uniform	Trumland
Syllable 19	7	Type 6	Uniform	Trumland
Syllable TS2	10	Type 7	Uniform	Trumland

Table 1: Syllable types and the number of examples of each. Also included are the song types each syllable was found in, the shape of the correlation histograms, and the location each syllable type was recorded at.

3.1.2: Within-Syllable Comparisons:

The spectral similarities for each group of syllable samples were computed using Avi-Soft SASLab Pro. The output of the auto-correlation function is a matrix of correlation coefficients for each comparison. For example, the output of the three syllables named: var1, var2, and var3, would be a 3 x 3 matrix of nine correlation coefficients. Table 2 is an example of the correlation matrix for Syllable 18 of the 1977 data.

Syllables	var1	var2	var3	var4	var5	var6	var7
var1	1	0.898	0.927	0.925	0.918	0.898	0.935
var2	0.898	1	0.92	0.918	0.937	0.829	0.917
var3	0.927	0.92	1	0.906	0.953	0.863	0.944
var4	0.925	0.918	0.906	1	0.944	0.861	0.892
var5	0.918	0.937	0.953	0.944	1	0.869	0.946
var6	0.898	0.829	0.863	0.861	0.869	1	0.866
var7	0.935	0.917	0.944	0.892	0.946	0.866	1

Table 2: The correlation matrix for the samples of Syllable 18. Each number represents the correlation coefficient between the corresponding variables in the left column and top row. The range of values is 0 to 1.0, with 1.0 signifying the two syllables are identical to one another.

Once correlation matrices for all syllables were computed, histograms for each matrix were used to determine if the distribution of coefficients was normal or bimodal. The distributions of Syllable 3, Syllable 5, Syllable 9, Syllable 14, and Syllable 16 were identified as being bimodal, while all other comparisons exhibited normal or unstructured distributions. A bimodal distribution results when sub-groups of similar variants exist within a syllable type. In this situation, one subset of variants are structurally similar to each other, but not to the other subset(s). The distribution of correlation coefficients therefore includes both high and low quantities. In the case of the five syllables mentioned above, the two modes are often centered at 0.5 and 0.8, representing the average similarity between and within subsets, respectively. Figure 1 shows an example of both the normal and bimodal distributions determined by the data.

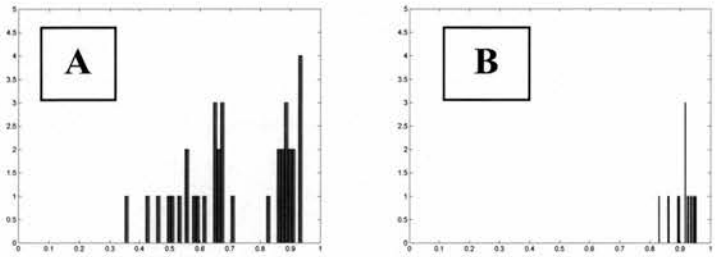

Figure 1: Histograms showing the distribution of correlation coefficients for: (A) Syllable 14 and (B) Syllable 18. Note the normal distribution of Syllable 18, a group of highly similar samples, as compared to the distribution of Syllable 14, which has subsets of variants with differing similarities.

In cases such as Syllable 14, where at least two different subsets of syllable variants exist, it is important to determine why such a situation has resulted. Cluster analysis was used to construct similarity dendrograms for each syllable type. From these dendrograms it is possible to see which syllable variants are more closely related, and also to determine the membership of any syllable type subsets. Using Syllable 14 as an example, the dendrogram reveals three groups of related syllables (Figure 2).

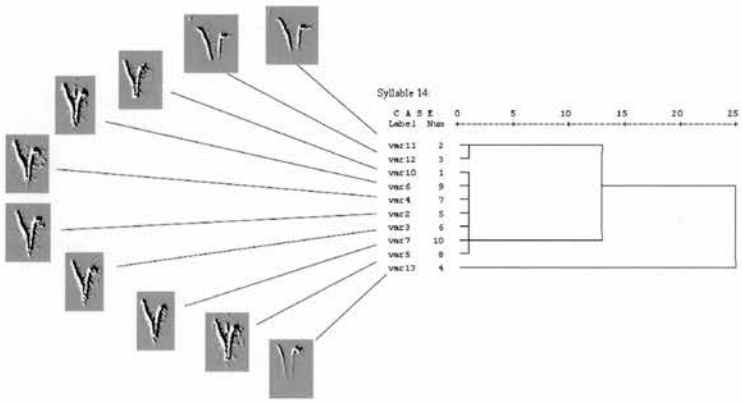

Figure 2: Dendrogram output for a cluster analysis of Syllable 14 examples. The gray boxes represent the spectrograms for each syllable compared. "Label" identifies each syllable example; "Num" identifies the order in which syllable pairs were grouped; and "Case" is an arbitrary unit used by the SPSS software to graphically represent similarity. Similarity distances are only determined along the X-axis; vertical distance along the Y-axis is inconsequential.

Syllable samples 2 through 10 are grouped together, and are therefore very similar to one another (so similar that the cluster analysis was not able to resolve any difference

between them). Syllable examples 11 and 12 are similar to one another, but not to examples 2 through 10. Sample 13 was unlike any of the other examples compared, and as a result, grouped singly. Examining where each syllable example was recorded, and from what song type they were taken provides an explanation for the differences in similarity. Syllable examples 2 through 10 were all recorded at the same location, Trumland Woods on Rousay Island, and taken from Song Type 6. Samples 11 through 13, on the other hand, were recorded at Balfour Castle on Shapinsay Island, and used instead for Song Type 5. In the case of Syllable 14, syllable variant subsets result when the same syllable is used in different locales, and for different song types. Whether or not these syllables should be deemed separate types, or just variants of the same type, is difficult to determine.

Syllable Types 3, 4, 5, 8, and 16 also have bimodal distributions of their correlation coefficients (Appendix D shows the histograms and dendrograms of the Slater 1977 syllables). The twenty examples of Syllable 3 were sorted into groups by the same cluster analysis procedure described above, and were examined for any consistencies with regard to syllable structure. Samples 1 through 9 were contained within one group, and samples 10 through 20 were grouped into another cluster (Figure 3).

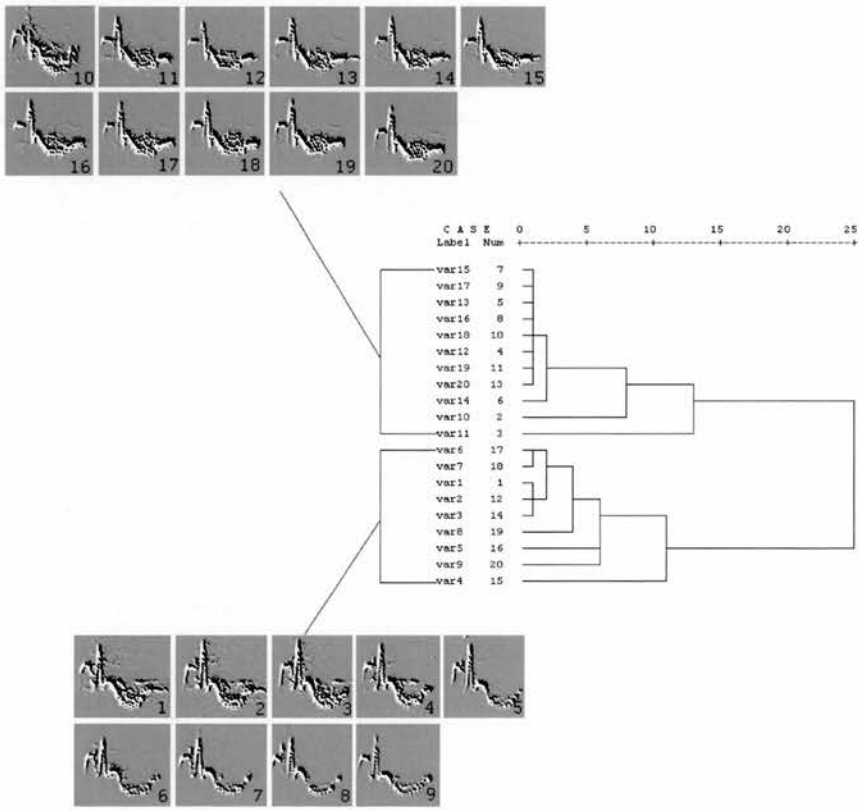

Figure 3: Dendrogram of Syllable Type 3. Similarity distances are determined solely by the X-axis and not by the Y-axis.

Looking at the recording location and song type for each syllable example reveals a pattern similar to that described for Syllable 14. Examples 1 through 9 were all recorded at Finstown Village, and were taken from Song Type 2; example 10 was recorded at Binscarth, and was also a Song Type 2 syllable; and examples 11 through 20 were recorded at Trumland Woods, and taken from Song Type 7. The clustering of Syllable 3 suggests that location is a more important factor to syllable structure than song type; examples 1 through 9 were from the same song type as example 10, but were structurally different as a result of recording location.

The bimodality of Syllable 4 and 5's correlation coefficients is also a result of recording site (Figure 4).

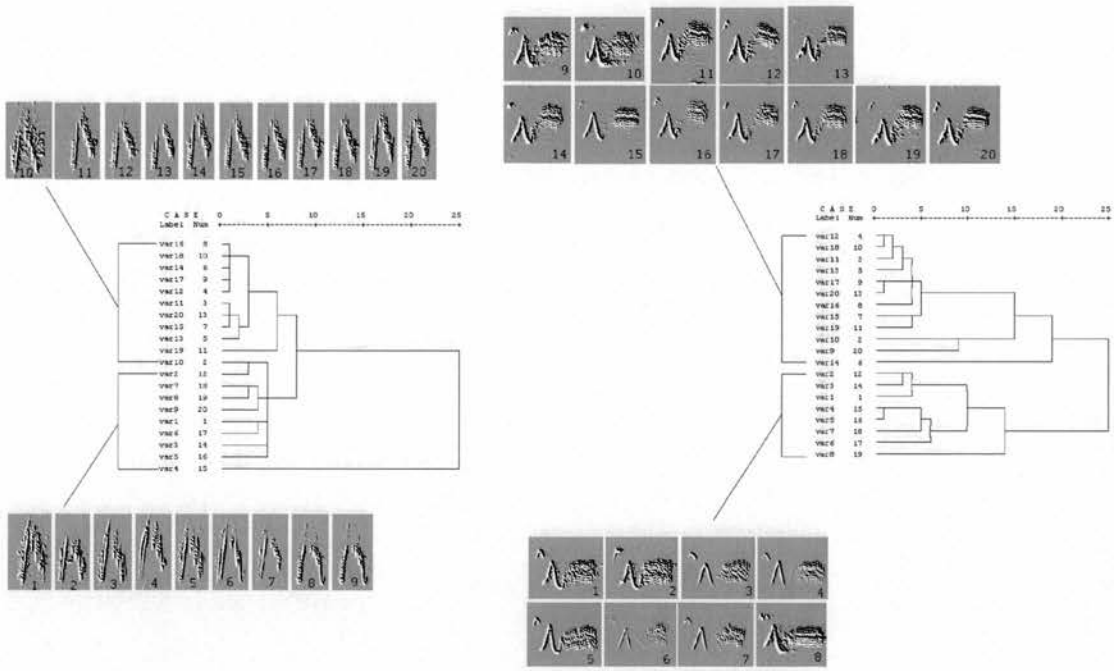

Figure 4: Dendrograms for Syllable Types 4 and 5. Type 4 is on the left, and Type 5 is on the right.

Syllable examples 1 through 9 of Type 4 were recorded at Finstown Village, example 10 was recorded at Binscarth, and examples 11 through 20 were recorded at Trumland Woods. Cluster analysis of Syllable Type 4 maintained location specific groupings, but not song type specific groupings (examples 1 through 10 are all from Song Type 2). The same pattern is seen in Syllable Type 5: samples 1 through 8 are from Finstown Village and Song Type 2; samples 9 and 10 from Binscarth and also Song Type 2; and examples 11 through 20 were recorded at Trumland Woods in Song Type 7. The clustering of Syllable Types 4 and 5 suggests once again that location is a more important factor in determining syllable structure than song type.

The correlation coefficients of Syllable Types 9, 10, 12 and 15 are not as high, and their distributions are borderline bimodal (Appendix D). The cluster analysis for Syllable Type 9 sorts samples 9 and 10 separate from the other eight, and these two

samples were the only ones recorded at Binscarth (samples 1 through 8 were recorded at Finstown Village). The clustering of Syllable Type 10 did not follow location specific trends, and it appears that recording quality is affecting the grouping analysis. A similar pattern is seen for Syllable Type 15. Example 11 is the only syllable sample considerably different from the rest, and it also happens to be the one with the poorest recording quality. Samples 10 and 11 were recorded at Berstane House, whereas all others were recorded at Balfour Castle. The clustering of Syllable Types 12 and 15 show a trend for song type specific differences in syllable structure, but recording quality has prevented conclusive results.

The syllables without bimodal distributions of their correlation coefficients provide more evidence for location specific modifications in syllable structure. Syllable Types 1, 6, 7, 18, 19, and TS2 were each recorded at the same location, and derived from the same song types (Appendix D). The correlation coefficients show high similarities within each syllable type, and the histograms are all normally distributed. These syllables do not appear to have variant subsets within each collection of samples.

3.1.3: Between Syllable Comparisons

One example of each syllable type was chosen (on the basis of its recording quality) to compare the structural similarities of all syllables. In a manner similar to the within-syllable comparisons, correlation coefficients were computed between each pair of syllable types, and histograms and dendrograms were constructed from these matrices (see Appendix G for all relevant graphs). The cluster analysis performed between syllable types did not exhibit any trends towards song type specific or location specific similarities. The more tonal syllables had a tendency to sort with each other, as did the

syllables containing harmonics and frequency sweeps. In general, the syllables of the 1977 recordings were noticeably different from one another, and the cluster analysis confirmed the syllable groupings that were identified visually.

3.2: Lachlan 1997 Data

3.2.1: Song Types and Syllable Selection

Twelve song types were identified in the recordings made during 1997 (see Appendix B for spectrograms of each song type). Twenty-two distinct syllable types (also shown in Appendix B) were visually identified; and 1 to 28 examples of each syllable were selected for analysis. Nine syllable types were found in more than one location, and eight syllable types were found in more than one song type. Table 3 summarizes general information on each syllable.

	Examples	Song Type	Histogram	Location
Syllable 1	2	Type 1	Uniform	Balfour
Syllable 2	2	Type 1	Uniform	Balfour
Syllable 3	2	Type 1	Uniform	Balfour
Syllable 4	28	Type 1, 4a, 4b, 5, and 9	**Bimodal**	Balfour, Finstown, Trumland
Syllable 5	12	Type 2	**Bimodal**	Balfour and Finstown
Syllable 6	10	Type 2	Uniform	Balfour and Finstown
Syllable 7	13	Type 2	Uniform	Balfour and Finstown
Syllable 8	4	Type 3	Uniform	Balfour
Syllable 9	14	Type 3, 7, and 12	**Bimodal**	Balfour, Finstown, Trumland
Syllable 10	10	Type 3, 6, and 11	Uniform	Balfour, Finstown, Trumland
Syllable 11	14	Type 4, 5, and 9	Uniform	Finstown and Trumland
Syllable 12	16	Type 4a, 4b, and 6	Uniform	Finstown
Syllable 13	17	Type 4a, 4b, 6 and 11	**Bimodal**	Finstown and Balfour
Syllable 14	3	Type 5	Uniform	Finstown
Syllable 15	7	Type 6 and 7	Uniform	Finstown
Syllable 16	10	Type 7, 9, and 12	Uniform	Finstown and Trumland
Syllable 17	8	Type 8	Uniform	Trumland
Syllable 18	8	Type 8	Uniform	Trumland
Syllable 19	8	Type 8	Uniform	Trumland
Syllable 20	1	Type 10	Uniform	Woodwick
Syllable 21	1	Type 10	Uniform	Woodwick
Syllable 22	1	Type 10	Uniform	Woodwick
Syllable 23	1	Type 11	Uniform	Balfour

Table 3: Syllable types and the number of examples of each. Also included are the song types each syllable was found in, the shape of the correlation histograms, and the location of the recordings made for each syllable type.

3.2.2: Within-Syllable Comparisons

Because there were fewer than four examples of seven of the twenty-three syllables identified in the 1997 recordings, only sixteen syllable types could be used for analyses. The auto-correlation function of Avi-Soft SASLab Pro was used to compute the structural similarities of Syllable Types 4 through 19, but Types 1 through 3, and 20 through 23 were not included in the analysis. Histograms of the correlation coefficients for each intra-syllable comparison were again used to determine if the distribution was normal or bimodal (see Appendix E for the histograms and dendrograms of each within syllable comparison).

Of the sixteen different syllables identified, only four exhibited non-normal distributions of their correlation coefficients: Syllable Types 4, 5, 9 and 13. The basis of these bimodalities is not as clear-cut in the 1997 recordings as it was in 1977; location does not always have a consistent effect upon syllable structure. This is exemplified in the dendrogram for Syllable Type 4 (Figure 5).

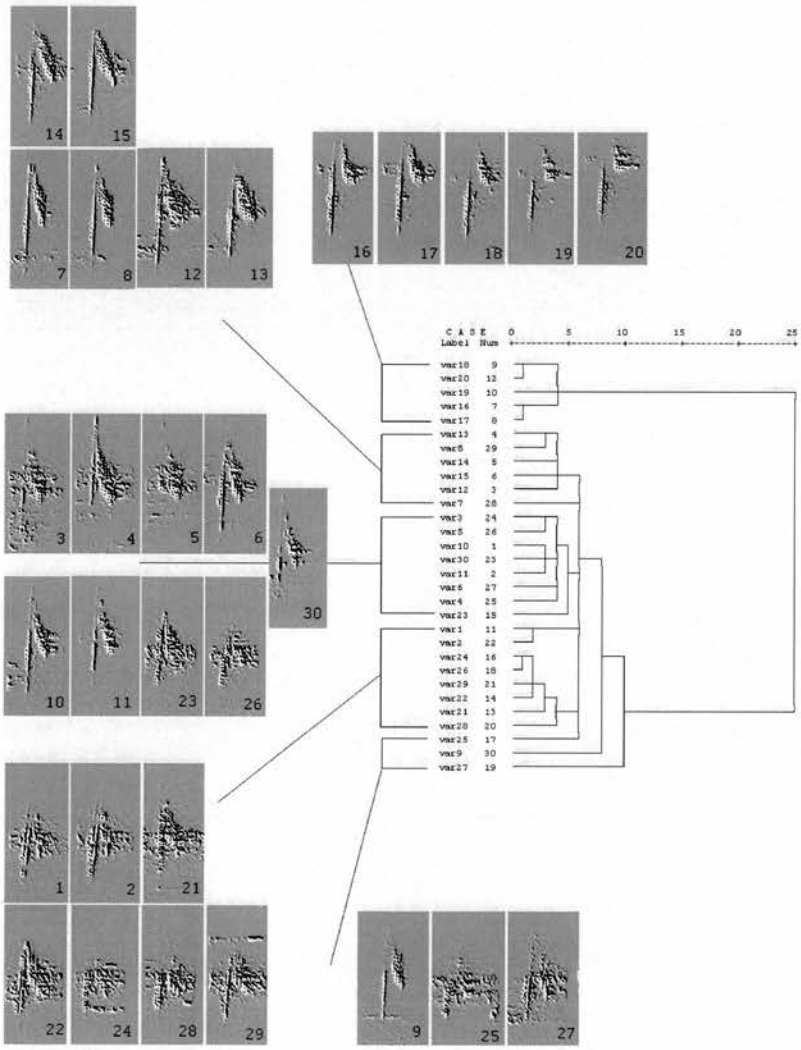

Figure 5: Dendrogram of Syllable Type 4. Similarity distances are defined by the X-axis and not the Y-axis.

Examples 1 through 15, and 21 through 30 are quite similar to one another as determined by their groupings. Examples 16 through 20 have been clustered separate from the rest, and these five syllables were the only samples recorded at Trumland Woods. The other 25 examples were recorded at Balfour Castle or Finstown Village, and were derived from five different song types. Except for examples 16 through 20, the groups determined by cluster analysis did not follow any trends based upon location or song type. This is partly the result of poor recordings. The spectrograms for many of the examples of Syllable Type 4 are contaminated with background noise, and this noise interferes with the proper sorting of each syllable sample.

Unlike Type 4, Syllable Type 9 does show a tendency for location specific syllable structures (Figure 6).

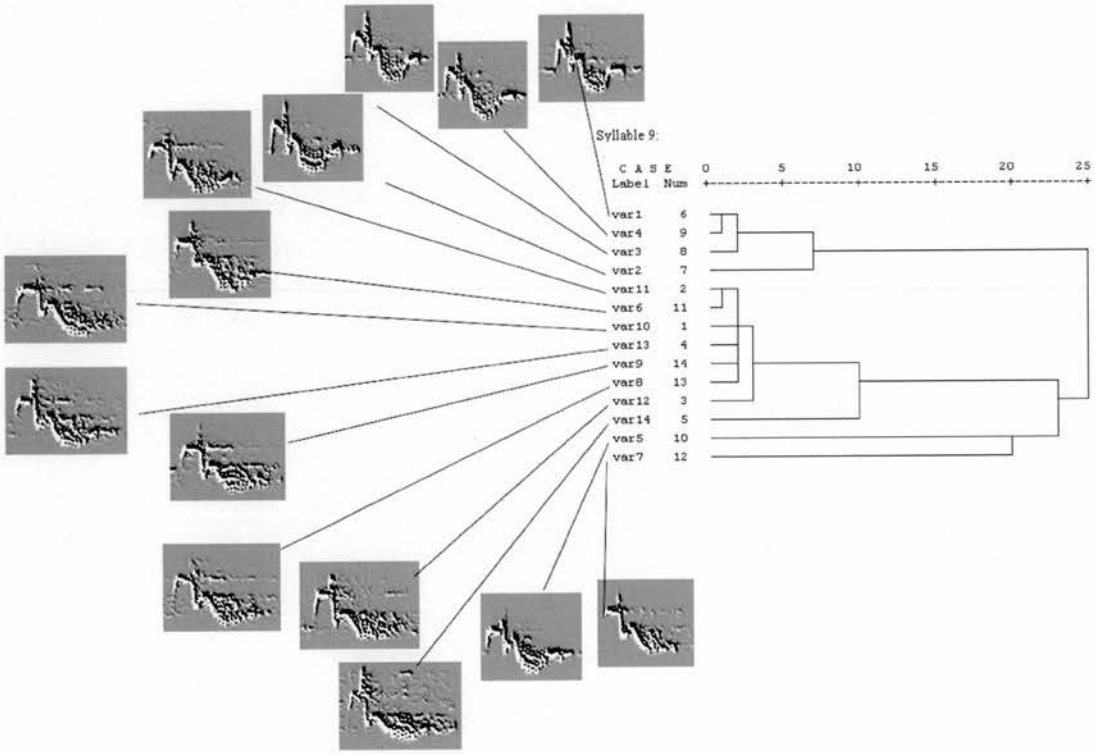

Figure 6: Dendrogram for Syllable Type 9.

Examples 1 through 4 sorted together and were recorded at Balfour Castle in Song Type 3. Example 5 was also found in Song Type 3, but was the only sample recorded at Finstown Village. This resulted in it being grouped by itself during the cluster analysis. Except for example 7, the rest of the examples of Syllable Type 9 were recorded at Trumland in Song Type 12, and received the same grouping. The failure to cluster example 7 with the rest of the Trumland data is most likely a result of low quality recordings.

The clustering of Syllable Type 13 appears to be much more random (Figure 7).

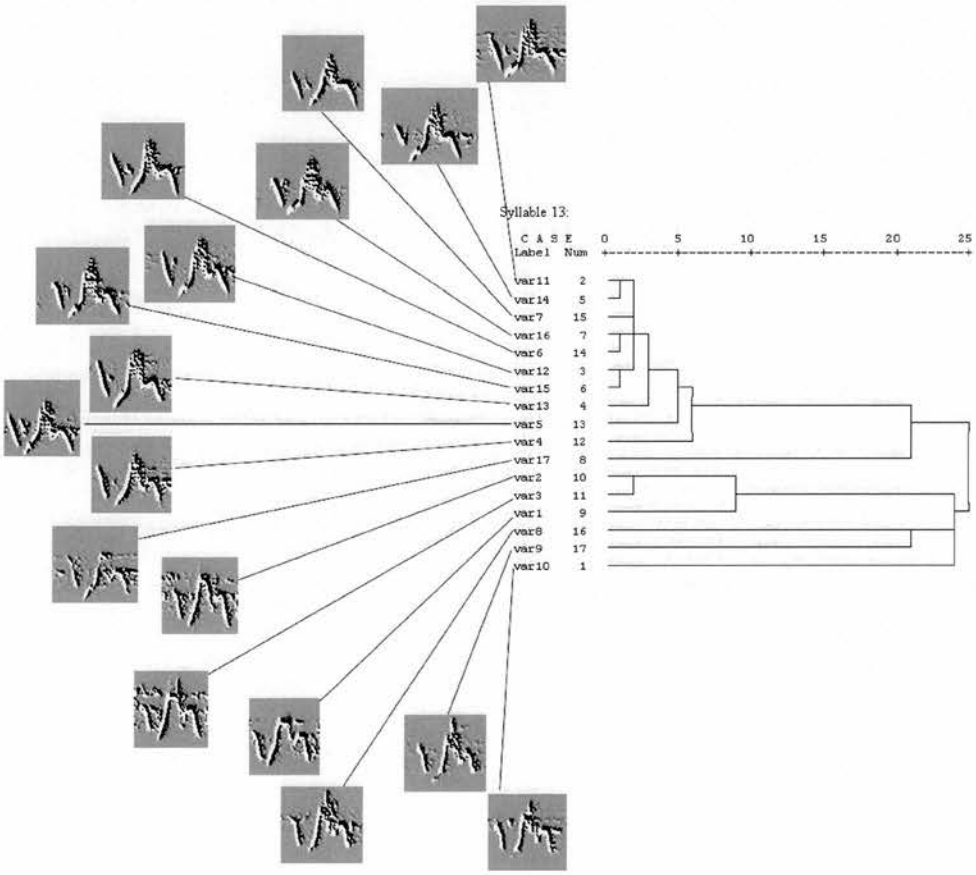

Figure 7: Dendrogram for Syllable Type 13.

Examples 1, 2, and 3 were grouped together, showing a trend for song type specific structures, but the trends ended there. All other examples of Type 13 failed to group according to location or song type.

The distributions of correlation coefficients for all other syllable types (6 through 8, 10 through 12, and 14 through 19) do not show evidence of bimodality (Appendix E). Syllable Types 6, 7, 10, 16, and 19 are borderline bimodal, but closer inspection reveals noise contamination to be responsible for the differences in correlation coefficients. Syllable Type 12 is an interesting illustration of location being a more important factor in determining syllable structure than song type. Syllable Type 12 was only recorded at Finstown Village, but it is found in three different song types. The distribution of correlation coefficients is centered at 0.7, and shows no sign of bimodality. For this syllable type, the use of the syllable (i.e. which song type it is used in) has no effect upon syllabic structure. Syllable Type 11 also lacks a bimodal distribution of its correlation coefficients, but there are location specific trends in the clustering scheme (Figure 8).

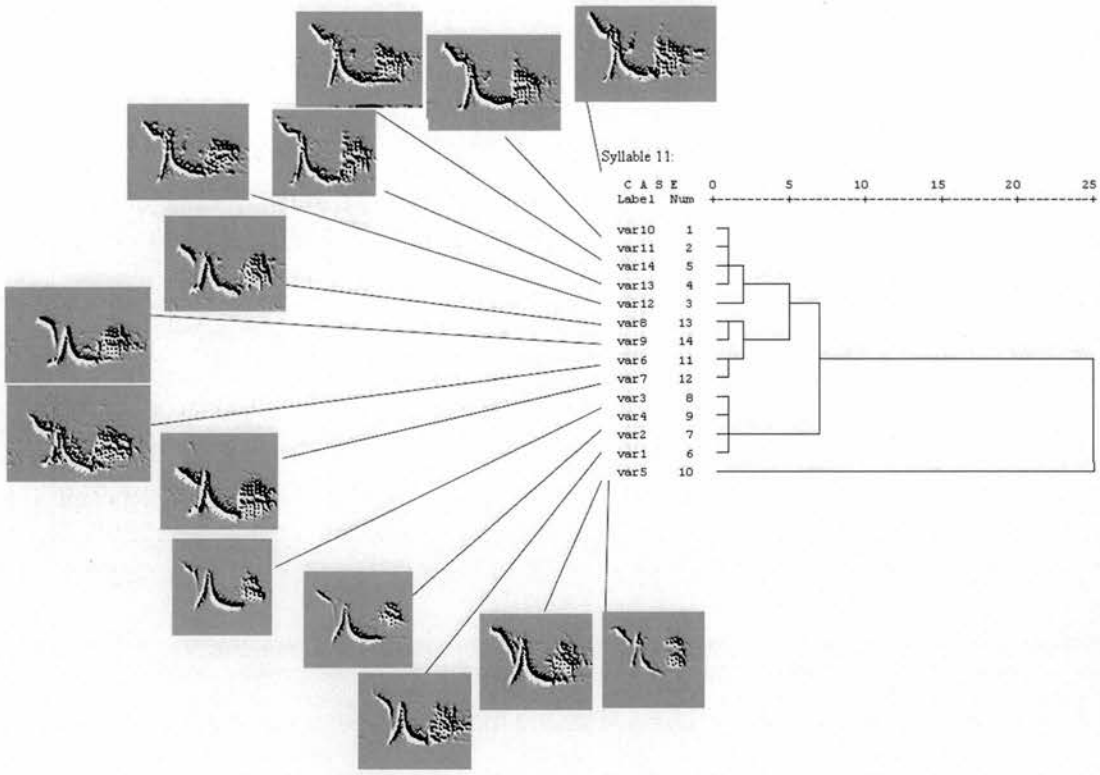

Figure 8: Dendrogram and spectrograms for Syllable Type 11 examples.

Examples 1 through 10 were recorded at Finstown Village, and examples 11 through 14 were recorded at Trumland. Generally, the examples of Syllable Type 11 recorded at a single site sorted together during the cluster analysis, but some inconsistencies are seen. Two of the examples, 5 and 10, were grouped outside their predicted clusters. Noise is probably the reason for example 5's nonconforming grouping. Example 10 from Finstown Village, however, is more structurally similar to the Trumland syllables. As a result, example 10 was grouped with Trumland syllables instead of with the Finstown Village syllables. Apart from examples 5 and 10, the sorting of Syllable Type 11 was strict with respect to recording location.

Trends with respect to location and/or song type could not be evaluated for the rest of the syllable types in the 1997 recordings. Syllable Types 8, 14, 15, 17 and 18

were each recorded at only one site, and found in one song type each (see Appendix E for dendrograms and histograms of these syllable types). These syllables do have comparatively high correlation coefficients, demonstrating that when location is consistent, the syllables are very similar to one another.

3.2.3: Between Syllable Comparisons

One example of each syllable type was chosen (on the basis of its recording quality) to compare the structural similarities of all syllables. In a manner similar to the within-syllable comparisons, correlation coefficients were computed between each pair of syllable types, and histograms and dendrograms were constructed from these matrices (see Appendix G for all relevant graphs). For the most part, the cluster analysis confirmed the syllable types visually identified, but a few syllables did appear to be similar to one another. Syllable Types 9 and 14, 8 and 16, and 10 and 4 are all pairs of syllables that are very similar in structure to each other, suggesting that these syllables may have been derived from a common ancestor. The divergence of syllable structure throughout the study period will be discussed below.

3.3: Wohlgemuth 2002 Data

3.3.1: Song Types and Syllable Selection

Sixteen song types were identified in the recordings made during 2002 (see Appendix C for spectrograms of each song type). Thirty-seven different syllable types (see Appendix C for these also) were used to construct these sixteen song types, and Syllable Types 10 and 11 came in 2 and 4 varieties, respectively. Sixteen of the total forty-one syllable types and variants were found in more than one location, and seven

were found in more than one song type. Table 4 summarizes general information regarding each syllable.

	Examples	Song Type	Histogram	Location
Syllable 1	10	Type 1	**Bimodal**	Binscarth
Syllable 2	10	Type 1	Uniform	Binscarth
Syllable 3	10	Type 1	Uniform	Binscarth
Syllable 4	10	Type 2	Uniform	Binscarth
Syllable 5	10	Type 2	Uniform	Binscarth
Syllable 6a	10	Type 2	Uniform	Binscarth
Syllable 6b	10	Type 5 and 9	Uniform	Binscarth, Finstown, and Balfour
Syllable 7	78	Type 2, 3, 4a-c, 5, 7, 9, 10, 14, 16,	Uniform	Binscarth, Moness, Finstown, Balfour, and Bu Farm
Syllable 8	8	Type 3	Uniform	Binscarth and Moness
Syllable 9	10	Type 3	**Bimodal**	Binscarth and Moness
Syllable 10a	18	Type 4a, 4c, and 10	Uniform	Binscarth and Balfour
Syllable 10b	6	Type 4b	**Bimodal**	Binscarth and Finstown
Syllable 11a	14	Type 4a and 7	Uniform	Binscarth and Balfour
Syllable 11b	6	Type 4b	Uniform	Binscarth and Finstown
Syllable 11c	6	Type 4c	Uniform	Balfour
Syllable 12	20	Type 5 and 9	Uniform	Binscarth, Finstown, and Balfour
Syllable 13	10	Type 5	Uniform	Binscarth, Finstown, and Balfour
Syllable 14	14	Type 6 and 8	Uniform	Balfour and Finstown
Syllable 15	4	Type 6	Uniform	Balfour
Syllable 16	5	Type 6	Uniform	Balfour and Finstown
Syllable 17	14	Type 6 and 8	Uniform	Balfour and Finstown
Syllable 18	8	Type 7	Uniform	Balfour
Syllable 19	8	Type 7	Uniform	Balfour
Syllable 20	8	Type 7	Uniform	Balfour
Syllable 21	6	Type 8	Uniform	Balfour
Syllable 22	10	Type 10	Uniform	Balfour
Syllable 23	8	Type 12	Uniform	Trumland and Westness
Syllable 24	9	Type 12	Uniform	Trumland and Westness
Syllable 25	10	Type 12	Uniform	Trumland and Westness
Syllable 26	10	Type 13	Uniform	Trumland
Syllable 27	10	Type 13	Uniform	Trumland
Syllable 28	10	Type 13	Uniform	Trumland
Syllable 29	10	Type 14	**Bimodal**	Moness
Syllable 30	10	Type 14	Uniform	Moness
Syllable 31	10	Type 14	Uniform	Moness
Syllable 33	10	Type 15	Uniform	Moness
Syllable 34	10	Type 15	Uniform	Moness
Syllable 35	10	Type 15	Uniform	Moness
Syllable 36	10	Type 15	Uniform	Moness
Syllable 37	10	Type 15	Uniform	Moness
Syllable 38	1	Type 16	Uniform	Bu Farm

Table 4: Syllable types and the number of examples of each. Also included are the song types each syllable was found in, the shape of the correlation histograms, and the location of the recordings made for each syllable type.

3.3.2: Within-Syllable Comparisons

Correlation matrices could be constructed for all syllable types except for Type 38 (there is only one record for this type). Unlike the previous years' data, just a small proportion of the correlation matrices have bimodal distributions (see Appendix F for the histograms and dendrograms of each within-syllable comparison). Only four of the 41 within-syllable comparisons have bimodal distributions of their correlation coefficients. These are Syllable Types 1, 9, 10b, and 29. The bimodality of Types 1 and 29 is not due to changes in location or song type, but rather recording quality, leaving only Types 9 and 10b with syllable sample groupings that are location specific. Syllable Type 9 was recorded at three different sites: Binscarth, Moness and Bu Farm; and the clustering procedure grouped the ten syllable samples according to these locations (Figure 9).

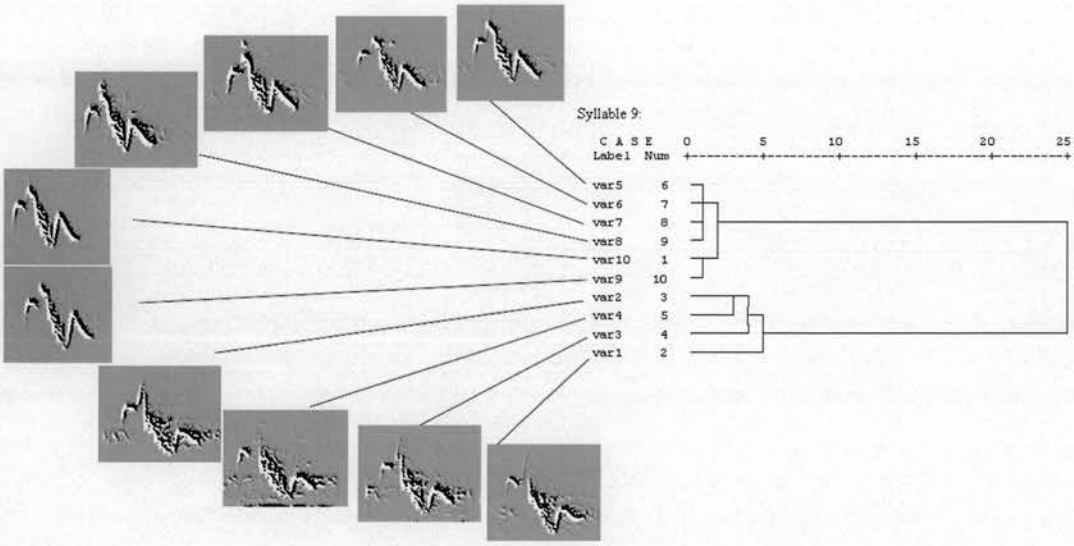

Figure 9: Dendrogram for Syllable Type 9.

Examples 1 through 4 were recorded at Binscarth, examples 5 through 9 at Moness, and example 10 was obtained at Bu Farm. All examples of Syllable Type 9 are from Song Type 3, substantiating the claim that location is a more accurate prediction of syllable structure than song type.

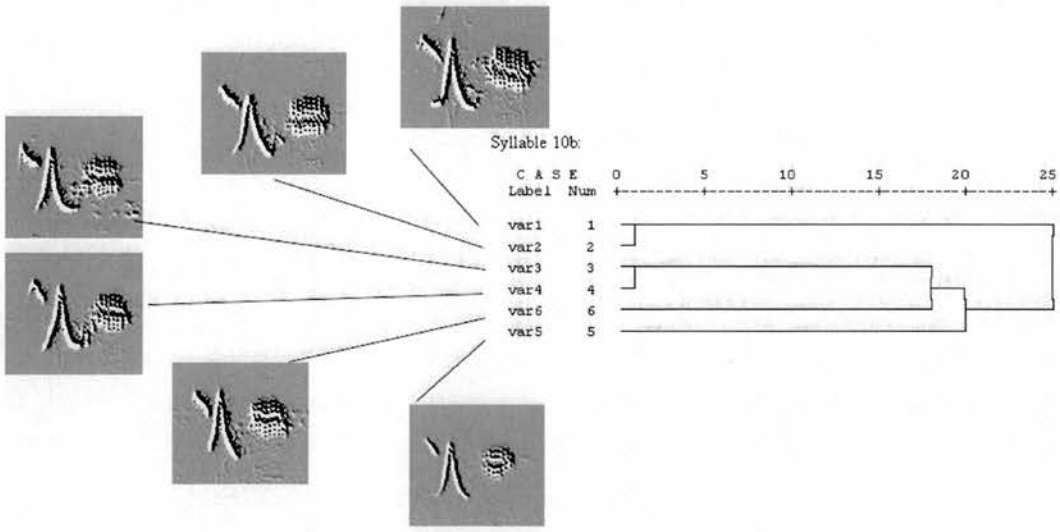

Figure 10: Dendrogram of Syllable Type 10b.

Samples of Syllable Type 10b are also clustered according to location (Figure 10). Examples 1 and 2 were recorded at Binscarth, while examples 4, 5, and 6 were recorded at Finstown Village. The examples of Syllable Type 10b are also derived from a single song type (Type 4b), corroborating a location specific trend in syllable structure.

Bimodality in the distribution of correlation coefficients was not found in any other syllable type, but Syllable Types 8, 11a, 13, 16, and 23 did sort according to collection site. The differences in syllable structure for each of these types were not great enough to result in variant subsets, but the differences were large enough to result in location specific sorting during cluster analyses. In Syllable Type 8, the first cluster (examples 1 through 4) was recorded at Binscarth, and the second (examples 5 through 9) at Moness; but all of the samples were found in Song Type 3 (Figure 11).

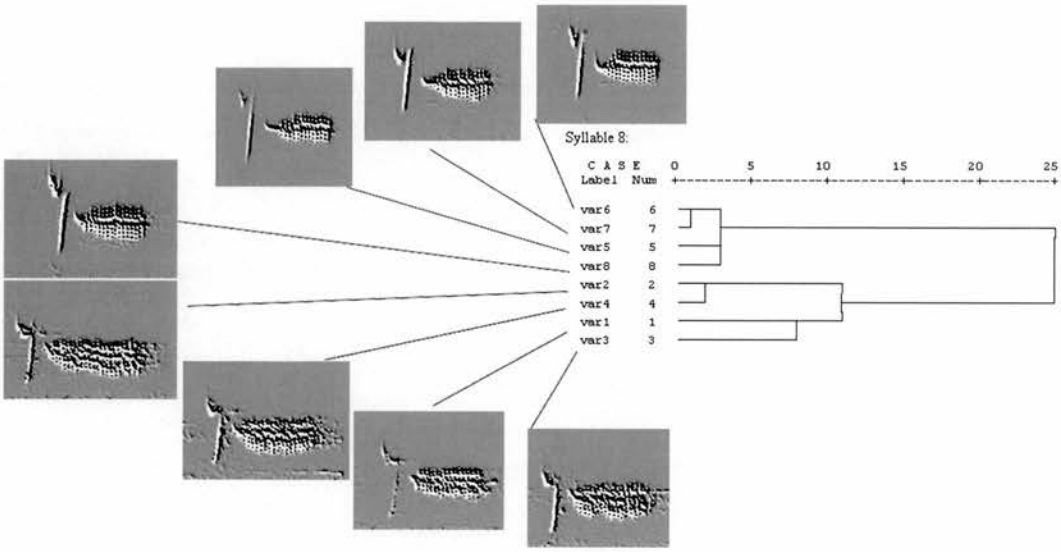

Figure 11: Dendrogram of Syllable Type 8.

Syllable Type 11a was found at two different locations: Binscarth and Balfour, and in two different song types: Song Type 4a and 7. The dendrogram for Type 11a clusters examples 1 through 6 in one group, and 7 through 14 in another. These two groups are consistent with both location and song type, making it difficult to determine which variable is responsible for the groupings. In contrast, the sorting of Syllable Type 13 is unaffected by differences in song type (Figure 12).

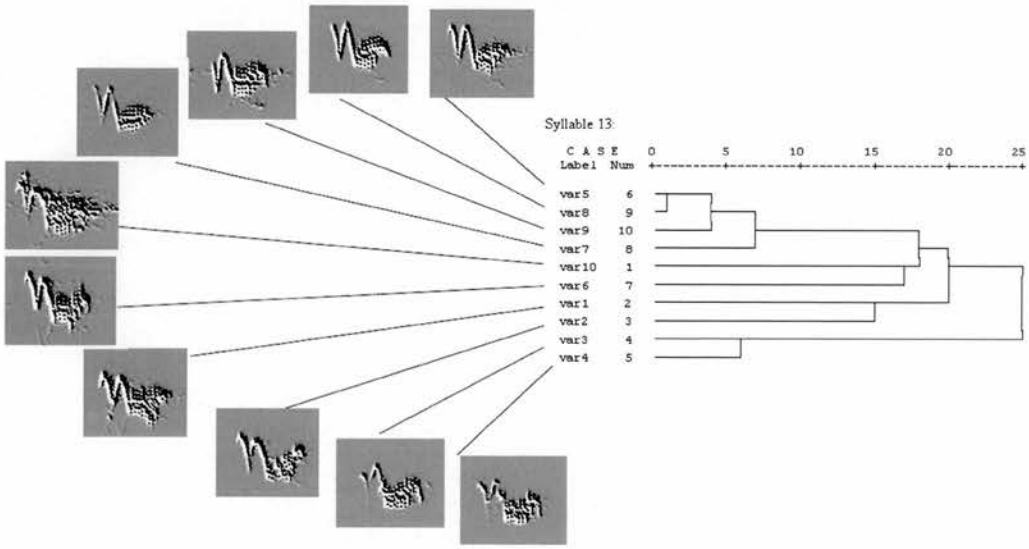

Figure 12: Dendrogram of Syllable Type 13.

Examples 1 through 4 were collected at Binscarth, 5 through 9 at Finstown Village, and example 10 was found at Balfour Castle. What is different about Syllable Type 13 is that all of the samples collected were from Song Type 5. Location is therefore the only determining factor for syllable structure in Type 13. The same is true for Syllable Types 16 and 23. Each pool of syllables for Types 16 and 23 was found in a single song type, but they were recorded at different locations, and grouped according to these locations. In total, seven of sixteen syllable types found at more than one site show location specific trends in their structure. The other nine syllable types found in more than one location (6b, 7, 10a, 11b, 12, 14, 17, 24, and 25) fail to demonstrate any trend in their sorting patterns. In the case of Syllable Type 7, the large quantity of examples precluded any precise observations, and the noise levels for Syllable Types 10a, 14, and 17 had deleterious effects upon the cluster analyses. The reasons why Syllable Types 6b, 11b, 24 and 25 failed to cluster according to their locations remain unclear. All other syllable types (2 through 5, 6a, 11c, 15, 18 through 22, 26, 27, 28, and 30 through 37) were each collected at one site and from one song type. The correlation coefficients for each of these syllables were comparatively very high, suggesting that consistencies in location result in consistencies of syllable structure.

3.3.3: Between Syllable Comparisons

One example of each syllable type was chosen (on the basis of its recording quality) to compare the structural similarities of all syllables. In a manner similar to the within-syllable comparisons, correlation coefficients were computed between each pair of syllable types, and histograms and dendrograms were constructed from these matrices (Appendix G). Syllable variants were more common in the 2002 recordings than for any

other year, and these variants sorted together during the cluster analysis. Examining the dendrogram for the 2002 syllables reveals common structures within each cluster of syllables (Figure 13).

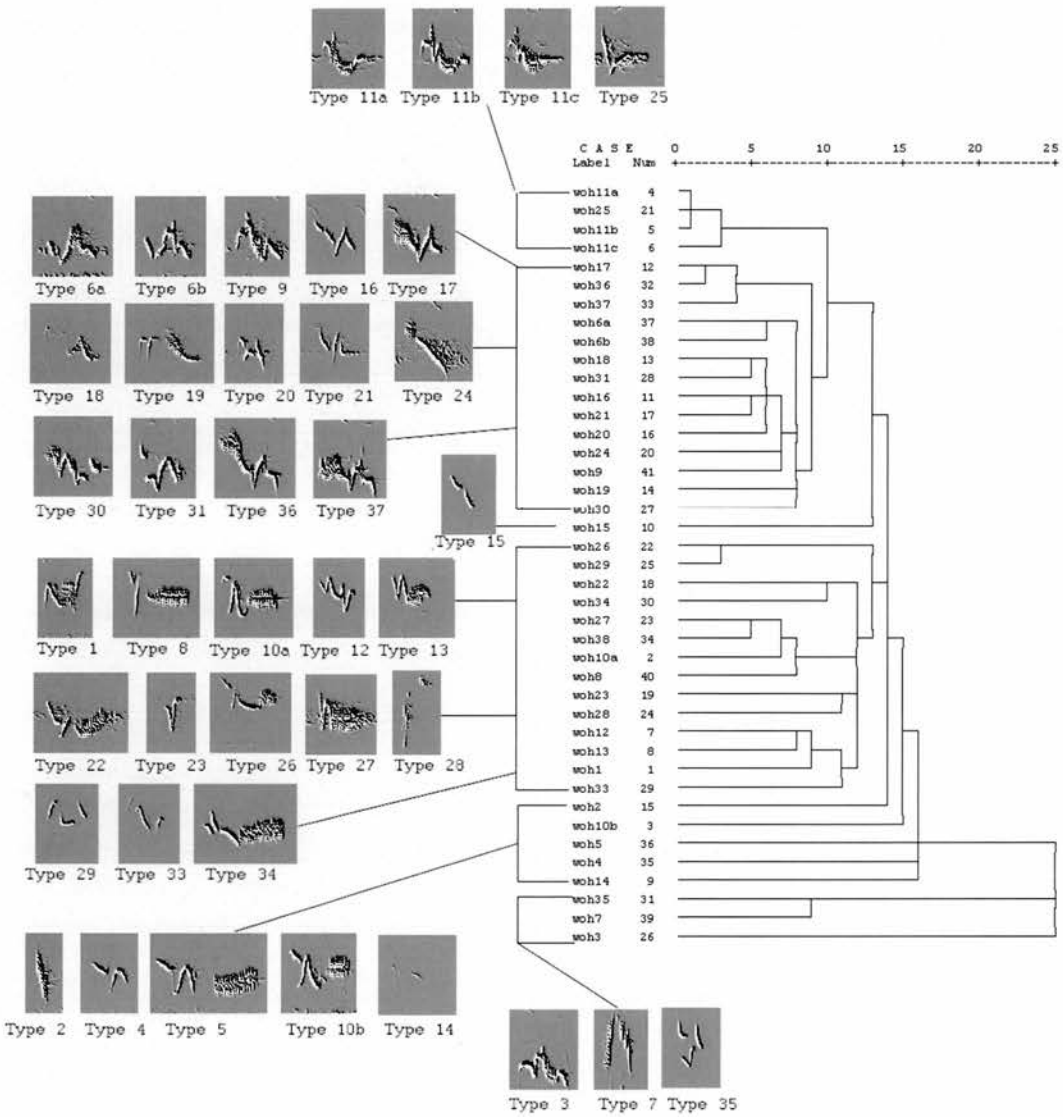

Figure 13: Dendrogram for 2002 Syllable Types.

The variants of Type 11 were grouped together with Type 25, and all of these syllables have descending sweeps of frequency modulation. The next group, Type 6a to 37, contains a few syllables with common structures. Types 16, 17, 30, 36, and 37 are all

similar in that they begin with a harmonic sweep, followed by oscillating, tonal modulations. The similarities between these syllable types suggest that they may have evolved from a single syllable. Syllable Types 8, 10, 13, 22, 26, 27, and 34 also have a stereotyped harmonic sweep, but in these instances, that sweep follows tonal modulations rather than preceding them. These syllables may also share a common ancestor. Although some consistencies in syllable structure are seen within each group, syllable differences were large enough to justify their separation into distinct types. The correlation coefficients between non-variant syllables were all below 0.7, except for the correlations between Types 36, 37, and 17; and 25, 11b, and 11c, substantiating the visual identification of syllable types.

3.4: Between Year Comparisons

The examples of each syllable type selected for within-year comparisons were pooled together and compared for longitudinal trends in syllable structure. This amounted to eighty different syllable types including variants. The auto-correlation function of Avi-Soft SASLab Pro was used to compute spectral similarities, and a hierarchical cluster analysis sorted the syllables into groups (Appendix G). The syllables clustered in a manner consistent with structural similarities, revealing groups of syllables that have conserved their structure throughout the 25 years of this study. For example, Syllable Type 19 from the 1977 recordings is found as Syllable Type 19 in the 1997 data, and as Syllable Type 25 in the 2002 recordings (Figure 14).

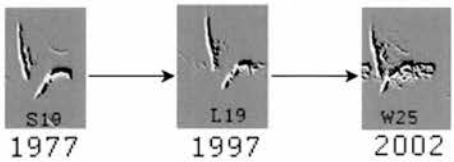

Figure 14: Examples of a single syllable that was found in all three years of the study.

Many of the same syllable types were found in each year of the study, prompting an analysis of site-specific trends. Three of the recording sites were surveyed in all three years of the study: Balfour Castle, Finstown Village, and Trumland Woods. The syllable types found at these locations were pooled and analyzed for similarities (see Appendix H for the relevant dendrograms). A few syllables from each location were recorded in all three years of the study, while others were only found in 1997 and 2002. The following syllables are those recorded in more than one year at Balfour Castle, Finstown Village, or Trumland Woods:

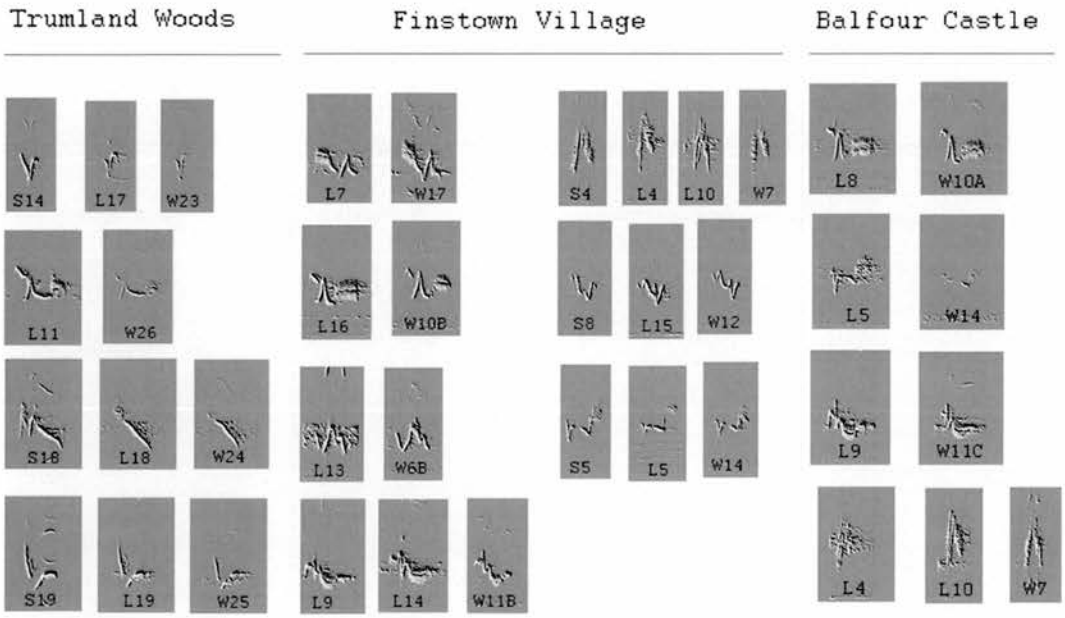

Figure 15: Groups of conserved syllables from three different recording sites in the Orkney Islands. The prefix "S" denotes 1977 data, "L" denotes 1997 data, and "W" the 2002 data.

The following four syllables (Figure 16), found in all three years of the study, were analyzed to determine if syllable structure changed with time.

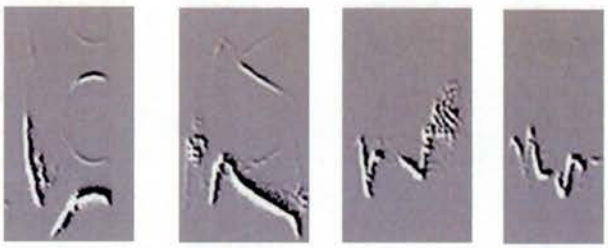

Figure 16: Spectrograms of the syllable types used to compare the effects of time on syllable structure. The numbers beneath each spectrogram correspond to the analyses performed below.

Four examples of each syllable from 1977, 1997, and 2002 were selected and their spectral similarity compared using the autocorrelation function of AviSoft SASLab Pro. In this analysis, syllables 1 and 2 were found in the same song type for all three years, but syllable types 3 and 4 mapped onto different song types in different years. Syllable 3 was found in 4 different song types (one in 1977 and 1997, and two in 2002), and syllable 4 was found in two different song types (one in 1977, and the same song types in 1997 and 2002). The number of songs each syllable is derived from will be important in determining which features of the cultural environment are influencing syllable structure.

A cluster analysis was performed for each syllable type and dendrograms constructed in order to determine the similarities between syllables recorded in different years. One-way ANOVA statistics and box plots were also calculated for the following four relationships: syllable similarity within the same year, similarity between 1977 and 1997, between 1977 and 2002, and between 1997 and 2002. The dendrogram constructed from Comparison 1 (the analysis for Syllable Type 1 in Figure 16 above) resulted in a sorting pattern consistent with the years in which each syllable was recorded (Figure 17).

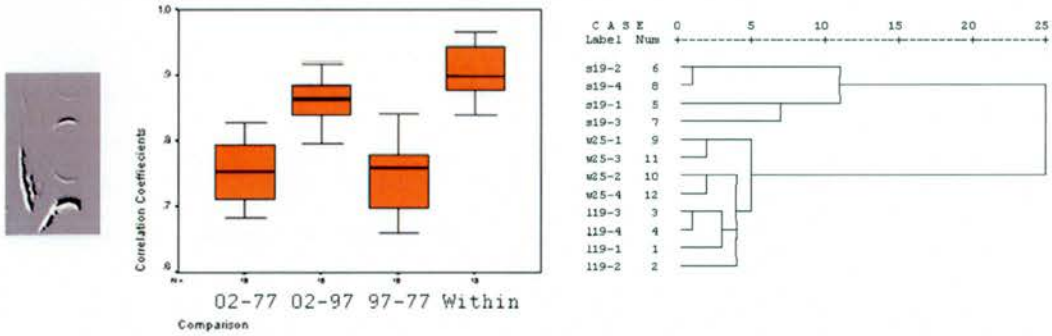

Figure 17: Spectrogram, box plot, and dendrogram for Syllable Comparison 1. Four examples for each year were selected and correlation coefficients generated for their structural similarities. The prefix "S" in the dendrogram represents syllables recorded in 1977, an "L" is used for 1997 syllables, and a "W" for those syllables recorded in 2002. For the box plot, the black bar indicates the mean of the correlation coefficients, the red bar the standard deviation, and the "T" bars the total distribution of values. One-way ANOVA statistics and post-hoc Tukey statistics are significant at $p < 0.05$ for all relationships except the 1997-1977 to 2002-1977 comparison ($p = 0.691$).

Syllables recorded in the same year were structurally more similar than those recorded in another year. The box plot of the correlation coefficients shows a more detailed pattern of similarity. Syllable similarity is highest between syllables recorded in the same year, with similarity decreasing as time increases. The correlation values between years 1997 and 1977, and 2002 and 1977 were significantly lower ($p < 0.05$) than within same year and 1997 versus 2002 values. The difference between correlation coefficients for 1997-1977 and 2002-1977 is not significant ($p=0.691$). Overall, syllables recorded in 2002 are more similar to those from 1997 than 1977, and the similarity between 1997 and 1977 syllables was not significantly different than between 2002 and 1977 syllables.

A different pattern is seen for Comparison 2 (Figure 18). The similarity is highest between syllables recorded in the same year, followed by the 1997-2002 comparison. Comparison 2 is unusual in that the 2002-1977 correlation values are significantly higher than those for 1997-1977 ($p < 0.05$). If syllable similarity decreases with time, it would be expected that the 25 years separating 2002 and 1977 data would result in less similar

syllables than the 20 years separating 1997 and 1977. For this syllable, an increase in time between recordings does not always equate to less syllable similarity. Generally, however, syllables recorded in 2002 are more similar to those recorded in 1997; and the similarity is higher between 2002 and 1977 syllables than it is between 1997 and 1977 syllables.

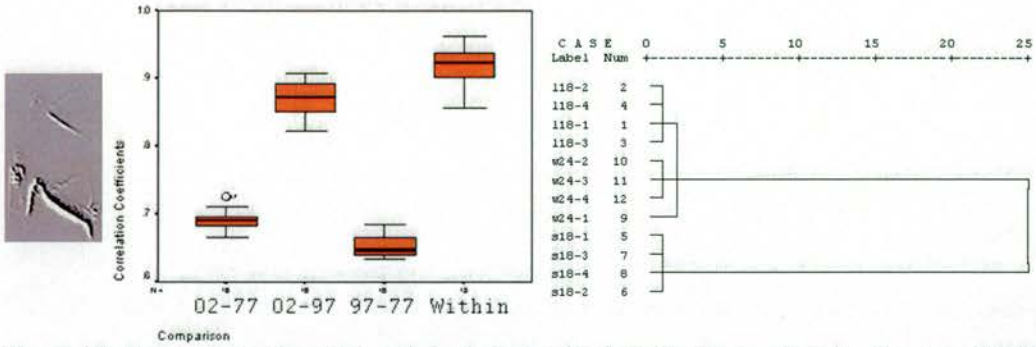

Figure 18: Spectrogram, box plot, and dendrogram for Syllable Comparison 2. One-way ANOVA statistics and post-hoc Tukey statistics are significant at $p < 0.05$ for all relationships. The parameters for the box plot and dendrogram are the same as those described above in Figure 15.

Syllable similarity as a function of time is more confused for Comparison 3 (Figure 19). The syllables recorded in the same year were again the most similar, but those recorded in 2002 were more similar to 1977 syllables than they were to 1997 syllables. Overall, the syllable similarity between years was quite low for this syllable type, suggesting that alterations in syllabic structure are quite common during song learning.

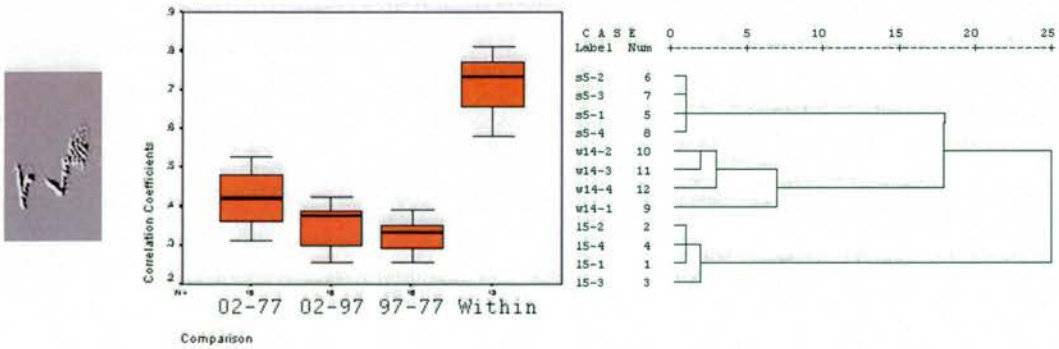

Figure 19: Spectrogram, box plot, and dendrogram for Syllable Comparison 3. One-way ANOVA statistics and post-hoc Tukey statistics are significant at $p < 0.05$ for all relationships except the 1997-2002 to 1997-1977 comparison ($p = 0.599$).

Syllable similarity between years for Comparison 4 follows the typical pattern of similarity decreasing with time (Figure 20). Syllables recorded in the same year are the most similar to each other, followed by those recorded in 2002 and 1997. Syllables from 1997 and 2002 were significantly less similar ($p < 0.05$) to those from 1977 than they were to each other. The difference in similarity between 1997-1977 and 2002-1977 comparisons was not significant.

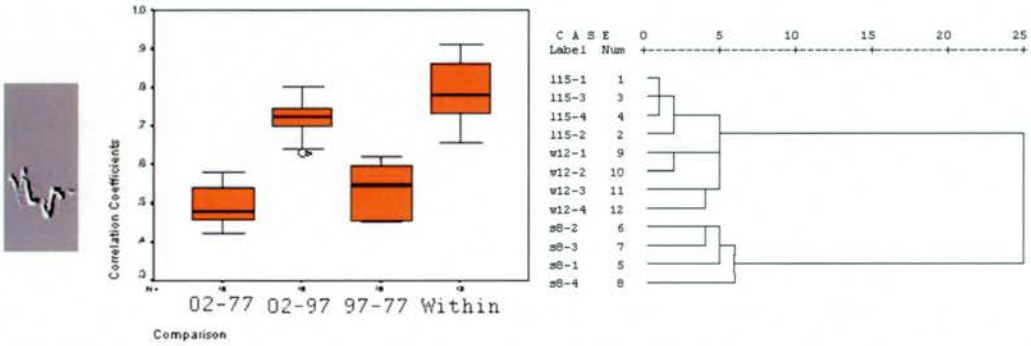

Figure 20: Spectrogram, box plot, and dendrogram for Syllable Comparison 4. One-way ANOVA statistics and post-hoc Tukey statistics are significant at $p < 0.05$ for all relationships except the 1997-1977 to 2002-1977 comparison ($p = 0.324$). The parameters for the box plot and dendrogram are the same as those described above in Figure 15.

The analyses for the four syllables found at a single site in all three years has one consistent conclusion: syllables recorded in the same year are more similar to one another than they are to syllables recorded in different years. Three out of four of the syllable types analyzed also show a significantly higher similarity between the 2002 and 1997 syllables than the 1977 syllables. None of the analyses, however, were able to resolve a significant difference between the 1997-1977 and 2002-1977 comparisons. This suggests that the changes in syllable structure over the course of 20 years are not significantly different than the changes in syllable structure over 25 years. Only at a 5-year time interval is syllable structure significantly more similar.

The four syllables used for the analyses above are not the only syllables conserved from year to year, but they are the only examples conserved at the same location. A total of 80 syllable types were identified for all three years combined, but this number can be reduced to 41 if the redundant syllables between years are removed.

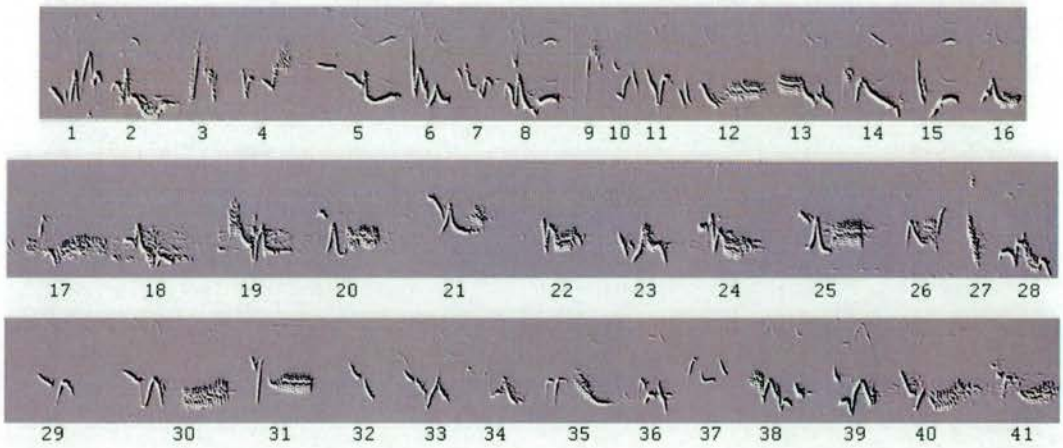

Figure 21: A compilation of the syllable types found in the 1977, 1997, and 2002 recordings with redundancies removed. The numbers used to identify unique syllable types in this figure are not consistent with those used in the rest of analysis.

These forty-one syllable types were used to construct the forty-two different song types found in the three years of recordings. Only four of the fifteen syllables identified in 1977 were absent in the 2002 data, exhibiting an extremely high retention rate for the single meme in chaffinch songs. Three of the four syllable types lost from the 1977 data set were contained within one song type, which also happened to be the least common song type from that year's recordings. The syllables contained in the most frequently recorded song types for 1977, 1997, and 2002 (Song Types 2, 3 and 4 respectively) were found in all three years. This does not necessarily equate to highly conserved syllable structure, however (see Table 5 for frequency statistics).

Year	Location Clusters	Song Type Clusters	No Cluster
1977	6 (60%)	1 (10%)	3 (30%)
1997	4 (36%)	1 (9%)	6 (55%)
2002	6 (38%)	2 (13%)	8 (50%)
Total	16 (43%)	4 (11%)	17 (46%)

Table 5: Frequency statistics on the syllable types found in multiple locations and/or song types. The columns represent the number (and percentage) of syllables clustering by location, clustering by song type, or not clustering at all (left to right) for each year and in total.

The above table shows that when clustering occurs, it is determined predominantly by location, and not by song type. The implications of this finding will be discussed in the next section.

Chapter 4.0: Discussion

Variations in the structure of chaffinch syllables are more dependent upon differences in location than they are on song type. Examples of the same syllable type recorded at different locations are less similar to each other, whereas syllables recorded at the same location but in different song types are highly similar to one another. It is believed that the bimodality of correlation coefficients seen is a result of subsets of syllable variants within the samples collected. These structurally similar subsets rarely span two different recording sites, suggesting location specific trends in syllable structure.

The conservation of syllable structure within a single location suggests that song learning in the chaffinch has high fidelity at the single meme level. Syllables used in different song types at the same location were remarkably similar to one another, implying that recombination is involved during song learning in the chaffinch. This has been shown for the chaffinches of New Zealand (Jenkins and Baker, 1984), as well as the chaffinches of the Atlantic Islands (Lynch and Baker, 1994). Young males learn the syllables of their local territory, and then recombine them to form new song types. In this way, chaffinches create a large variety of song types from just a few different syllables.

The longevity of a syllable at a specific location is proportional to its abundance in the population (Lynch et al 1989). The most common syllables have a greater likelihood of transmission than those that are rare. This is substantiated by the observation that syllables from the most plentiful song types were found in the recordings of all three years. These syllables have experienced minor modifications in their structure over the course of the study. The syllables of the most common song types in

the 2002 recordings also happened to be the most common syllable types. These types were also found in the greatest number of varieties (Syllable Types 10 and 11 have 2 and 3 variants respectively). This is probably a result of their prevalence in many different recording locations: local traditions in syllable structure result in more syllable variants for those syllables found in multiple sites.

The differences in syllabic structure between locations are most likely the result of two different factors: immigrating individuals who first introduced the syllable type could have inaccurately copied it; or, local modifications in syllable structure may have occurred post-introduction. It is most likely a combination of both factors that has resulted in the syllable similarity at a given site. Not all immigrating individuals would have inaccurately copied their tutor's syllables, and the highly similar syllabic structure within a single type imply that local modifications to syllables are rare. It is possible for slight changes made to syllabic structure to add up over time, and eventually result in new syllable types. In a manner similar to the cultural evolution of chaffinch song types (Lynch and Baker, 1986), immigration can spread novel syllables types to other locations, and new local traditions in syllable structure would begin again. The most common syllables in a location should therefore be the oldest, and would have experienced more modifications than rare, novel types at a particular location. This was seen in Syllable Types 10 and 11 of the 2002 data. These syllables comprised the most common song type (Type 4), and were also the ones with the greatest number of syllable variants. The proportion of syllables in each year with bimodal distributions further corroborates this hypothesis. The number of bimodal distributions decreased for each successive year as the number of syllable types increased. The variation seen in Syllable

Type 11 of the 2002 data is indicative of this type of divergence, and may very well be the beginning of three new syllable types.

The longevity of a syllable at a specific location is proportional to its abundance in the population (Lynch et al 1989), because in a neutral meme system, the most common syllables have a greater likelihood of transmission than those that are rare. This is substantiated by the observation that syllables from the most plentiful song types were found in the recordings of all three years (Song Type 2 of 1977, Song Type 3 of 1997, and Song Type 4 of 2002).

The data indicate that within a single location, variations in syllable structure are kept to a minimum. This conservation led to 11 of 15 syllable types originally found in 1977 to be recorded again after 25 years in 2002, and three of the four syllable types missing from the 1977 data in 1997 and 200, were contained within one, rare song type. Contrary to previous work, however (Lynch et al 1989; and Baker and Jenkins, 1987), the single meme does experience structural modifications within the same location over time. Syllable types recorded at the same location in 1997 and 2002 were often more similar to each other than the same type recorded in 1977, but this was not always the case. The results of syllable type comparisons from different years within the same site suggest an unlearned component of syllable structure that remains constant regardless of the learning process. If syllable structure was determined solely by the auditory experiences of young males, then the same syllable types recorded at a five-year interval should be more similar than at a 20 or 25-year interval. The results of Comparisons 2 and 3 show that syllables of the same type recorded 5 years apart to be less similar than those recorded 25 years apart. It is believed that this is indicative of an unlearned template for syllable

structure that allows for a certain amount of jitter during song acquisition. This is supported through laboratory studies of young male chaffinches during song learning. Chaffinches deafened before any auditory experience crystallize songs lacking the finer structures of normal adult song, but still very similar to their species-specific vocalizations (Nottebohm, 1968). The same is true for Kasper-Hauser chaffinches: their songs are abnormal as compared to wild birds, but their songs still contain the basic structural and temporal attributes of typical chaffinch song (Thorpe, 1958). These studies speculate that there is an unlearned component of chaffinch song, and the variations seen in chaffinch song syllables of this study support this hypothesis. From these results, it is believed that immigration plays a far greater role in the addition of single memes to an individual population of chaffinches than miscopying during song learning. It is possible to take this assertion one step further and say that the chaffinch has a finite, unlearned collection of syllable templates from which all song types are created, much like the indigo bunting (Baker and Boylan, 1995). Because song matching is beneficial to the chaffinch (Slater, 1981), young males could benefit from only have to learn the proper syllable ordering and local traditions in syllable modification from adjacent males in their first spring, and not the entire songs. A paradigm where behavioral transmission can be simplified will be more successful than those that have greater costs, and maintained during selection.

Chapter 5: References

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APPENDIX A
Song Types and Syllables Types Of the 1977 Recordings

(Numbers underneath each song type represent specific syllable types)

Slater 1977 Song Types

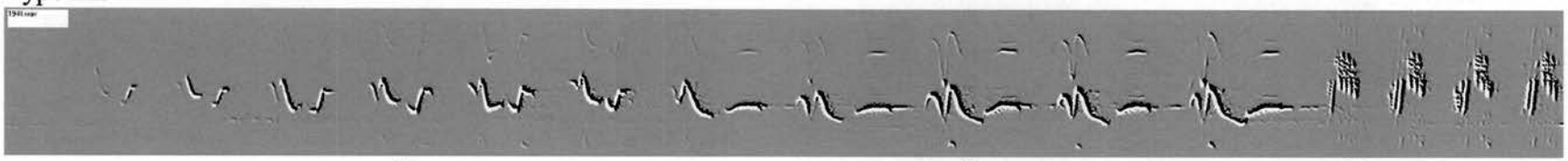
Type I:

6 1 7

Type II:

5 3 4

Type III:

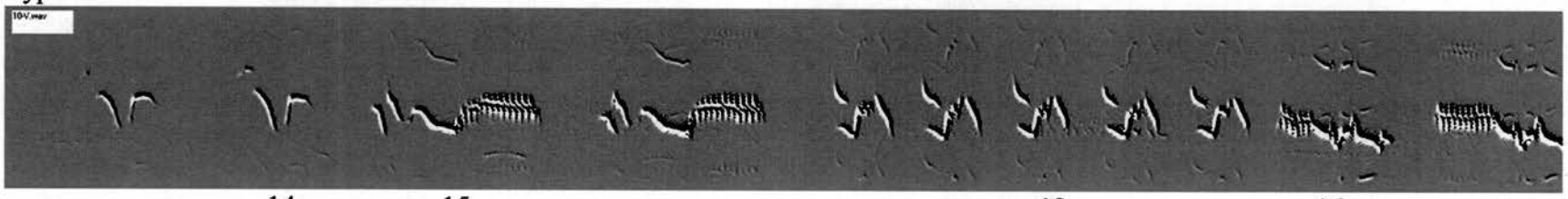


8 9 10

Type IV:

15 12 16

Type V:

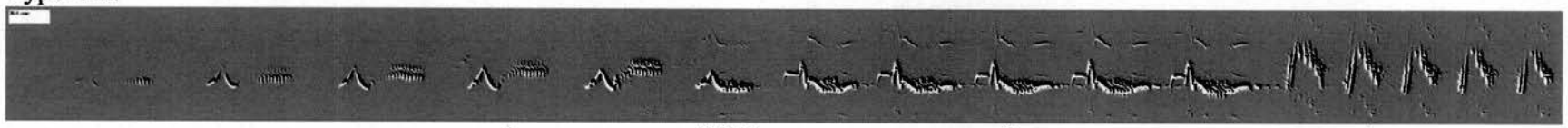


14 15 12 16

Type VI:

14 18 19

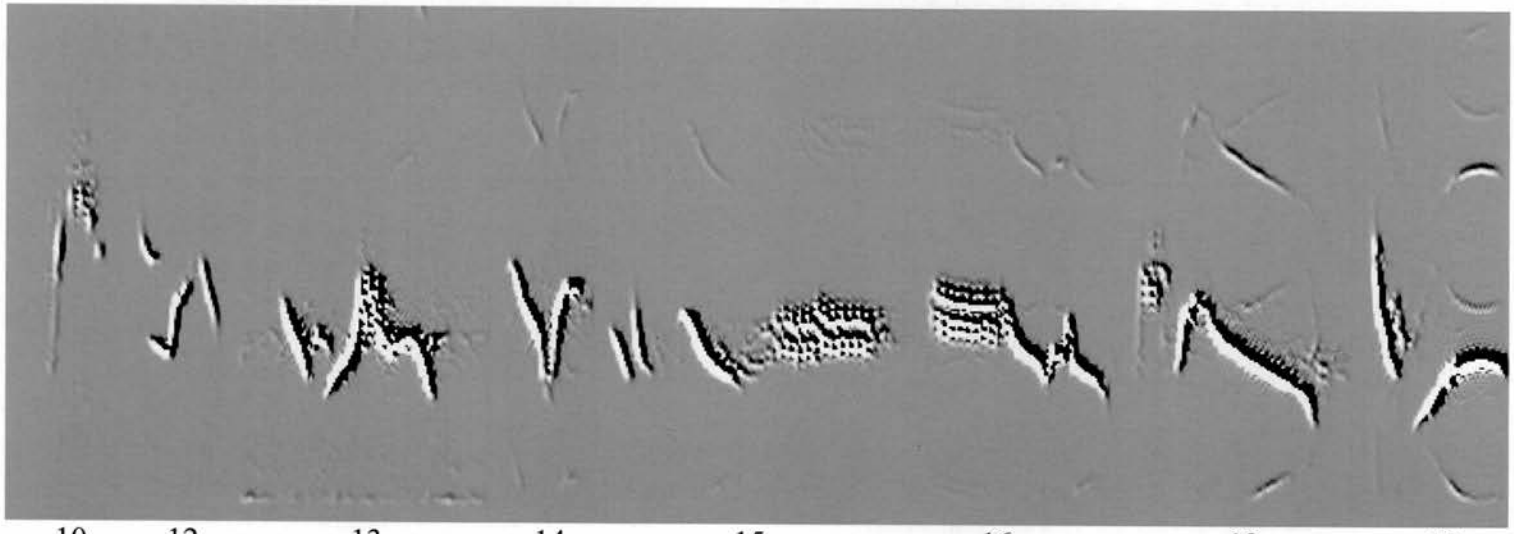
Type VII:



5 TS-2 3 4

Slater 1997 Syllable Types

1 3 4 5 6 7 8 9



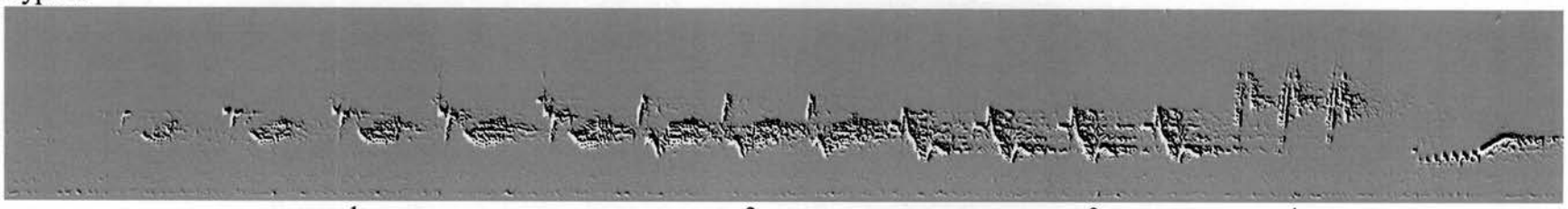
10 12 13 14 15 16 18 19

APPENDIX B
Song Types and Syllables Types Of the 1997 Recordings

(Numbers underneath each song type represent specific syllable types)

Lachlan 1997 Song Types

Type I:

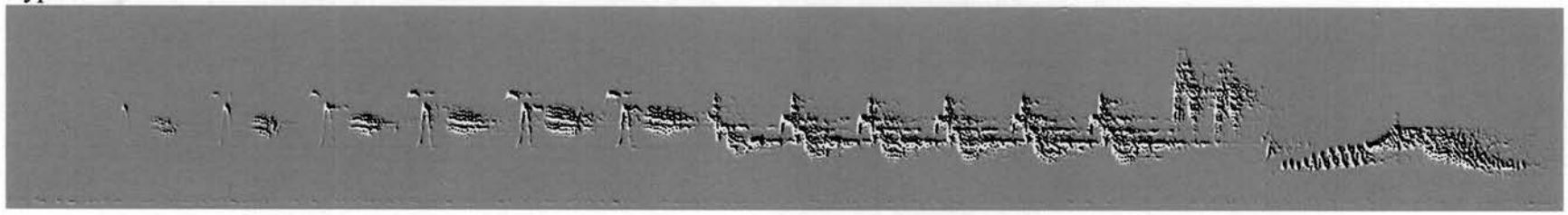


1 2 3 4

Type II:

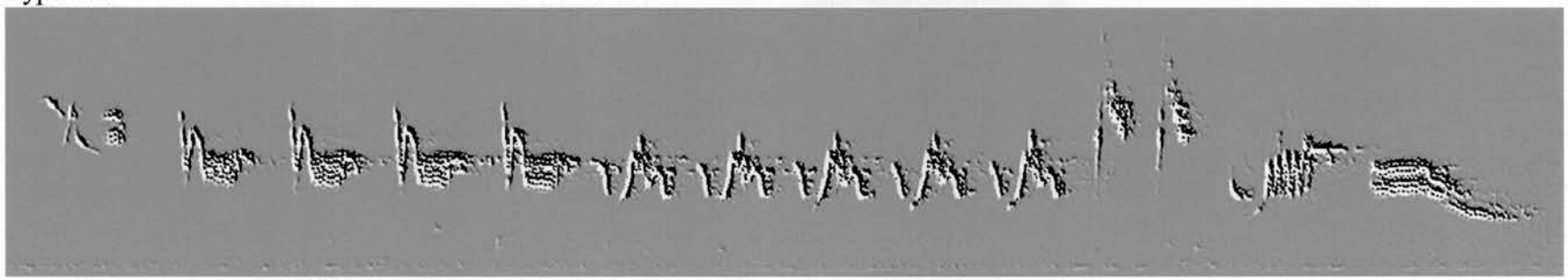
5 6 7

Type III:



8 9 10

Type IV:

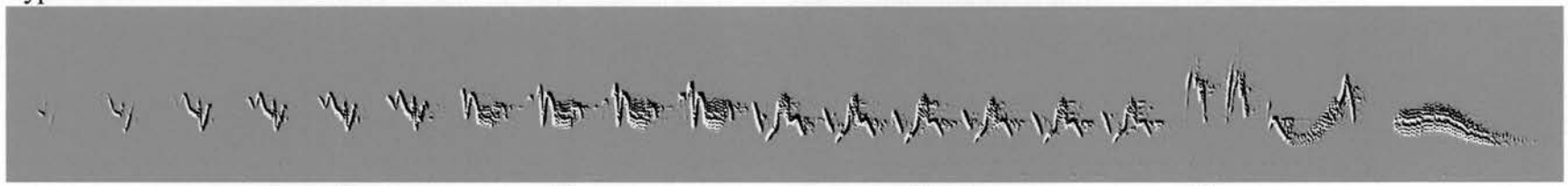


11 12 13 4

Type V:

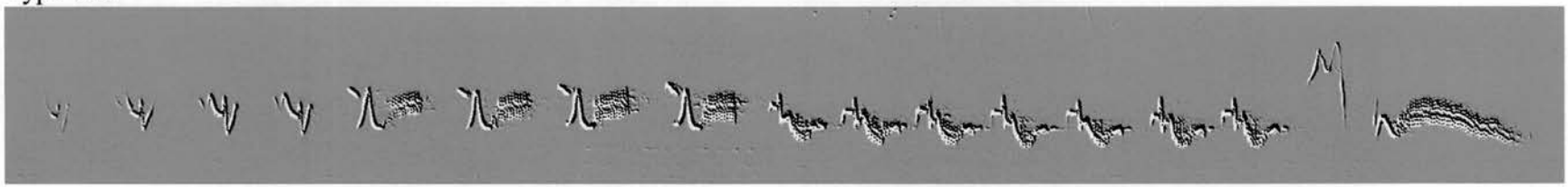
11 14 4

Type VI:



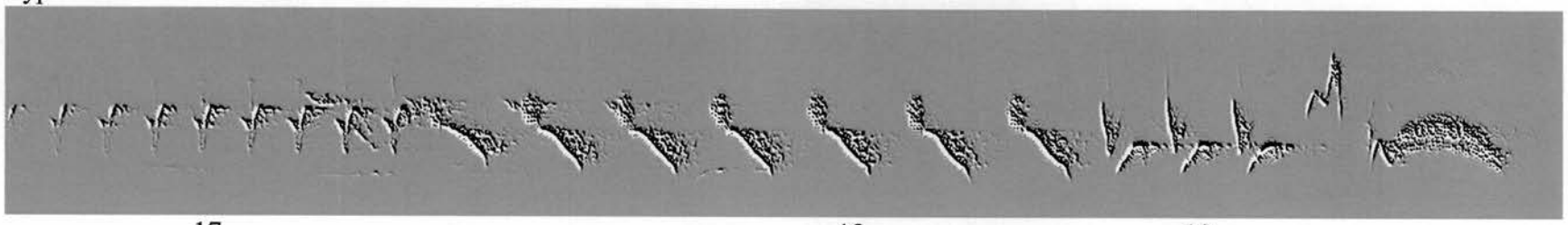
15 12 13 10

Type VII:



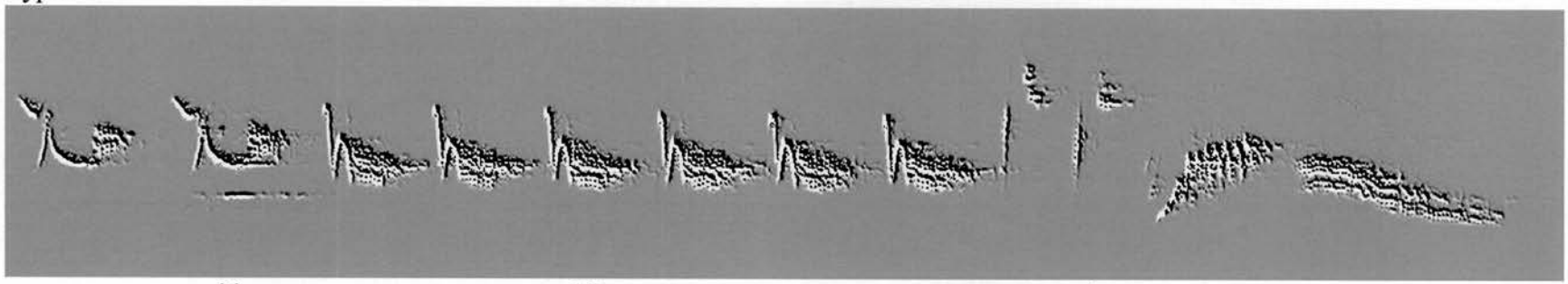
15 16 9

Type VIII:



17 18 19

Type IX:

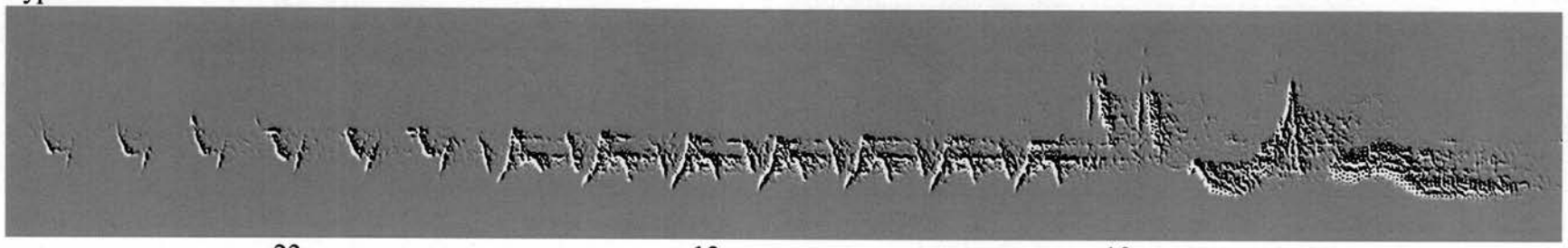


11 16 4

Type X:

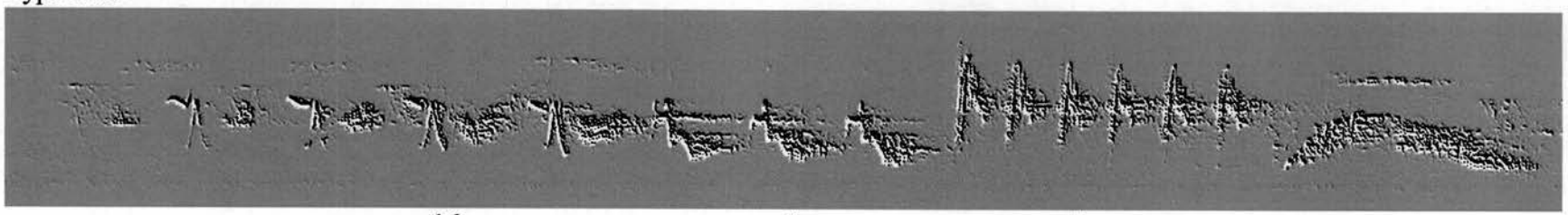
20 21 22

Type XI:



23 13 10

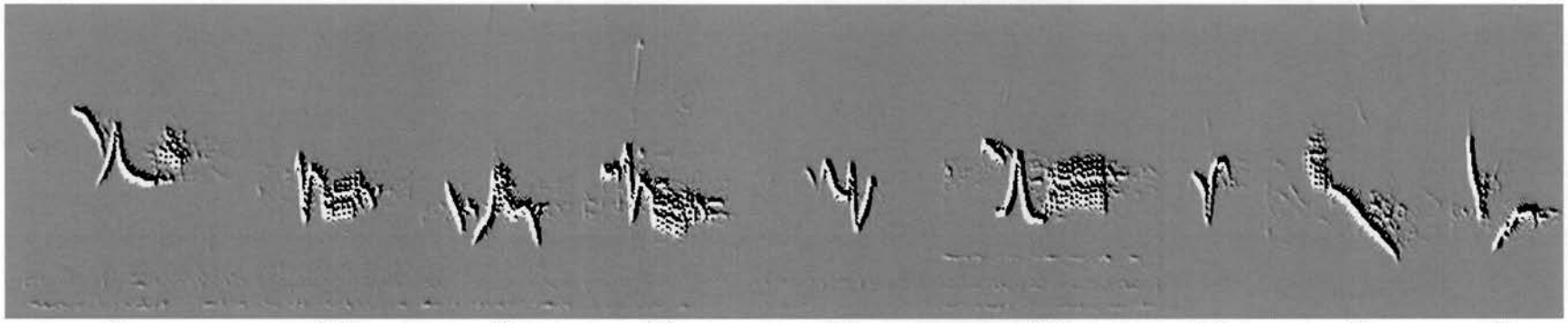
Type XII:



16 9 4

Lachlan 1997 Syllable Types

1 2 3 4 5 6 7 8 9 10



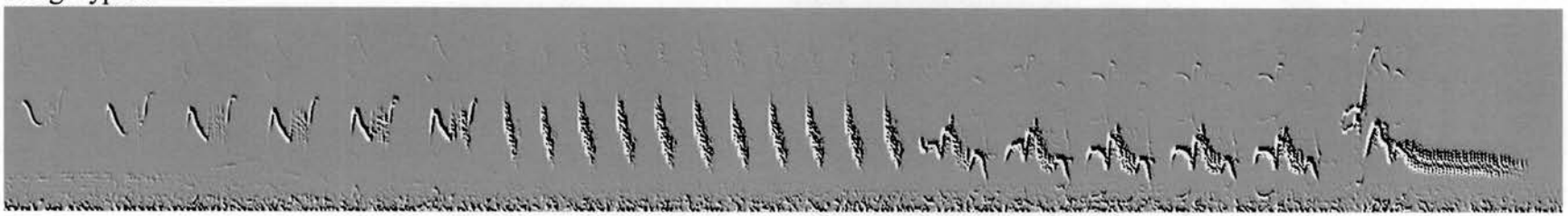
11 12 13 14 15 16 17 18 19

APPENDIX C
Song Types and Syllables Types
Of the 2002 Recordings

(Numbers underneath each song type represent specific syllable types)

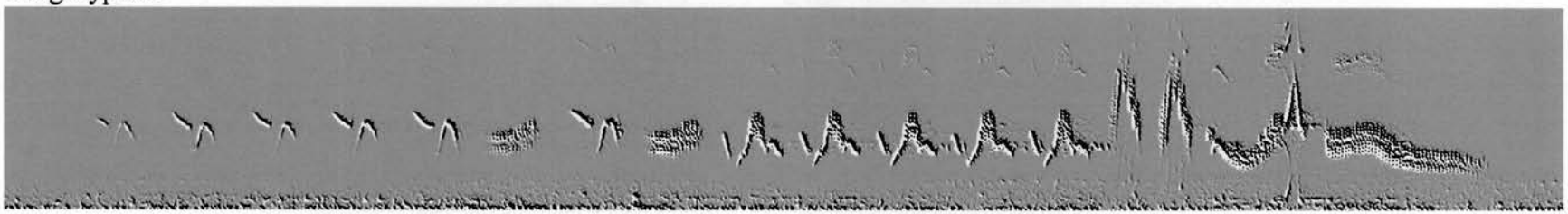
Wohlgemuth 2002 Song Types

Song Type I:



1 2 3

Song Type II:

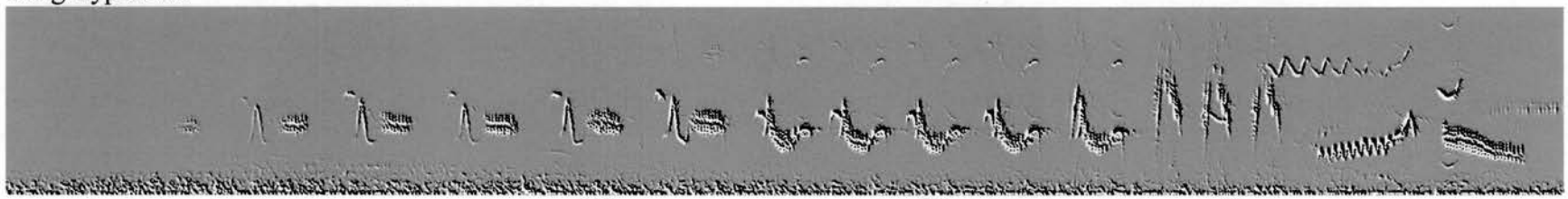


4 5 6a 7

Song Type III:

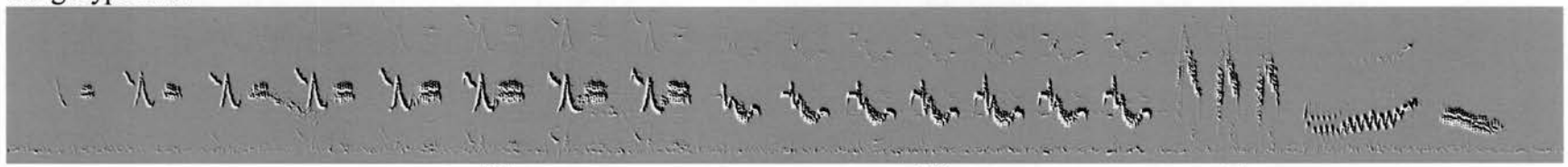
8 9 7

Song Type IVa:



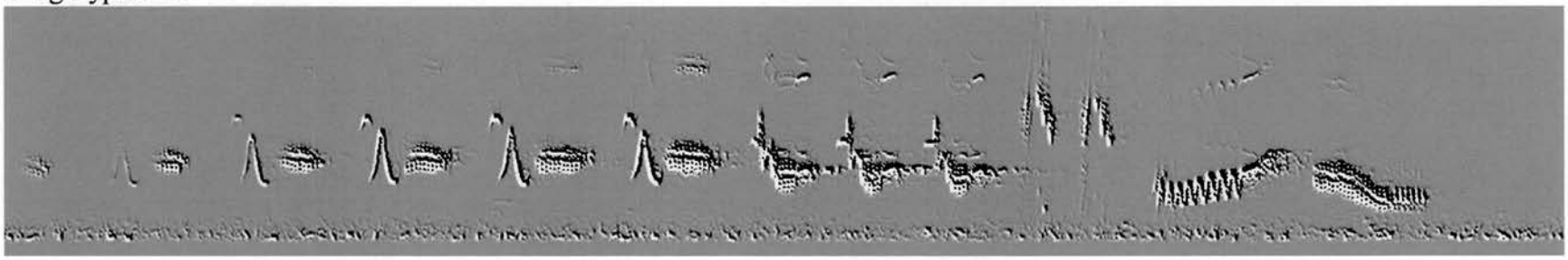
10a 11a 7

Song Type IVb:



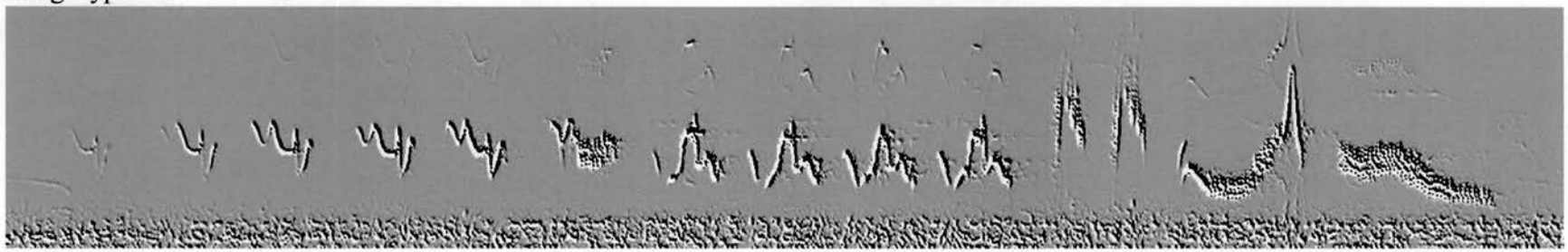
10b 11b 7

Song Type IVc:



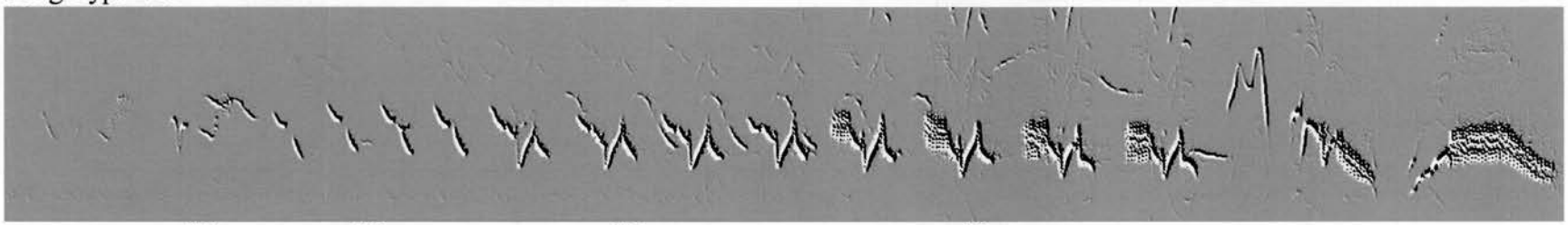
10a 11c 7

Song Type V:



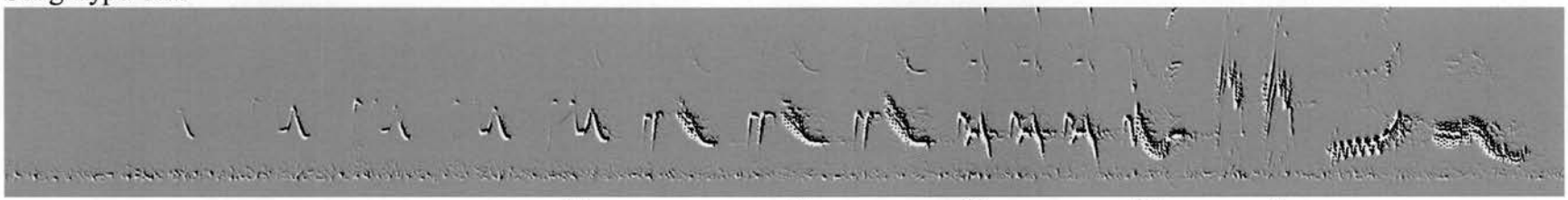
12 13 6b 7

Song Type VI:



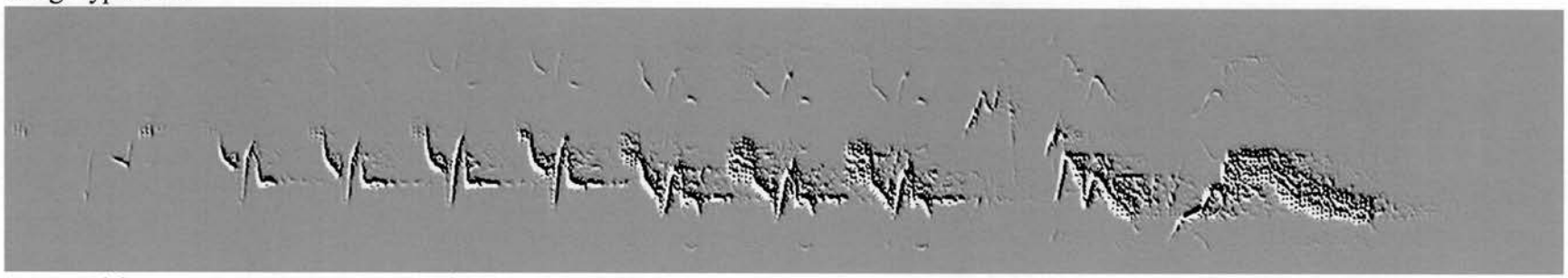
14 15 16 17

Song Type VII:



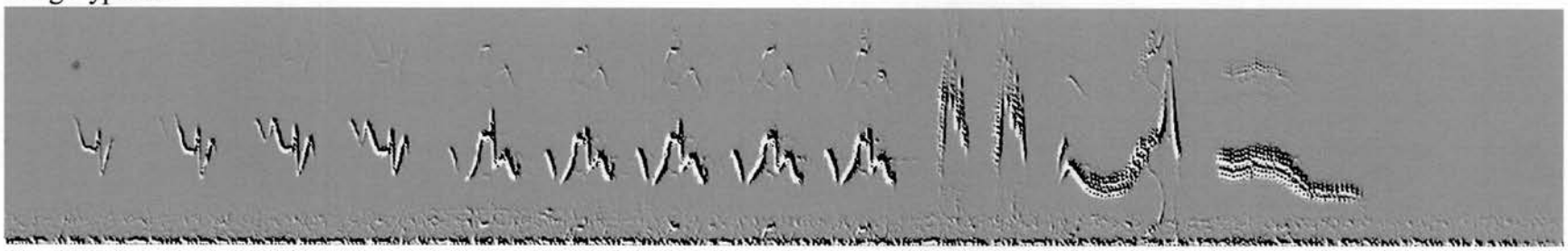
18 19 20 11a 7

Song Type VIII:



14 21 17

Song Type IX:

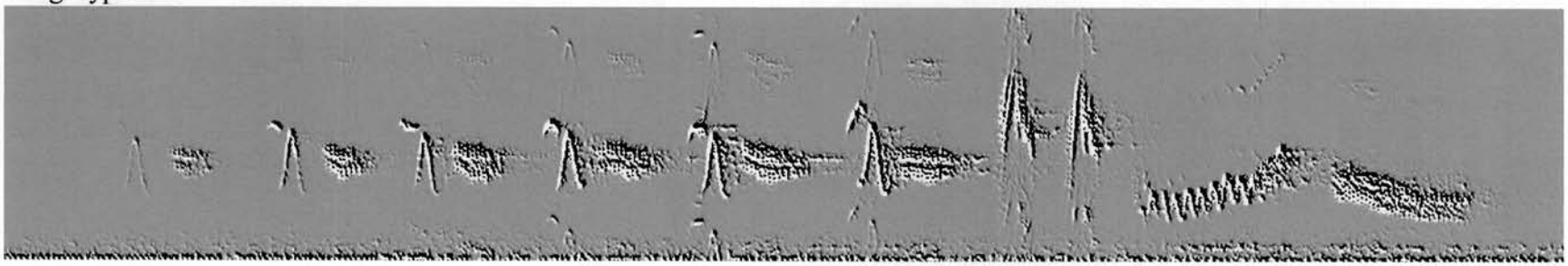


12 6b 7

Song Type X:

10a 22 7

Song Type XI:

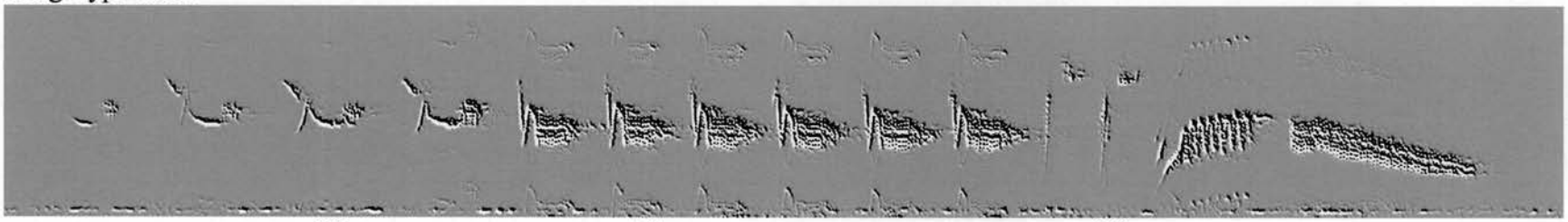


10a 7

Song Type XII:

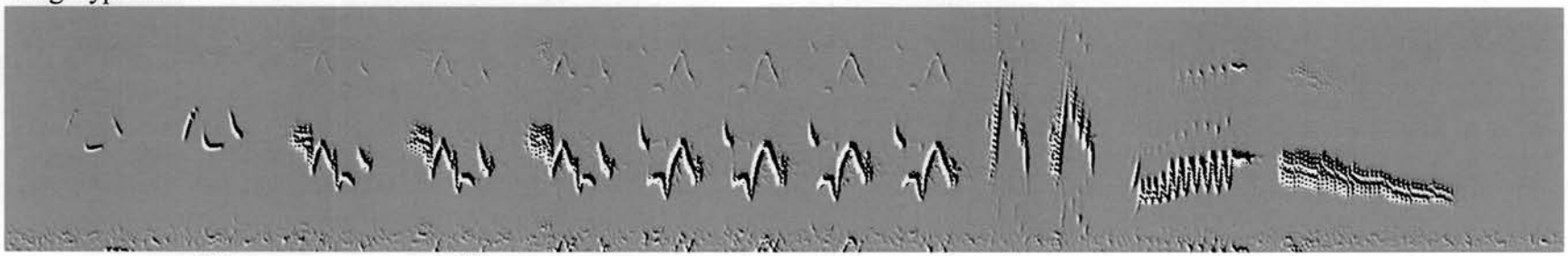
23 24 25

Song Type XIII:



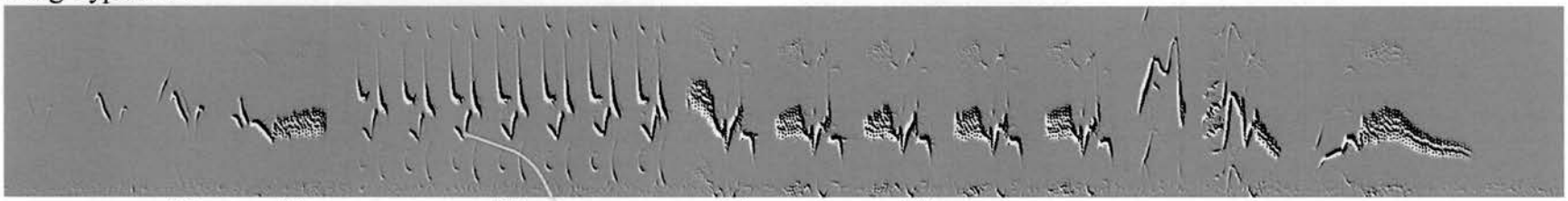
26 27 28

Song Type XIV:



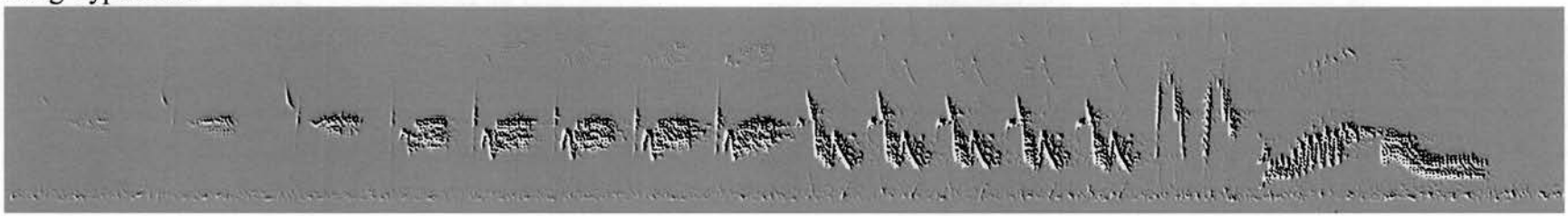
29 30 31 7

Song Type XV:



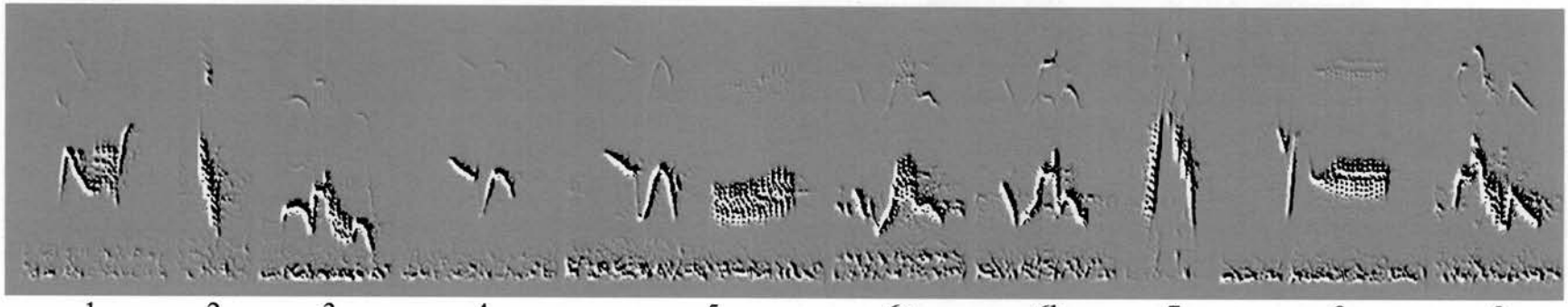
33 34 35 36 37

Song Type XVI:

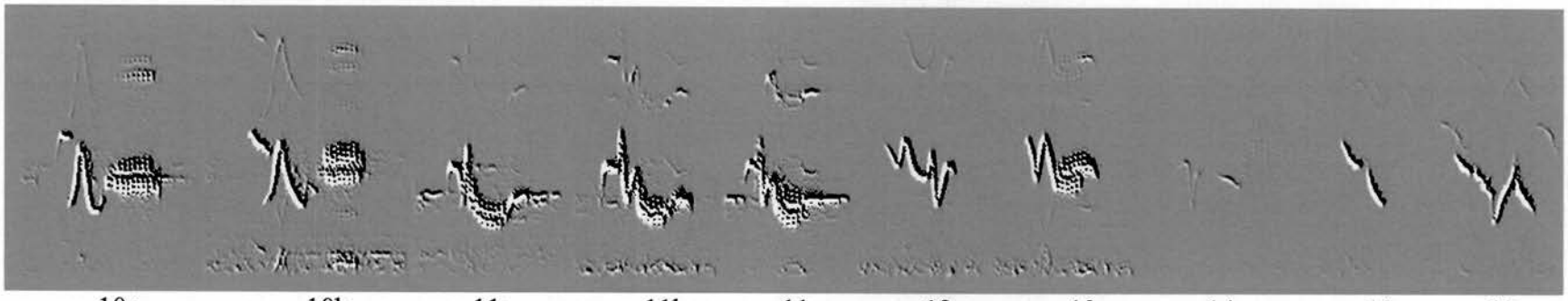


8 38 9 7

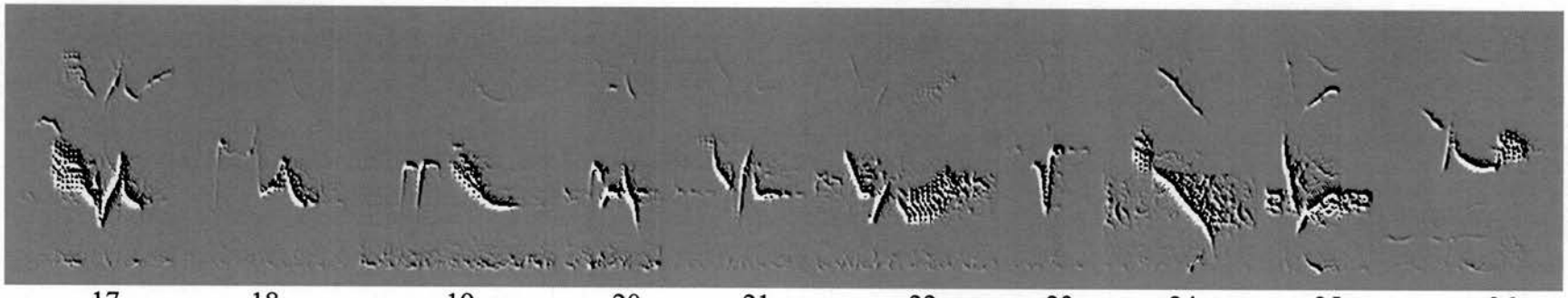
Wohlgemuth 2002 Syllable Types



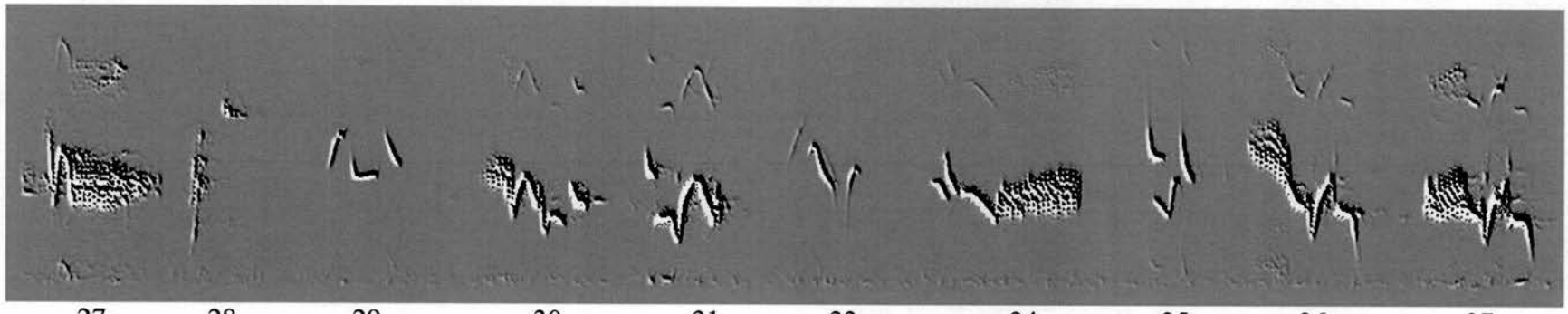
1 2 3 4 5 6a 6b 7 8 9



10a 10b 11a 11b 11c 12 13 14 15 16



17 18 19 20 21 22 23 24 25 26

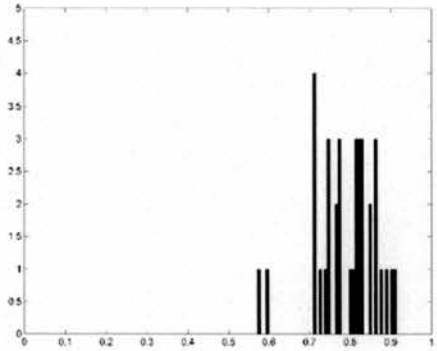


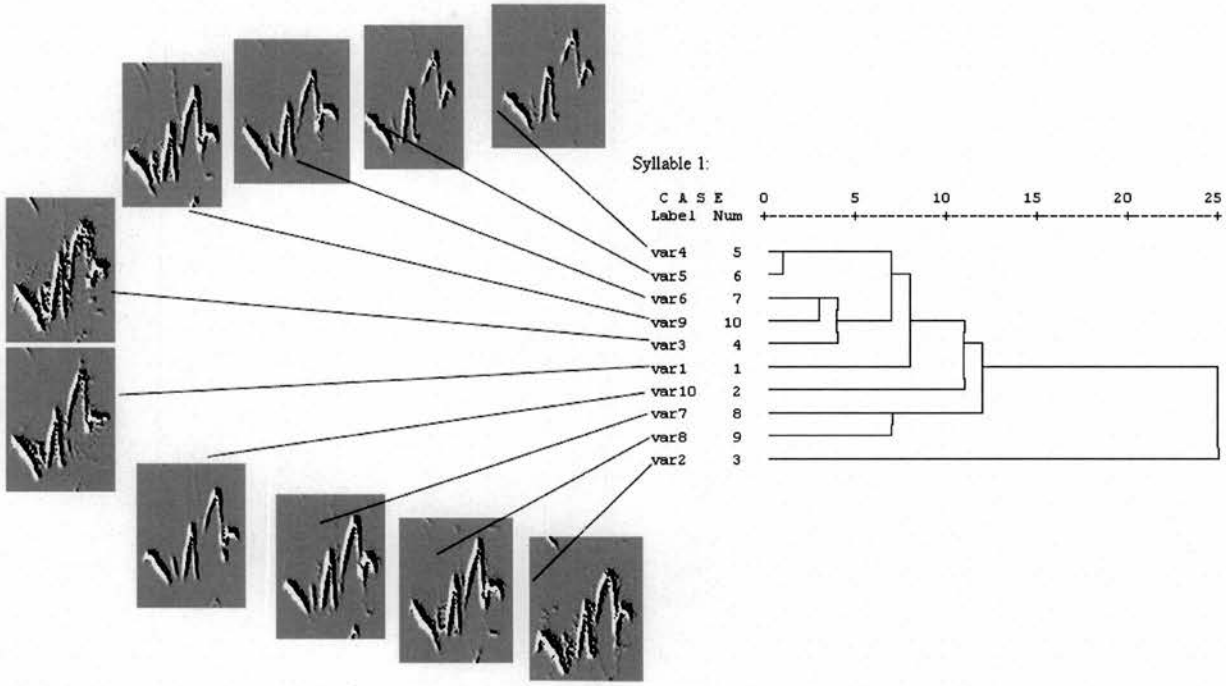
27 28 29 30 31 33 34 35 36 37

APPENDIX D
Within-Syllable Comparisons For the 1977 Recordings

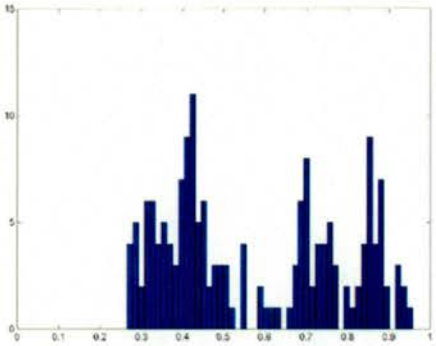
Figures include histograms of the correlation coefficients for each syllable, and dendrograms constructed from nearest-neighbor cluster analyses. Spectrograms for each syllable sample compared are also included with each dendrogram.

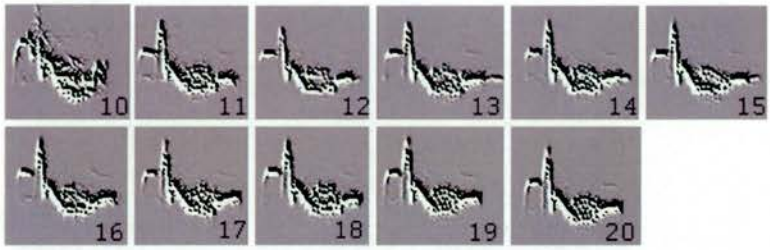
Syllable 1:

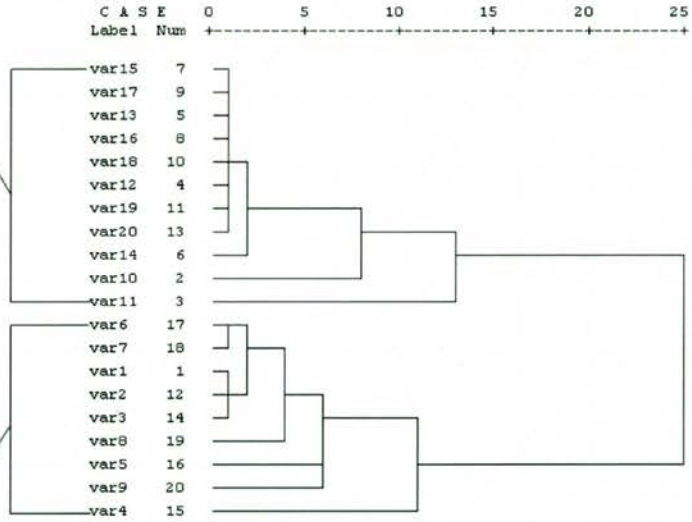


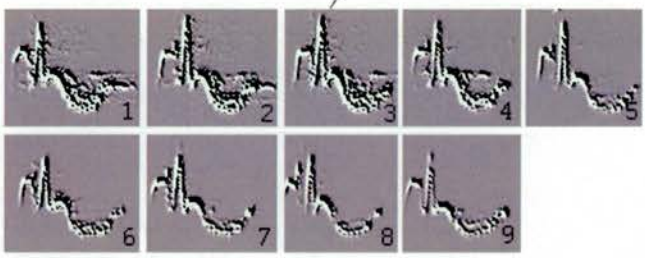

Syllable 1:
C A S E
Label Num
0 5 10 15 20 25
var4 5
var5 6
var6 7
var9 10
var3 4
var1 1
var10 2
var7 8
var8 9
var2 3

Syllable 3:




10
11
12
13
14
15
16
17
18
19
20


C A S E
Label Num
0 5 10 15 20 25
var15 7
var17 9
var13 5
var16 8
var18 10
var12 4
var19 11
var20 13
var14 6
var10 2
var11 3
var6 17
var7 18
var1 1
var2 12
var3 14
var8 19
var5 16
var9 20
var4 15


1
2
3
4
5
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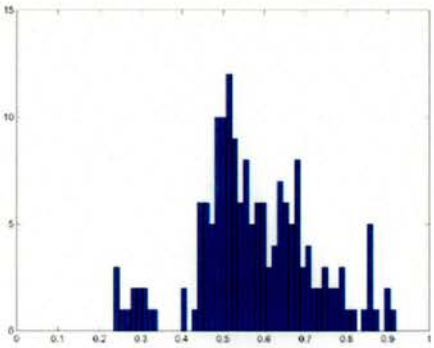
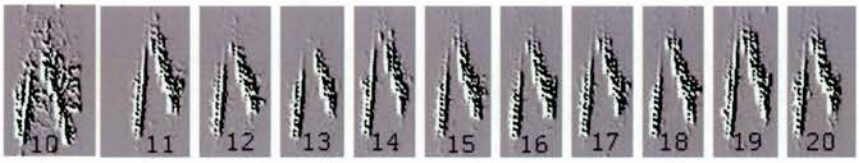
7
8
9

Syllable 4:


15
10
5
0
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1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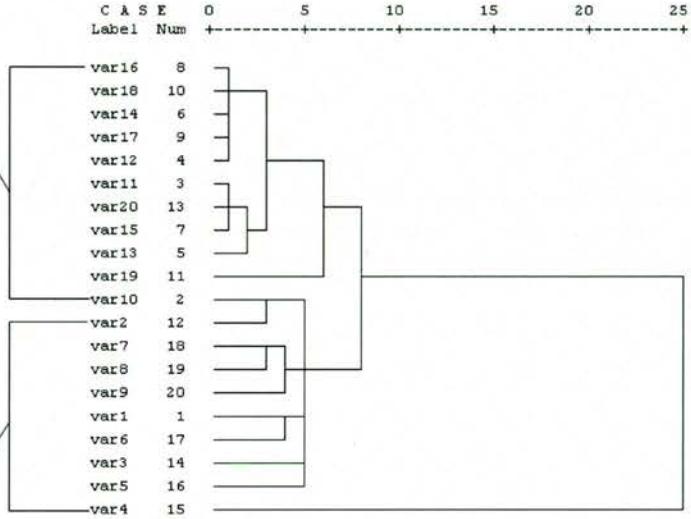
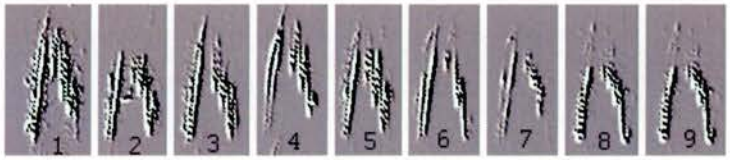
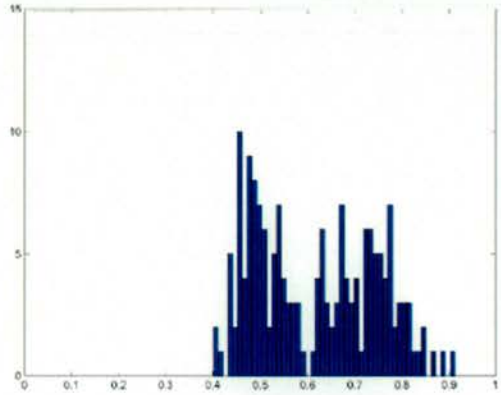
11
12
13
14
15
16
17
18
19
20


C A S E
Label Num
0
5
10
15
20
25
var16 8
var18 10
var14 6
var17 9
var12 4
var11 3
var20 13
var15 7
var13 5
var19 11
var10 2
var2 12
var7 18
var8 19
var9 20
var1 1
var6 17
var3 14
var5 16
var4 15


1
2
3
4
5
6
7
8
9

Syllable 5: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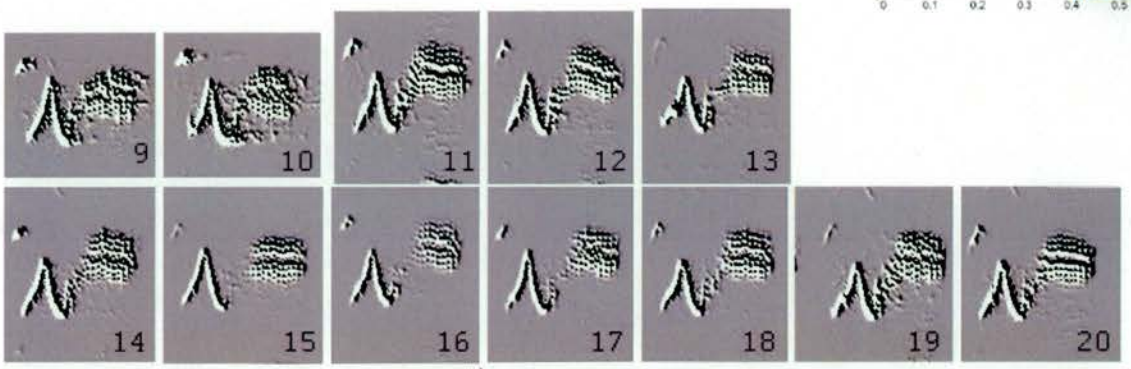
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1


9
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11
12
13
14
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16
17
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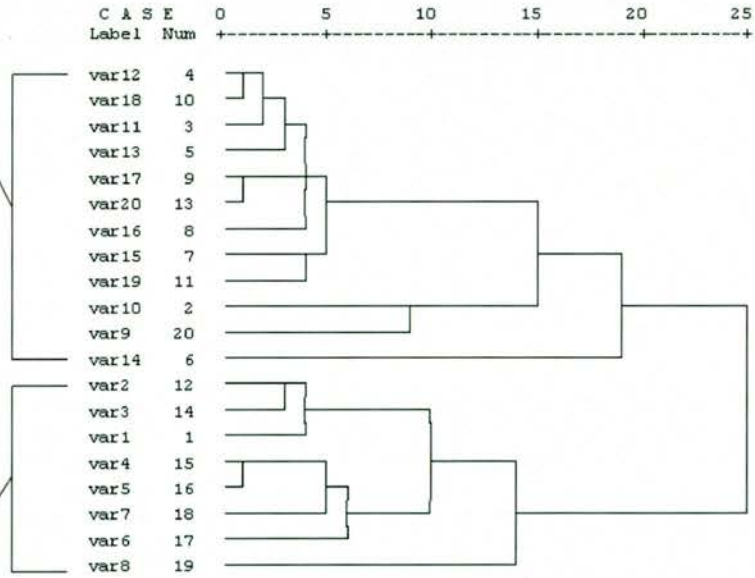
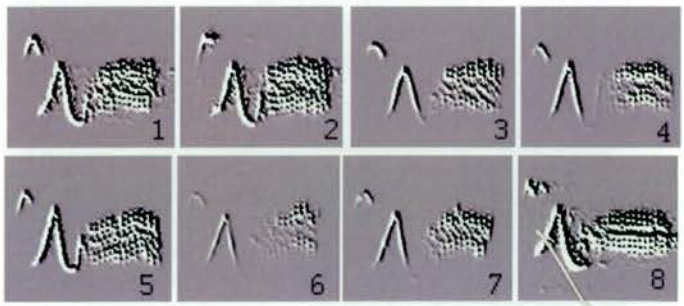
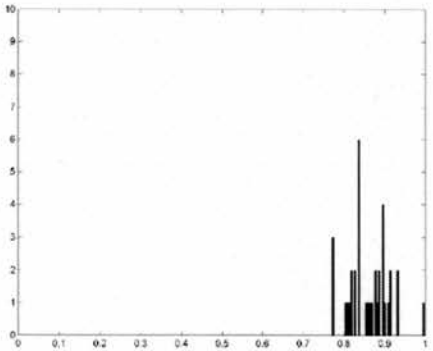
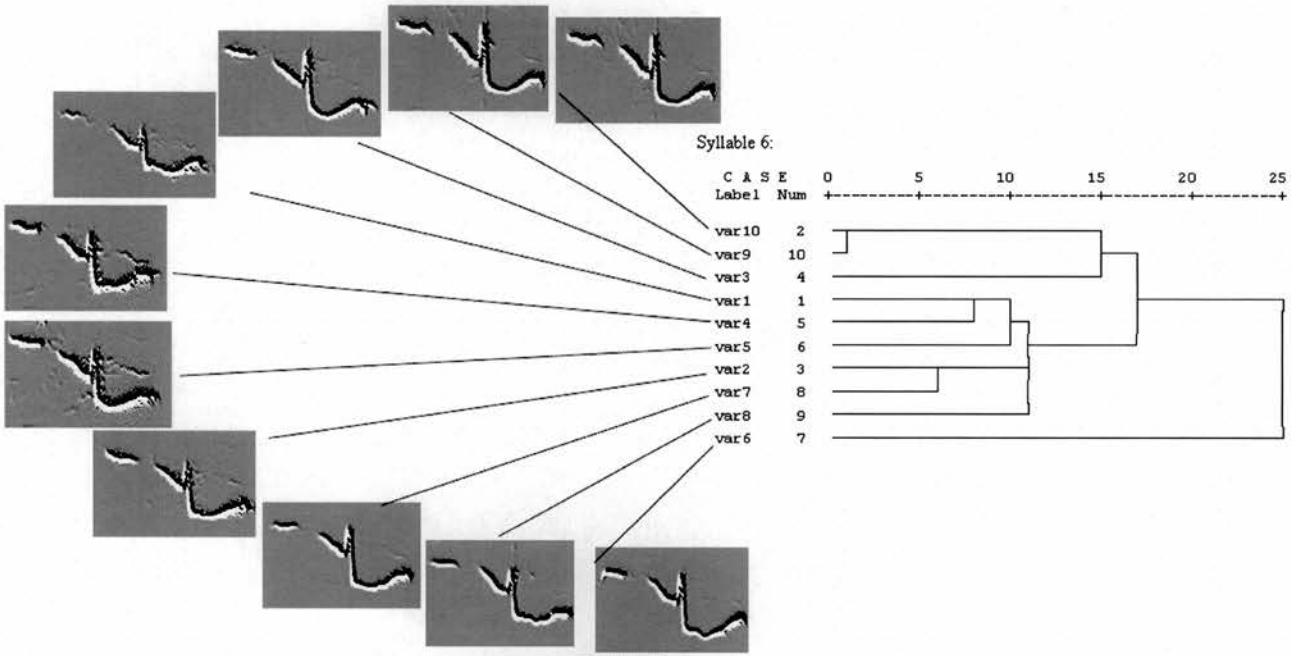
19
20


C A S E
Label Num
0 5 10 15 20 25
var12 4
var18 10
var11 3
var13 5
var17 9
var20 13
var16 8
var15 7
var19 11
var10 2
var9 20
var14 6
var2 12
var3 14
var1 1
var4 15
var5 16
var7 18
var6 17
var8 19


1
2
3
4
5
6
7
8

Syllable 6:





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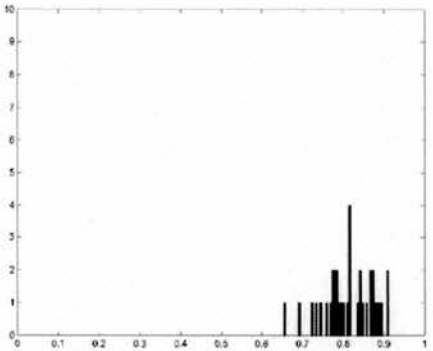
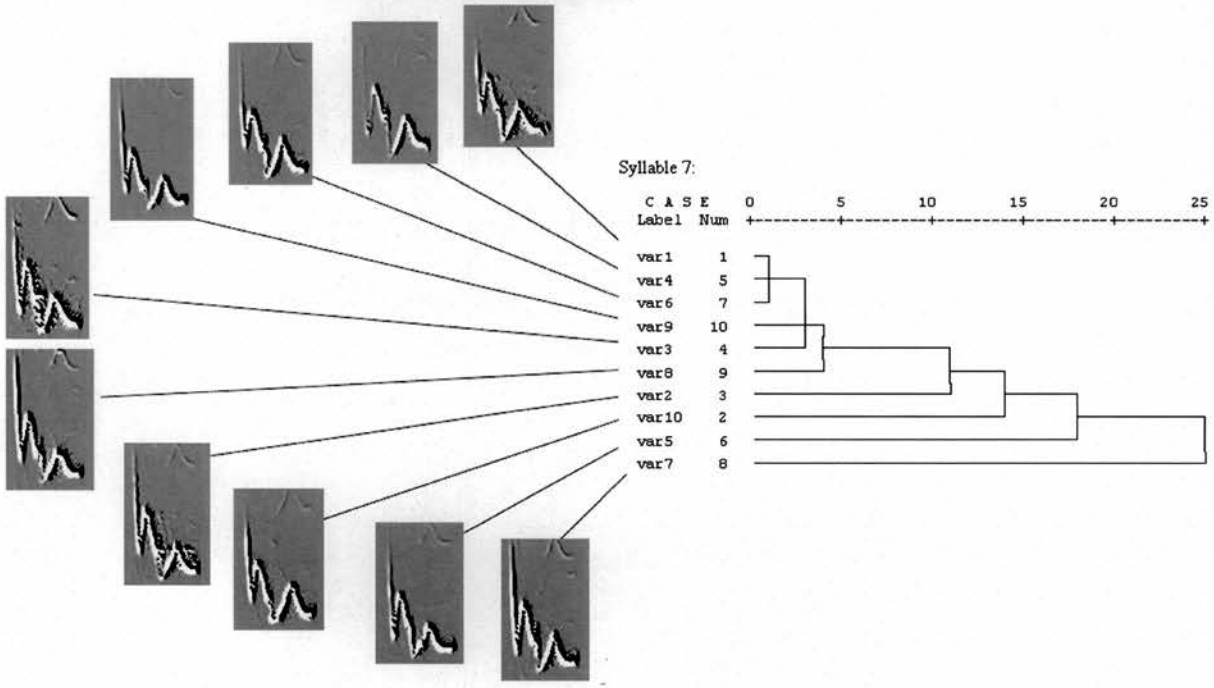
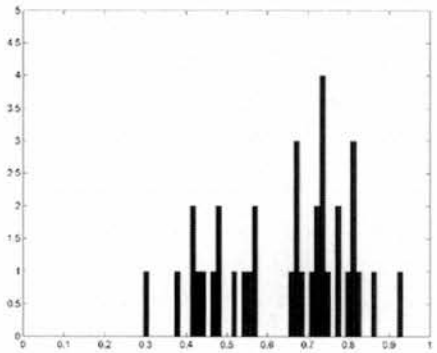
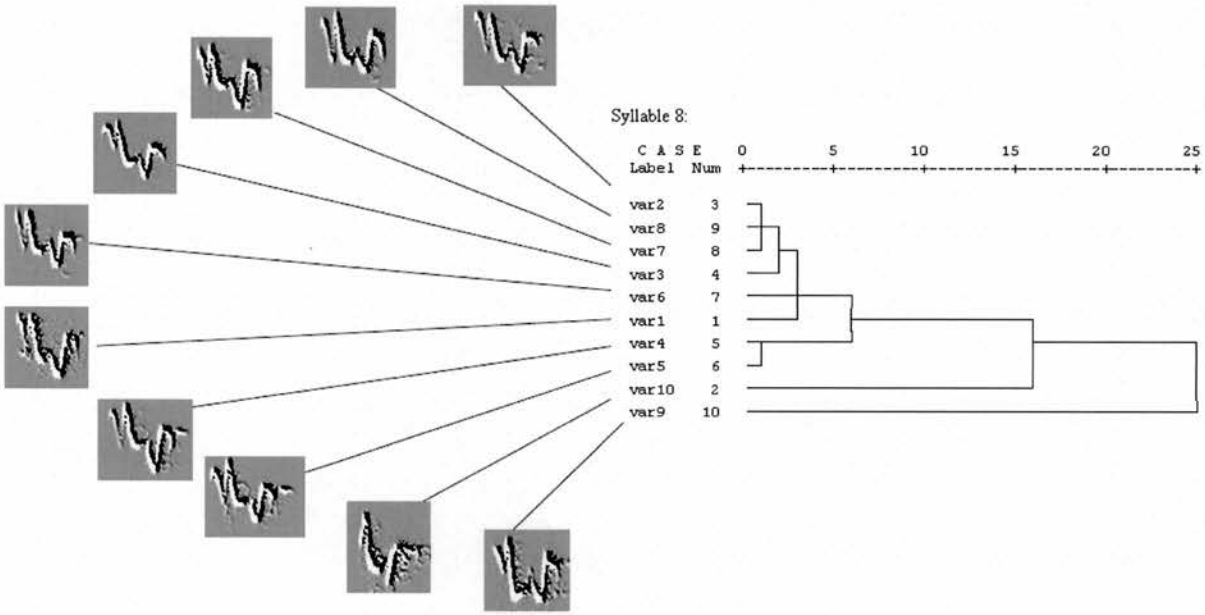


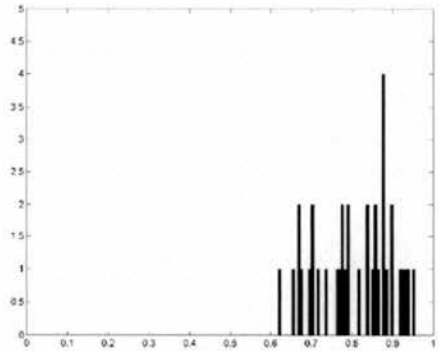


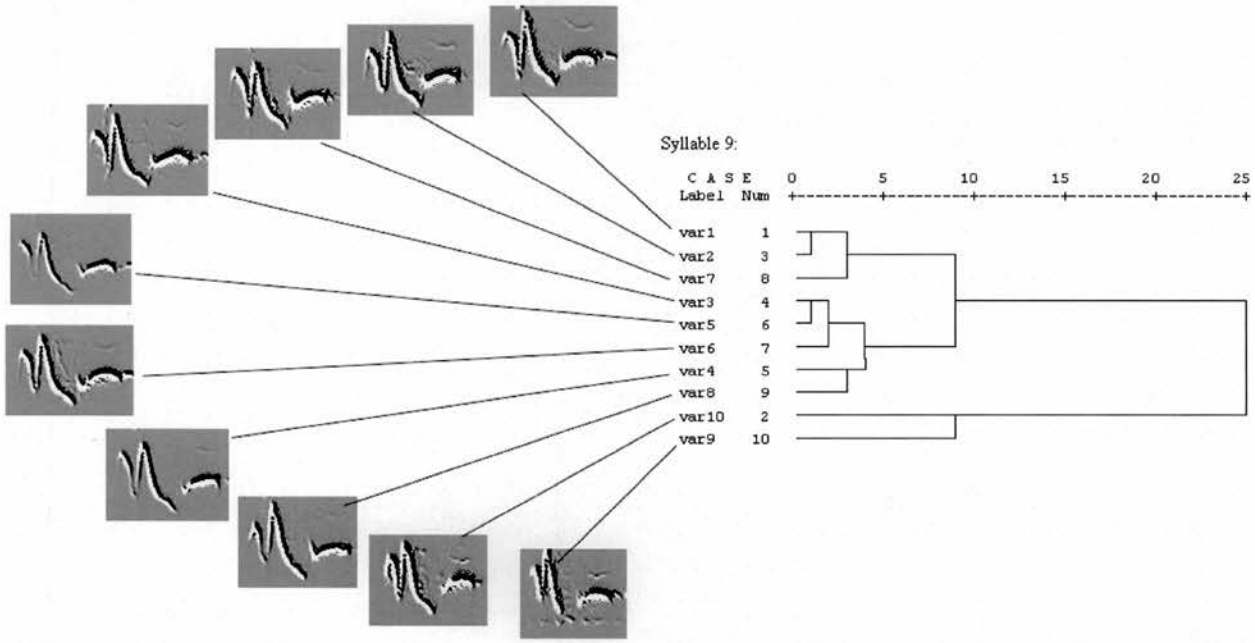
Syllable 8:



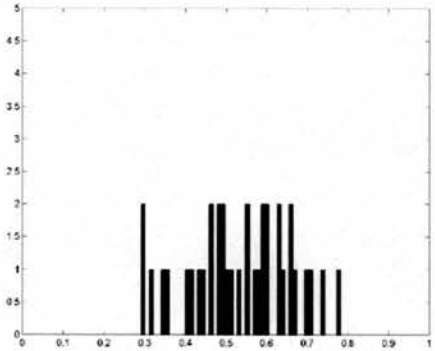


Syllable 9:





Syllable 10: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3
3.5
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0.9
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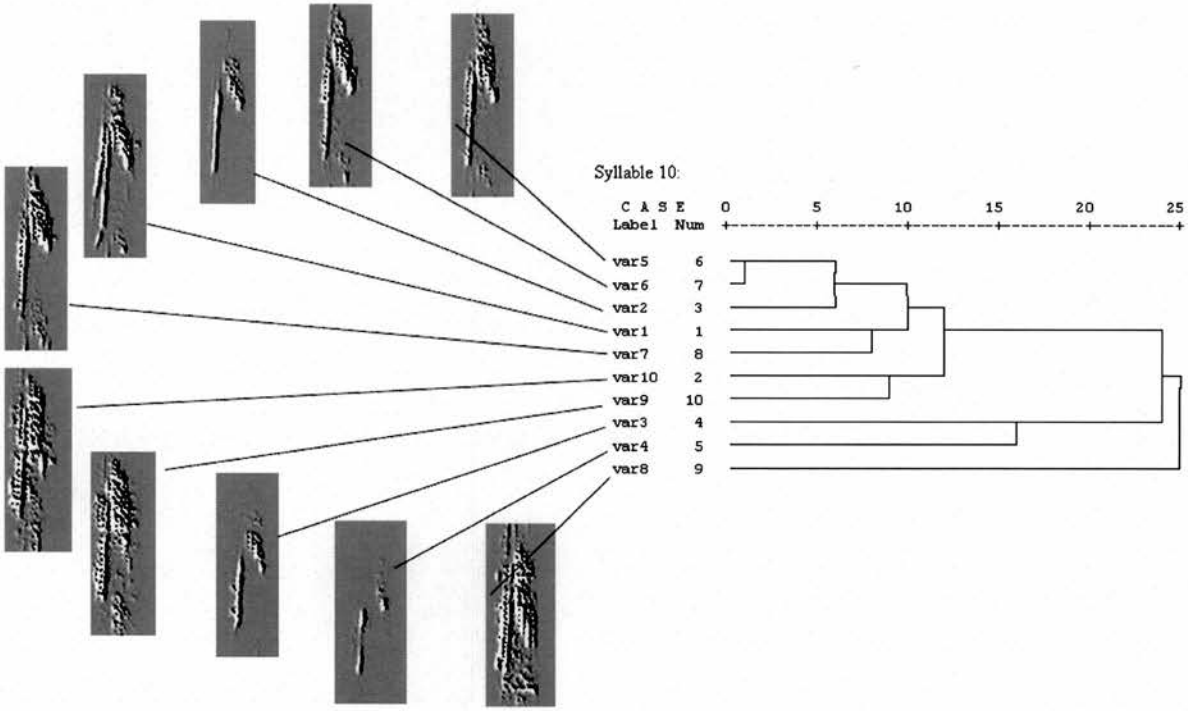
Syllable 10:
C A S E
Label Num
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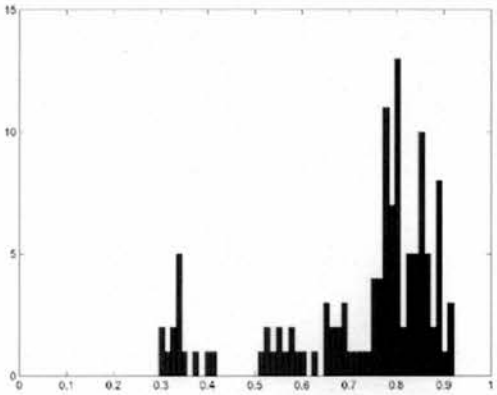
var2 3
var1 1
var7 8
var10 2
var9 10
var3 4
var4 5
var8 9

Syllable 12: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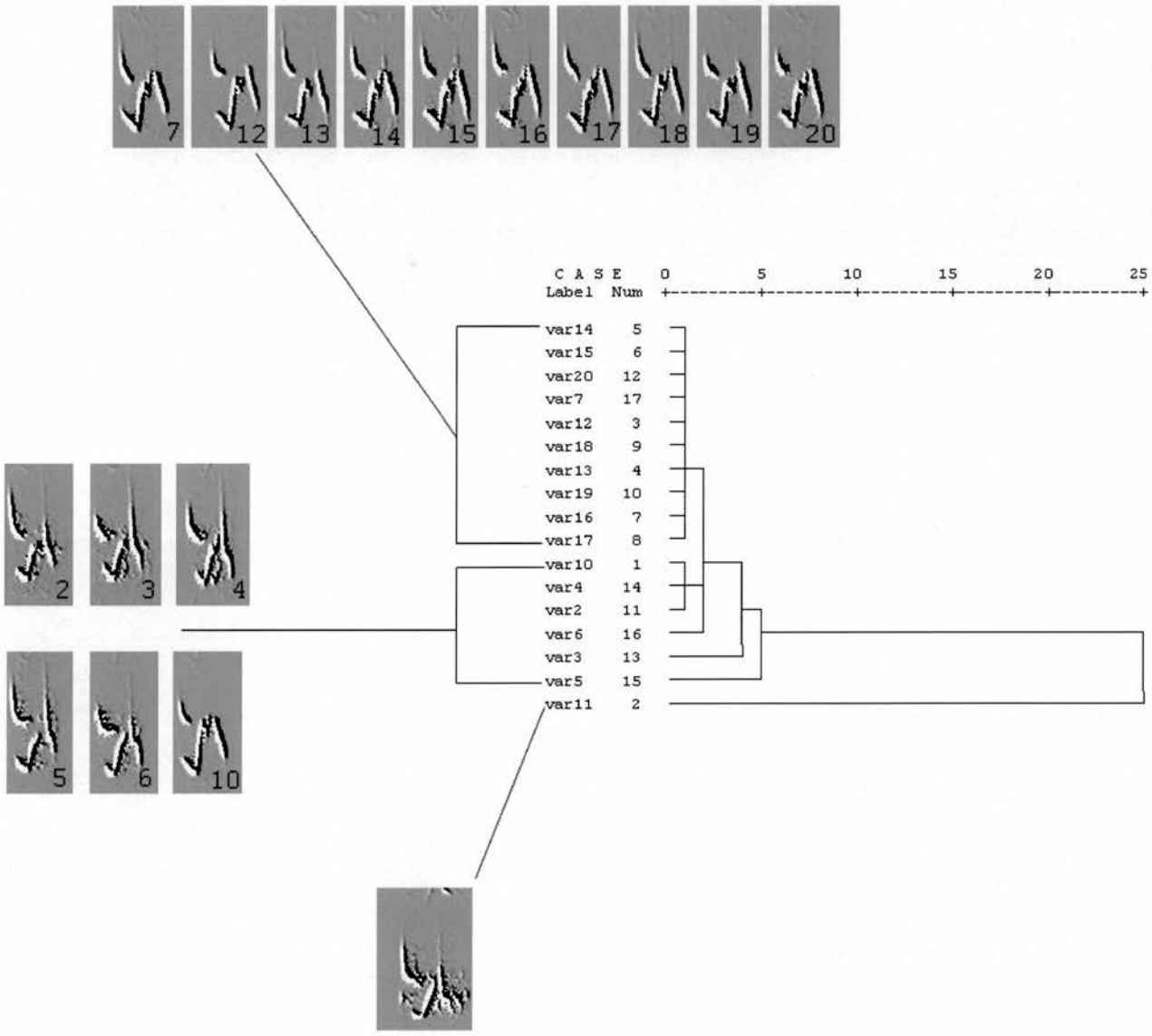
0.9
1


7
12
13
14
15
16
17
18
19
20
C A S E
Label Num
0
5
10
15
20
25
var14 5
var15 6
var20 12
var7 17
var12 3
var18 9
var13 4
var19 10
var16 7
var17 8
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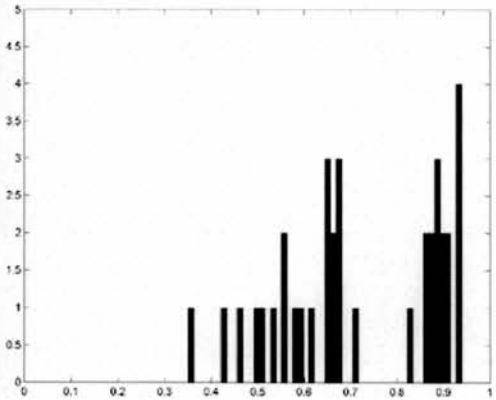
var6 16
var3 13
var5 15
var11 2
2
3
4
5
6
10

Syllable 14: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2
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3
3.5
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0.2
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0.6
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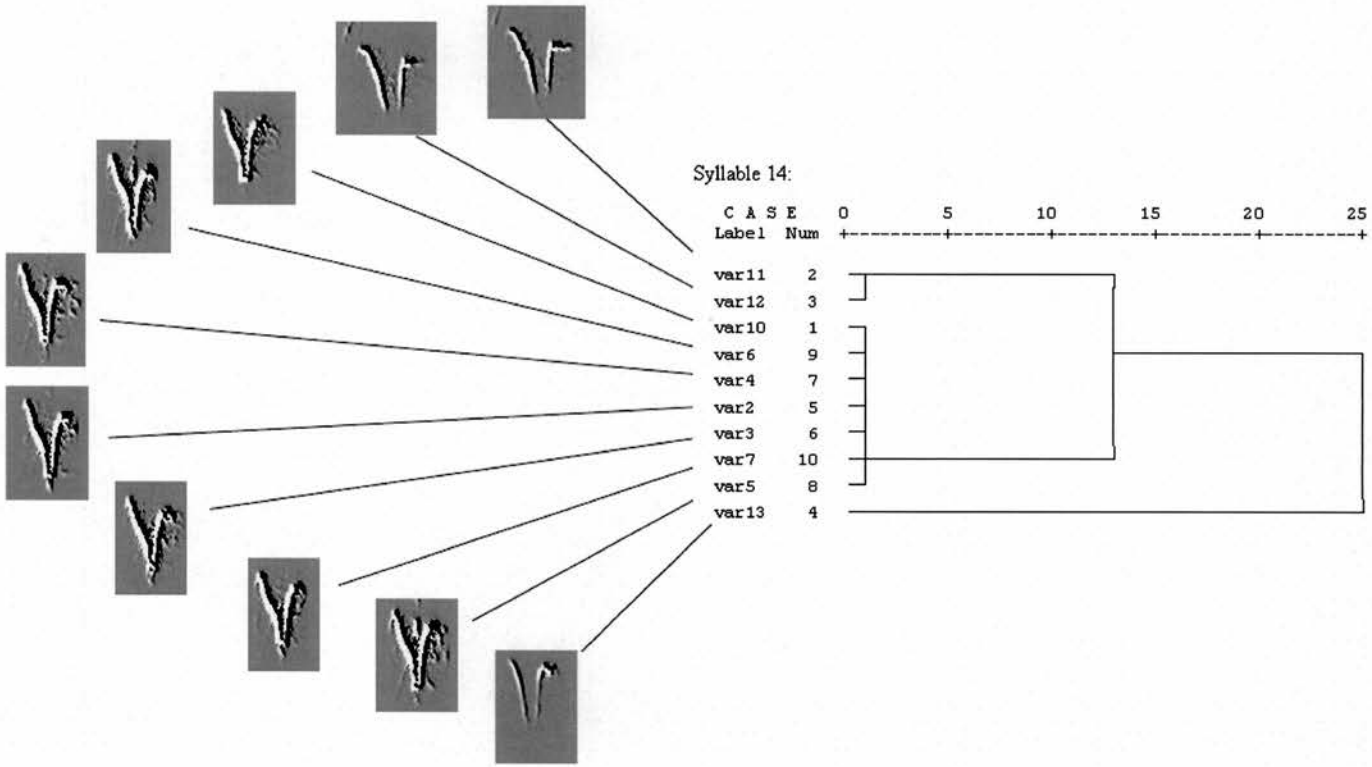
0.8
0.9
1


Syllable 14:
C A S E
Label Num
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10
15
20
25
var11 2
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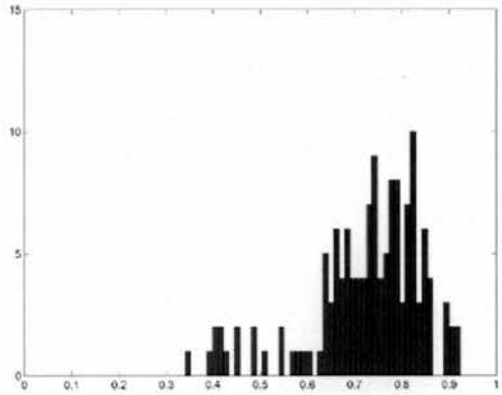
var10 1
var6 9
var4 7
var2 5
var3 6
var7 10
var5 8
var13 4

Syllable 15: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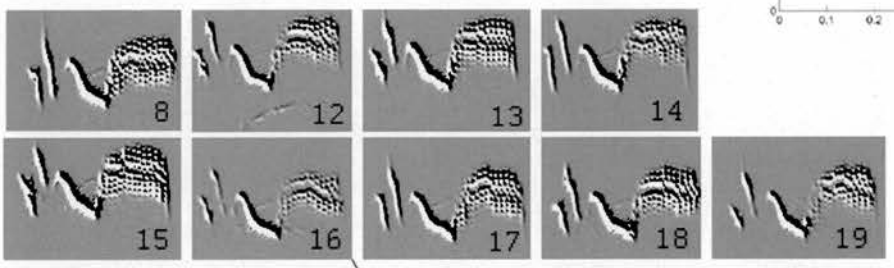
0.5
0.6
0.7
0.8
0.9
1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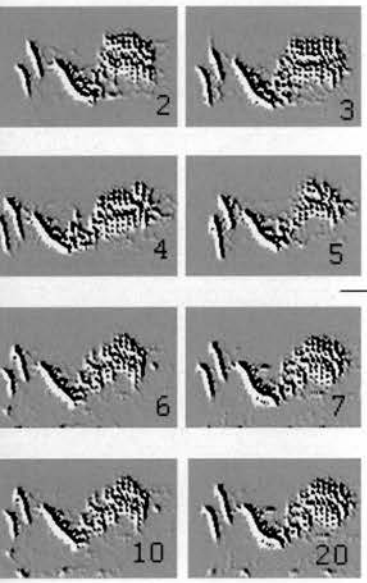
2
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4
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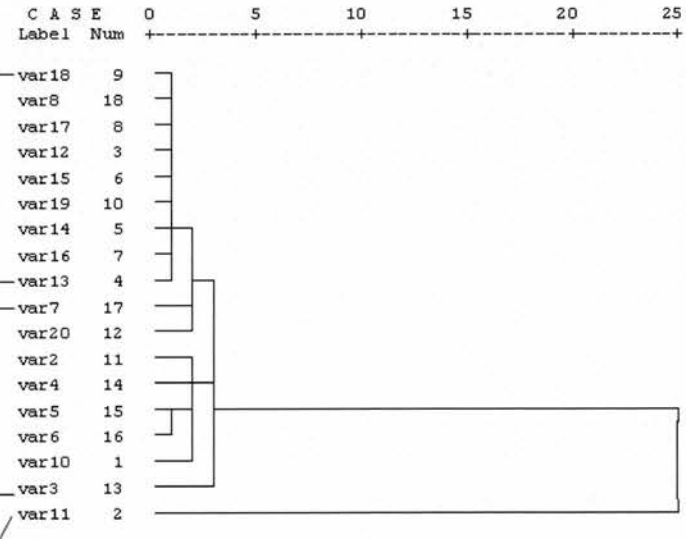
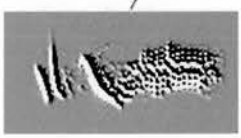
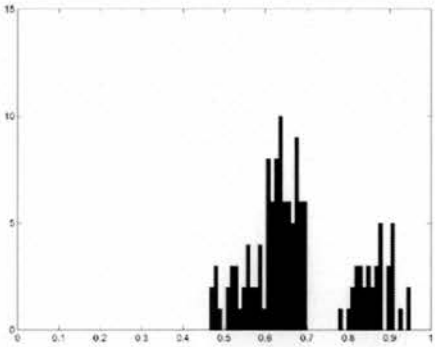
6
7
10
20


C A S E
Label Num
0
5
10
15
20
25
var18 9
var8 18
var17 8
var12 3
var15 6
var19 10
var14 5
var16 7
var13 4
var7 17
var20 12
var2 11
var4 14
var5 15
var6 16
var10 1
var3 13
var11 2



Syllable 16: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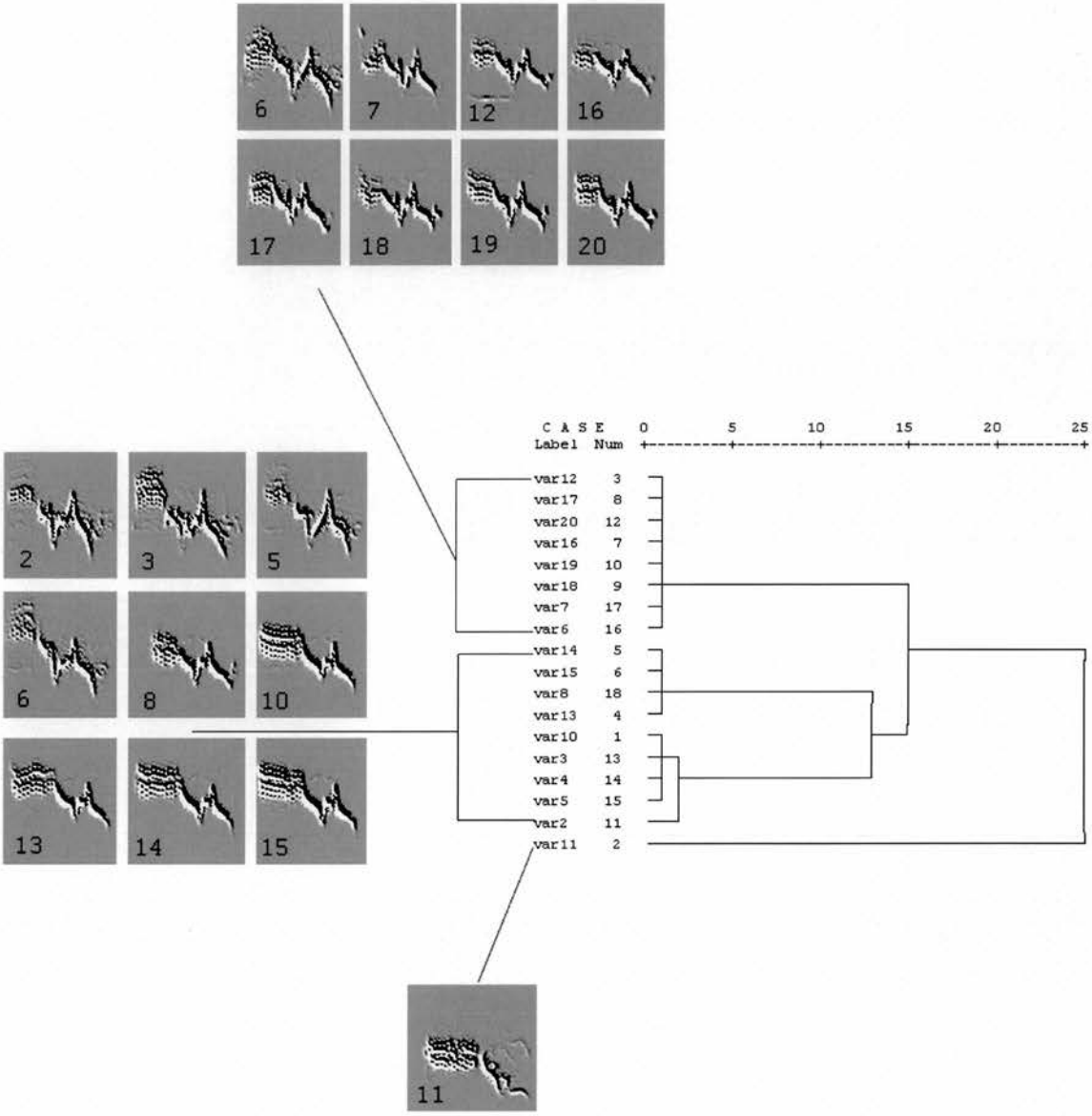
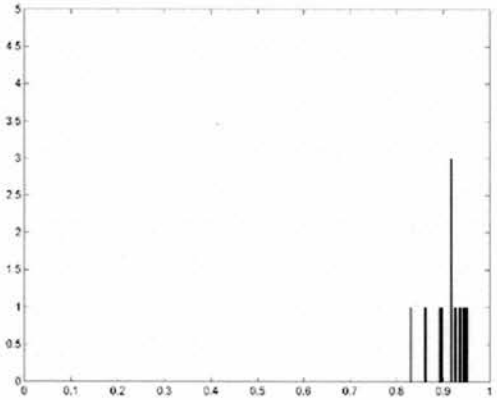
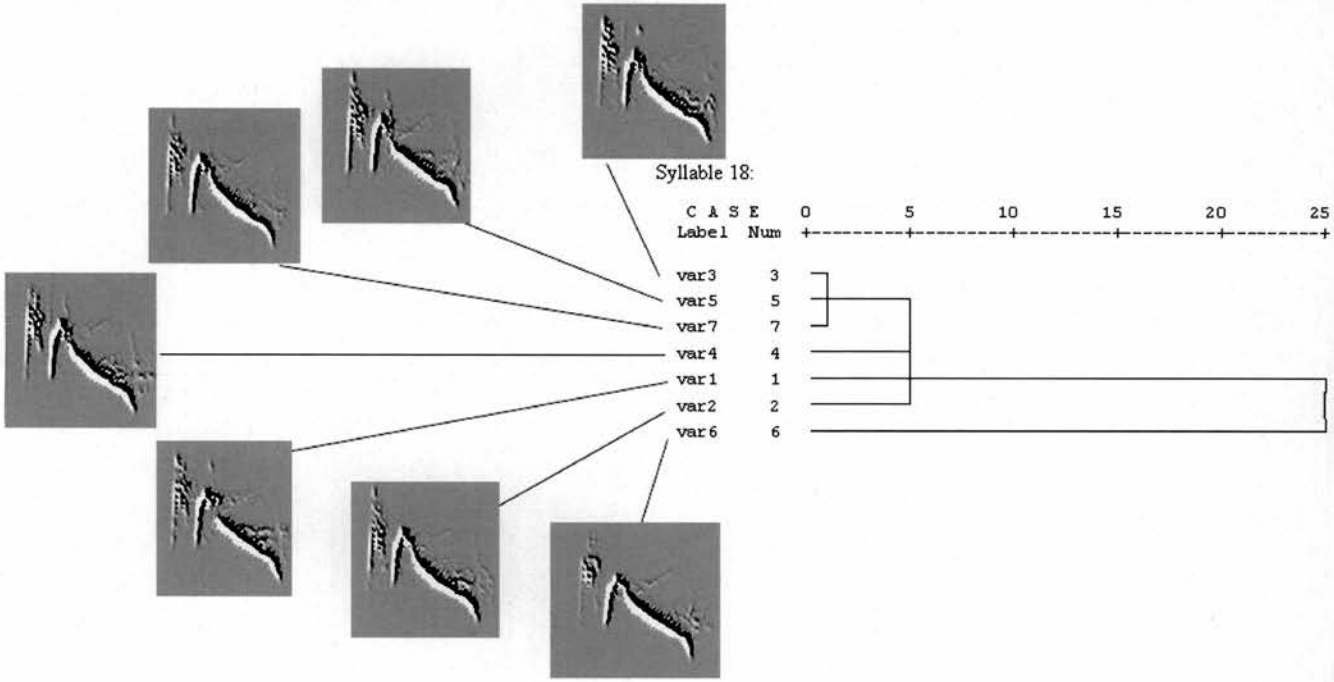
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1

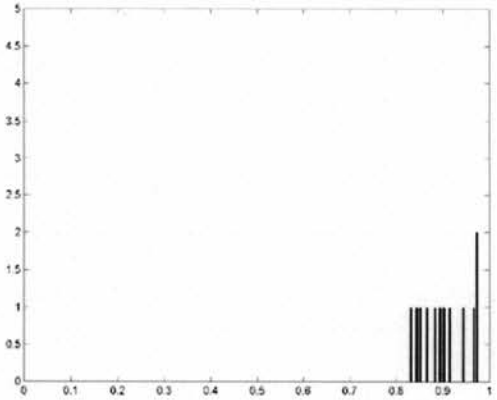

6
7
12
16
17
18
19
20
2
3
5
6
8
10
13
14
15
11
C A S E
Label Num
0
5
10
15
20
25
var12 3
var17 8
var20 12
var16 7
var19 10
var18 9
var7 17
var6 16
var14 5
var15 6
var8 18
var13 4
var10 1
var3 13
var4 14
var5 15
var2 11
var11 2

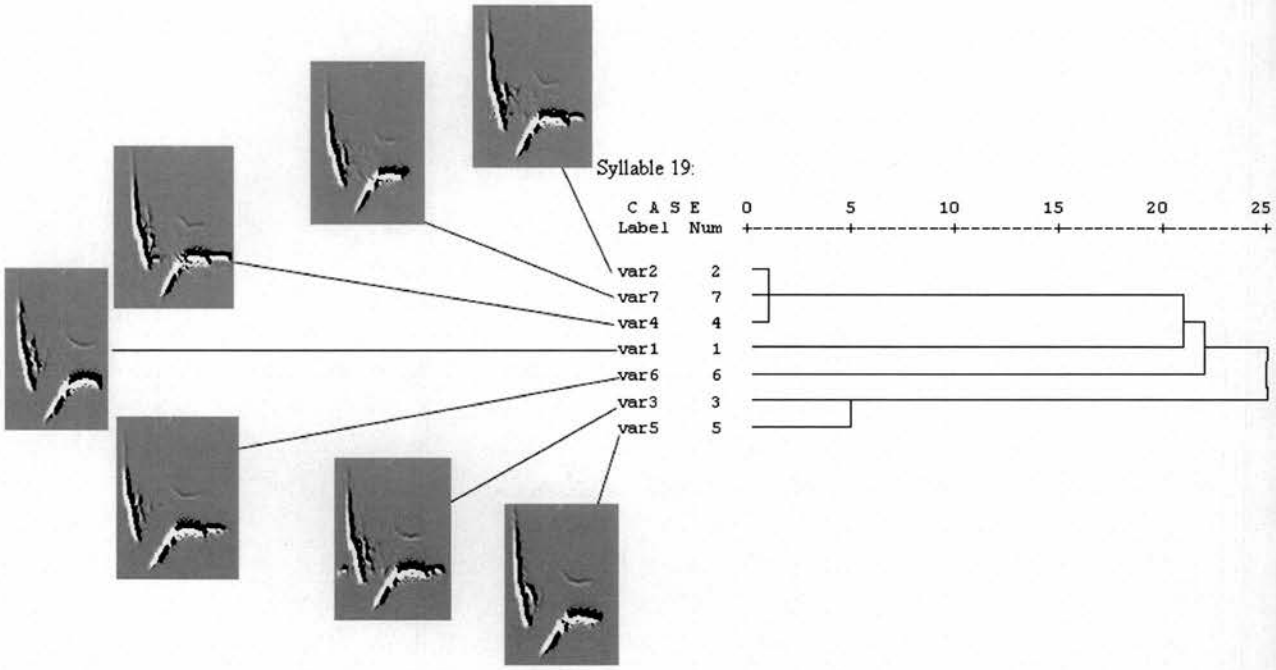
Syllable 18:



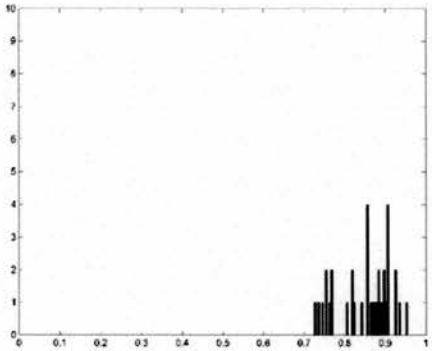


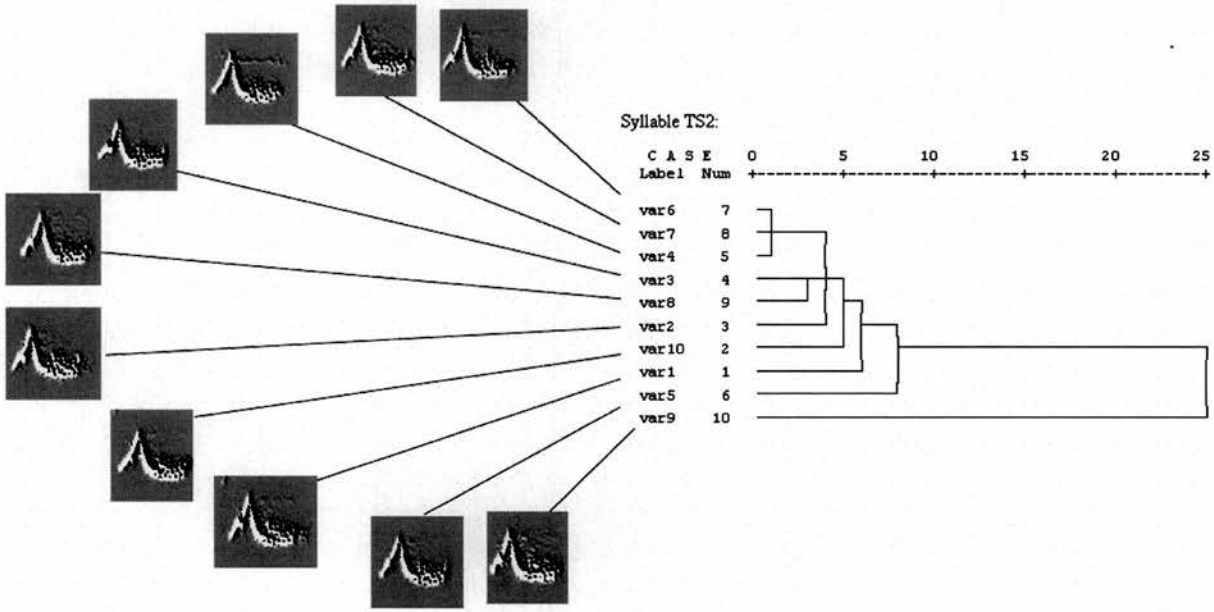
Syllable 19:





Syllable TS2:

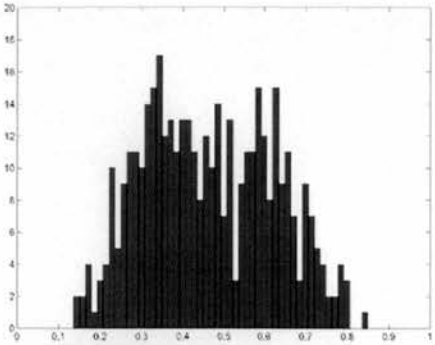


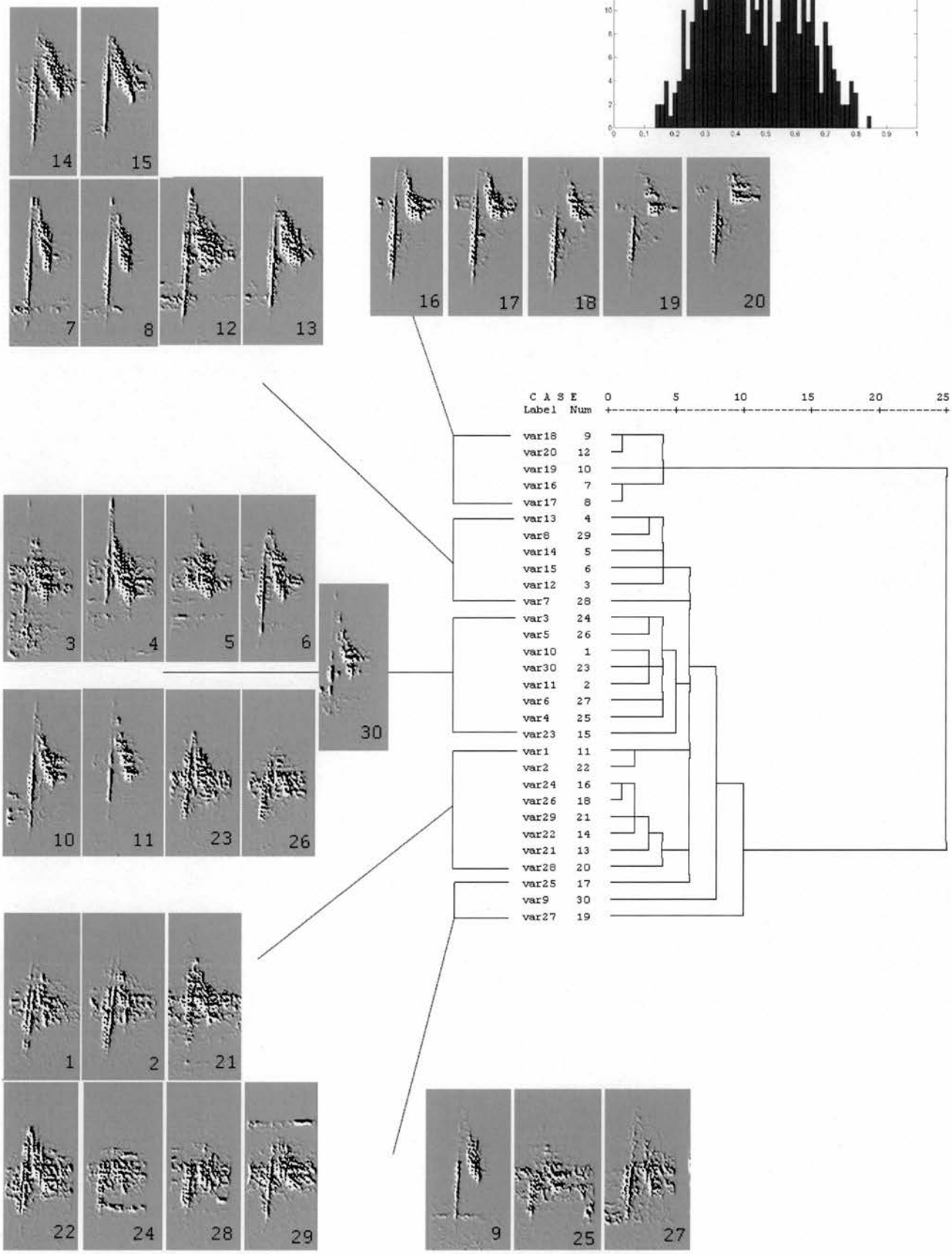


APPENDIX E
Within-Syllable Comparisons For the 1997 Recordings

Figures include histograms of the correlation coefficients for each syllable, and dendrograms constructed from nearest-neighbor cluster analyses. Spectrograms for each syllable sample compared are also included with each dendrogram.

Syllable 4:




C A S E
Label Num
0 5 10 15 20 25
var18 9
var20 12
var19 10
var16 7
var17 8
var13 4
var8 29
var14 5
var15 6
var12 3
var7 28
var3 24
var5 26
var10 1
var30 23
var11 2
var6 27
var4 25
var23 15
var1 11
var2 22
var24 16
var26 18
var29 21
var22 14
var21 13
var28 20
var25 17
var9 30
var27 19
14
15
7
8
12
13
16
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18
19
20
3
4
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10
11
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1
2
21
22
24
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29
9
25
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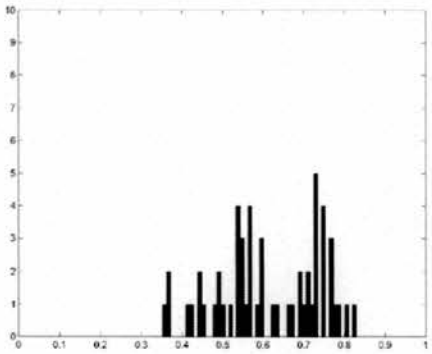
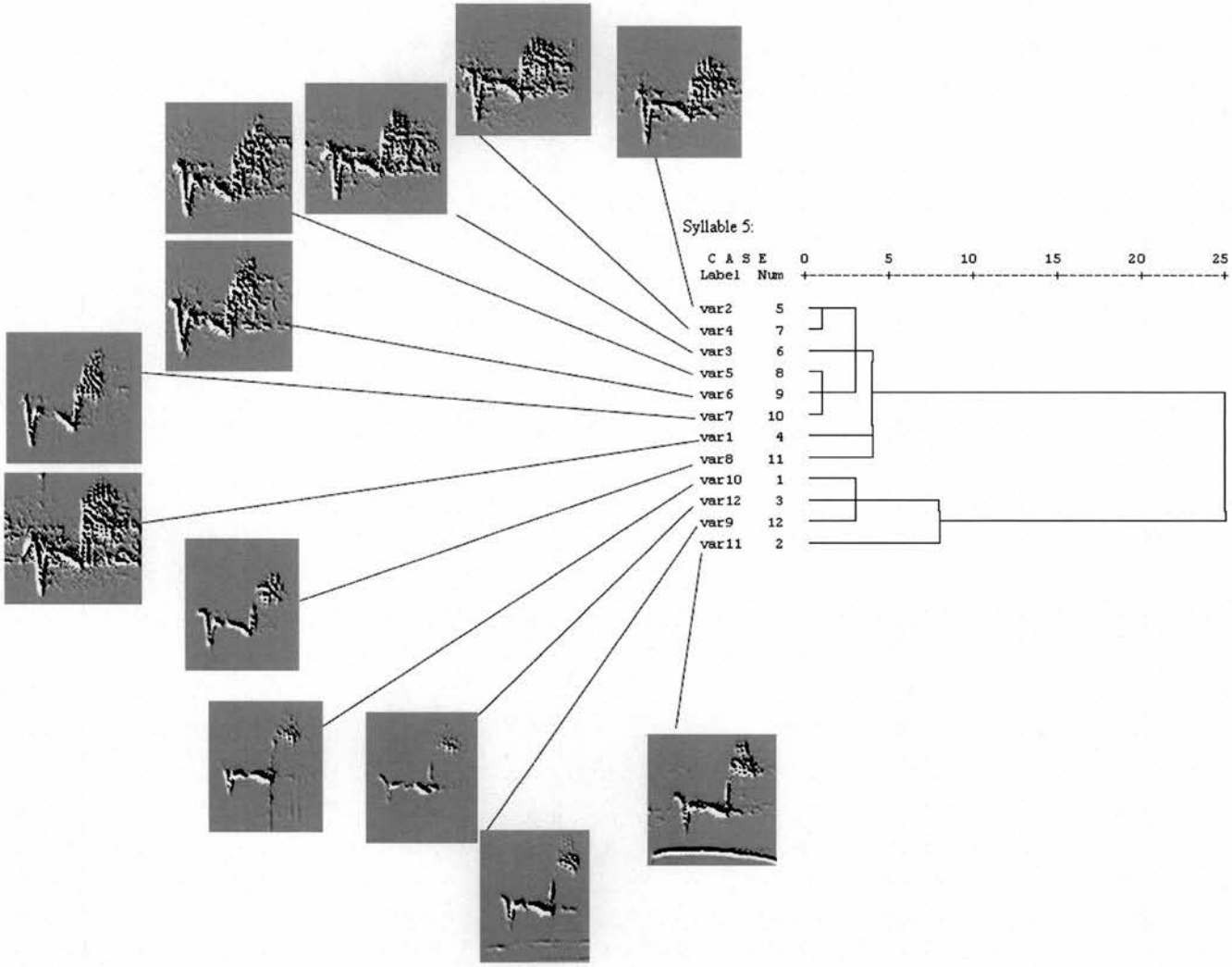
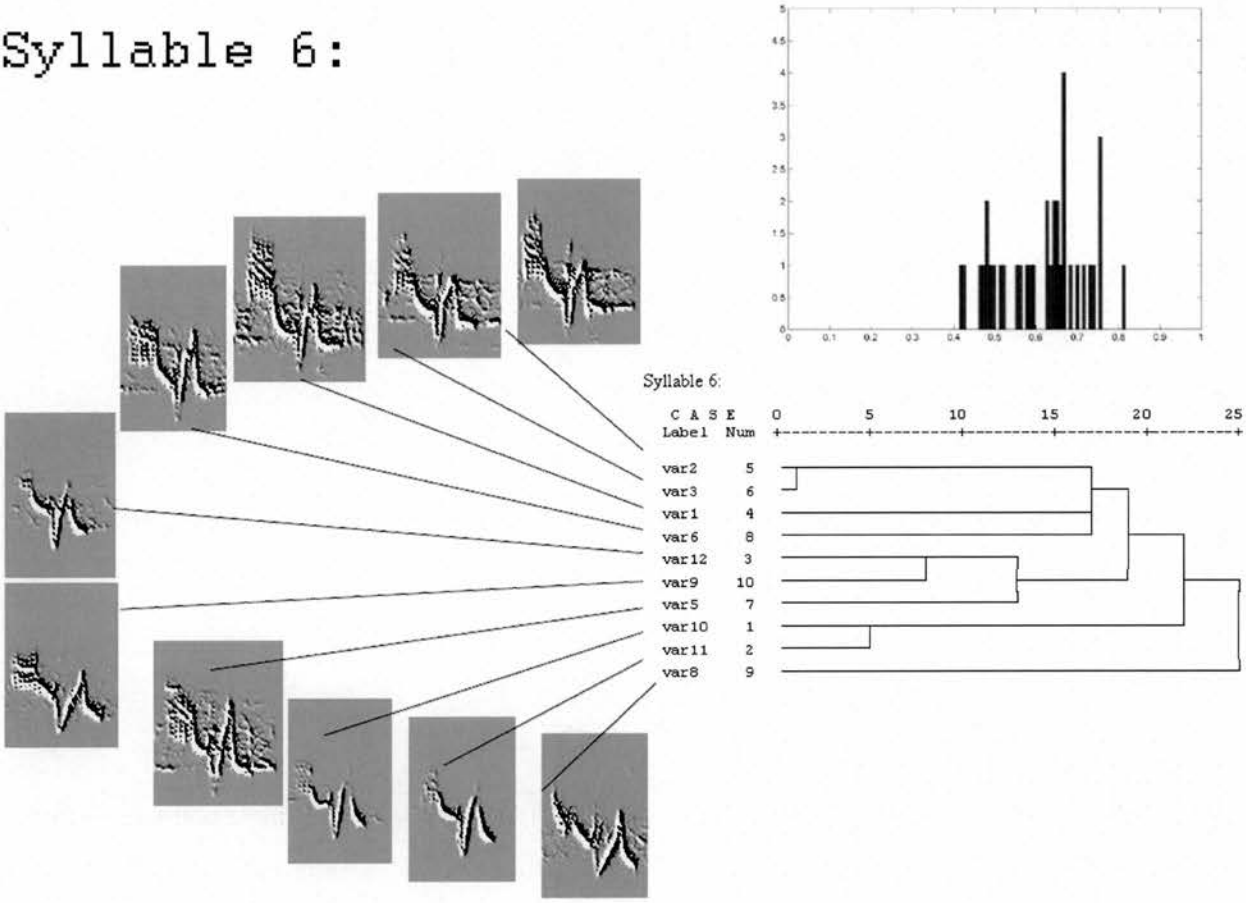
Syllable 5:

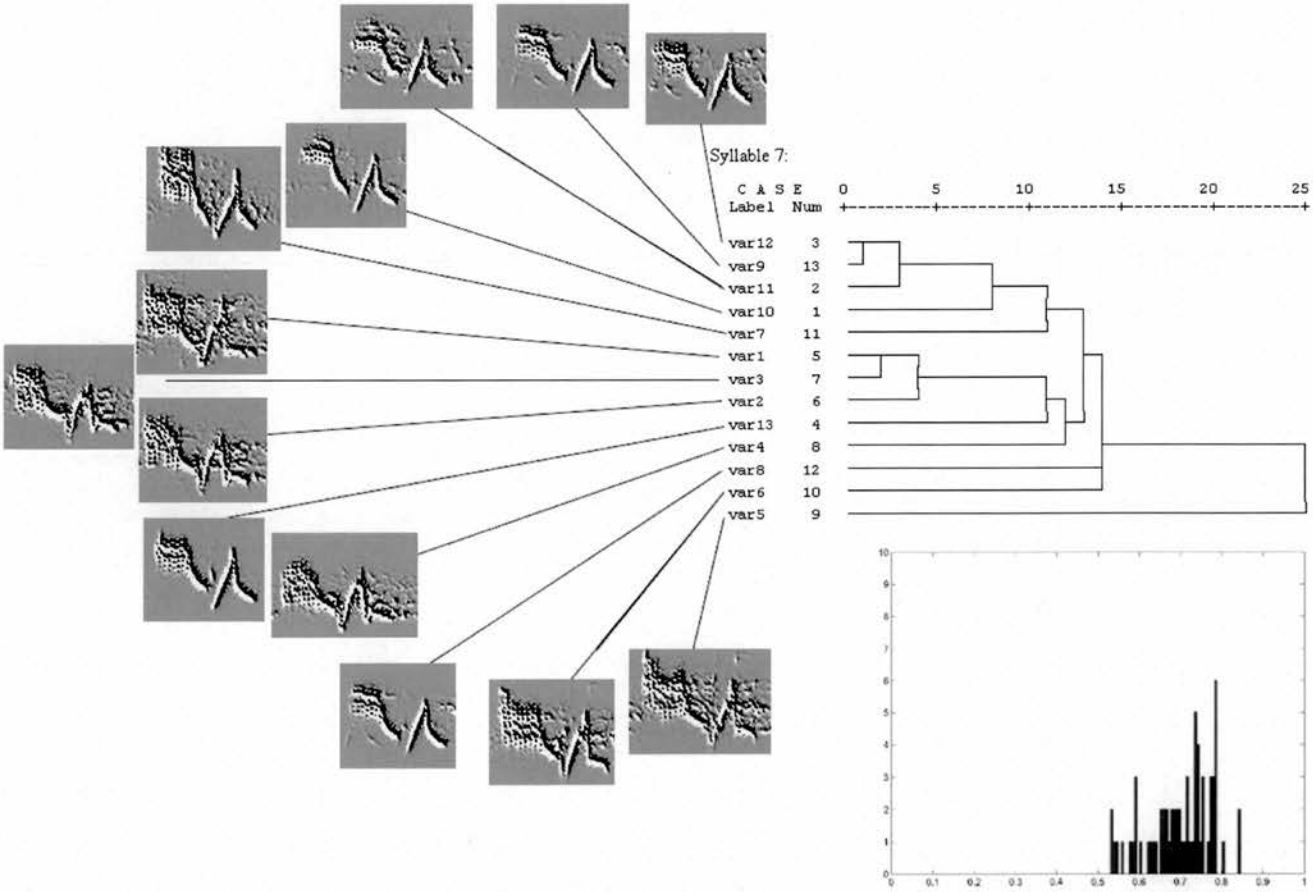



Syllable 5:
C A S E
Label Num
0 5 10 15 20 25
var2 5
var4 7
var3 6
var5 8
var6 9
var7 10
var1 4
var8 11
var10 1
var12 3
var9 12
var11 2

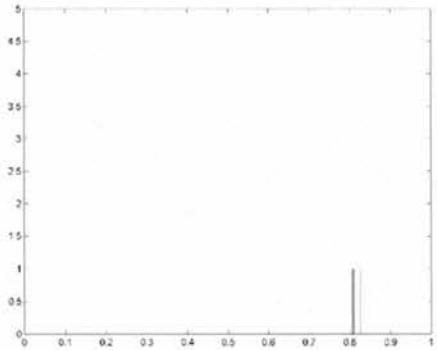
Syllable 6:



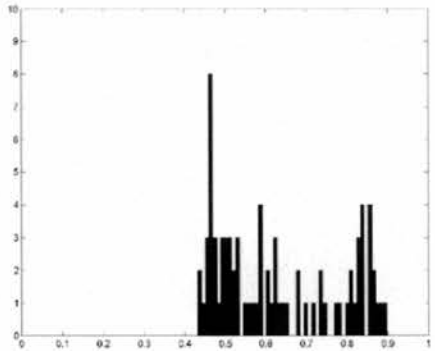
Syllable 7:

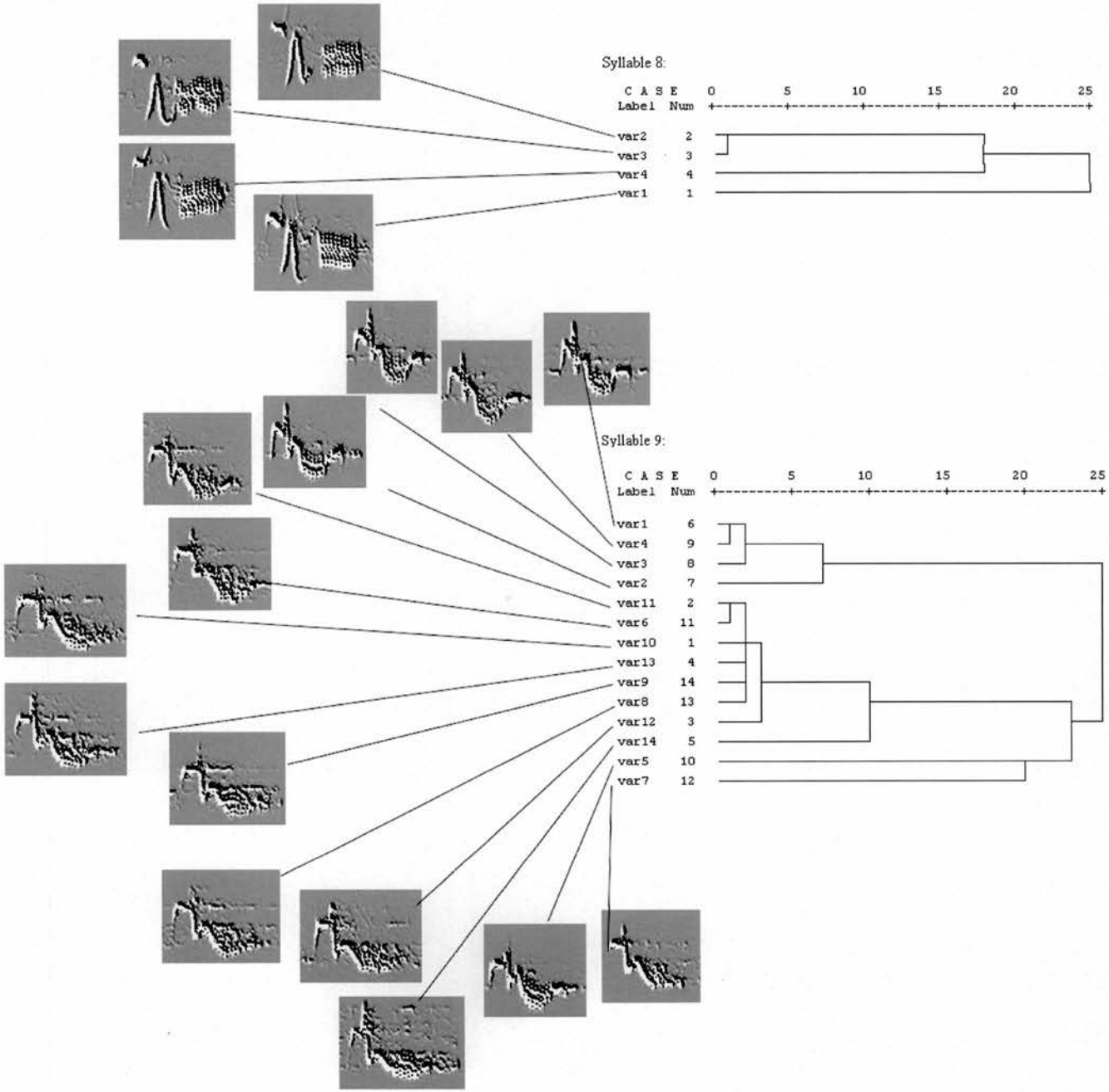


Syllable 8:

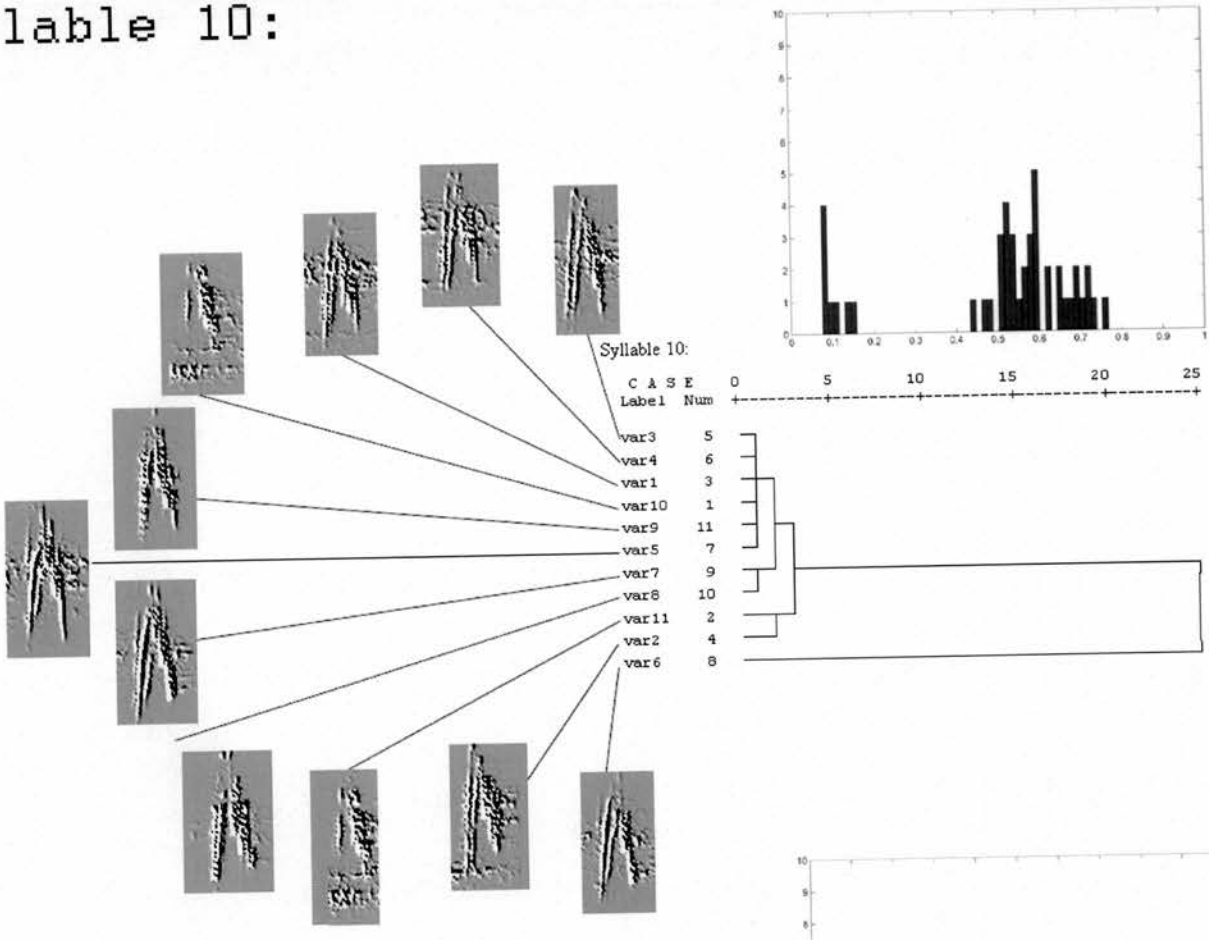


Syllable 9:

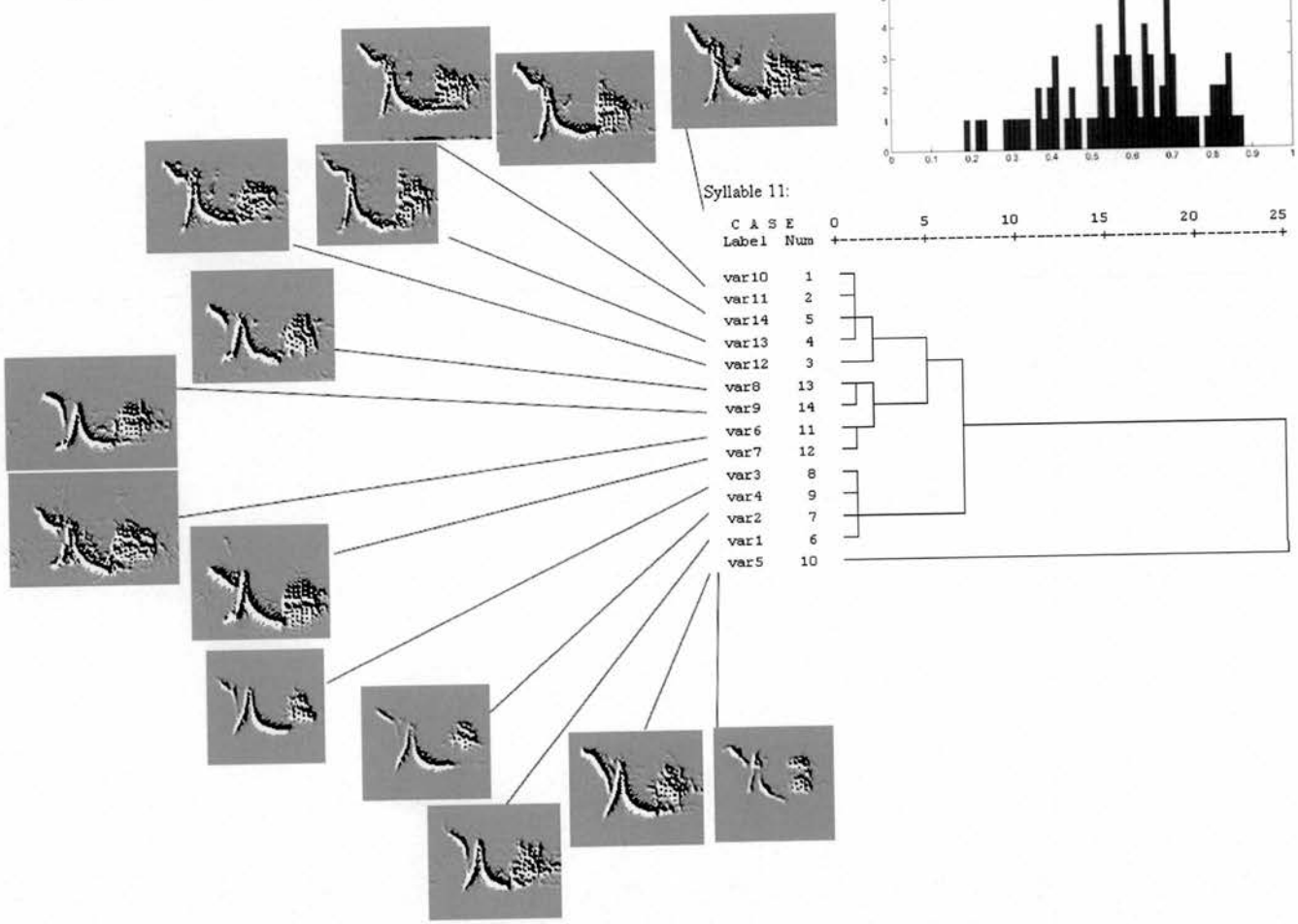




Syllable 10:



Syllable 11:



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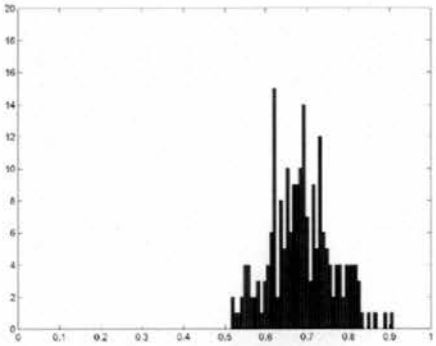

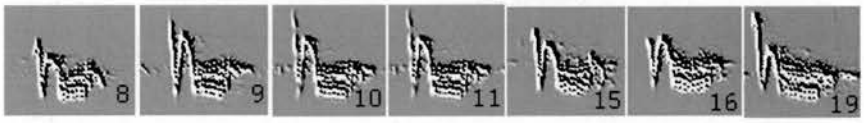
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11
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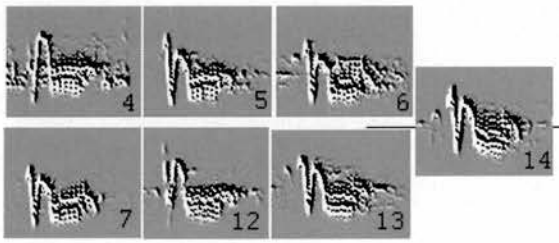
16
19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14
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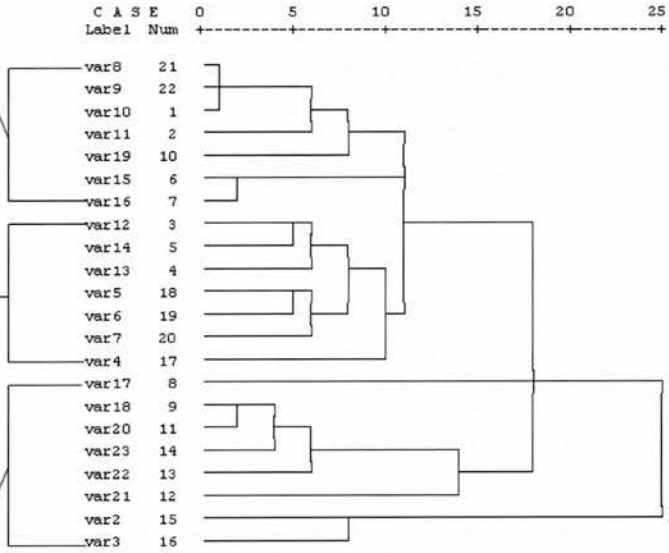
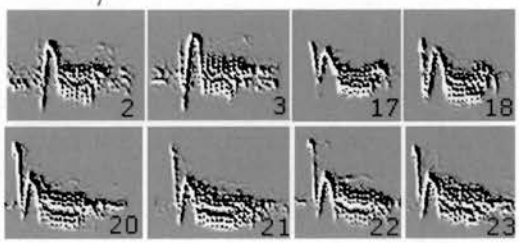
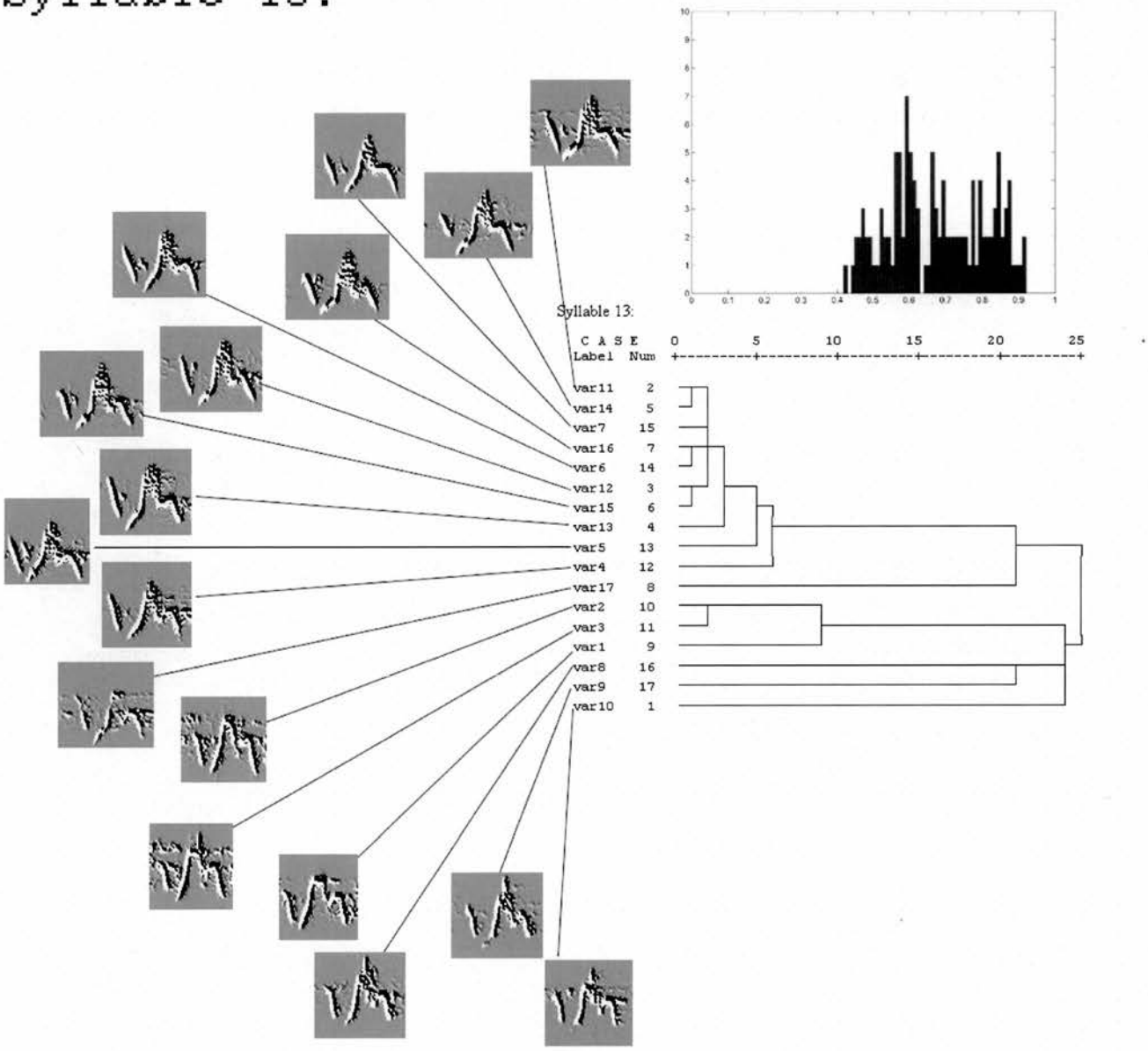
12
13

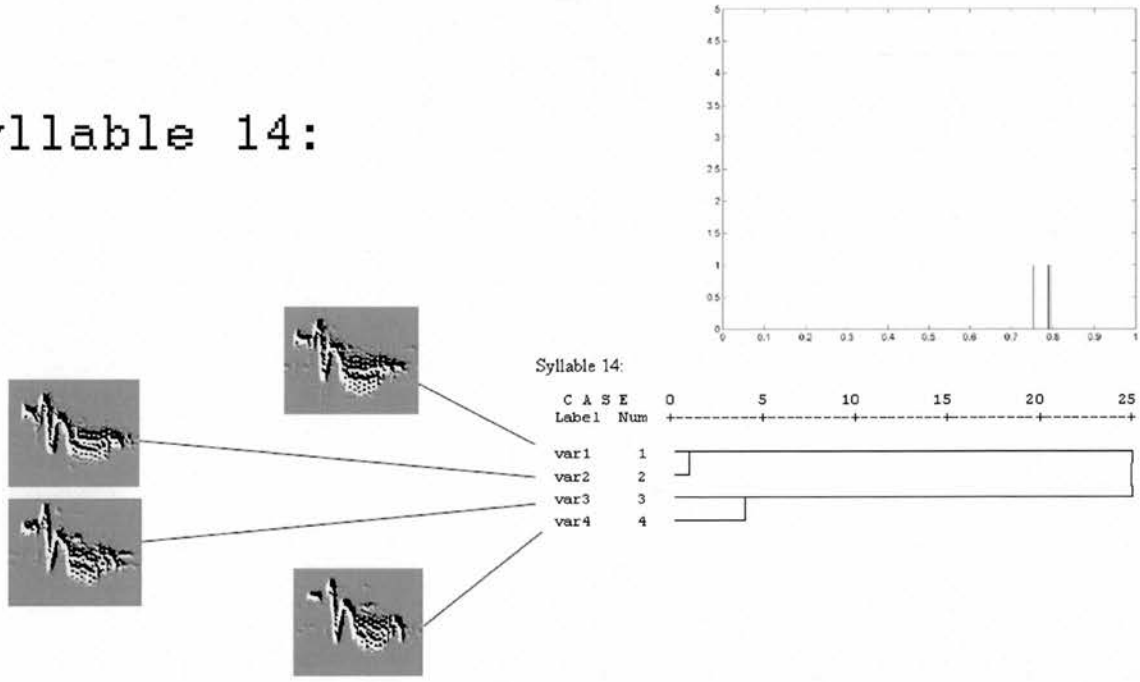

Syllable 12:
C A S E
Label Num
0 5 10 15 20 25
var8 21
var9 22
var10 1
var11 2
var19 10
var15 6
var16 7
var12 3
var14 5
var13 4
var5 18
var6 19
var7 20
var4 17
var17 8
var18 9
var20 11
var23 14
var22 13
var21 12
var2 15
var3 16


2
3
17
18
20
21
22
23

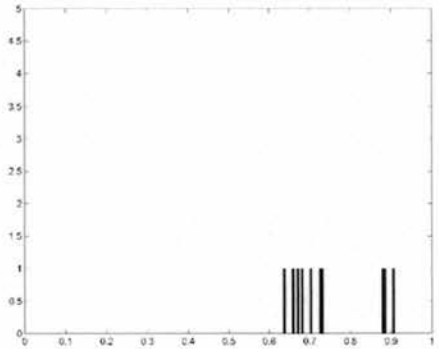
Syllable 13:

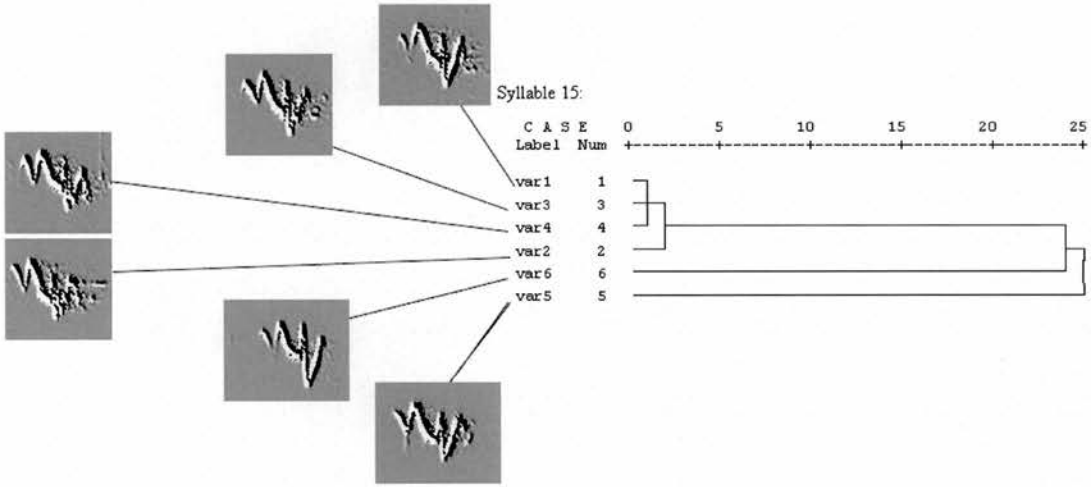


Syllable 14:

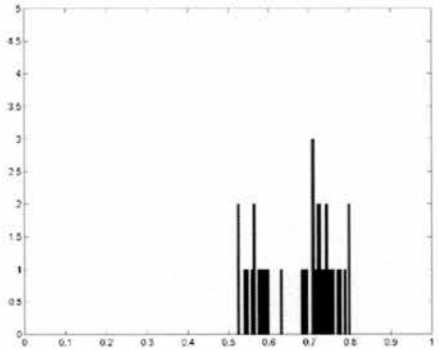


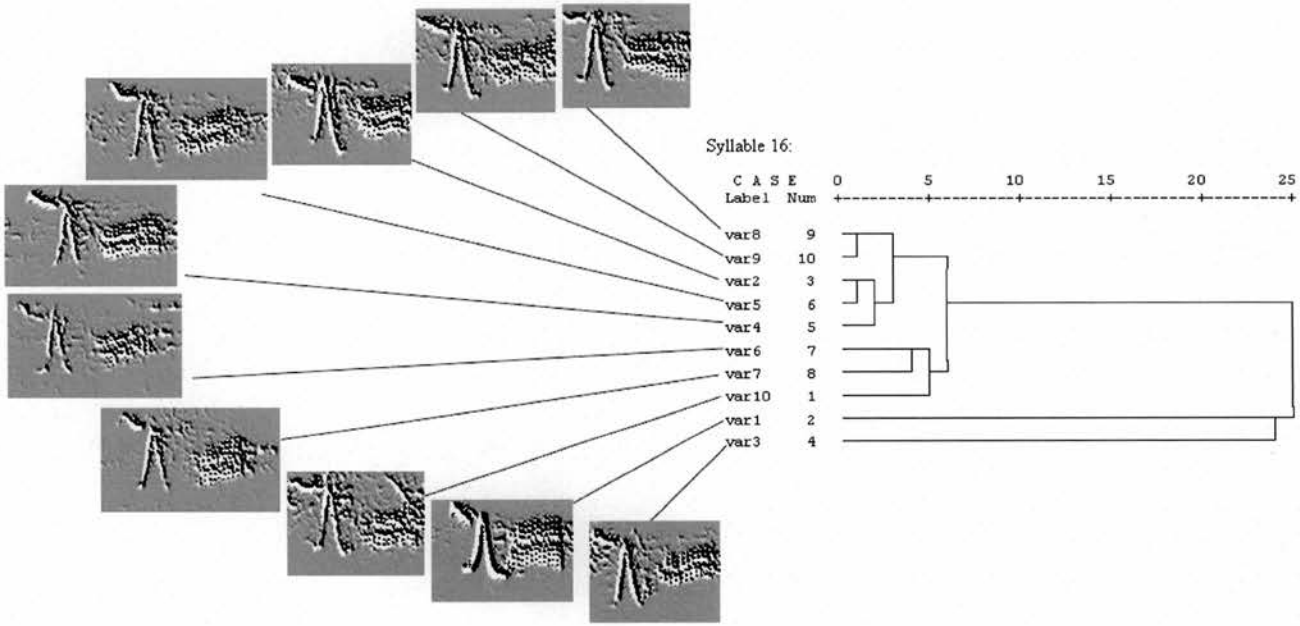
Syllable 15:



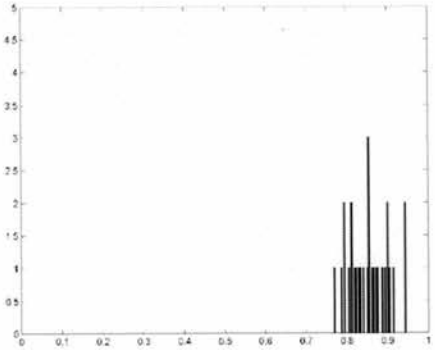


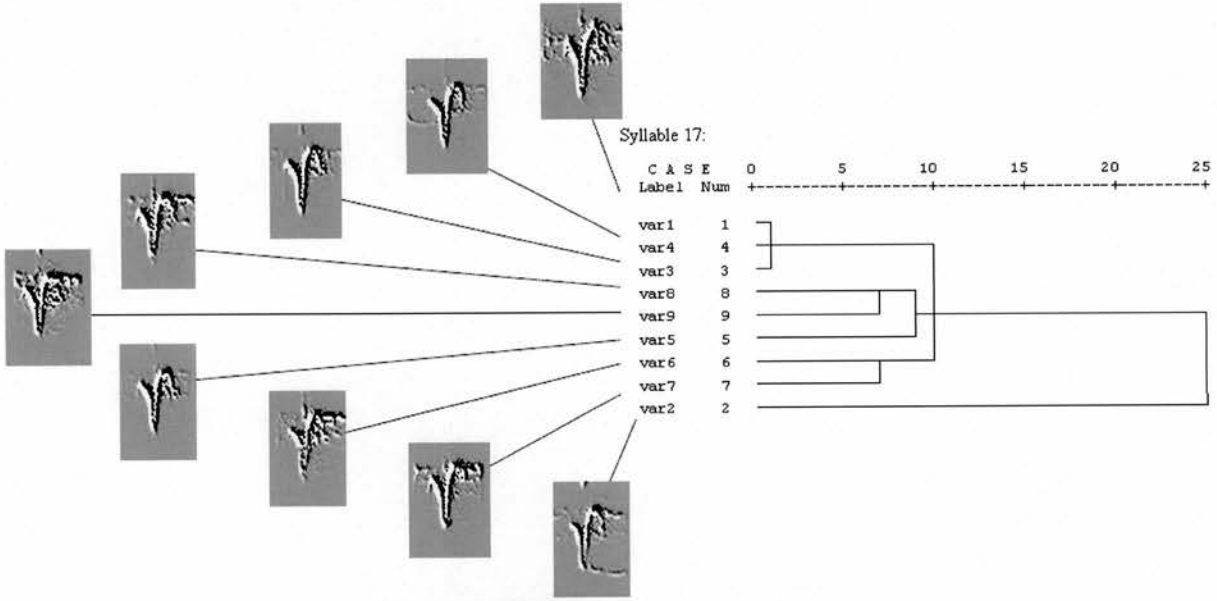
Syllable 16:





Syllable 17:





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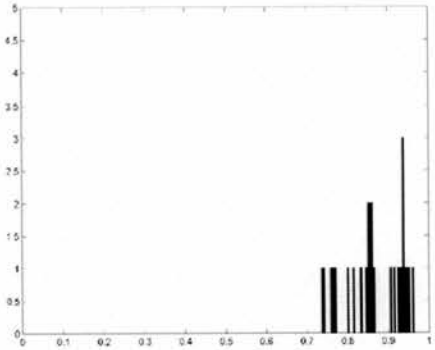

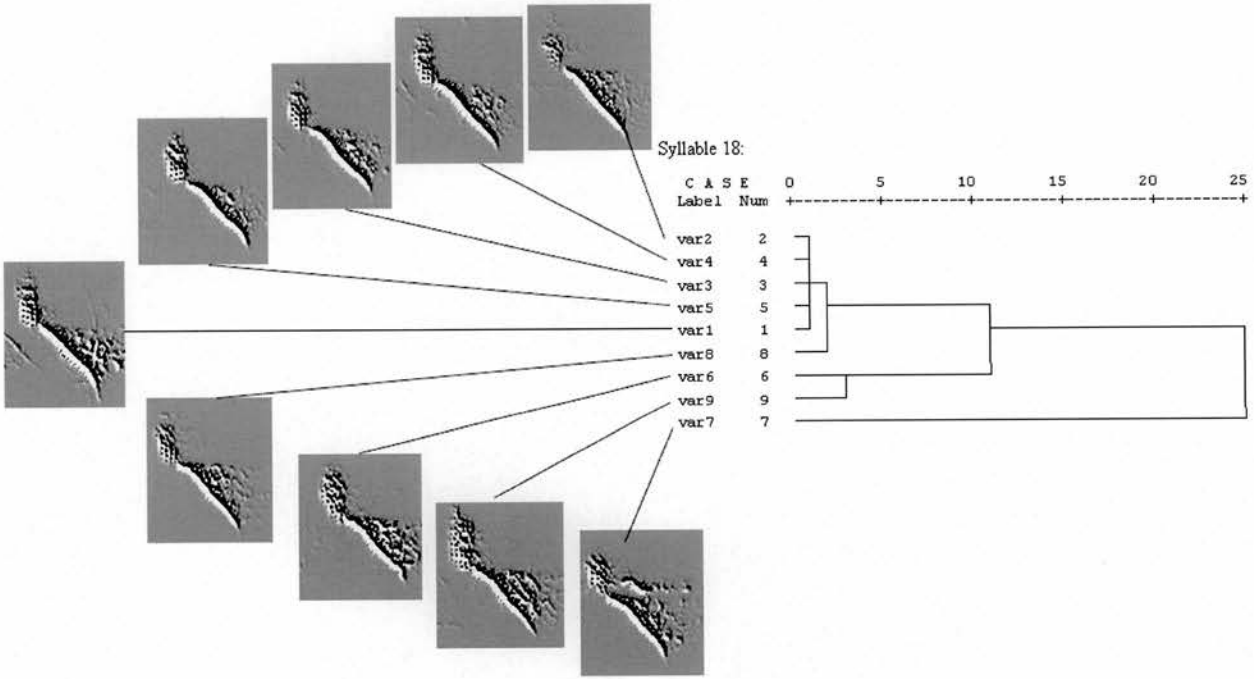

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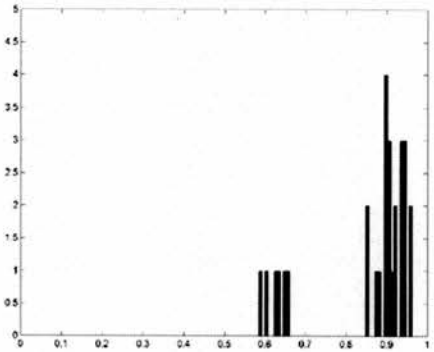
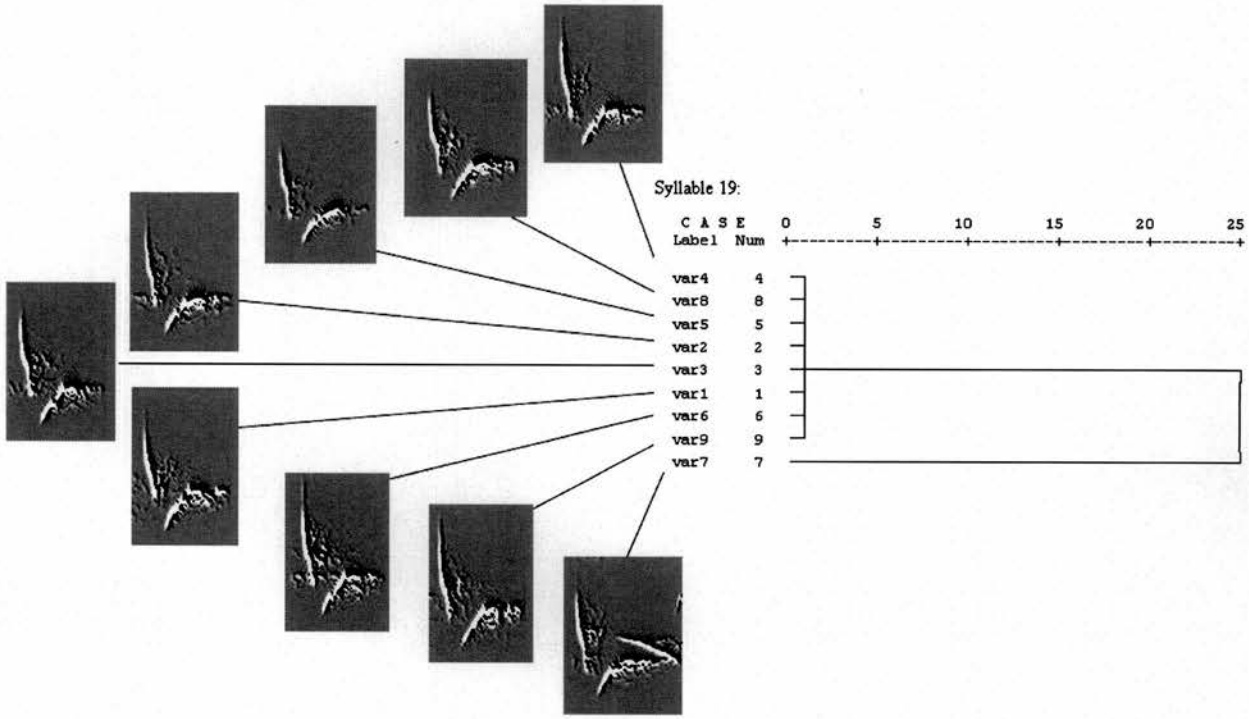
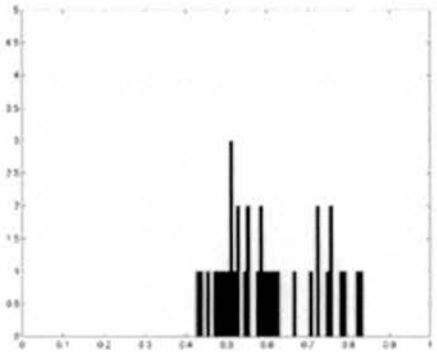


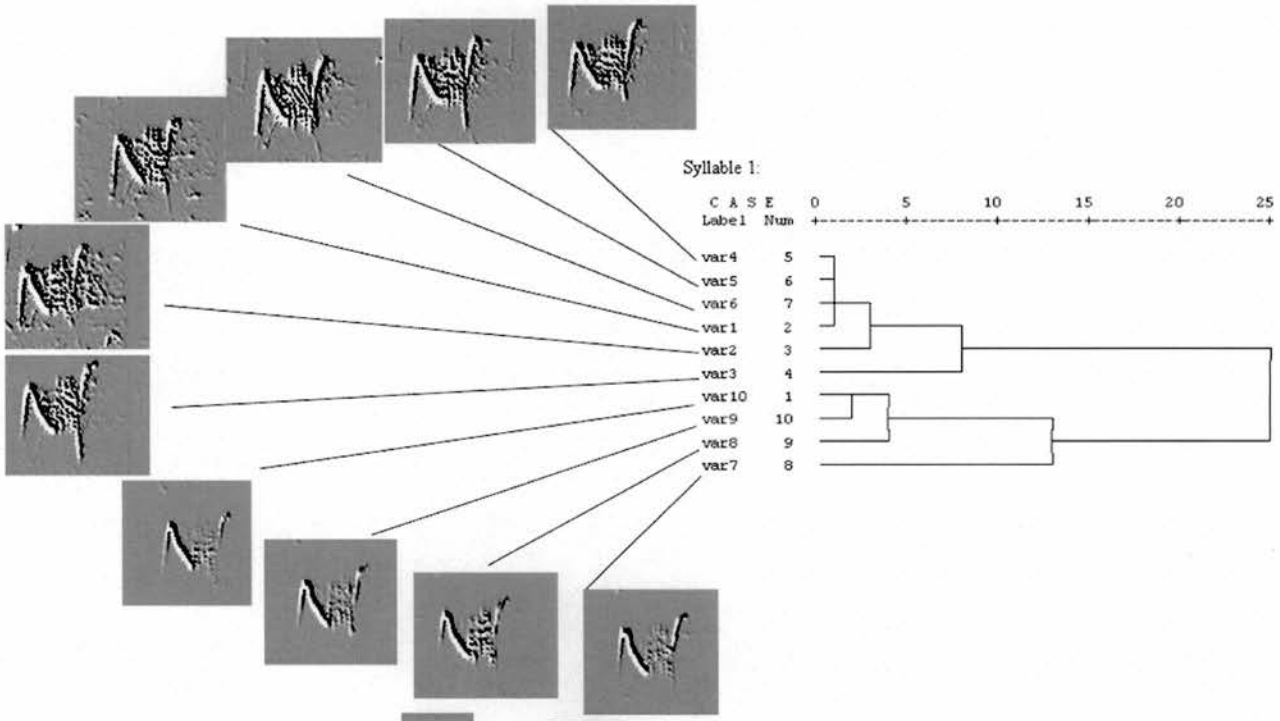

Syllable 19:
C A S E
Label Num
0 5 10 15 20 25
var4 4
var8 8
var5 5
var2 2
var3 3
var1 1
var6 6
var9 9
var7 7

APPENDIX F
Within-Syllable Comparisons For the 2002 Recordings

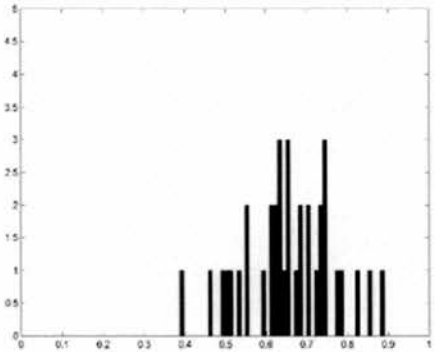
Figures include histograms of the correlation coefficients for each syllable, and dendrograms constructed from nearest-neighbor cluster analyses. Spectrograms for each syllable sample compared are also included with each dendrogram.

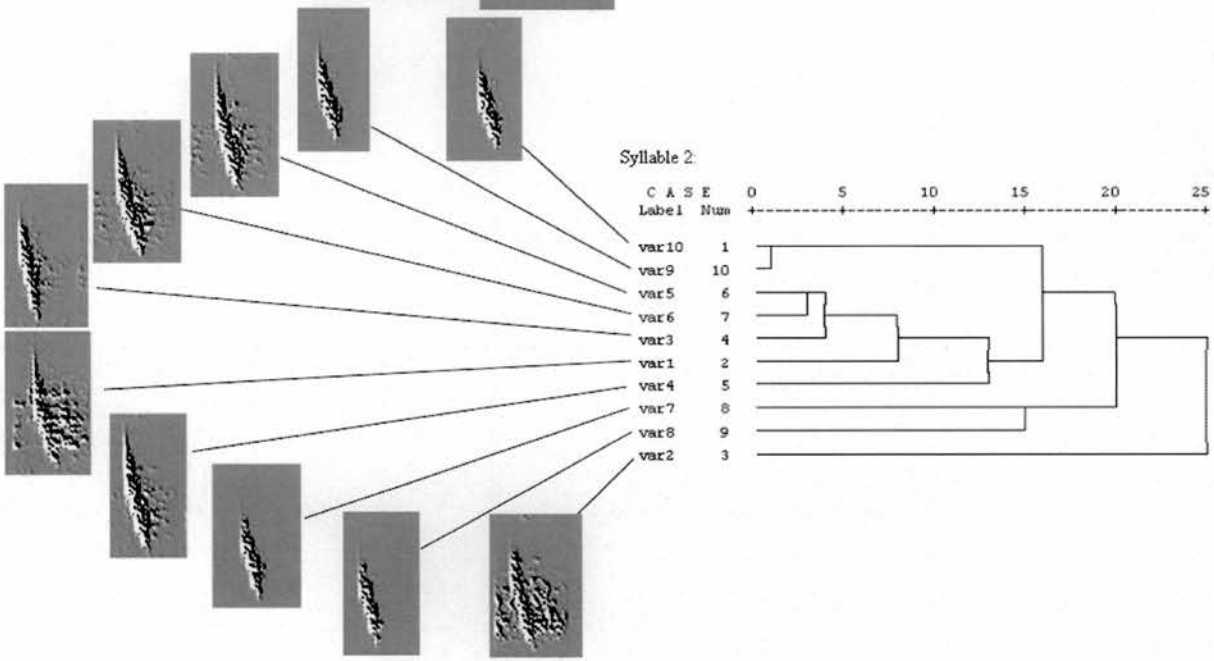
Syllable 1:



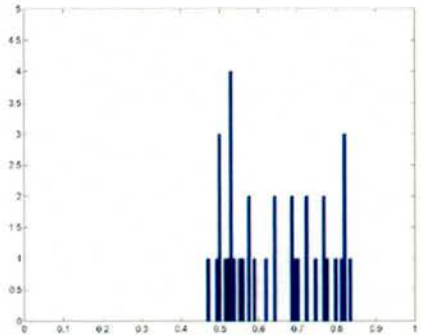


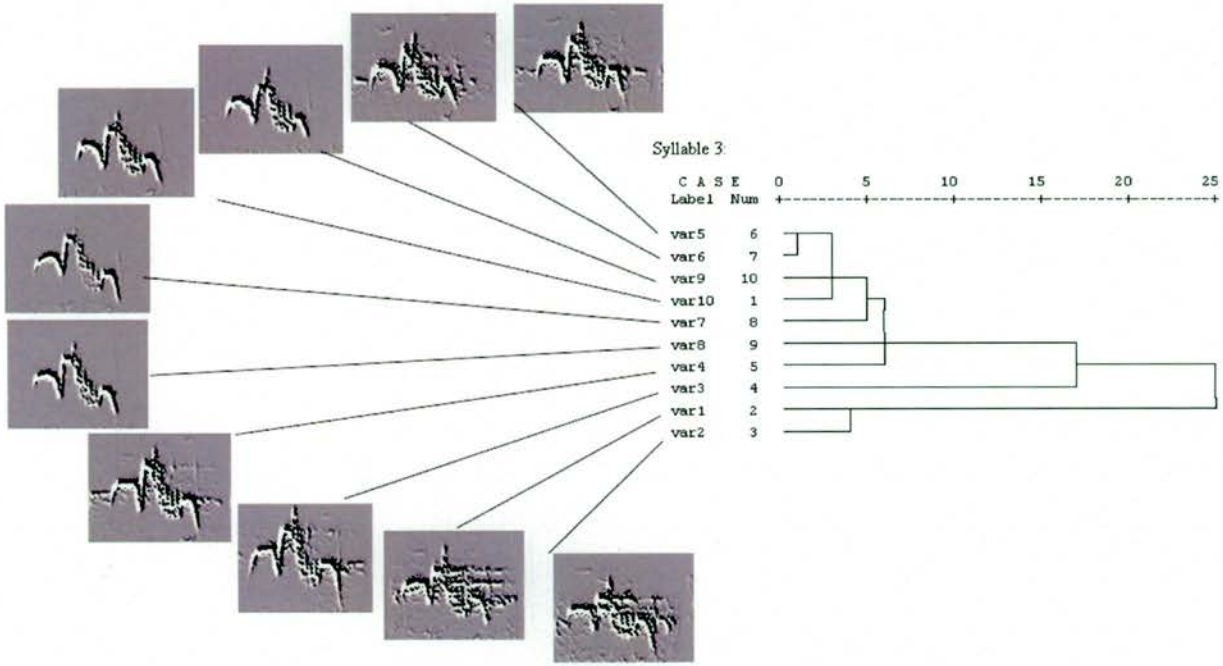
Syllable 2:



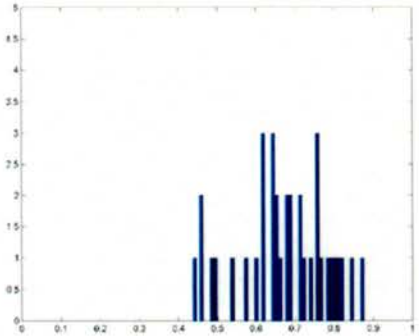


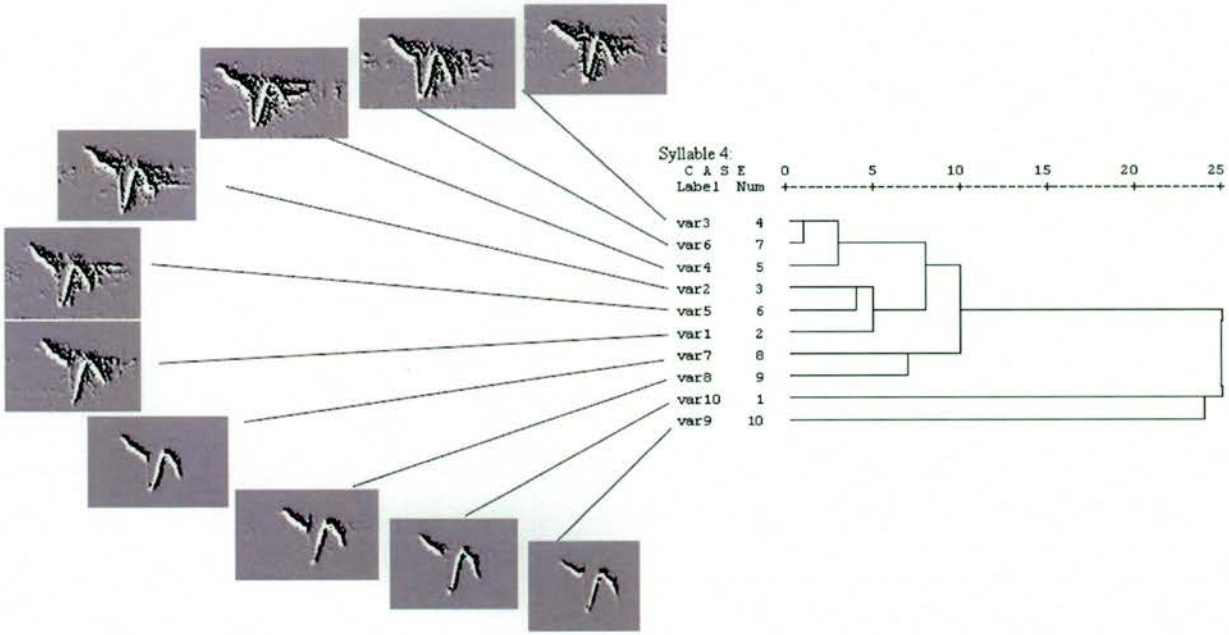
Syllable 3:



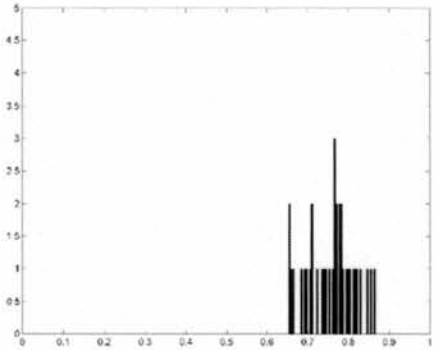


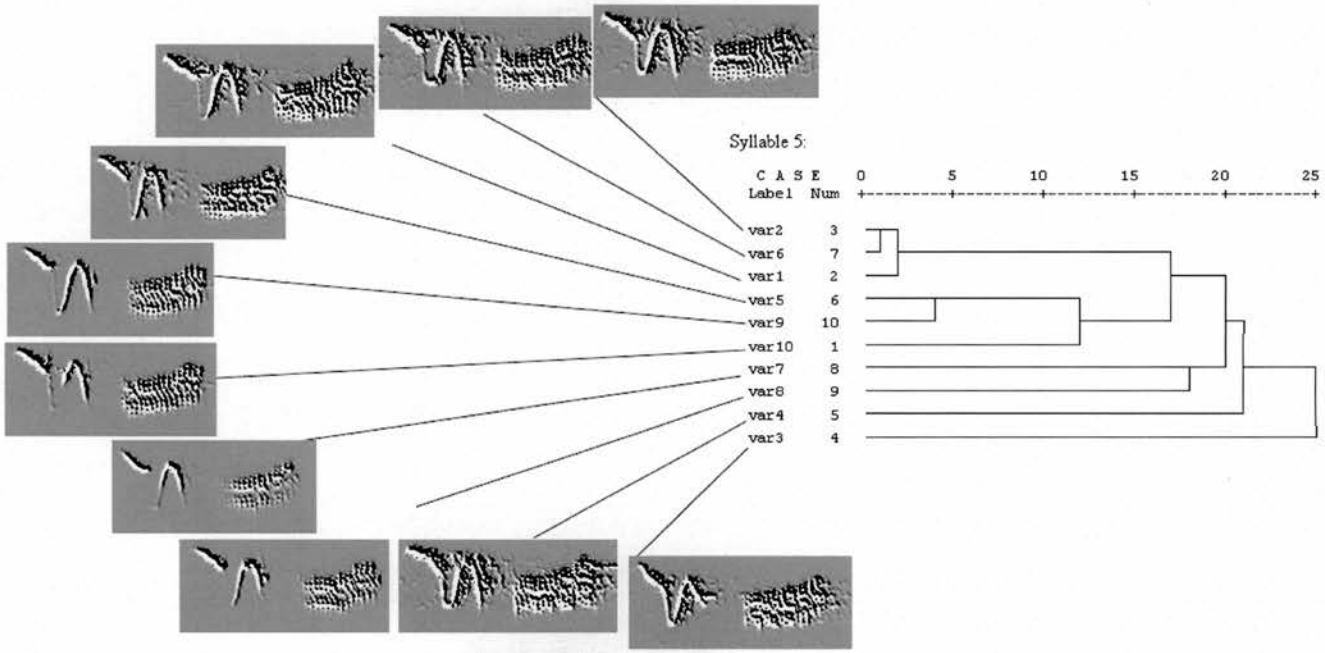
Syllable 4:



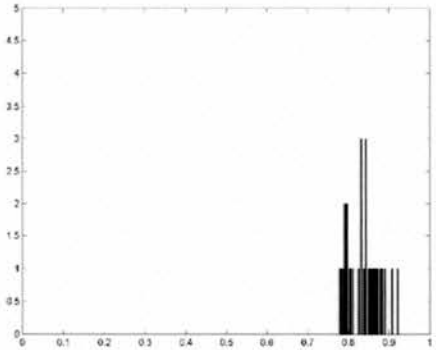


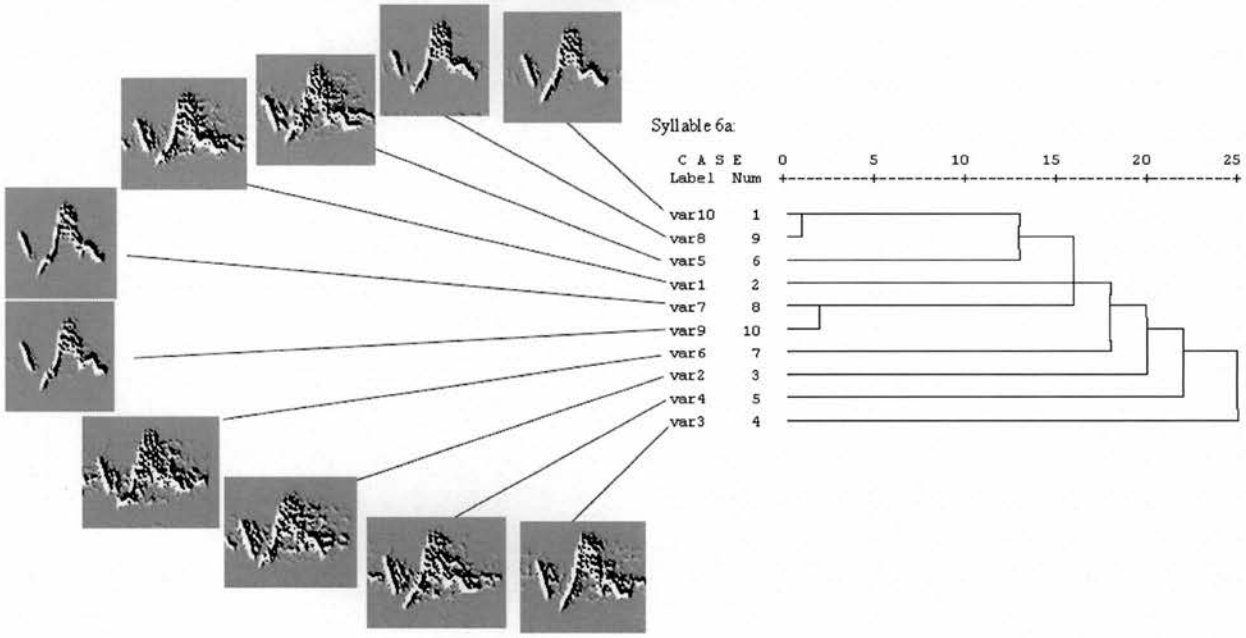
Syllable 5:



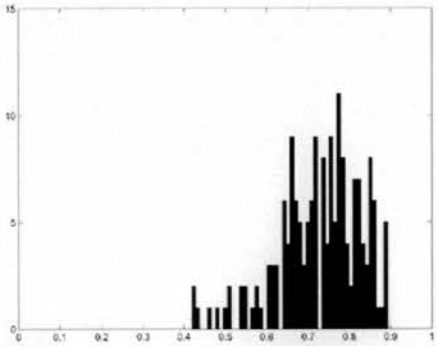


Syllable 6a:





Syllable 6b:


15
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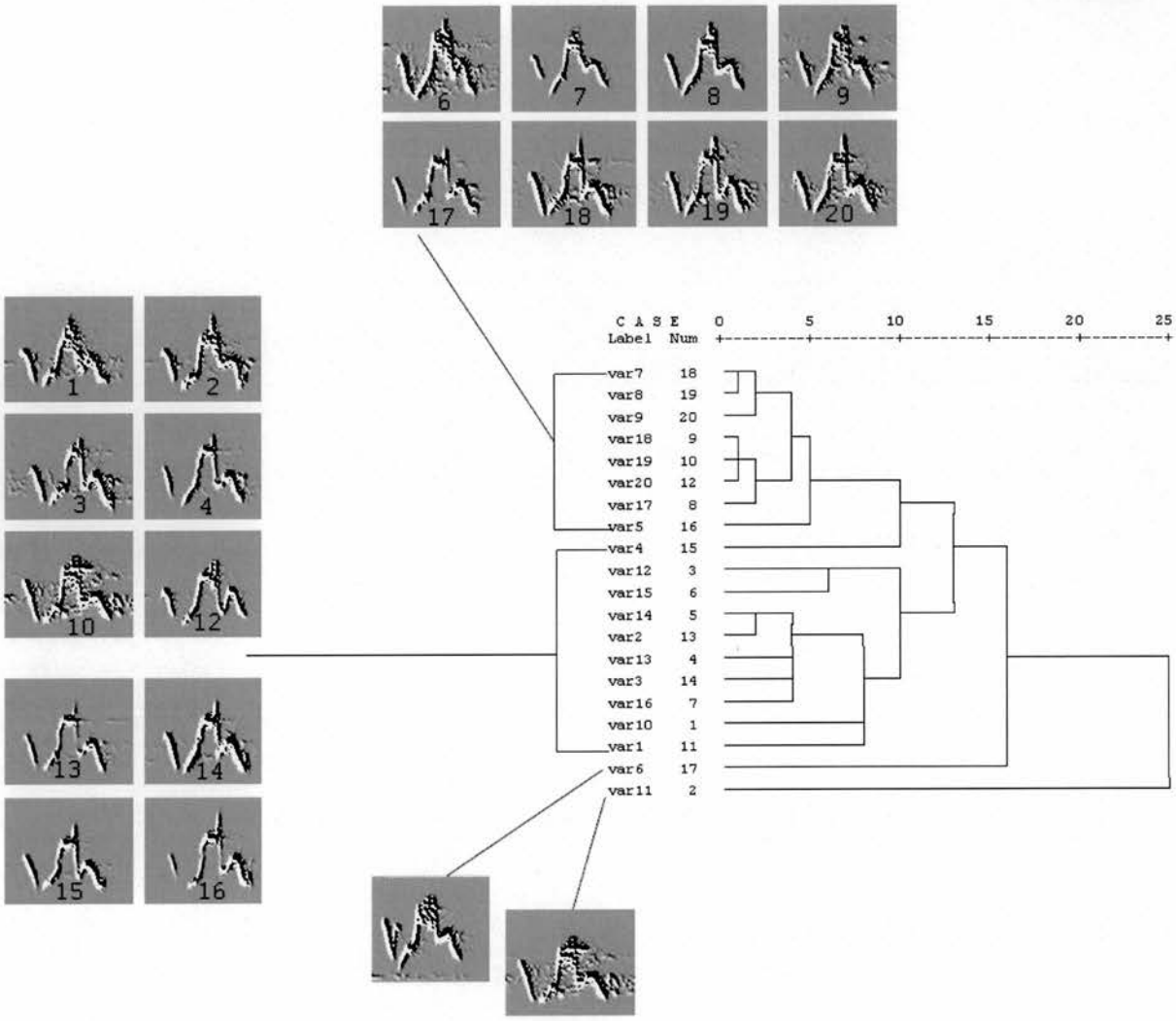
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1


6
7
8
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17
18
19
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1
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3
4
10
12
13
14
15
16
C A S E
Label Num
0
5
10
15
20
25
var7 18
var8 19
var9 20
var18 9
var19 10
var20 12
var17 8
var5 16
var4 15
var12 3
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var2 13
var13 4
var3 14
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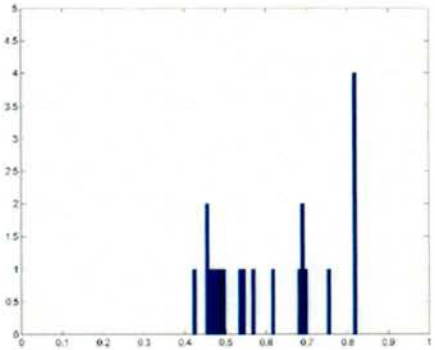
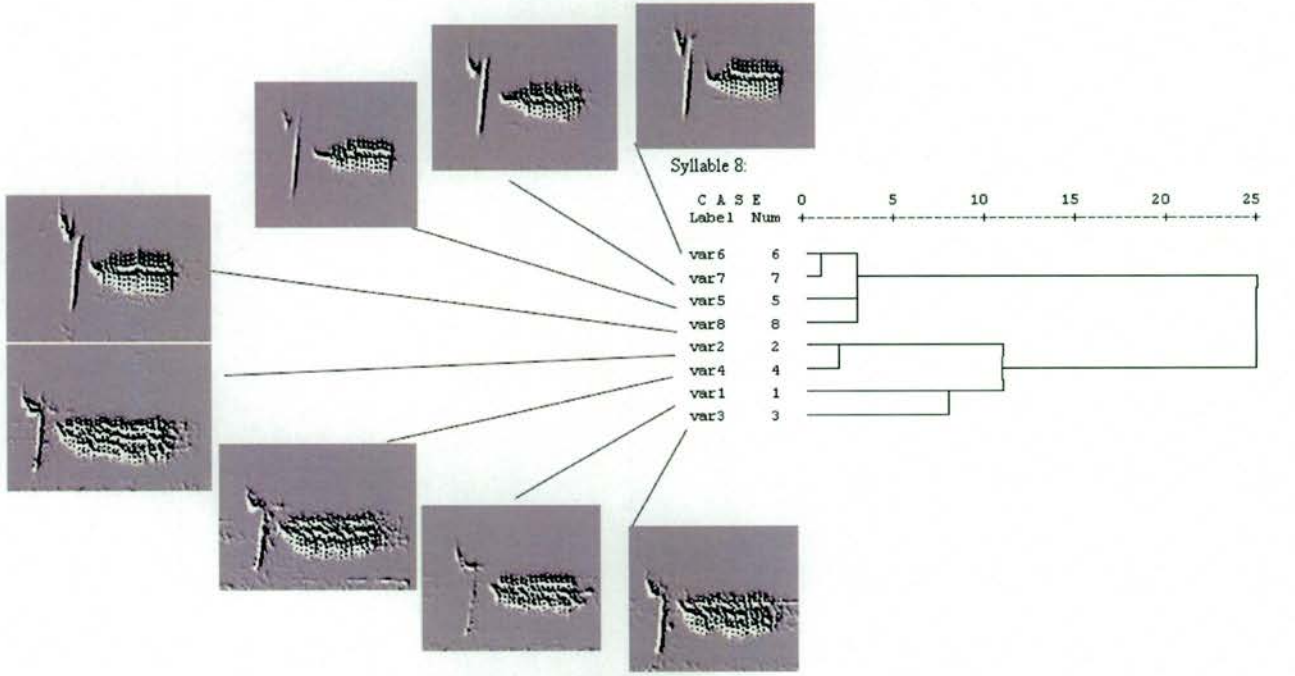
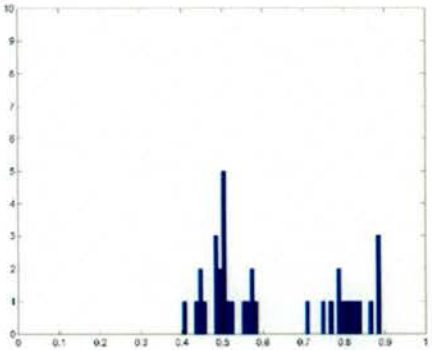
var10 1
var1 11
var6 17
var11 2

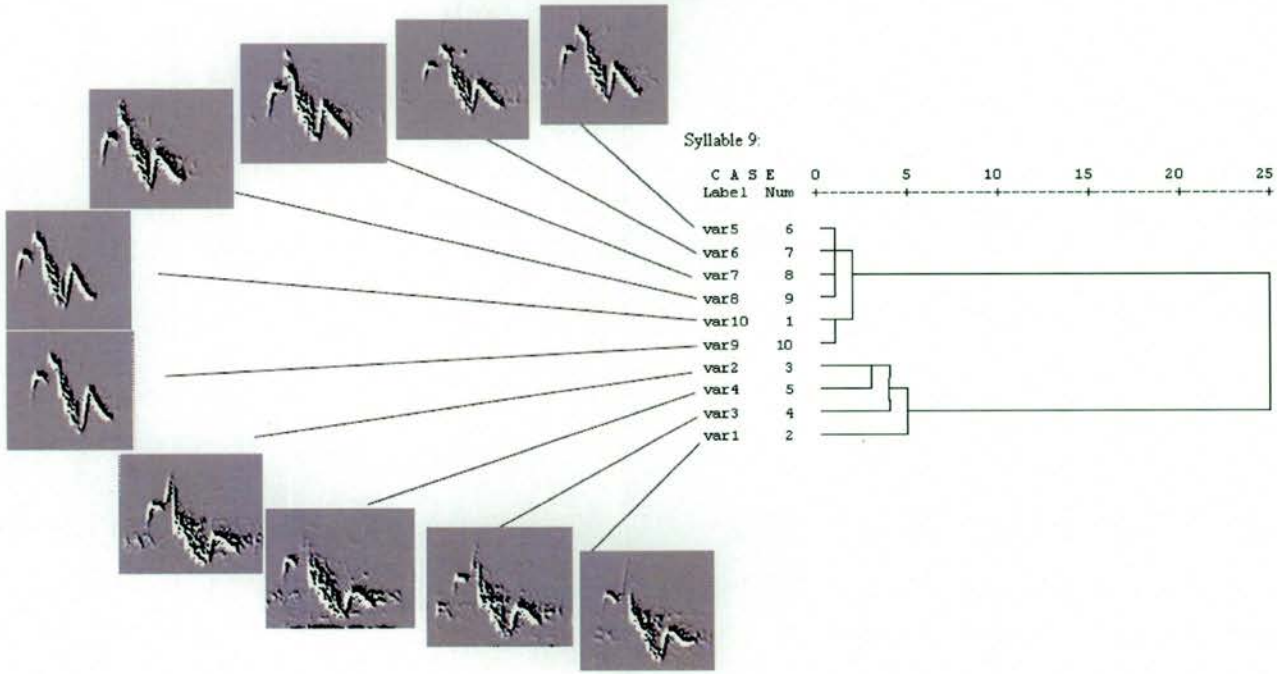
Syllable 8:



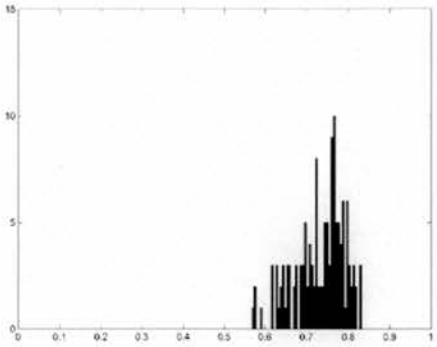


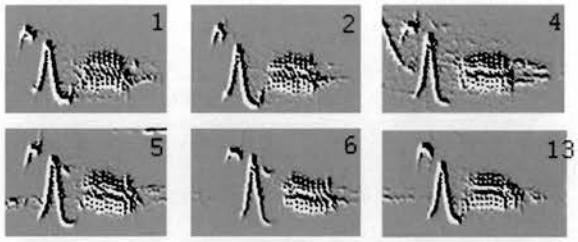
Syllable 9:

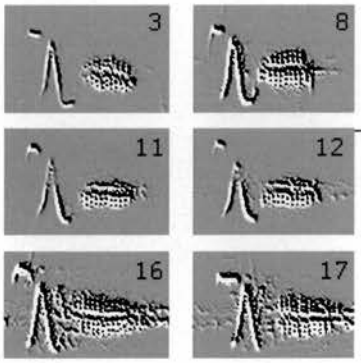


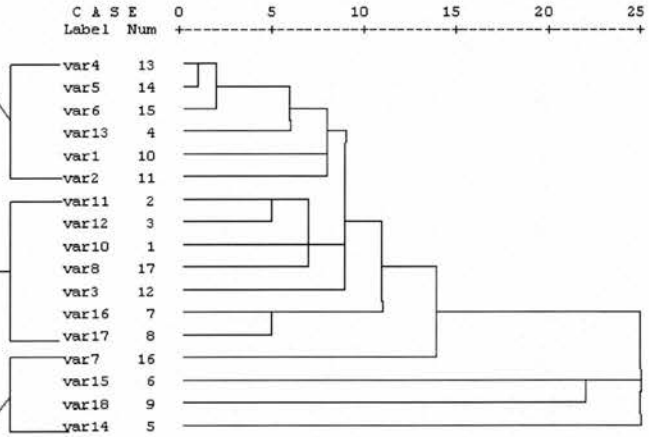


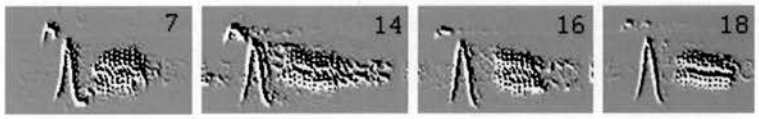
Syllable 10a:



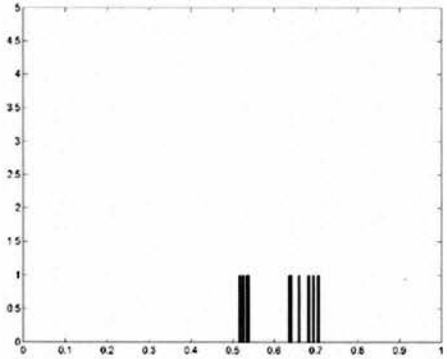


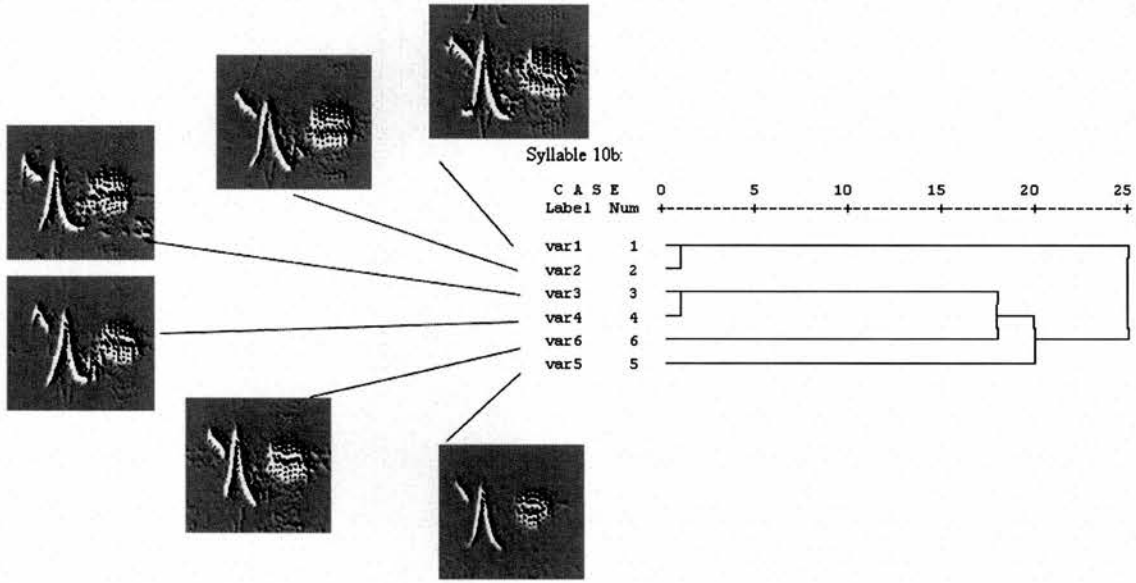






Syllable 10b:





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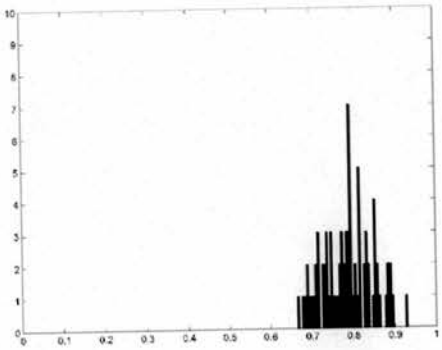

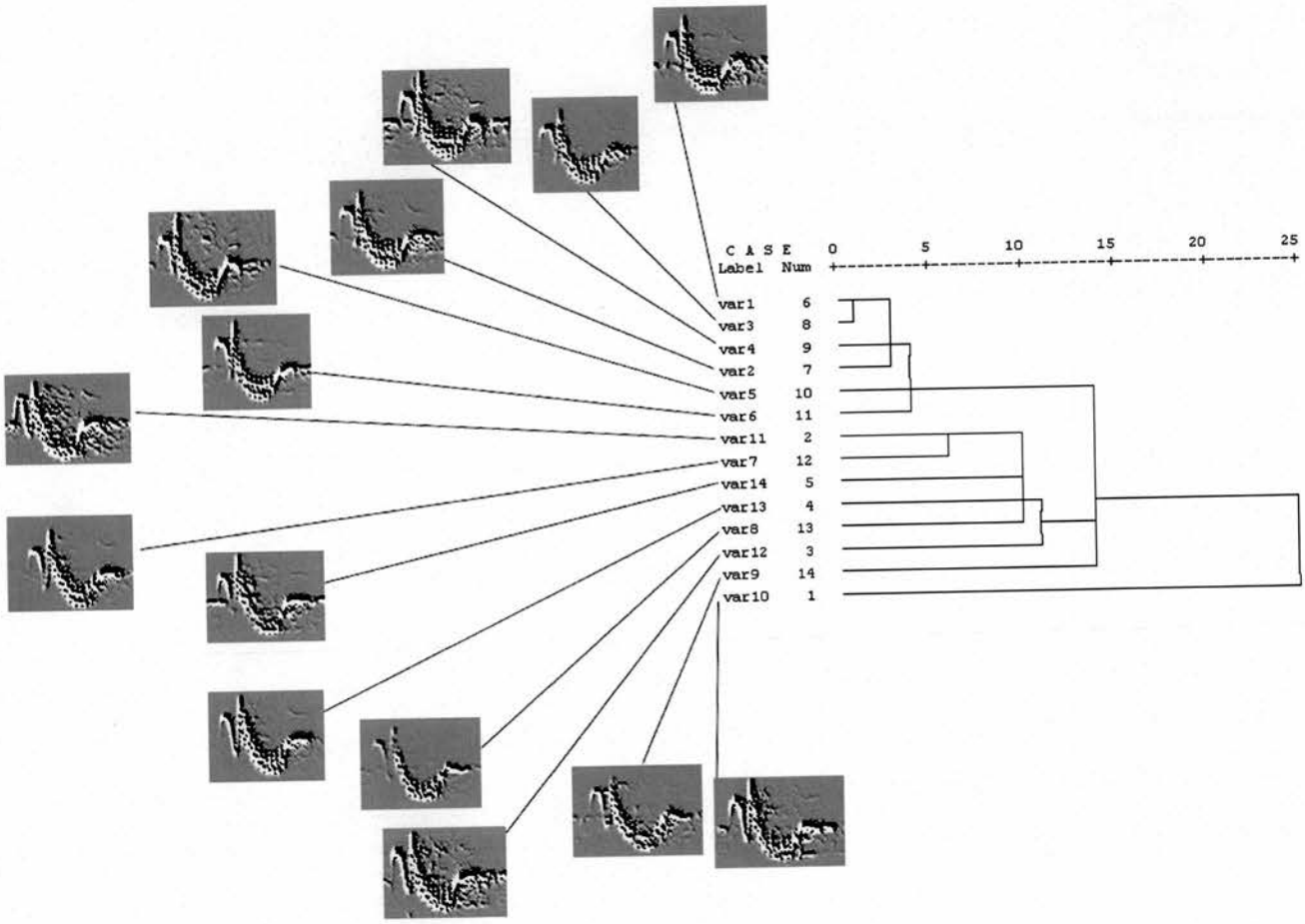

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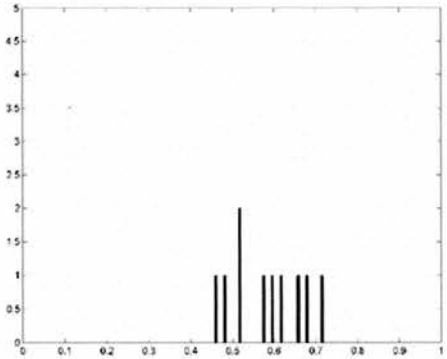

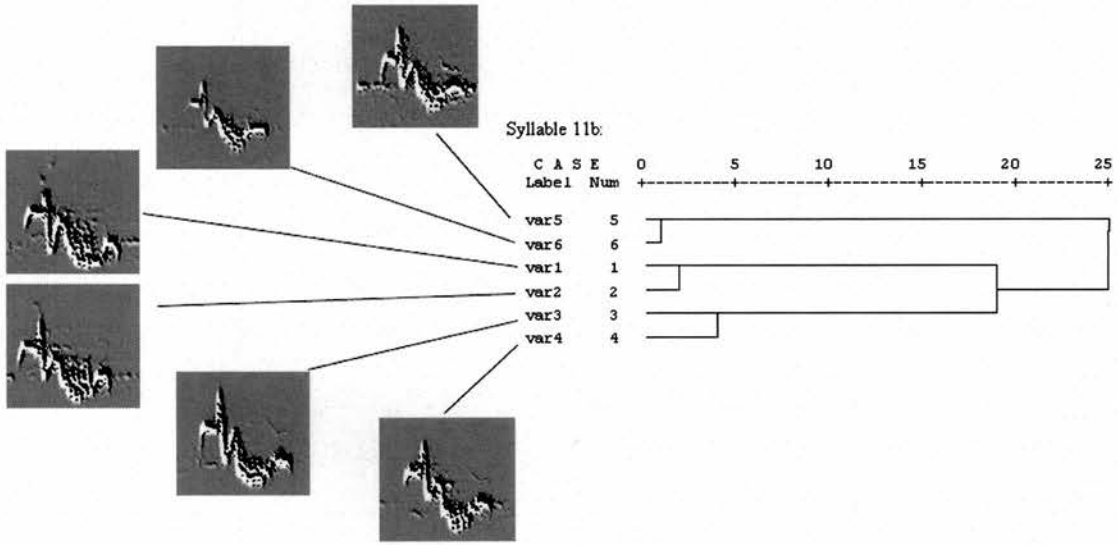

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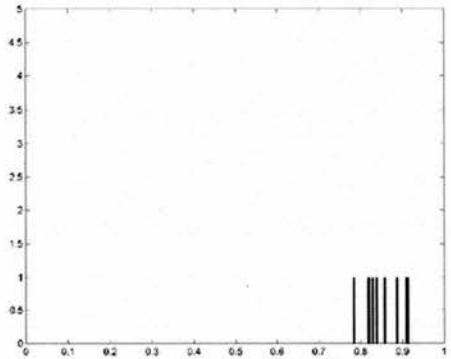

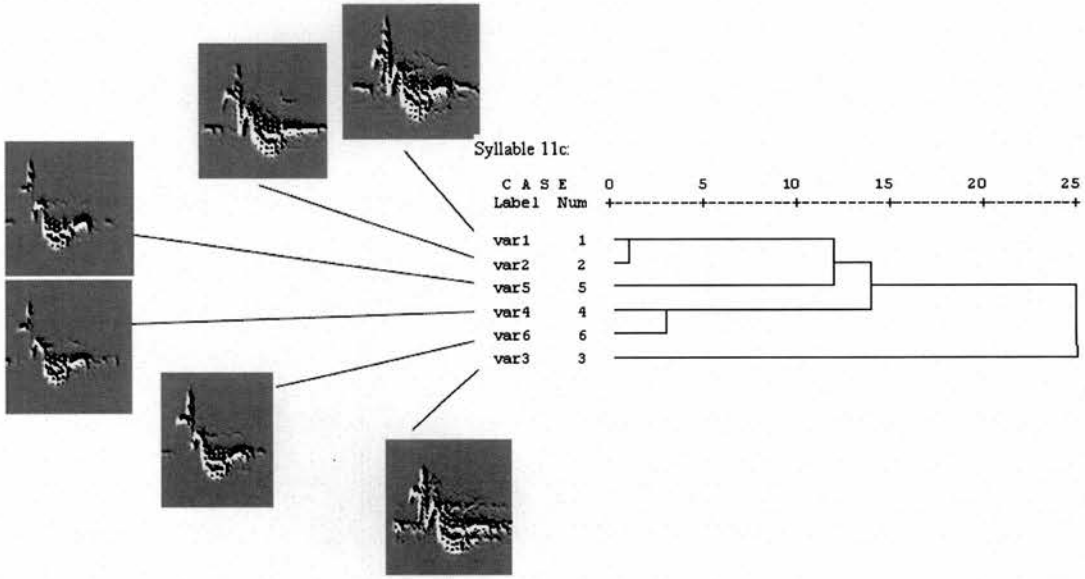

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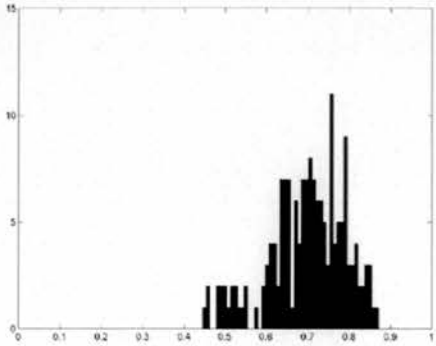
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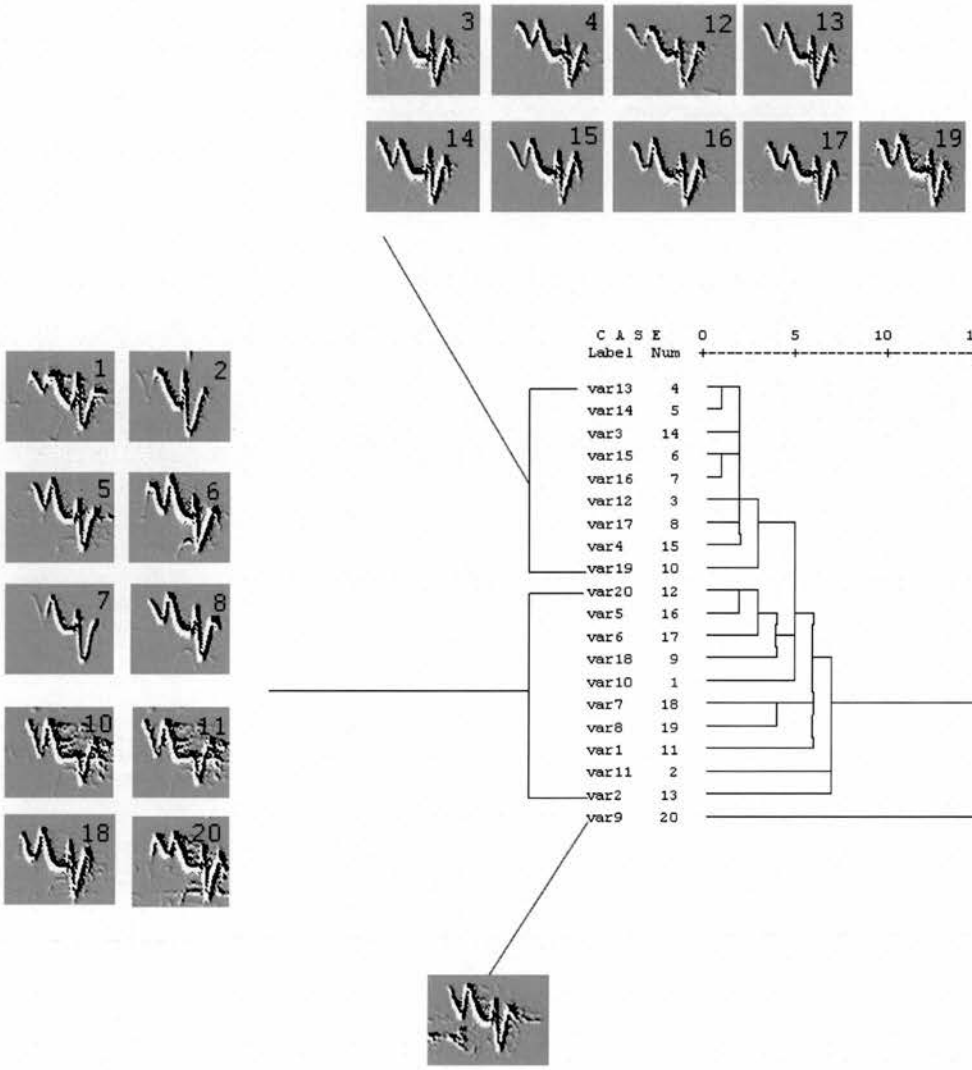
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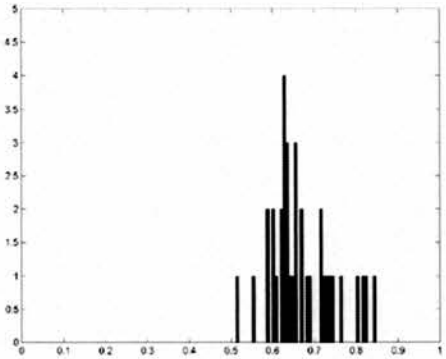

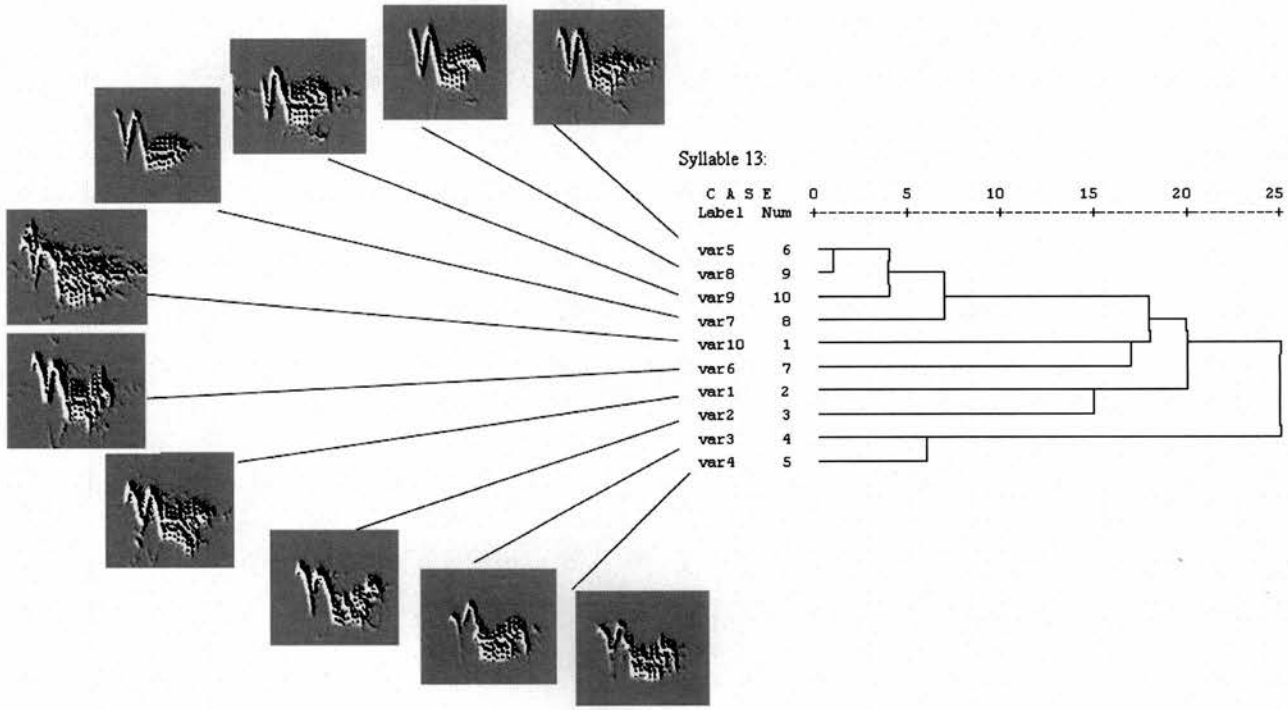
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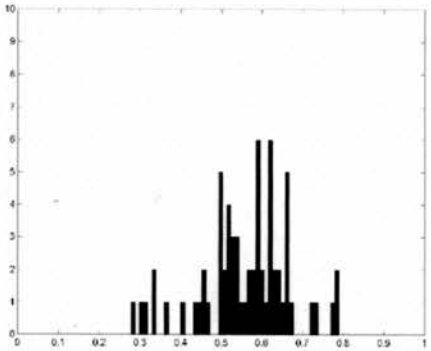

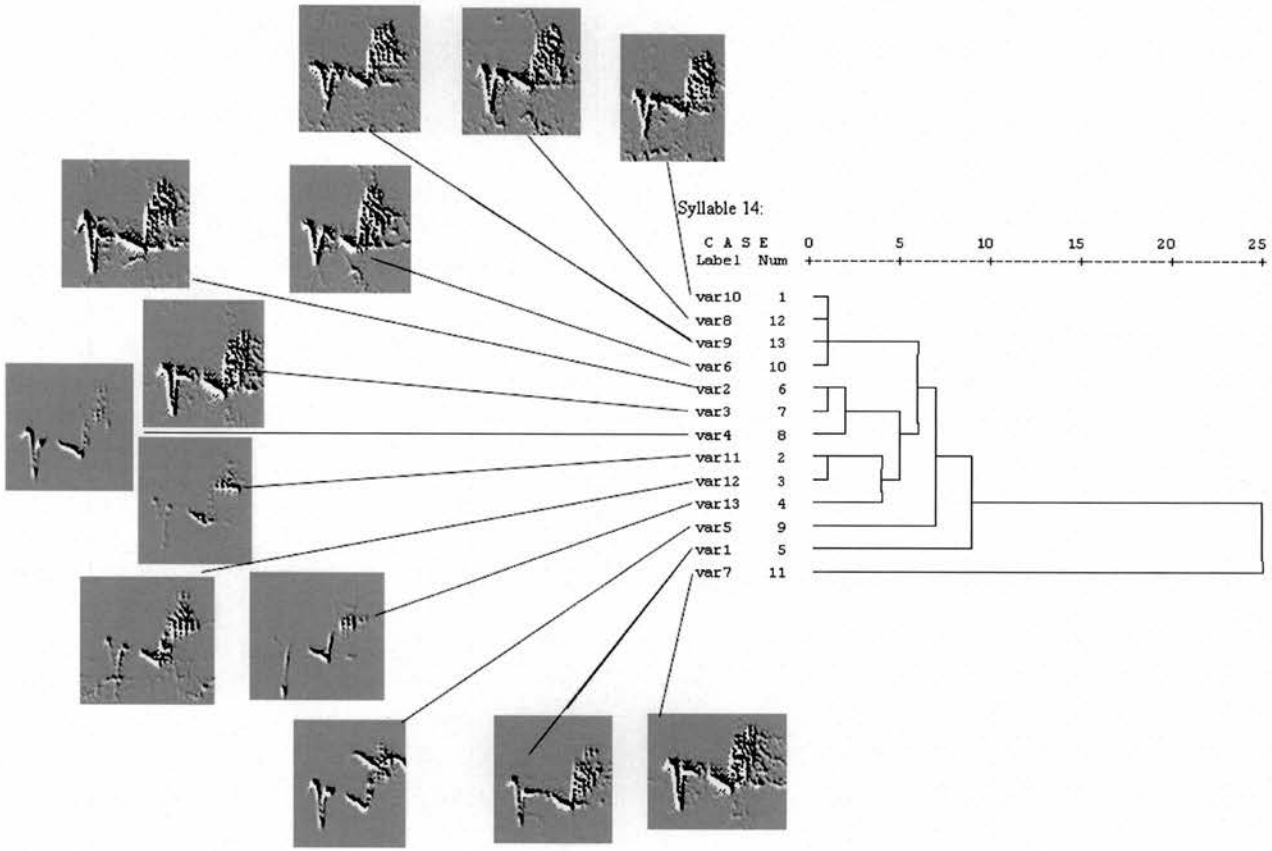

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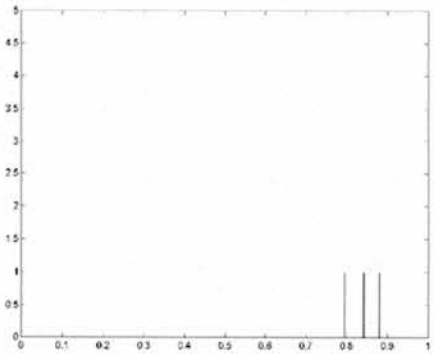

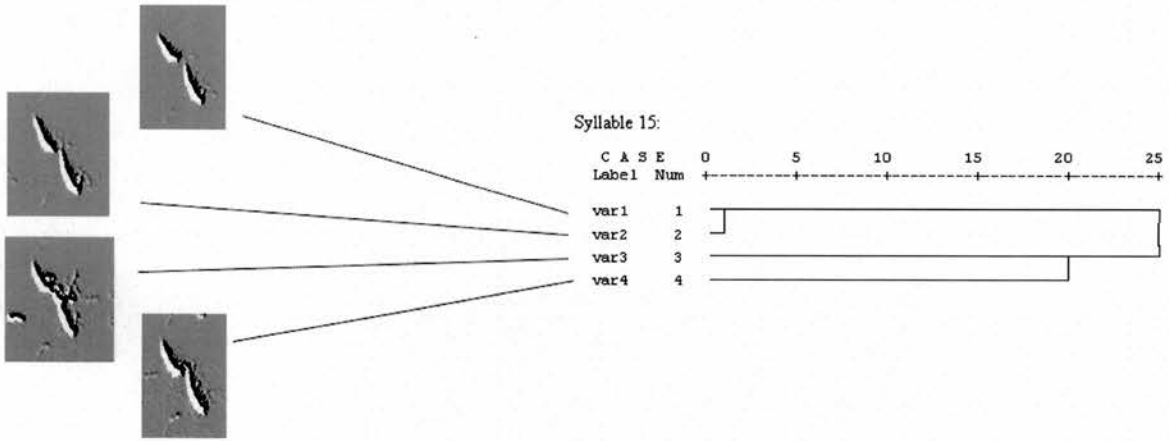

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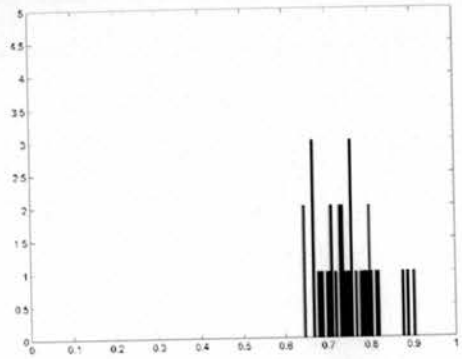

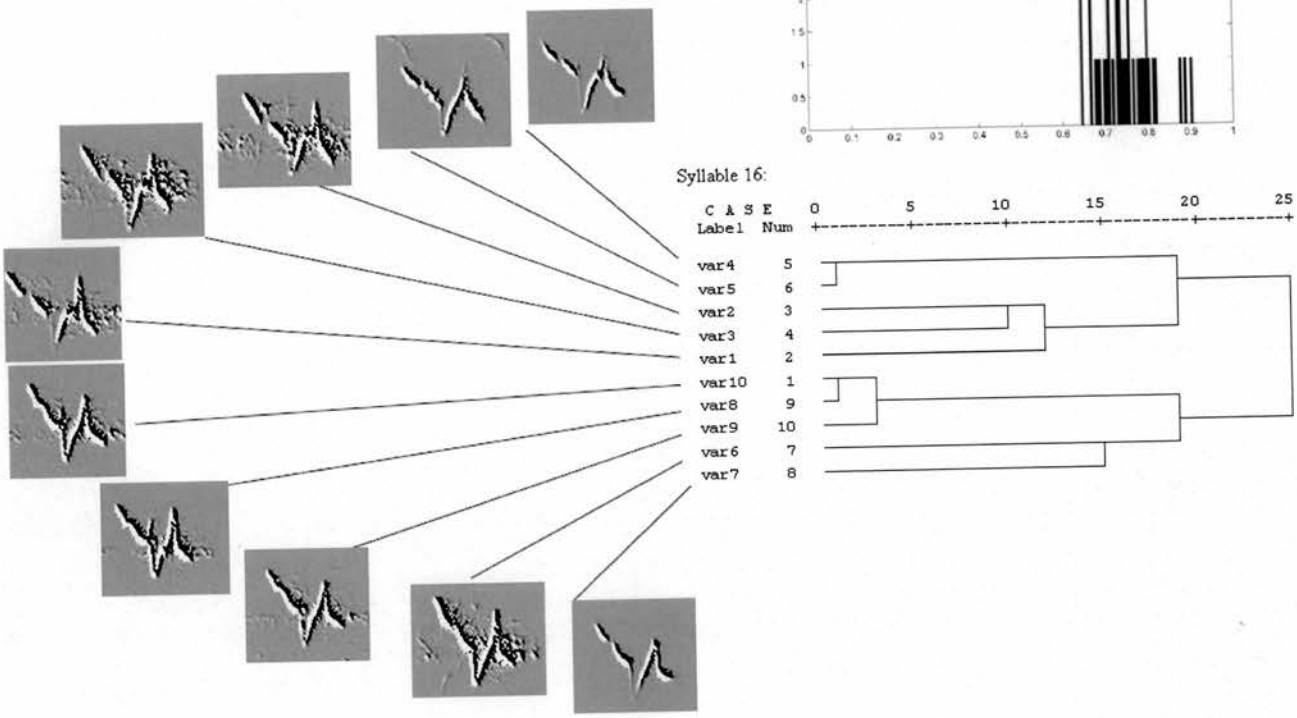

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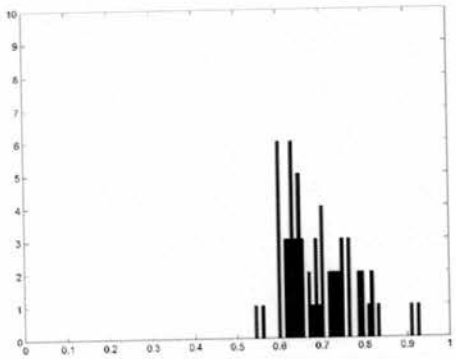

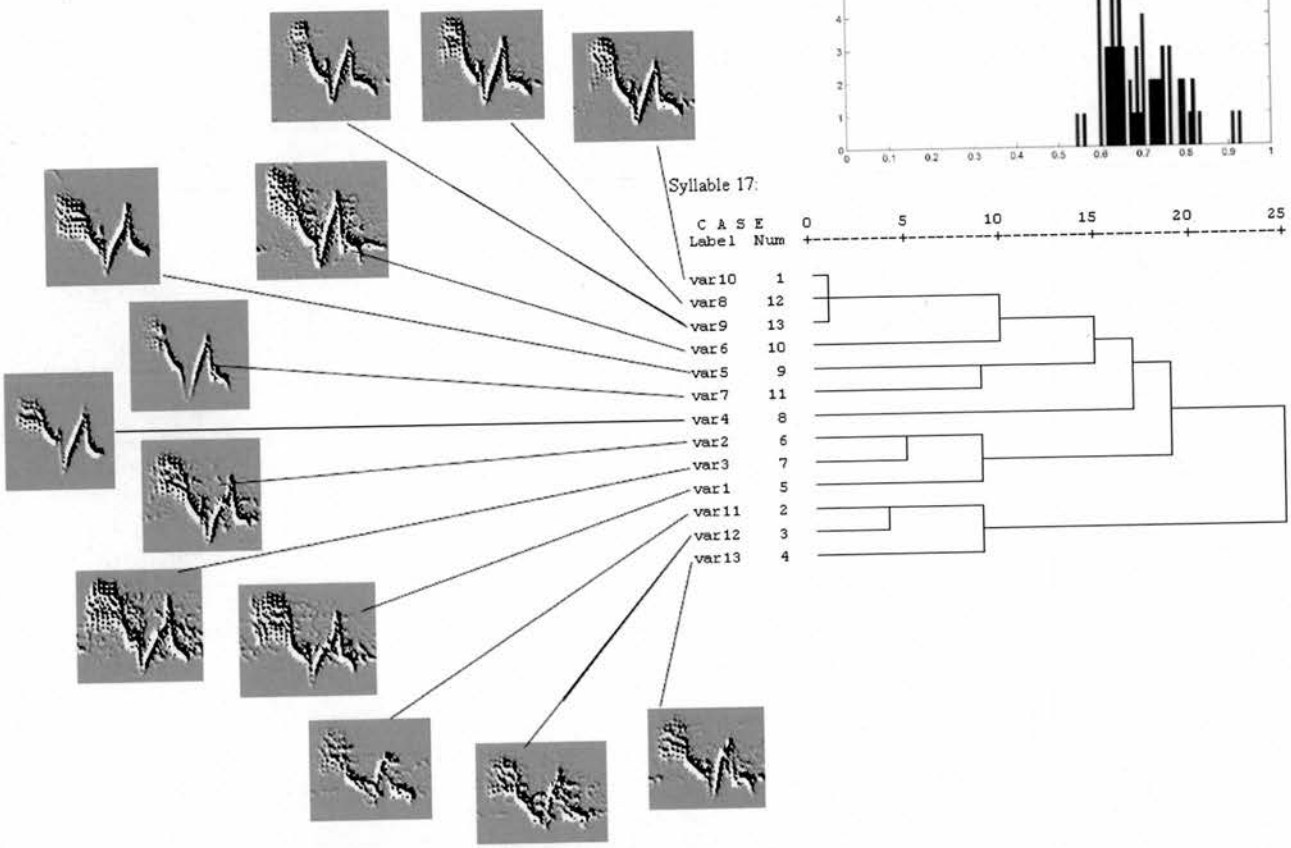

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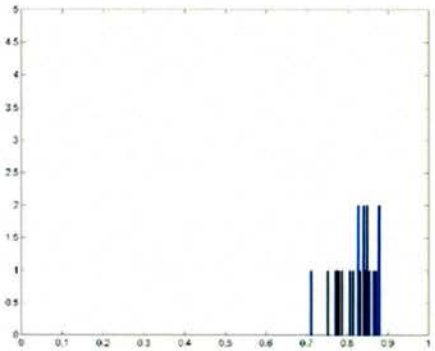

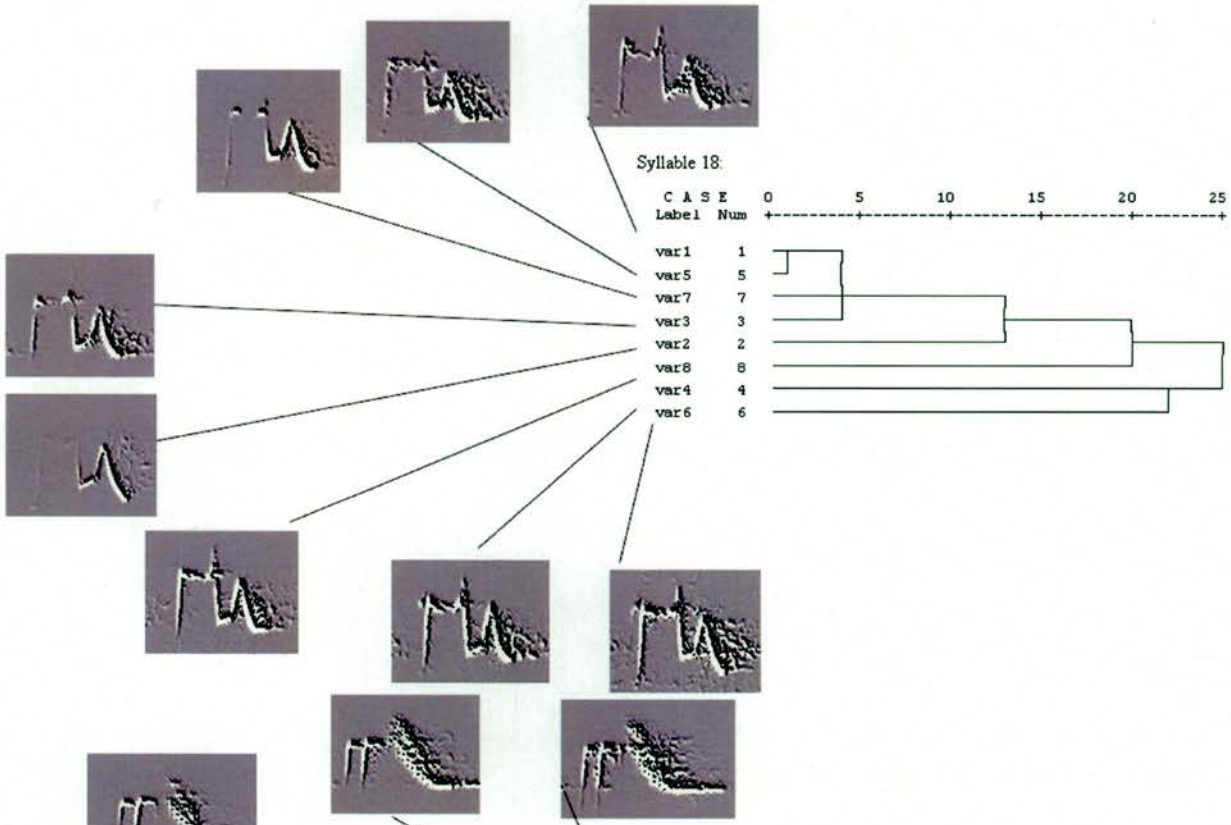

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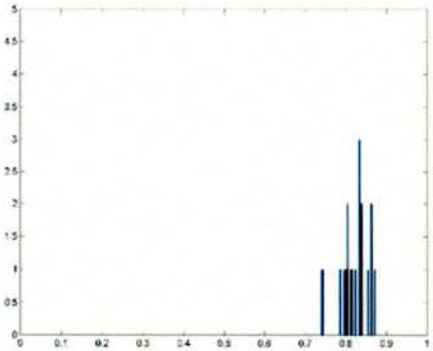

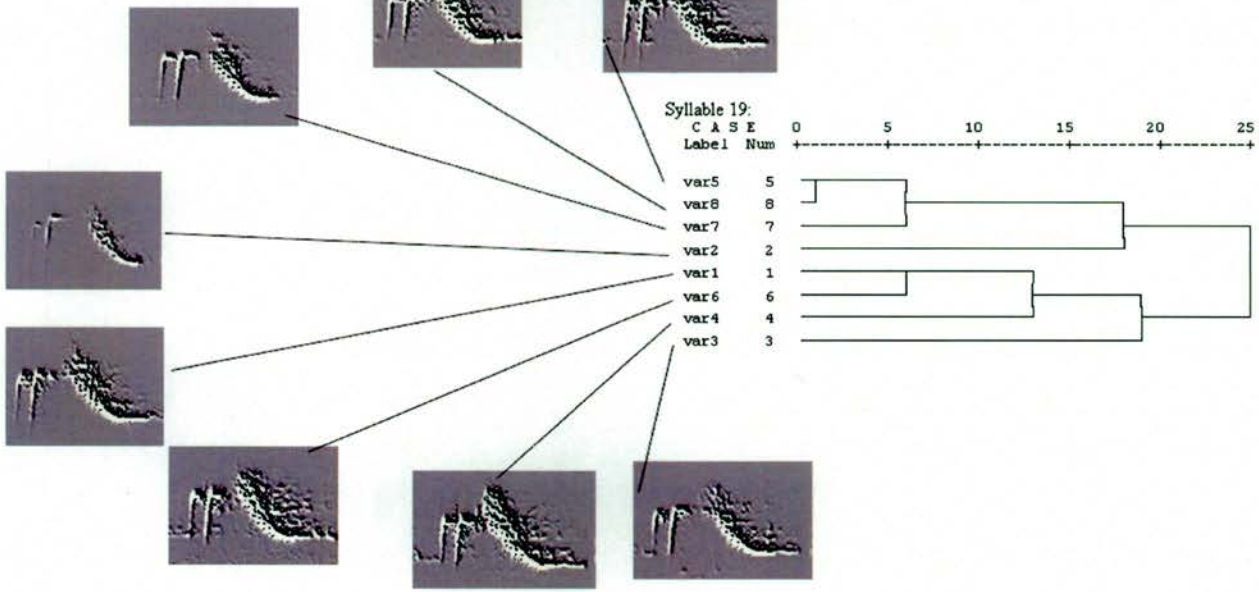

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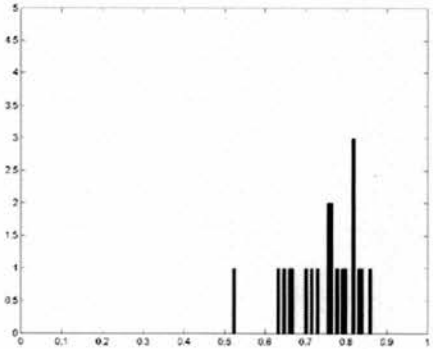
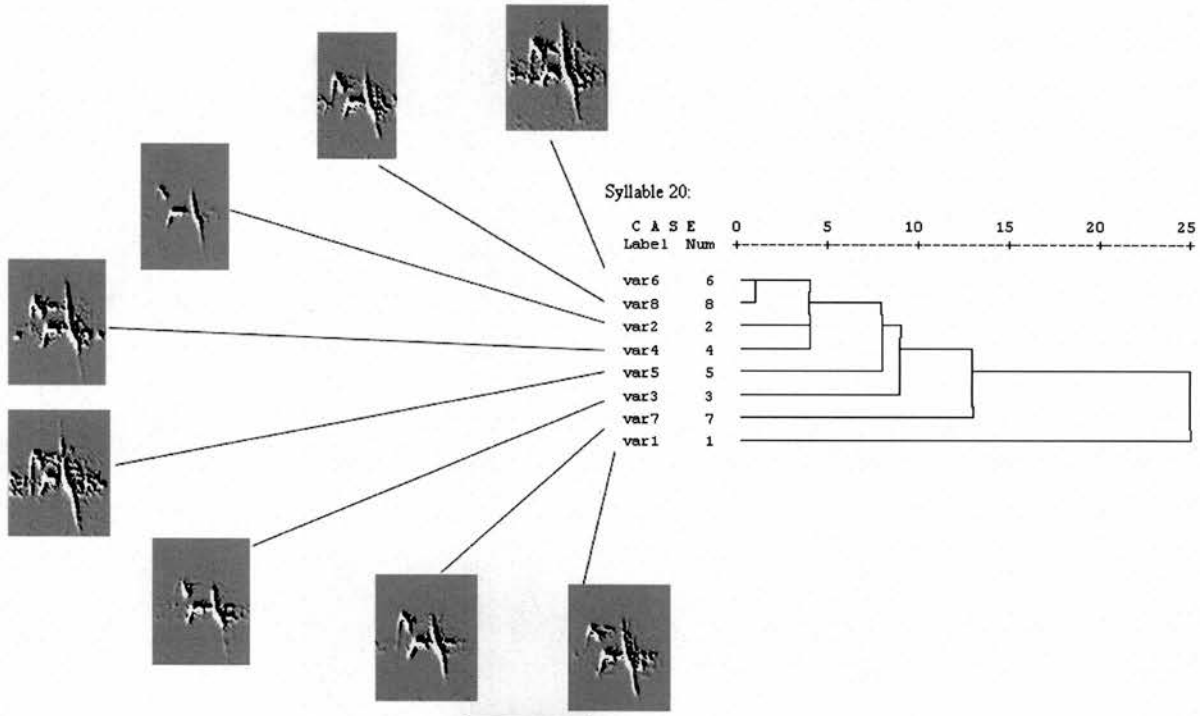
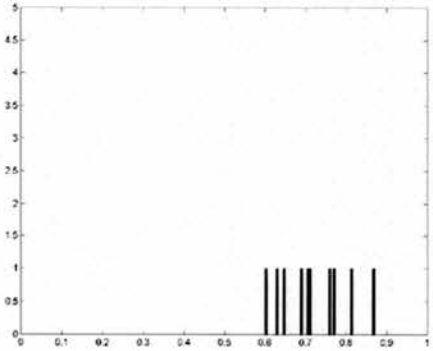
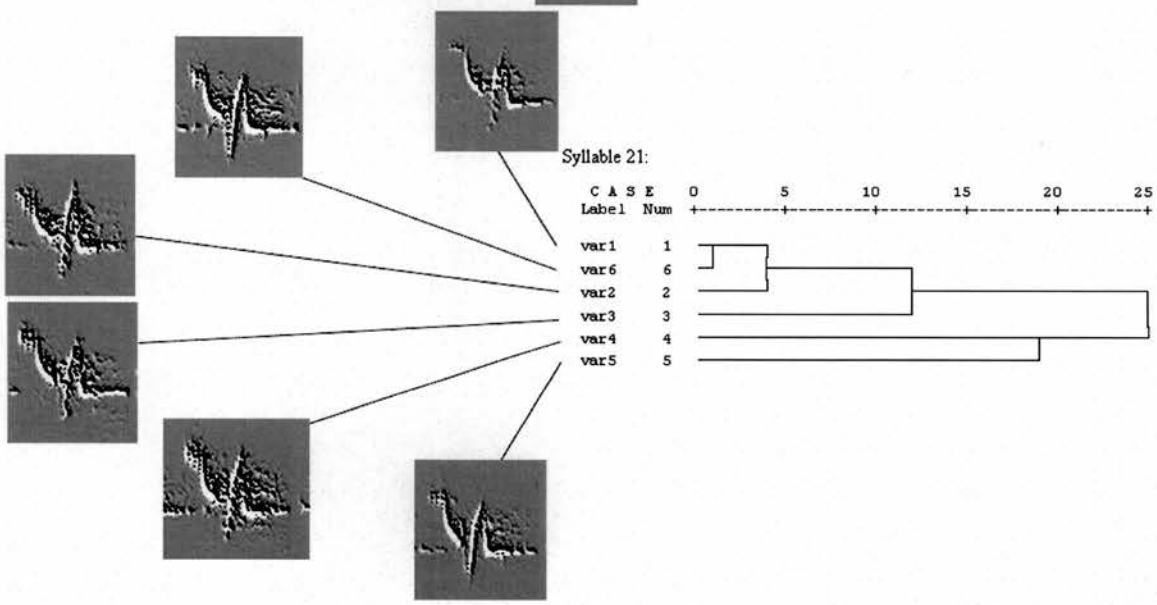




Syllable 21





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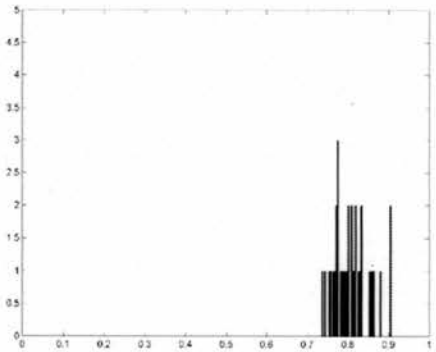

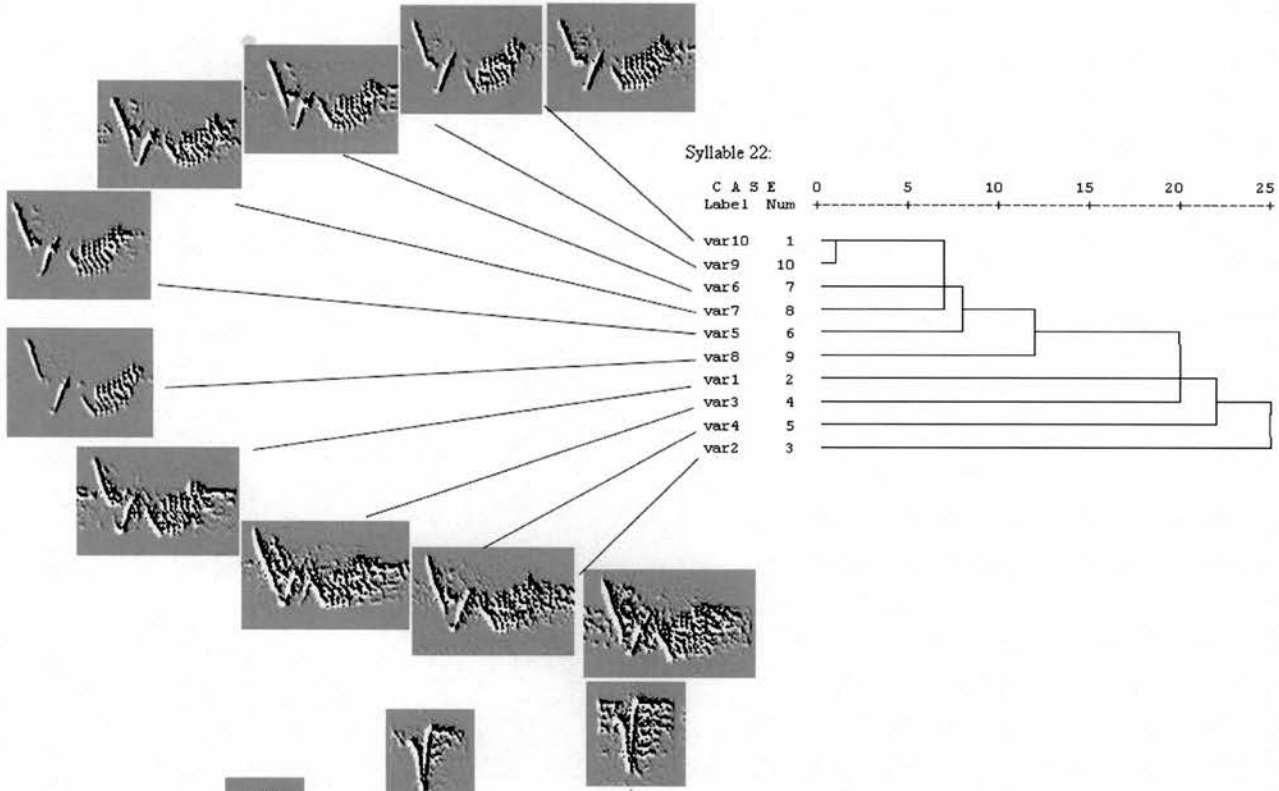

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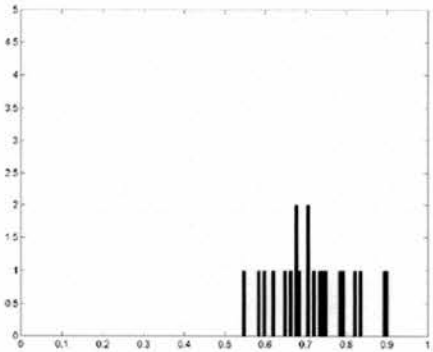

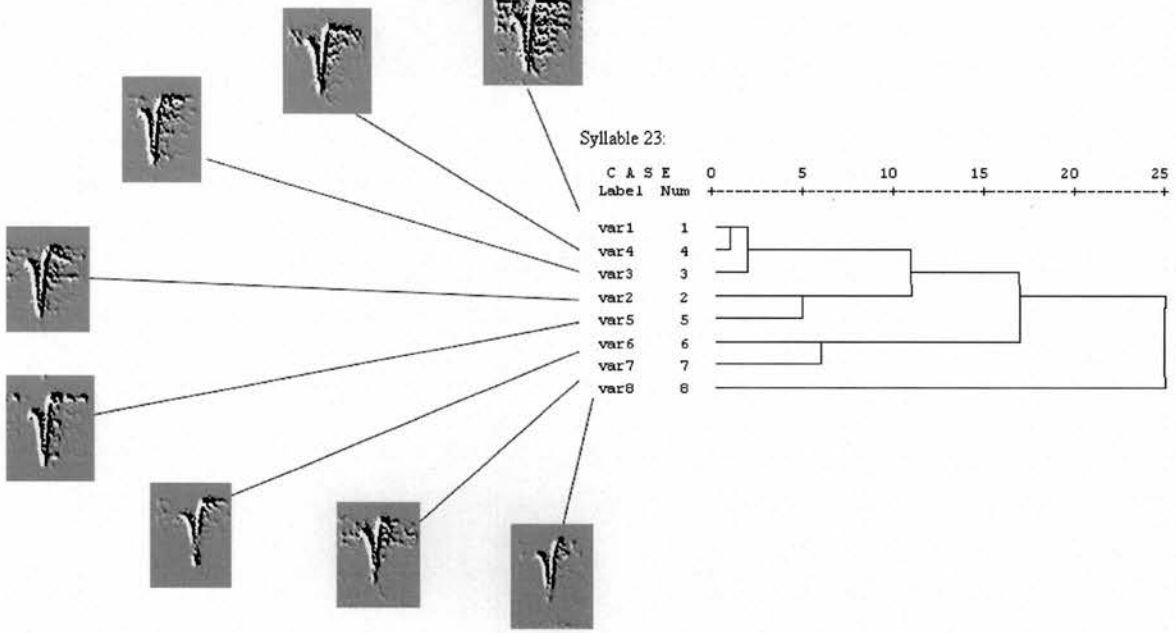

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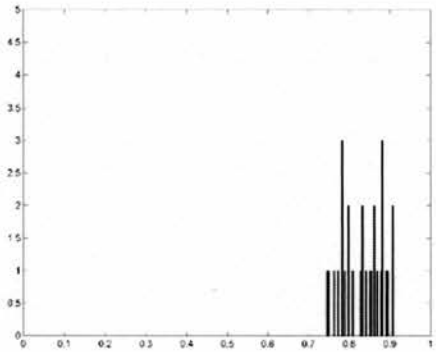

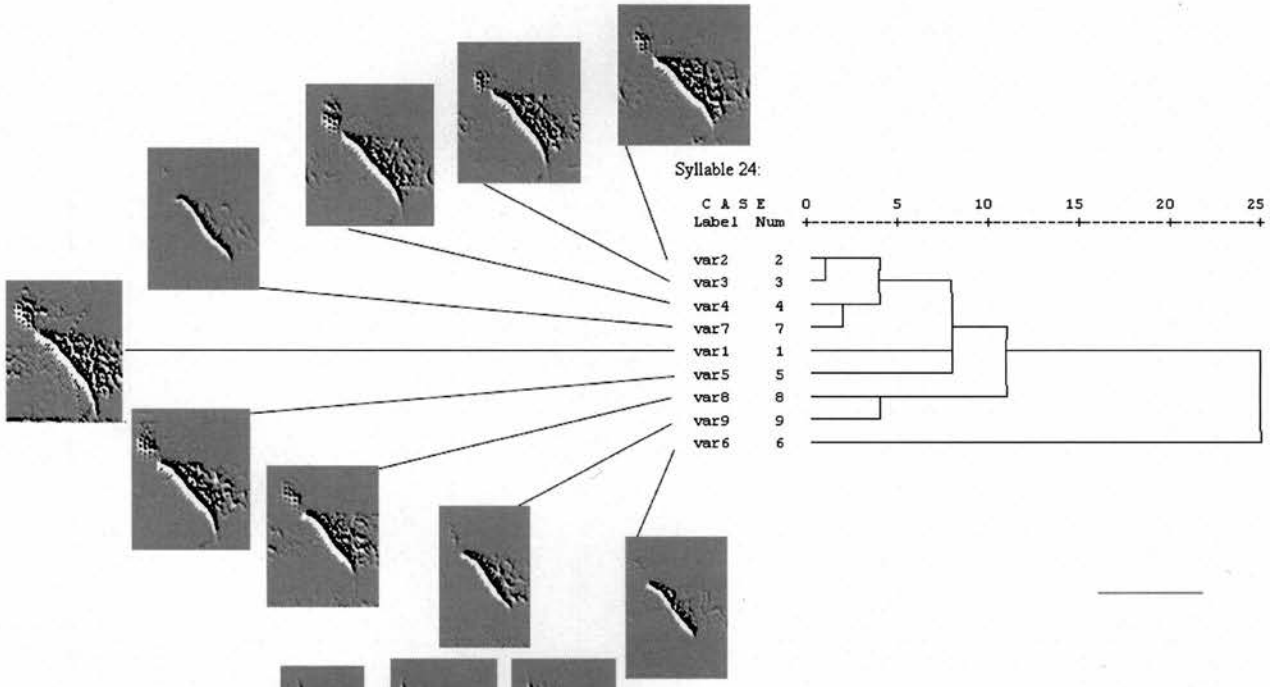

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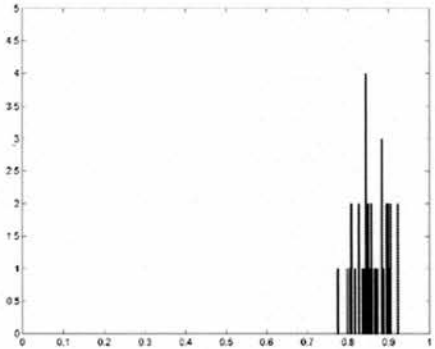

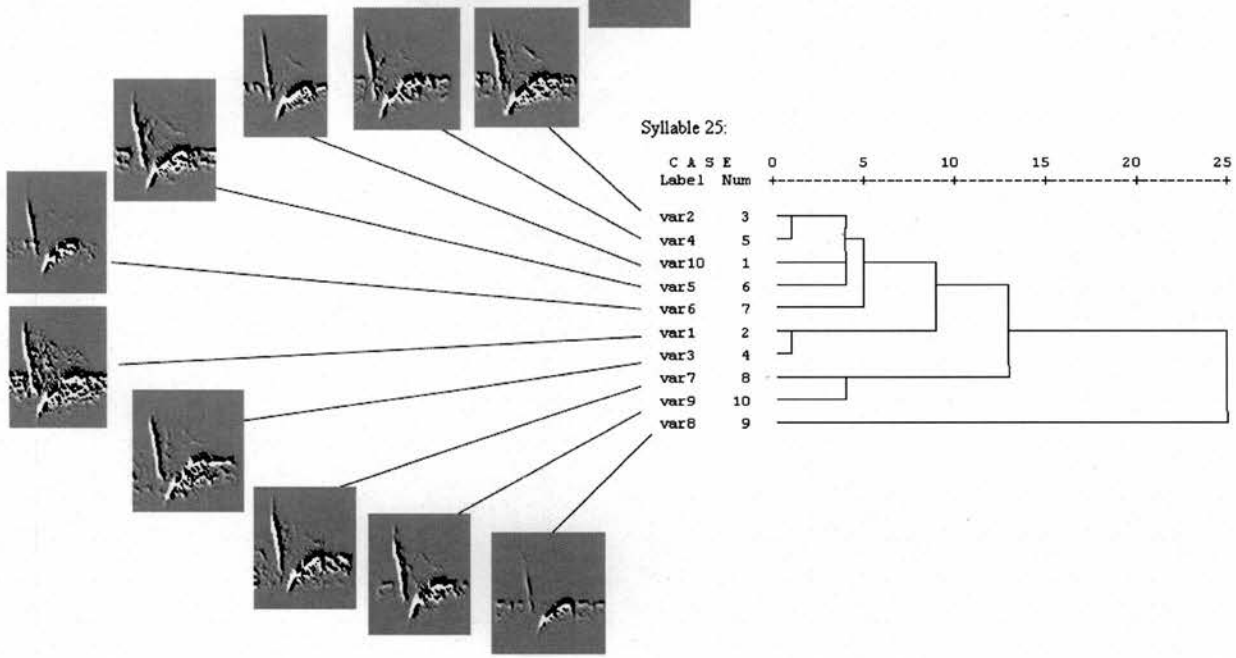

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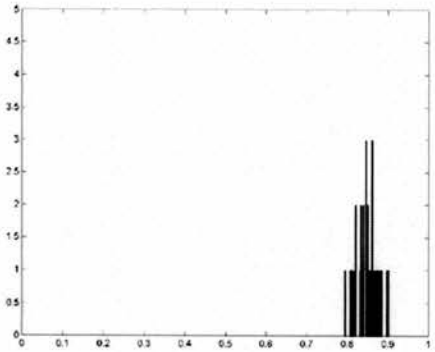
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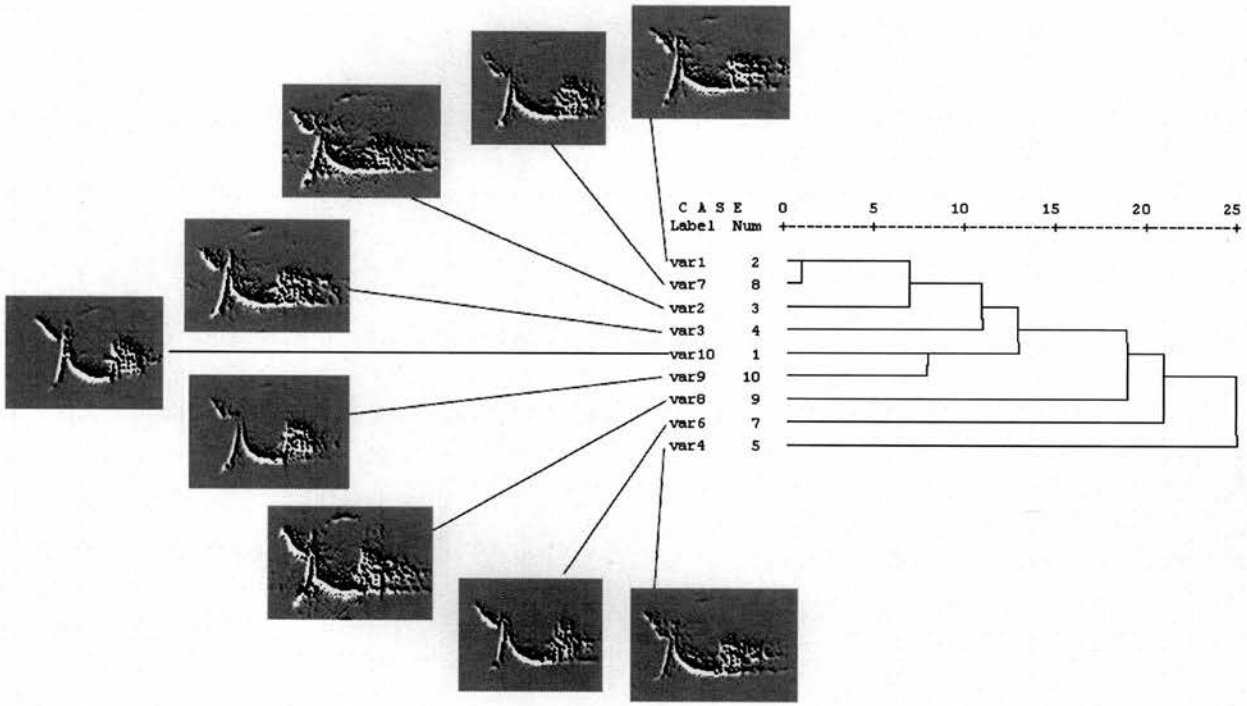
C A S E
Label Num
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var6 7
var4 5

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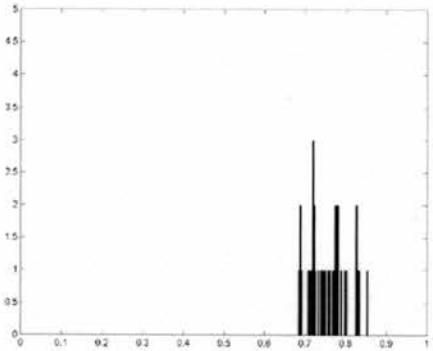

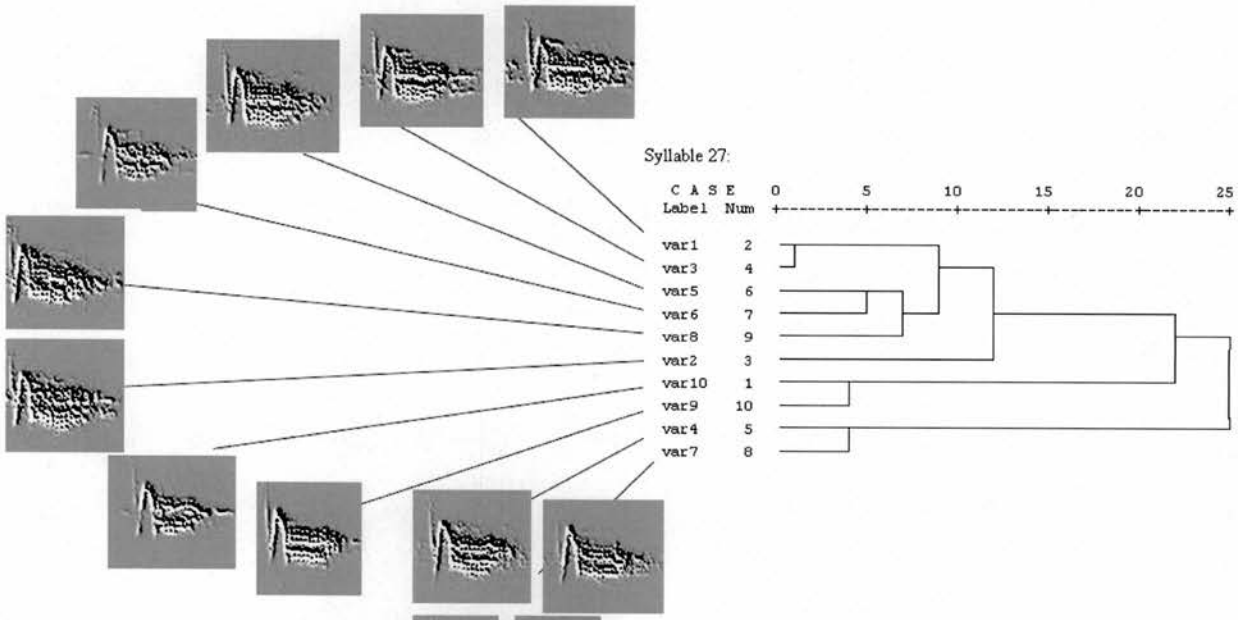

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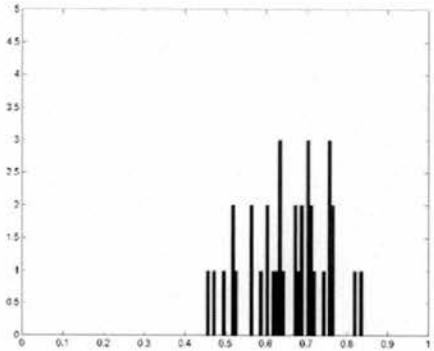

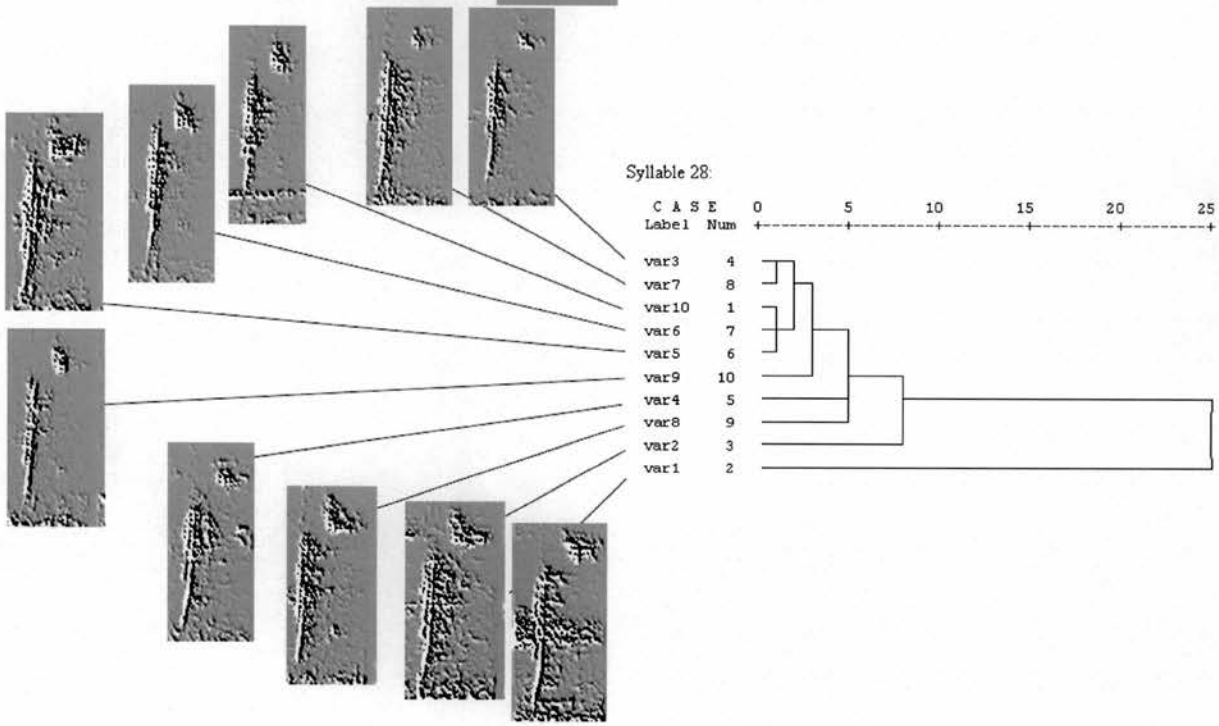

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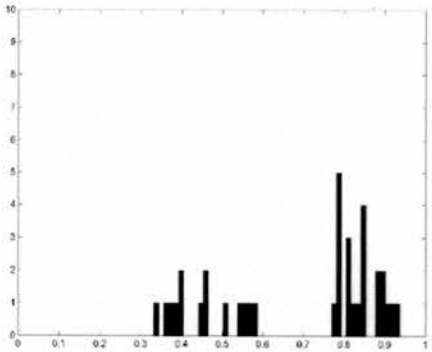

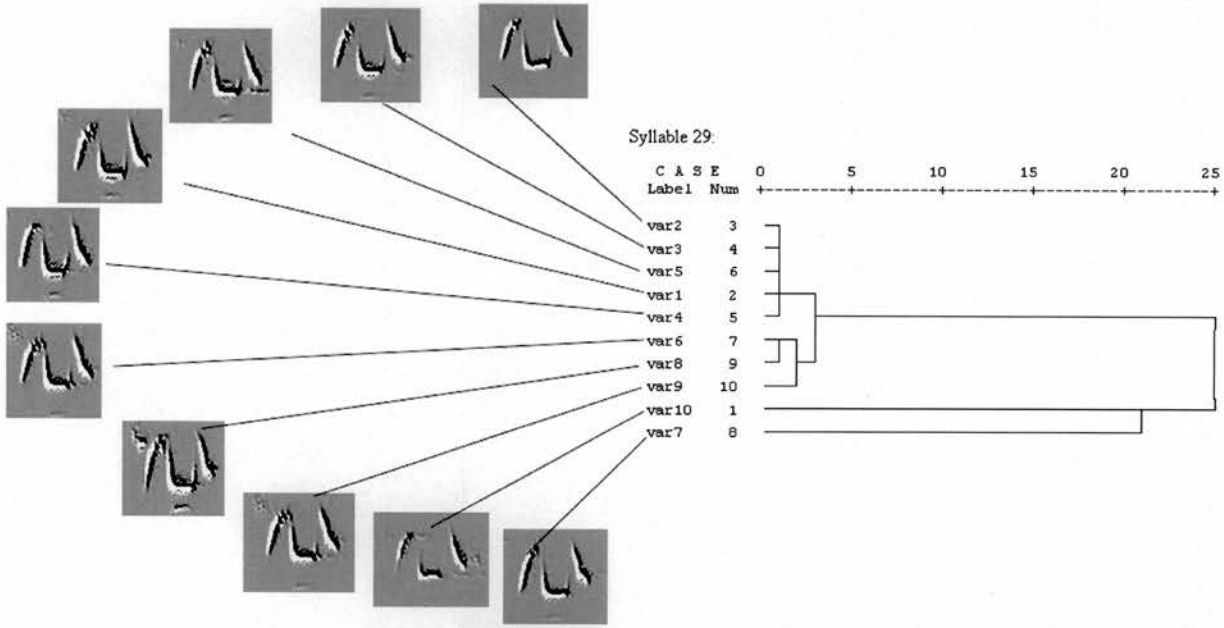

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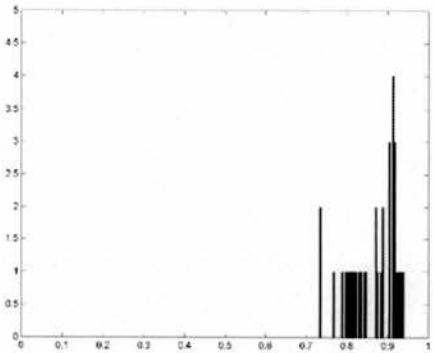

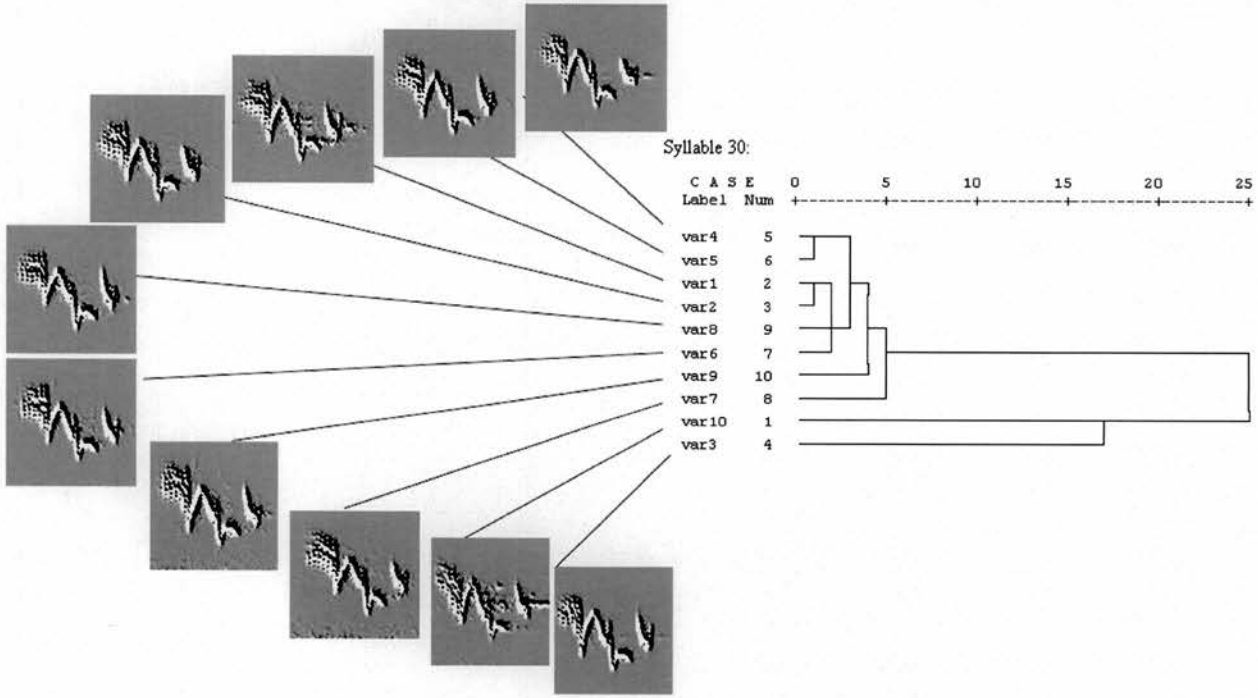

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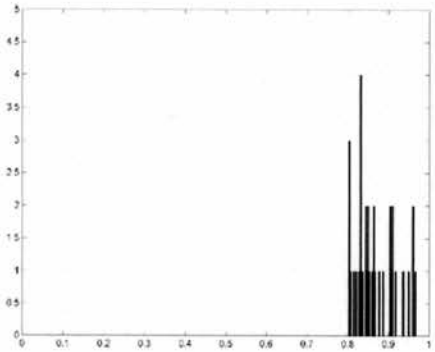

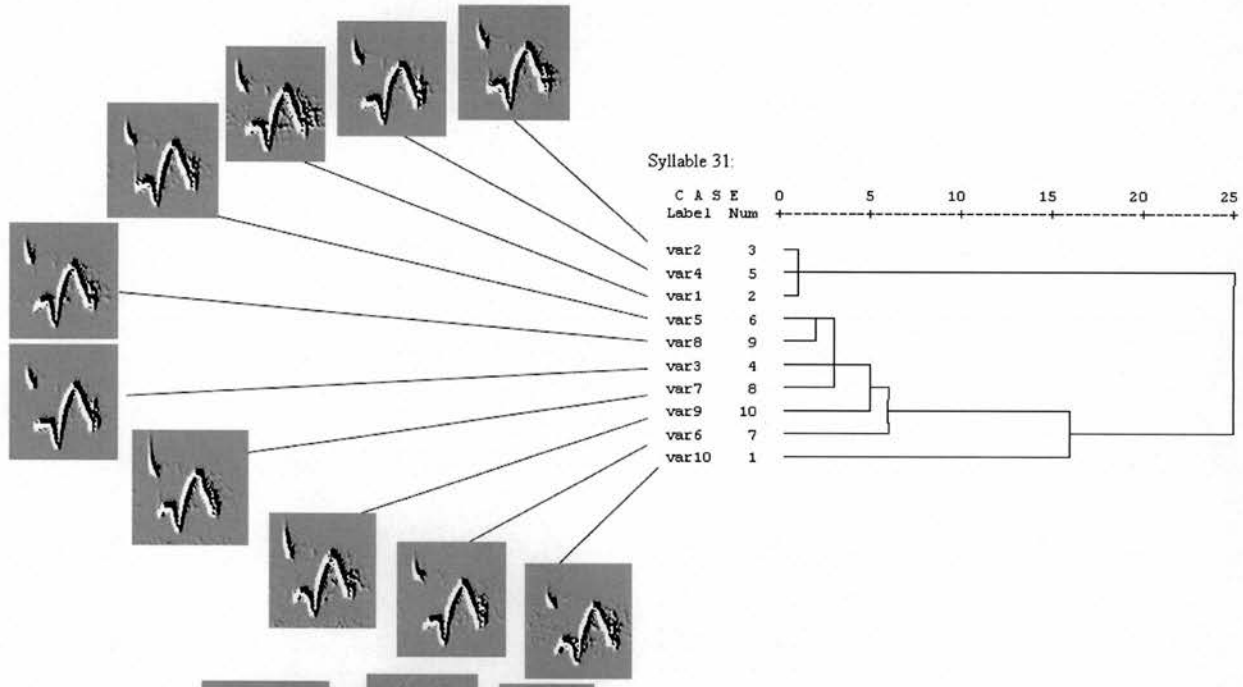

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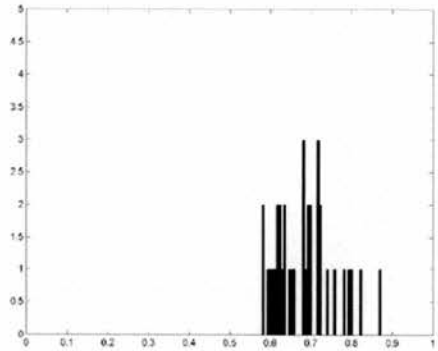

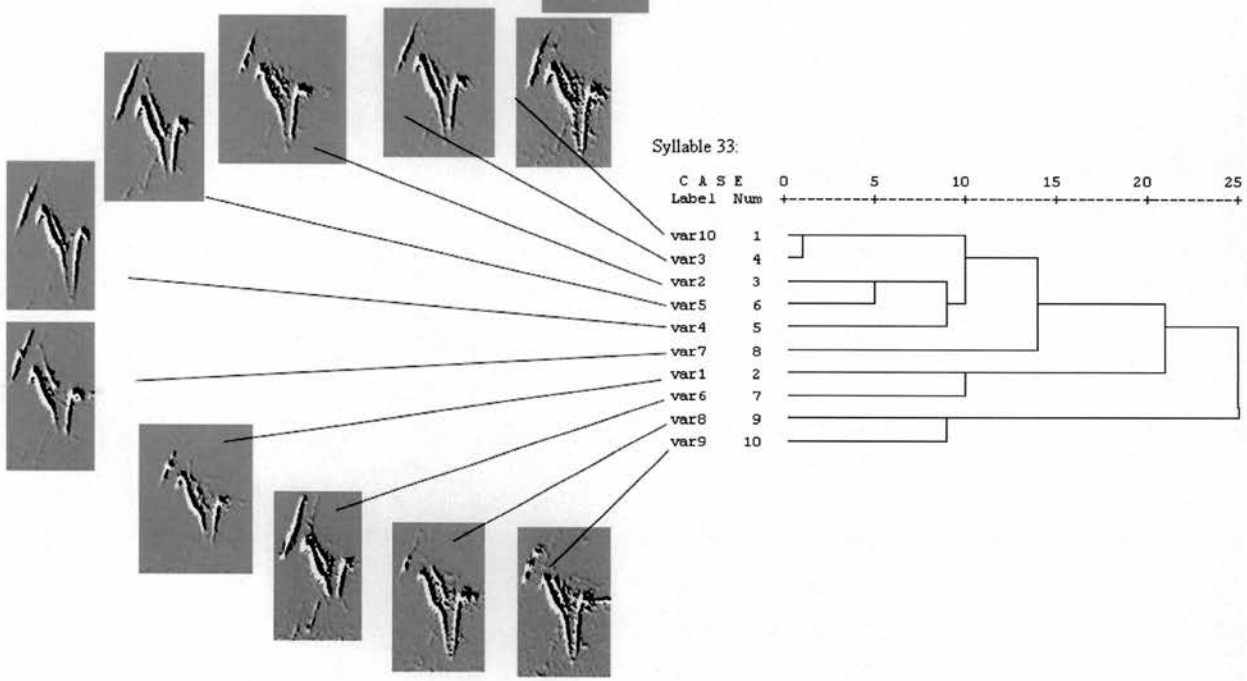

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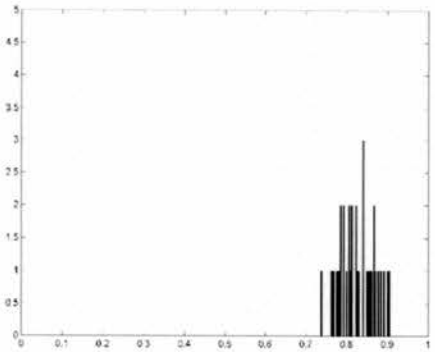

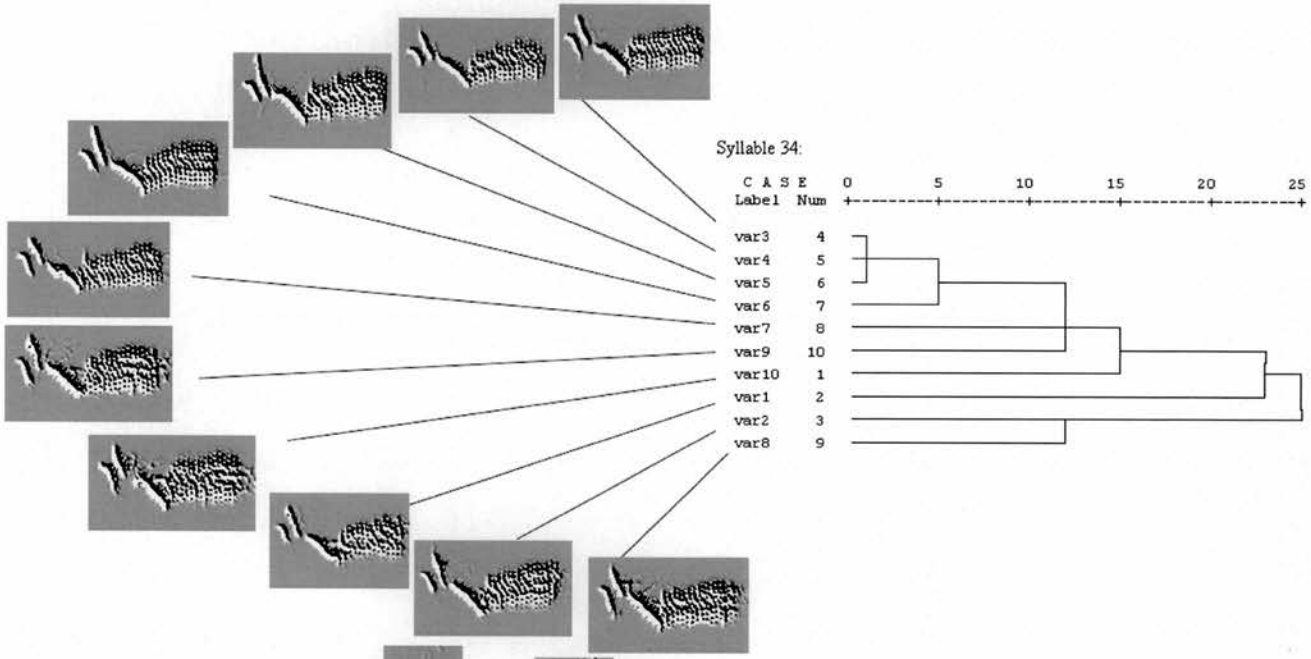

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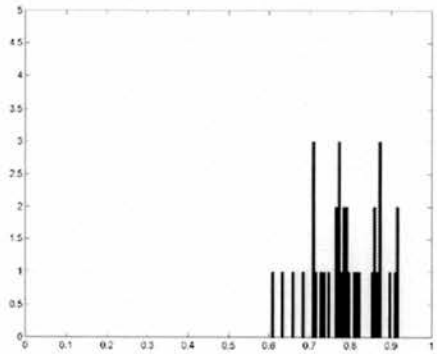

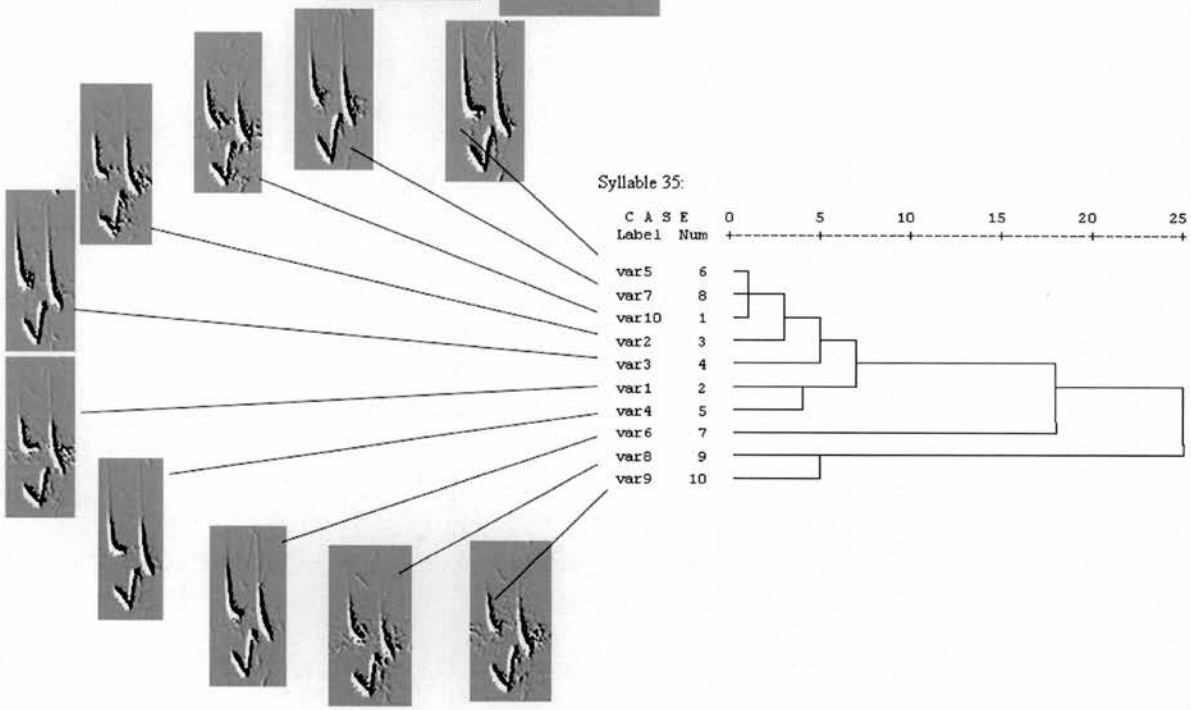

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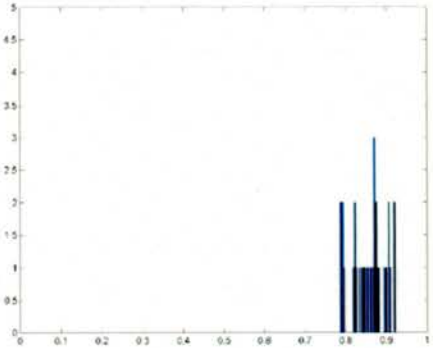

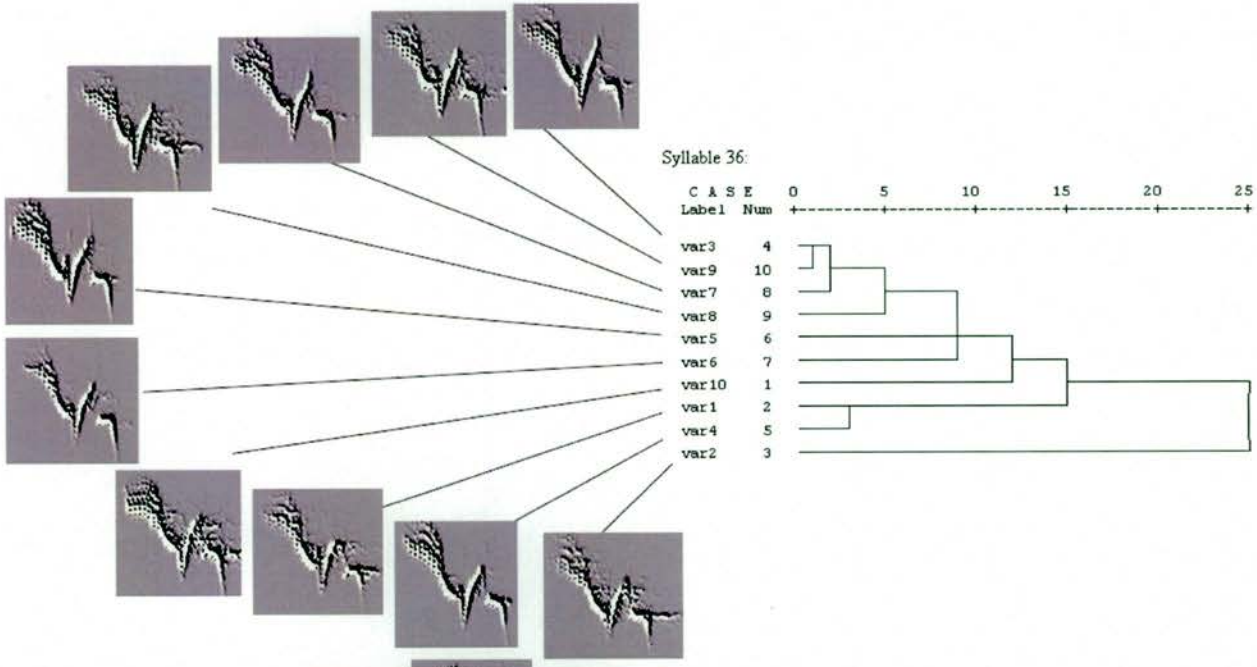

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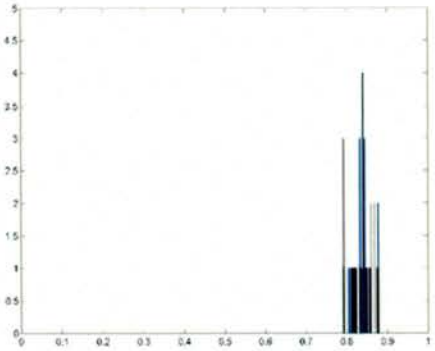
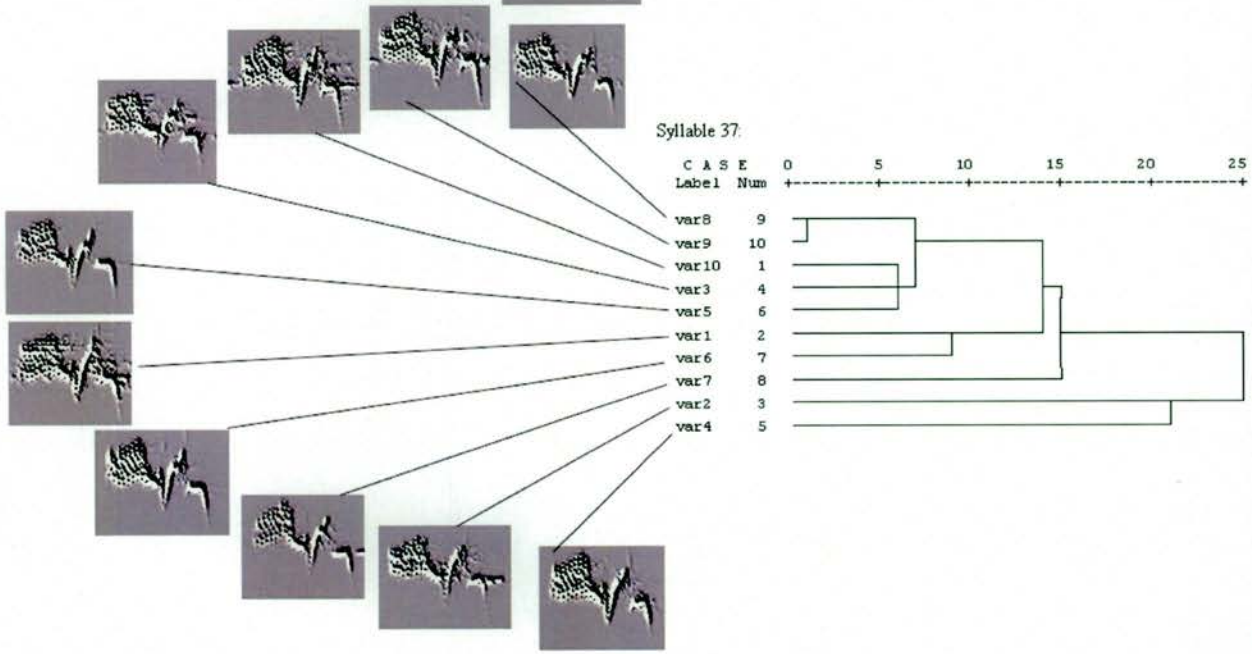
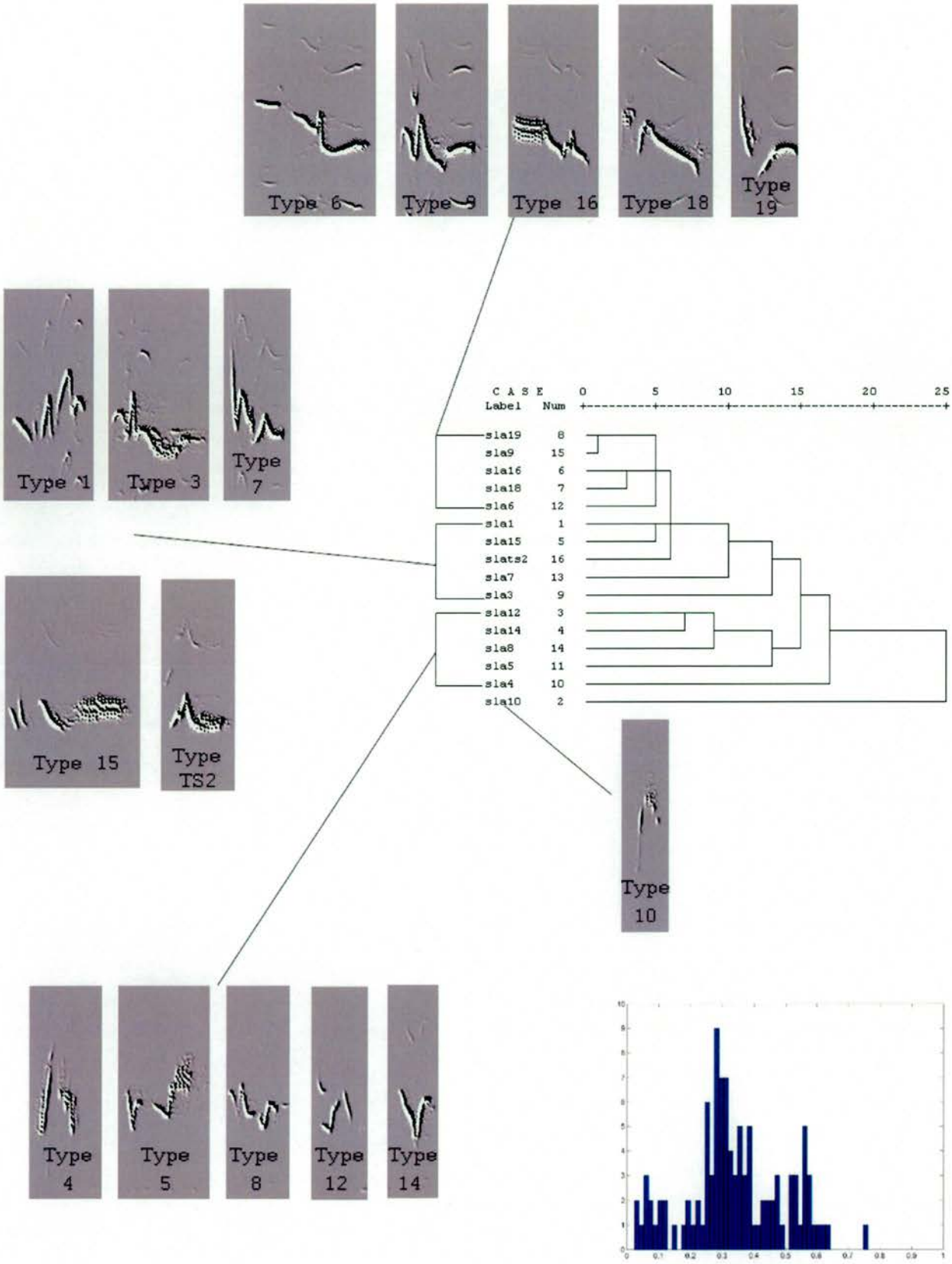




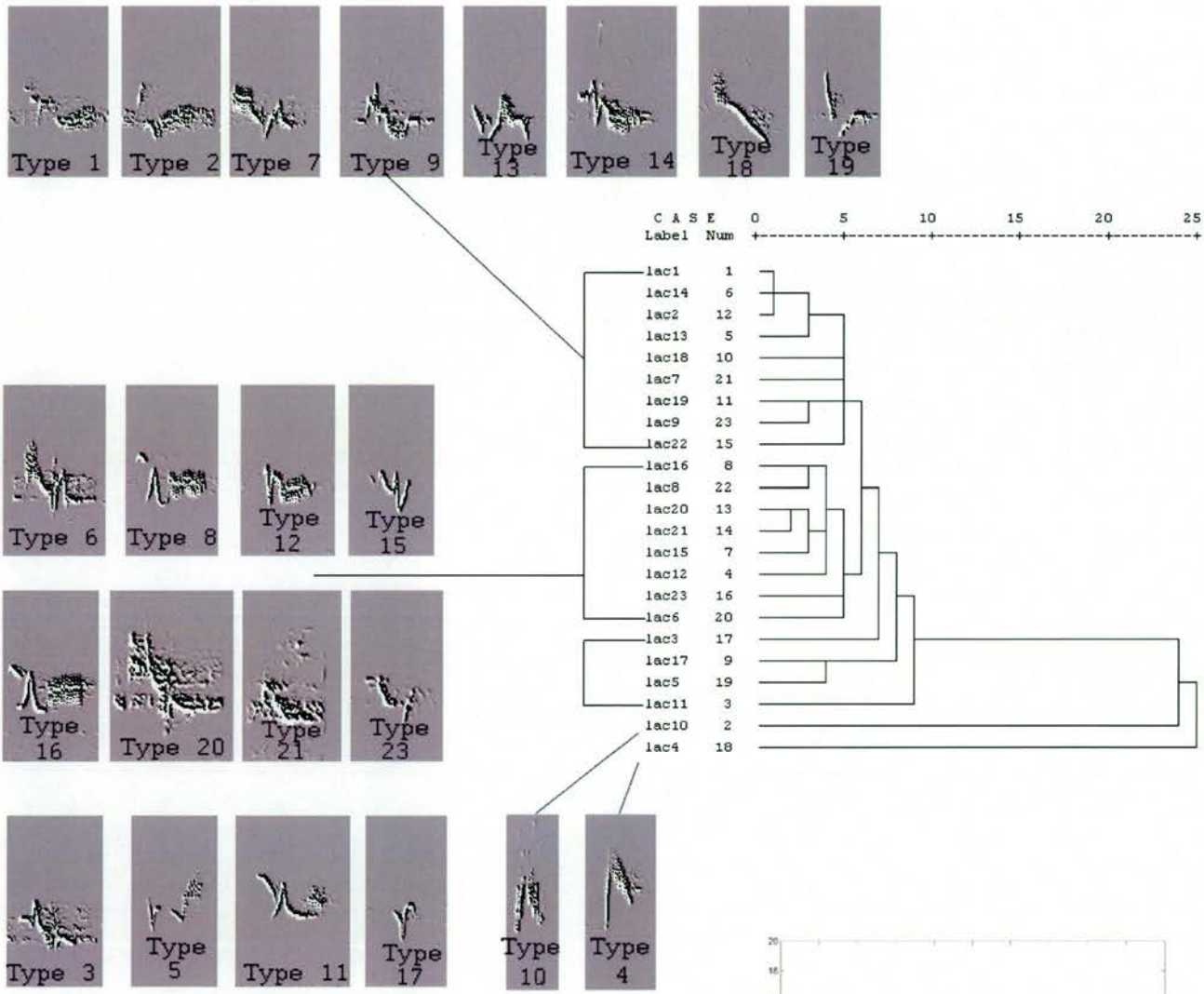
APPENDIX G
Between-Syllable Comparisons For the 1977, 1997, and 2002 Recordings

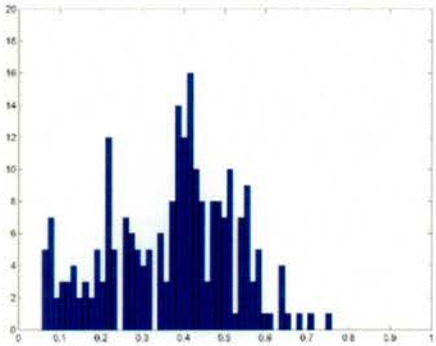
Figures include histograms of the correlation coefficients for each syllable, and dendrograms constructed from nearest-neighbor cluster analyses.

1977 Syllables:

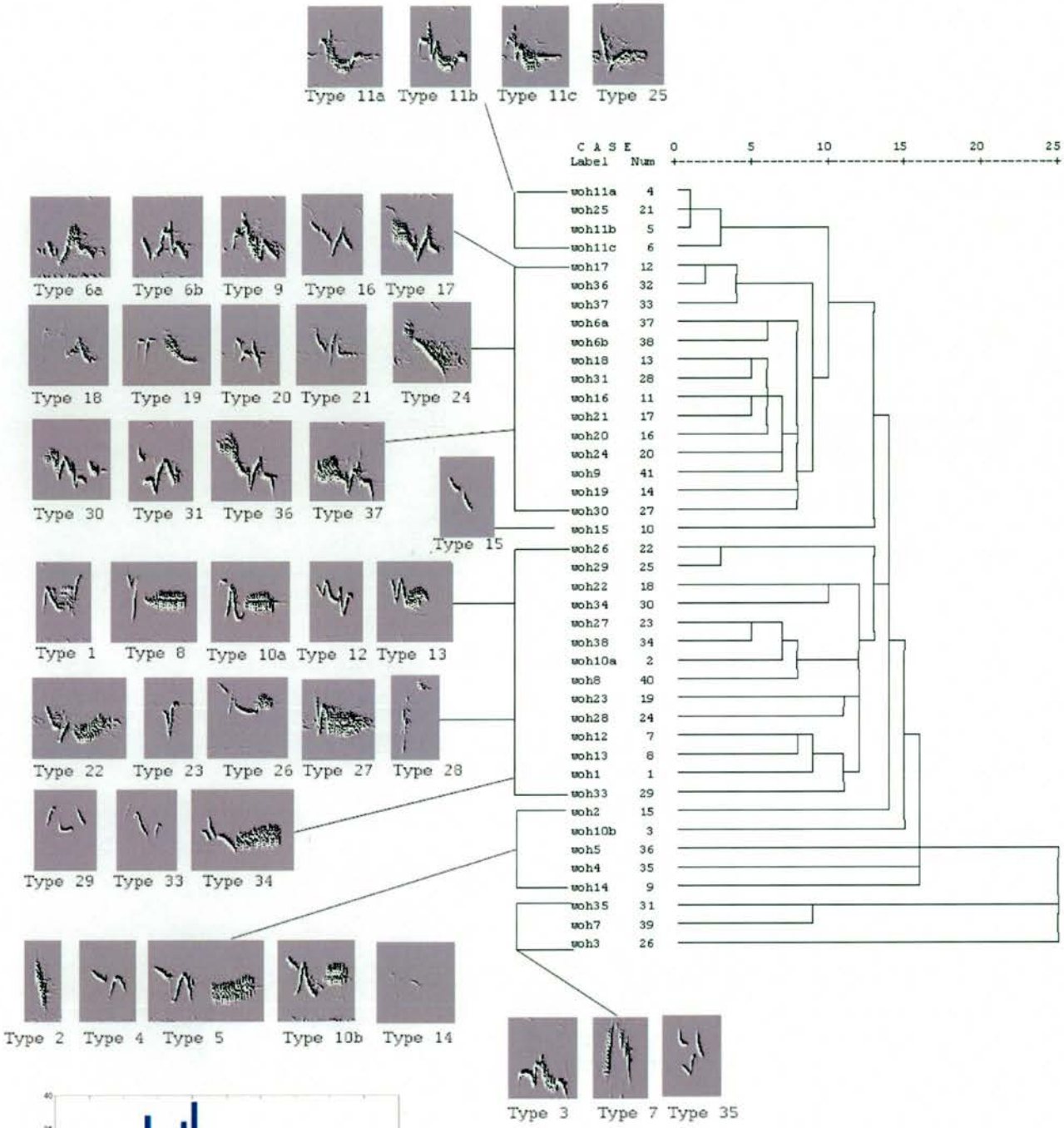


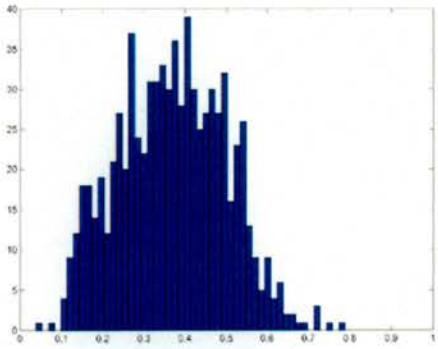
1997 Syllables:



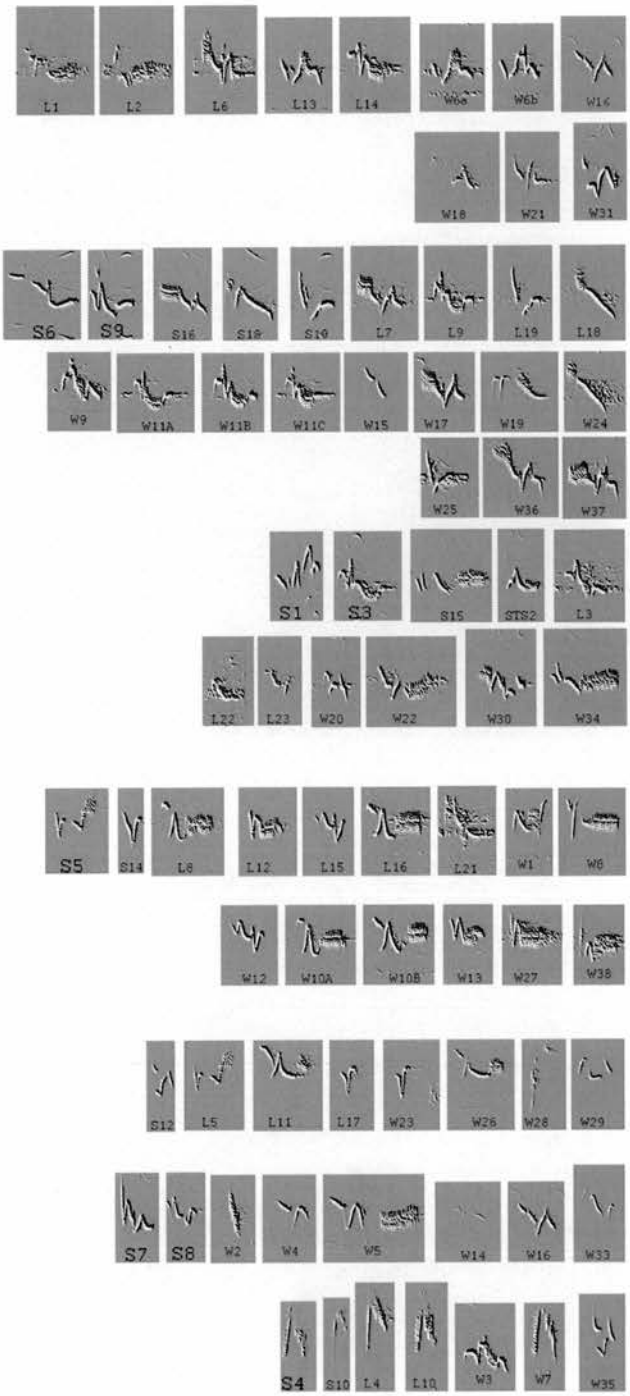


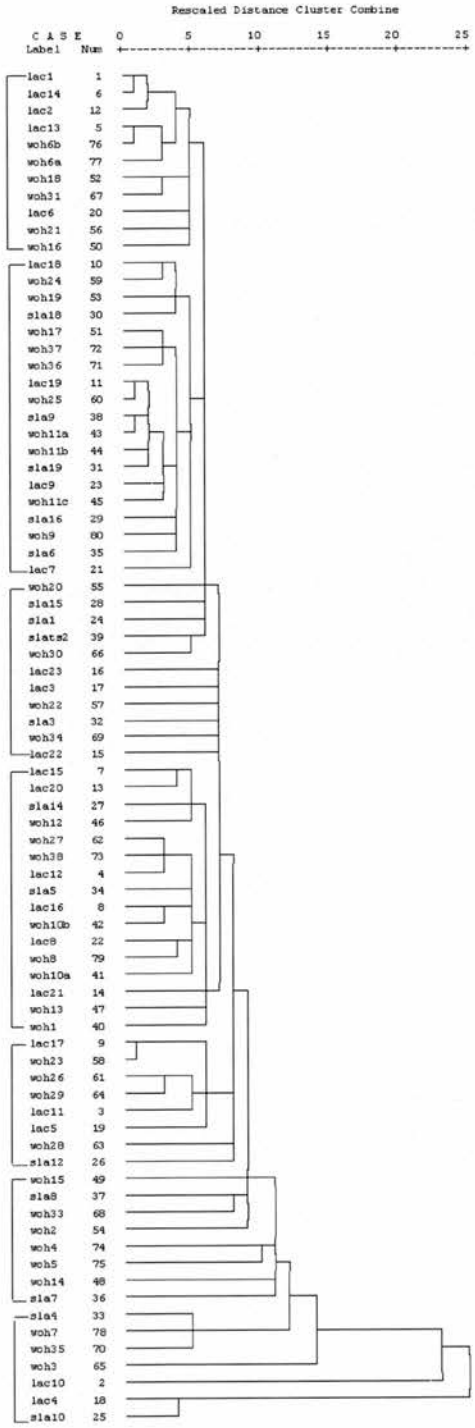
2002 Syllables:

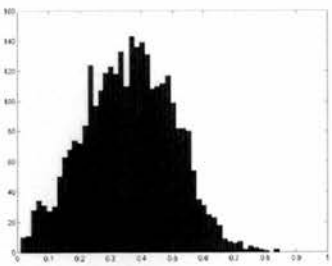




Syllables from 1977, 1997, and 2002:



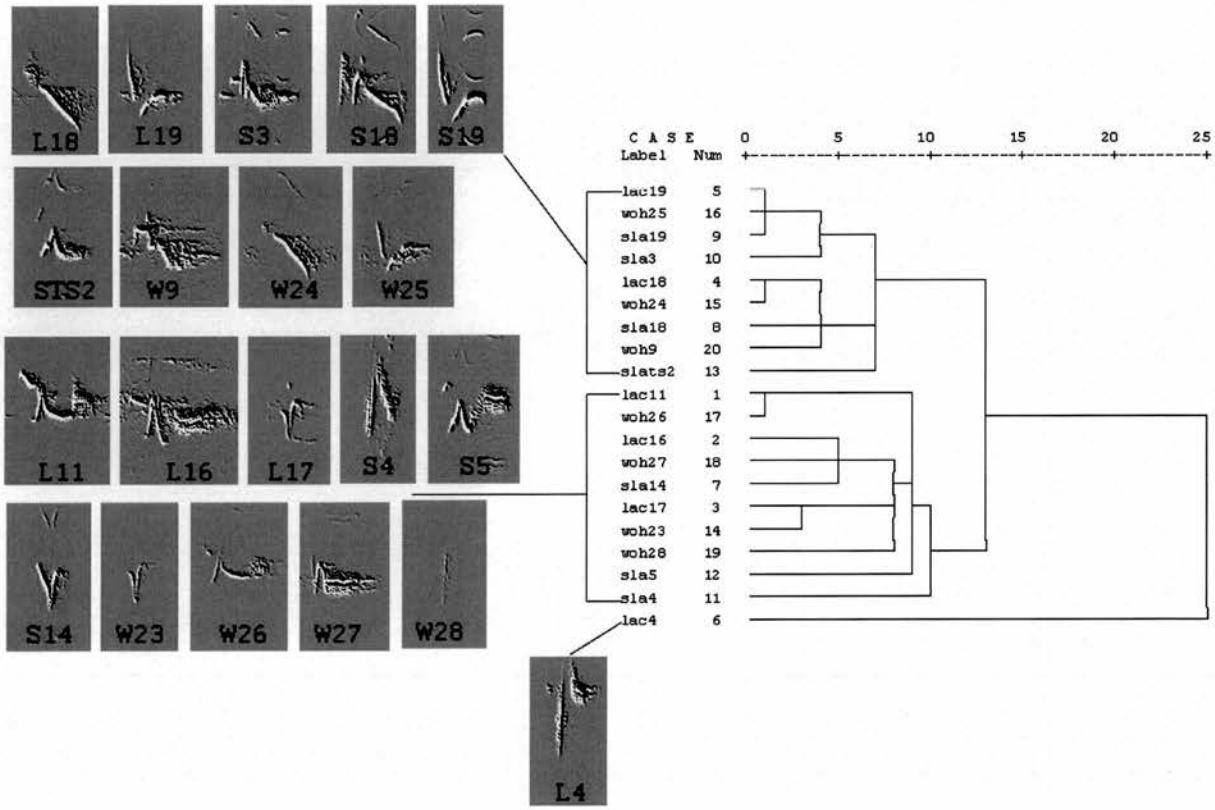




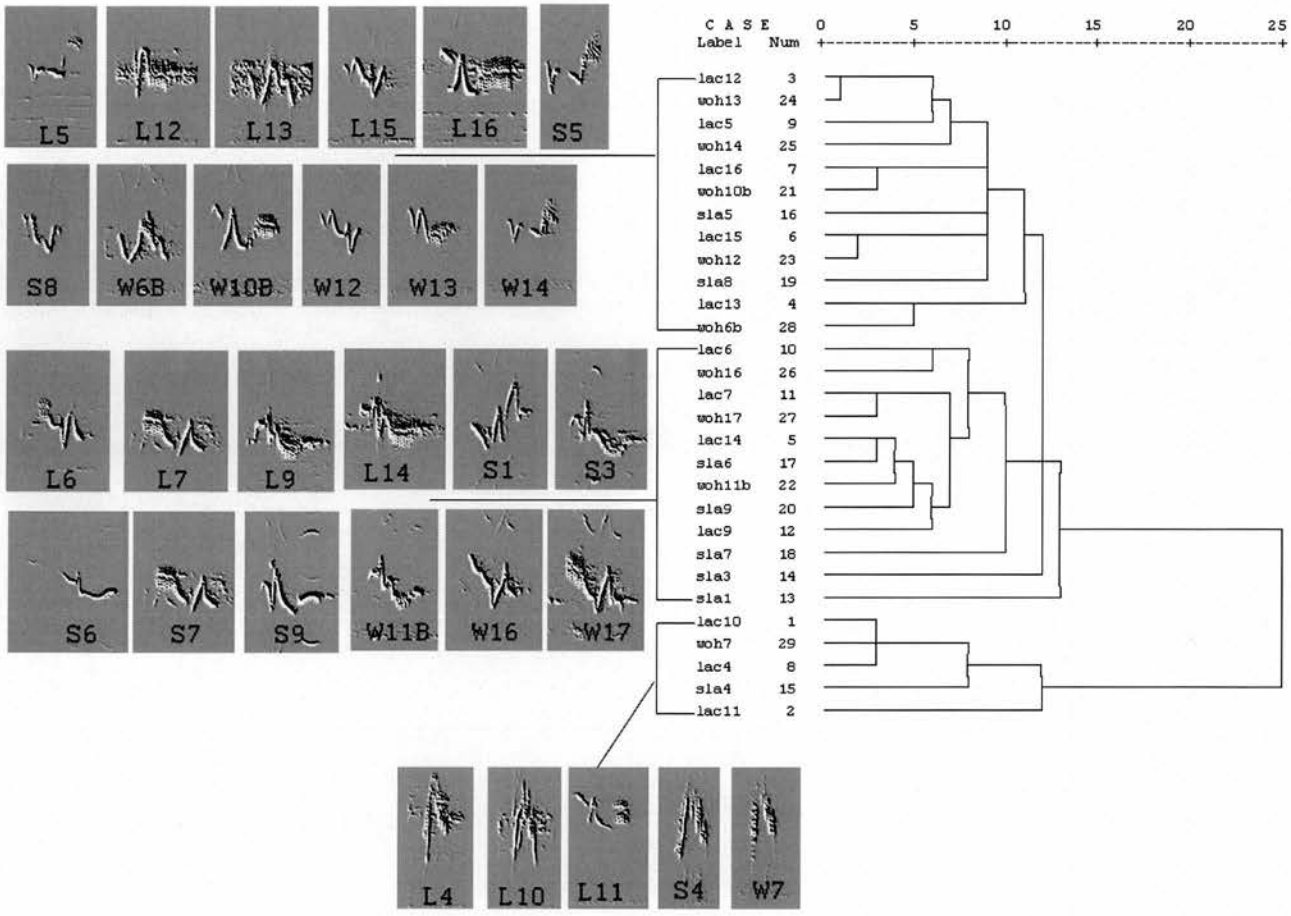
APPENDIX H
Site Comparisons
For the 1977, 1997, and 2002 Recordings

Figures include dendrograms constructed from nearest-neighbor cluster analyses for comparisons of syllables recorded at the same site in all years.

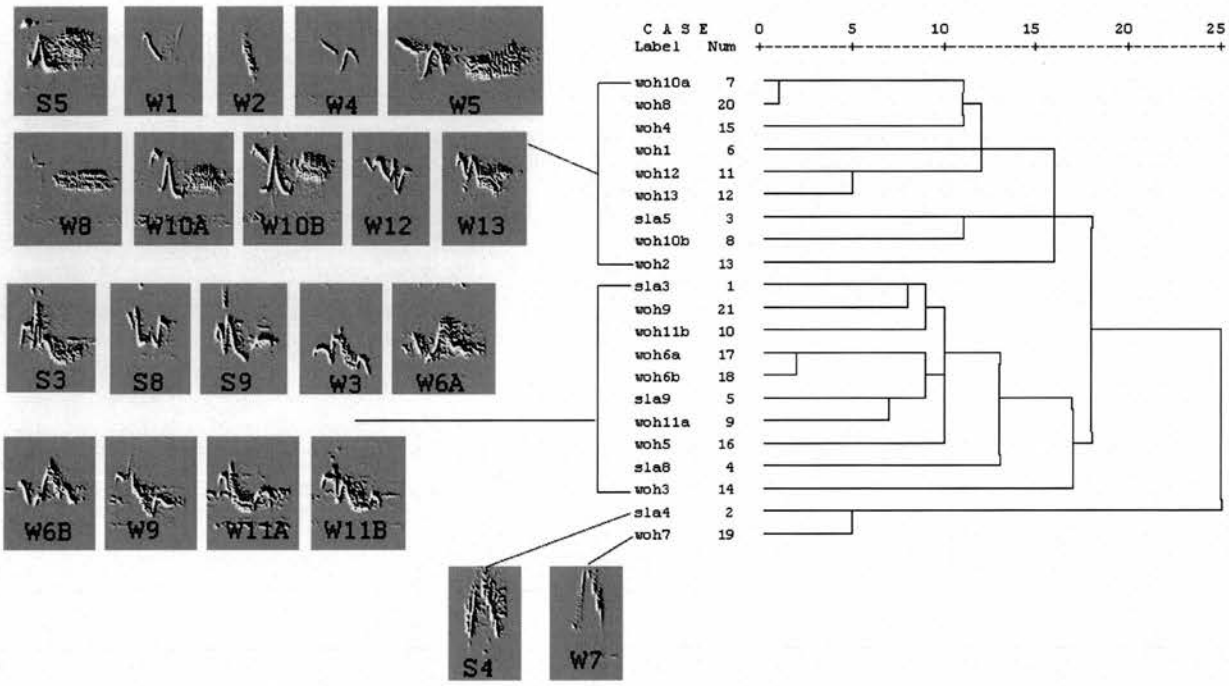
Trumland Syllables:



Finstown Syllables:



Binscarth Syllables:



Balfour Syllables: