CHAPTER ELEVEN

Secular Trends in Craniofacial Asymmetry Studied by Geometric Morphometry and Generalized Procrustes Methods

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INTRODUCTION

Previous work on the secular trends of growth, size, and shape of American craniofacial form over the past 200 years documents significant morphological change and increased variability. For example, Jantz and Meadows Jantz (2000) demonstrated that the American cranial vault has become longer and narrower over time. While the face was less affected by secular change, modifications were noted in its height and width. Interestingly, secular change in shape

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was more pronounced than that determined for size. Increased phenotypic variance, like that noted by Jantz and Meadows Jantz (2000), is compounded by many influential genetic factors (i.e., homozygosity and directional selection) and their interaction with nutritional stress or parasitic load. Such genetic and environmental factors disrupt the development process and alter the phenotype. One well-studied manifestation of this is the asymmetrical development of bilateral traits. Developmental stability and canalization, on the other hand, are buffering mechanisms that provide an individual with the ability to overcome this developmental noise (Sciulli et al., 1979; Siegel et al., 1977; Waddington, 1957). As buffering mechanisms act to overcome developmental noise and stabilize development, they modify the gene-to-phenotype relationship (Rutherford, 2000). This leads to the question of whether periods of rapid morphological change affect such buffering mechanisms and are accompanied by increased asymmetry.

Traditional morphometric techniques have been used to measure asymmetry in a wide range of traits from soft to hard tissue, such as dermatoglyphics (Jantz and Brehme, 1993), dentition (Hershkovitz et al., 1993), and various skeletal elements (Farkas and Cheung, 1981; Peck et al., 1991). More recently, geometric morphometric techniques have been applied to the study of size and shape asymmetry of skeletal and soft tissue structures (Klingenberg et al., 2001; Mardia et al., 2000).

Geometric morphometrics, as defined by Slice et al. (1996), is the study of size and shape based on the multivariate analysis of Cartesian coordinate data and has been applied to the study of developmental stability by a number of researchers (Klingenberg and McIntyre, 1998; Klingenberg et al., 2001; Leamy et al., 2000; Richtsmeier, 1987). Typically, methods of geometric morphometry include the estimation of mean shapes and descriptions of sample variation in shape through the use of geometric principles, such as Procrustes distances (Slice et al., 1996). Since Procrustes methods inherently allow for shape and size variables to be analyzed separately, they are quite useful for the study of developmental stability through the measurement of asymmetry. The multivariate statistical procedures needed for analysis of developmental stability are easily applied to coordinate data.

While a comprehensive comparison between traditional methods of calculating asymmetry and geometric morphometrics has been made by Auffray and colleagues (1996), a few comments on the differences between these approaches, as they relate to asymmetry, are worthwhile. Beneficially, Procrustes methods allow for analysis of size and shape variables using three-dimensional (3D) visualization, in depth analysis of directionality, and in our experience, lower interobserver or repeated measurement error. Further, in some past studies of craniofacial landmarks (Peck et al., 1991), construction of a midline was needed for structures, such as the face, from which one could measure left and rights points. The creation of such a midline often leads to bias or inaccuracies because asymmetry usually involves the measure of very small deviations between left and right sides. Procrustes methods as used in this analysis allow for the elimination of a defined midline.

MATERIALS AND METHODS

The purpose of this chapter is to investigate the secular change of developmental stability in the craniofacial region of Americans through measurement of fluctuating and directional asymmetry using the generalized Procrustes analysis (Gower, 1985) of paired craniofacial landmark coordinates in the manner of Klingenberg and McIntyre (1998); refer also to Mardia and coworkers (2000) for more recent methods. Previous work on the secular trends of growth, size, and shape of American cranial form leads to the question of whether periods of rapid morphological change are accompanied by increased fluctuating asymmetry in American craniofacial morphology. To test for fluctuating and directional asymmetry and their association with rapid morphometric change, 3D coordinate data from 526 American males and females of African and European descent who were born between the years 1820–1980 A.D. were analyzed (Table 1). All craniofacial data used in this investigation were collected from skeletons of identified individuals, ensuring that accurate birth date or minimally, the years of birth are known.

The skeletal remains in this analysis originated from several national collections: The Robert J. Terry Anatomical Skeletal Collection located at the National Museum of Natural History, Smithsonian Institution in Washington, D.C.; the William M. Bass Donated Collection housed at the University of Tennessee, Knoxville; the Forensic Data Bank that includes forensic cases from throughout the United States, but is maintained by the Forensic Anthropology Center also at the University of Tennessee, Knoxville; and the Civil War Collection housed at the National Museum of Health and Medicine of the Armed Forces Institute of Pathology in Washington, D.C.

The majority of data were collected from the R. J. Terry Anatomical Collection representing skeletons that were retrieved from the medical cadavers of people who lived and died in St. Louis, Missouri, between the years

Table 1. Sex and ancestral distribution by decade of birth

YOB	White males	White females	Black males	Black females	Total sample
1820–1829	5	—	—	1	6
1830–1839	13	1	1	1	16
1840–1849	14	5	8	7	34
1850–1859	10	10	9	10	39
1860–1869	12	14	12	15	53
1870–1879	10	12	10	13	45
1880–1889	11	11	10	12	44
1890–1899	10	10	10	11	41
1900–1909	10	12	18	15	55
1910–1919	12	11	12	10	45
1920–1929	19	17	7	7	50
1930–1930	21	6	7	2	36
1940–1949	12	4	4	2	22
1950–1959	12	3	2	—	17
1960–1969	10	0	6	3	19
1970–1979	—	—	3	—	3
1980–1989	—	1	—	—	1
Total	181	117	119	109	526

of 1820–1940 A.D. The birth places for these individuals varies nationwide. The W. M. Bass Donated sample consists of 127 skeletons retrieved from the donated cadavers of people who predominantly lived and died in East Tennessee, between the years of 1900–1980 A.D. Data collected from the Forensic Data Bank came from 27 forensic cases investigated at various universities and morgues throughout the United States. These individuals were born between the years of 1840–1980 A.D. Finally, the Civil War Collection consists of the crania of 28 Civil War veterans who died in battle and were born between the years of 1820–1840 A.D. in various parts of the United States.

Cartesian coordinate data were collected using a Microscribe-3DX 3D digitizer for the seven bilateral facial landmarks (dacryon, frontomalare anterior, frontomalare temporale, zygomaxillare, zygoorbitale, zygion, and asterion). The landmarks (Figure 1) were defined using W. W. Howells (1973) standard definitions.

While investigations into the buffering mechanisms of individuals may lead to greater understanding of observed variation, its precise measurement is more elusive. There are two different types of asymmetry commonly recognized that will be discussed here. Directional asymmetry is the propensity for a particular side of a trait to develop more than the other. In directional asymmetry, the

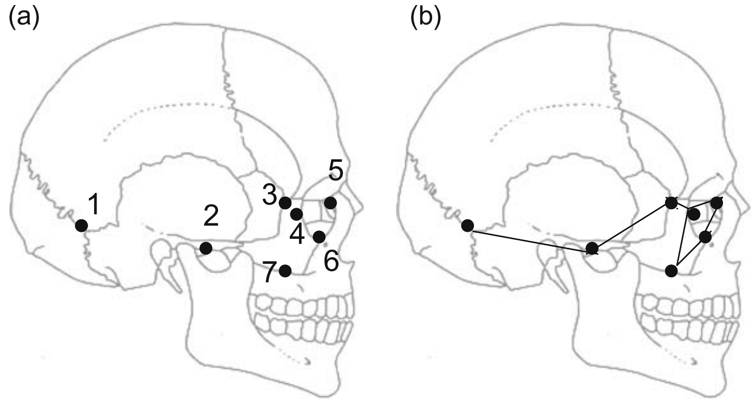

Figure 1. (a) Craniofacial landmarks: 1, asterion; 2, zygion; 3, frontomalare temporale; 4, frontomalare anterior; 5, dacryon; 6, zygoorbitale; 7, zygomaxillare. (b) The second panel illustrates the geometric abstraction of landmarks that is used throughout this study.

mean right minus left (R − L) trait values have a normal distribution with the mean value deviating from zero (Palmer and Strobeck, 1992), and it is typically argued to be genetically based. This differs from fluctuating asymmetry, which is the measure of random deviations from a normal distribution of right minus left values with a mean value of zero (Palmer and Strobeck, 1992) and is thought to result from disruptions to the buffering mechanisms during growth (i.e., environmental and genetic noise). The (R − L) landmark distributions were also checked for a third pattern, antisymmetry, the tendency of a random side to significantly deviate in size or shape, through scatter plots. None was noted.

There are many ways to measure fluctuating asymmetry. Most commonly, the absolute value of right-minus-left measurements, |R − L|, is used to compare individuals, and the variance of |R − L| is the measure of asymmetry at the level of the population. In contrast, directional asymmetry is measured as the signed differences between left and right sides. Various methods, such as a two-way (multivariate) analysis of variance models, test whether significant levels of directional and fluctuating asymmetry are present (Klingenberg and McIntyre, 1998).

Procrustes methods of superimposition offer one approach to the analysis of shape, the geometric properties of an object invariant to orientation, location, and scale (Slice et al., 1996). While there have been several studies investigating the asymmetry of shape, the overwhelming body of research in the area of developmental stability focuses on asymmetry in terms of size. In this study, size and shape are analyzed as separate variables.

Figure 2 illustrates the construction of shape asymmetry variables used in this analysis for a single individual. Landmark coordinates for the left and right structures of the individual are superimposed using Procrustes superimposition (see Chapter 14). The data are individually scaled to unit centroid size, reflected, and optimally (in the least-squares sense) translated and rotated to achieve a best fit. Once so superimposed, individual coordinate differences between the right and left structures provide a detailed multivariate description of shape asymmetry. To produce a univariate summary of this asymmetry, we compute the square root of the sum of squared coordinate differences (Procrustes distance) between the two configurations.

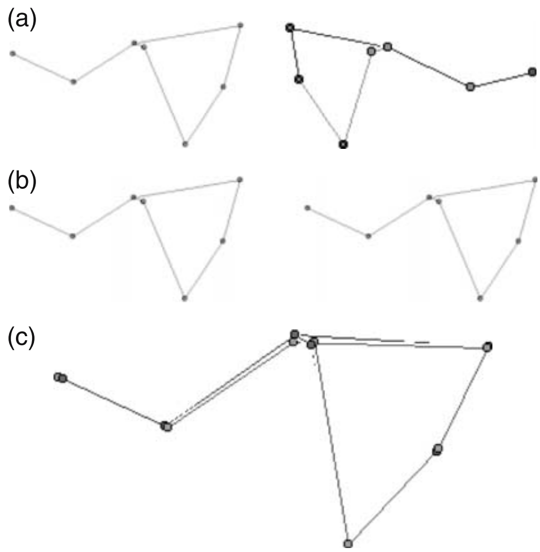

Figure 2. This figure illustrates the construction of shape asymmetry variables used in this analysis for a single individual. Landmark coordinates for the left and right structures of the individual are superimposed using Procrustes superimposition. In this example, using only two specimens, ordinary Procrustes analysis (OPA) is demonstrated. The entire sample of right and left sides from all individuals are fitted through GPA so that differences between left and right sides may be computed. (a) Paired homologous craniofacial landmarks, (b) both sides scaled to centroid size and one side reflected, (c) paired configurations superimposed and rotated for maximum fit. The square root of the sum of the differences between the left and right landmark coordinates is the measure of shape asymmetry.

The illustration is for two specimens and uses ordinary Procrustes analysis (OPA). To jointly process the samples, right and left data for multiple individuals were combined and subjected to generalized Procrustes analysis (GPA). This will produce slightly different numerical results since GPA optimally superimposes individual data to an interactively computed sample mean, while OPA produces optimal pairwise superimpositions (see Slice, 2001 and Chapter 14). The multivariate shape asymmetry data from a GPA were used in the MANOVAs testing Side, Individual, and their interaction following Klingenberg and McIntyre (1998), while the individual pairwise distances (after GPA) were used for the regression analyses.

Centroid size was used for analyses of size asymmetry. The sizes of right and left structures were used for the ANOVA analyses, while the absolute value of their difference was used for the regressions.

Two-way ANOVA models with repeated measures were used to test the main effects of Side, Individual, and the interaction between Side and Individual on size (ANOVA) and shape (MANOVA) for both sex and ancestral subgroups (as defined by Klingenberg and McIntyre, 1998; Palmer and Strobeck, 1986). The Side variable was a fixed factor, representing the signed difference between the right and left configurations, and was a measure of the directional asymmetry component. The Individual was a random factor and was a measure of interindividual variation. The interaction term between Side and Individual was the measure of fluctuating asymmetry. Note that the degrees of freedom for the shape analysis were calculated for the 3D data as the number of landmarks times the number of dimensions, minus seven for the number of translations, rotations, and scaling (Bookstein, 1991). Finally, repeated measures were not available for the entire sample. Therefore, the individuals for whom repeated measures were available ($n = 19$) were analyzed and included in the generalized Procrustes superimposition. The variance between the two repeated measures was assumed to be consistent for the entire sample and was applied to the overall model so that a direct test of the presence of fluctuating asymmetry was obtained.

Polynomial regression was used to assess secular change in the craniofacial region of American White and Black male and female subgroups. To assess the secular trend of fluctuating asymmetry among the total sample and the four subgroups, the size and shape asymmetry variables (centroid size differences and shape distances) were regressed separately on the year of birth by polynomial regression, including linear and quadratic terms. Cubic terms were also tested, but the results were consistent with the quadratic terms. They are not presented here. Birth-years were divided into decade cohorts ranging from 1820–1990. The midpoint of each decade was used as the birth-year cohort term in the polynomial regression analysis. The mean fluctuating asymmetry scores from individuals born within each decade were used for each decade cohort. Since the sample sizes of each decade vary between one and fifty-seven, Weighted Least Squares (WLS) analysis was used to weigh the analysis for the sample size of each decade. Procrustes and statistical analyses and the creation of plots were performed using the programs Morpheus et al. (Slice, 1998) and SPSS, Inc. (SYSTAT, 1998).

RESULTS

The Presence and Types of Size Asymmetry

Table 2 presents a two-way ANOVA model with repeated measures used to test the main effects of Side and Individual and the interaction between the two on the total size variation. The degrees of freedom (df), sum of squares (SS), mean

Table 2. Total size variation. Two-way ANOVA tests for directional and fluctuating asymmetry

	df	SS	MS	F
White males				
Side	1	7.22	7.22	1.40
Individual	180	7879.02	43.77	8.47[a]
Individual × Side	180	930.07	5.167	11.52[a]
Measurement	38	17.05	0.4487	
White females				
Side	1	37.15	37.15	6.83[a]
Individual	116	4411.76	38.03	6.99[a]
Individual × Side	116	631.03	5.44	12.13[a]
Measurement	38	17.05	0.4487	
Black males				
Side	1	21.00	21.00	4.09[b]
Individual	118	5574.08	47.24	9.19[a]
Individual × Side	118	606.41	5.139	11.45[a]
Measurement	38	17.05	0.4487	
Black females				
Side	1	19.43	19.43	4.46[b]
Individual	108	4780.79	44.27	10.16[a]
Individual × Side	108	470.77	4.359	9.72[a]
Measurement	38	17.05	0.4487	

Notes:
[a] $p < 0.001$.
[b] $p < 0.05$.

Table 3. Total shape variation. Two-way MANOVA tests for directional and fluctuating asymmetry

	df	SS	MS	F
White males				
Side	14	0.000047	0.0000033	0.023
Individual	2520	0.422570	0.0001676	1.143[a]
Individual × Side	2520	0.369590	0.0001466	2.560[a]
Measurement	532	0.030484	0.0000573	
White females				
Side	14	0.000254	0.0000181	0.097
Individual	1624	0.306240	0.0001885	1.143[a]
Individual × Side	2520	0.30606	0.0001466	2.560[a]
Measurement	532	0.030484	0.0000573	
Black males				
Side	14	0.00014	0.00001	0.052
Individual	1652	0.30609	0.0001852	0.9719
Individual × Side	1652	0.31767	0.0001905	3.325[a]
Measurement	532	0.030484	0.0000573	
Black females				
Side	14	0.00021	0.000015	0.9009
Individual	1512	0.28998	0.0001917	1.155[a]
Individual × Side	1512	0.25418	0.000168	2.934[a]
Measurement	532	0.030484	0.0000573	

Note:
[a] $p < 0.001$.

sum of squares (MS), and F statistic are provided for each group. Note that Side was significant for White females and Black females and males, indicating the presence of directional asymmetry. As expected, individual variation was significant in all four subgroups. The presence of fluctuating asymmetry (the interaction term between Side and Individual) was also significant for all groups, ranging from the highest among White females to the lowest among Black females.

The Presence and Types of Shape Asymmetry

As with the analysis of size, a two-way MANOVA model with repeated measures was used to test the main effects of Side and Individual and their interaction on total shape variation (Table 3). No directional asymmetry (Side) was present. Individual variation was significant among all groups, except Black males. Black females exhibited the largest amount of individual variation ($F = 11.51$, $p < 0.001$). Finally, all groups exhibited significant levels of fluctuating shape asymmetry.

Table 4. Test for secular change in craniofacial fluctuating size asymmetry, which is regressed onto year of birth for pooled data and by subgroup, showing polynomial regressions

	df	R^2	MS	MSE	F
Total sample term					
Linear	1	0.012	1.02	2.25	0.17
Quadratic	2	0.012	0.42	2.28	0.08
White males term					
Linear	1	0.133	10.77	2.32	2.01
Quadratic	2	0.152	6.13	2.38	1.08
White females term					
Linear	1	0.072	4.06	2.01	1.00
Quadratic	2	0.093	2.66	2.07	0.62
Black males term					
Linear	1	0.081	4.58	1.99	1.15
Quadratic	2	0.081	2.290	2.08	0.53
Black females term					
Linear	1	0.157	13.99	2.50	2.23
Quadratic	2	0.176	7.89	2.58	1.18

Secular Change of Fluctuating Asymmetry Assessed through Polynomial Regression

To explore the secular trends of fluctuating asymmetry for the data as a whole and within each group, polynomial regression was performed on the fluctuating asymmetry of size and birth cohort (the midpoint of each decade of birth) (Table 4). Since no directional asymmetry was noted for White males, the absolute right minus left difference was used as the fluctuating asymmetry score. For the other three subgroups, where directional asymmetry was observed, the directional component (the signed difference between the mean left and right sides) was subtracted so that only fluctuating asymmetry was tested. No significant overall association was detected for size asymmetry and decade of birth.

To further test the relationship between secular patterns in shape asymmetry within each group, polynomial regression was used to test the relationship between fluctuating shape asymmetry (R − L distance) on birth cohort (Table 5). Interestingly, Black females show the only significant linear ($F = 11.92$, $p = 0.005$) and quadratic ($F = 5.48$, $p = 0.024$) relationship between fluctuating shape asymmetry and the decade of birth. The bivariate Pearson's correlation between year of birth and shape asymmetry was 0.669

Table 5. Test for secular change in craniofacial fluctuating shape asymmetry, which is regressed onto year of birth for pooled data and by subgroup, showing polynomial regressions

	df	R^2	MS	MSE	F
Total sample term					
Linear	1	0.072	1648.47	13.31	1.09
Quadratic	2	0.247	3.77	1.32	2.14
White males term					
Linear	1	0.000	1.78	2.13	0.00
Quadratic	2	0.052	1.08	1.79	0.33
White females term					
Linear	1	0.002	0.13	2.09	0.03
Quadratic	2	0.290	7.64	1.84	2.25
Black males term					
Linear	1	0.051	9.44	3.66	0.70
Quadratic	2	0.055	5.06	3.80	0.35
Black females term					
Linear	1	0.520	3540.66	17.23	11.92[a]
Quadratic	2	0.523	1780.46	18.02	5.48[b]

Notes:
[a] $p < 0.001$.
[b] $p < 0.05$.

($p = 0.009$) for the total sample. While significant levels of fluctuating shape asymmetry were present among Black males, White males, and White females, no secular association of fluctuating asymmetry and birth year was present for either linear or quadratic terms.

Patterns in the Secular Trends in Fluctuating Asymmetry

The mean values of size and shape asymmetry were plotted by birth decade for White males (Figure 3) and females (Figure 4), who exhibit similar patterns. The level of fluctuating shape asymmetry appears to remain relatively constant over time, whereas there is a slight trend (though nonsignificant association) for fluctuating size asymmetry to increase over time.

The mean values of size and shape asymmetry were plotted by decade for Black males (Figure 5) and illustrate a similar pattern. Only Black females (Figure 6) exhibit a statistically significant increase in shape asymmetry over time.

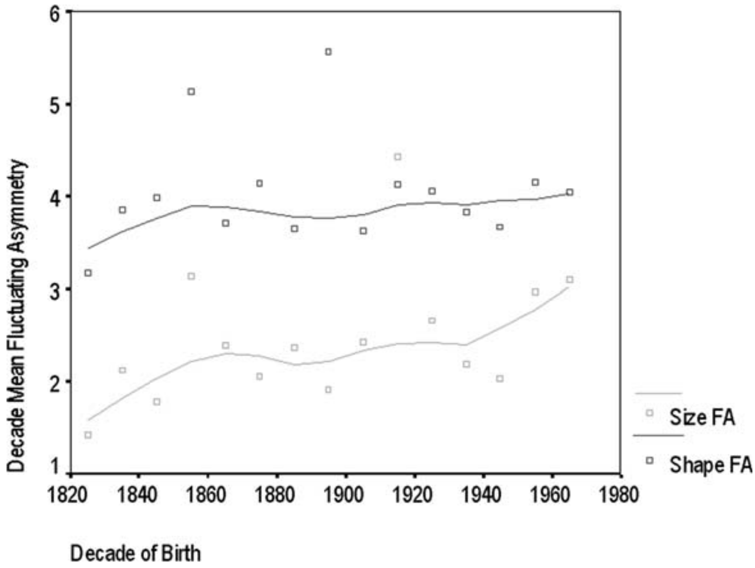

Figure 3. Secular trend of mean fluctuating size and shape asymmetry by decade of birth for White males, with fitted Lowess line.

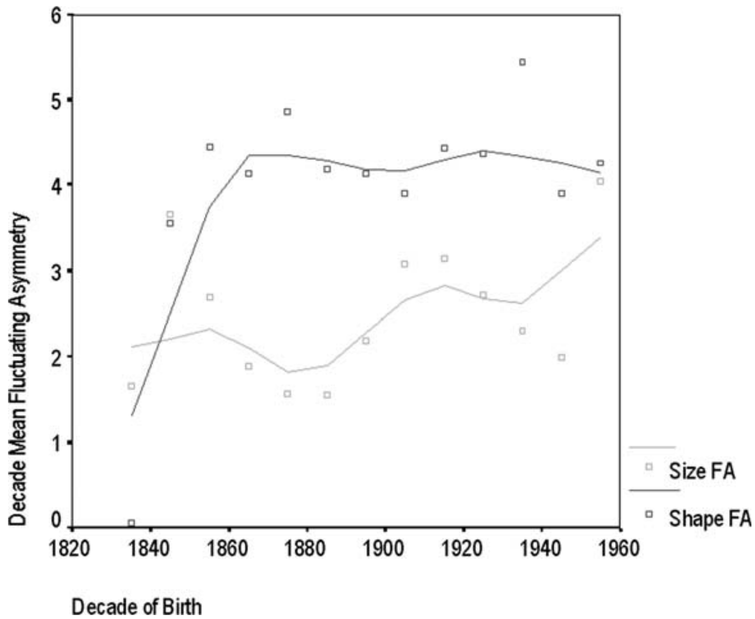

Figure 4. Secular trend of mean fluctuating size and shape asymmetry by decade of birth for White females, with fitted Lowess line.

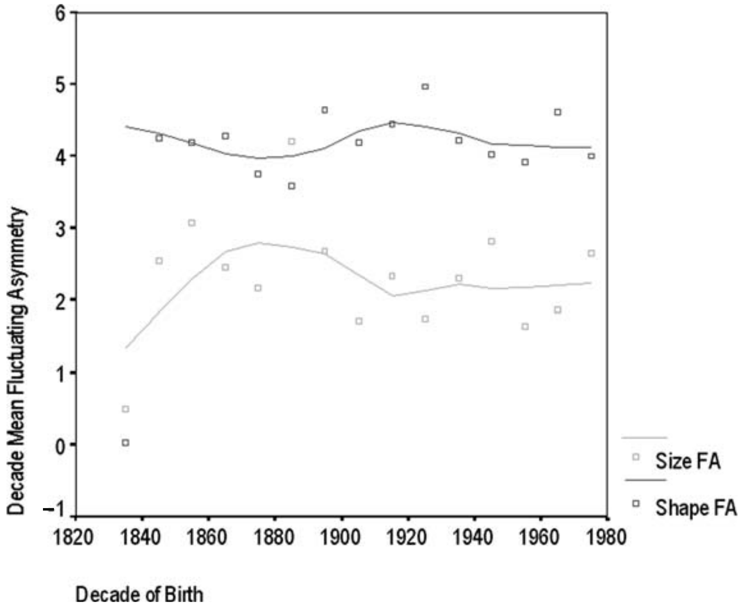

Figure 5. Secular trend of mean fluctuating size and shape asymmetry by decade of birth for Black males, with fitted Lowess line.

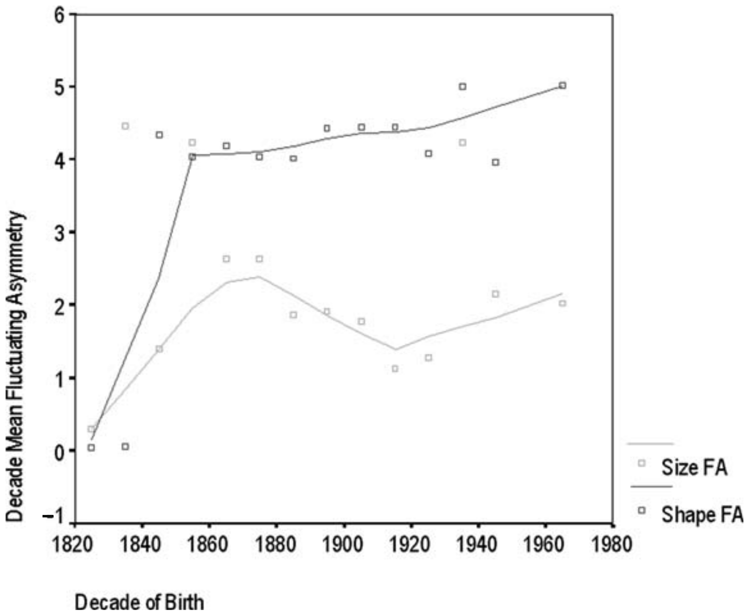

Figure 6. Secular trend of mean fluctuating size and shape asymmetry by decade of birth for Black females, with fitted Lowess line.

DISCUSSION

The purpose of this chapter was to explore a 200-year period of American craniofacial form to determine if morphological change and increased variability is accompanied by changes in the amount or type of asymmetry observed using geometric morphometrics. Both fluctuating and directional asymmetry in the size of craniofacial form are present, with the exception that no directional component is found among White males. Overall, high levels of individual variation are significant among all groups but the highest levels are among African Americans. In contrast, no directional component is found for shape asymmetry in either racial or sex group. Individual variability in shape is significant in all subgroups, except for Black males, yet Black females rank the highest for this value. Further, fluctuating shape asymmetry is present in all groups.

To assess the trends of fluctuating shape and size asymmetry over time, these associations were investigated through polynomial regression. We find that the only significant association of fluctuating shape or size asymmetry and the birth-year cohort is for shape for Black females. This finding suggests facial morphology among this group is becoming less symmetrical over time and may reflect a decline in developmental stability and increasing levels of individual variation. Yet, only about half of the variation observed for Black females can be explained by decade of birth ($r^2 = 0.523$). From the scatter plots, we observe similar, nonlinear patterns in the secular trends of fluctuating asymmetry among all of the groups; shape asymmetry remains relatively constant while size asymmetry fluctuates with a slight increase, although significant associations among three of these groups cannot be substantiated at this time.

Due to the overall tendency toward low r^2 values, a cursory attempt was made to determine whether those individuals with the highest levels of fluctuating asymmetry, particularly during the early 19th century, shared any common life history factors. The cause of death, age at death, geographic location of birth, and even the collection in which the skeletal remains are housed were compared. To date, the only patterns observed are those for birth year.

Economic historians use the secular change of biological variables as a reflection of changing socioeconomic conditions. This is analogous to many studies of developmental stability in anthropology. However, interpreting the causal mechanisms of developmental instability is challenging given the various genetic and environmental components which may, under given conditions, result in asymmetry. In the case of American craniofacial morphology, several influential components have changed. Environmental variants known to result in high levels of asymmetry, such as nutritional deficiencies, infectious disease, and parasitic load have markedly declined in America over the time period in which we are interested. Consequently, we would expect the developmental stability of Americans to increase. Instead, the pattern observed is that developmental stability remains constant, except for Black females who show a decline. Of course, improving environmental conditions does not have a linear relationship with time. Various individuals used in this study had been subject to wide-ranging environmental and material conditions including Slavery during the 19th century, followed by the American Civil War and the Reconstruction Period in the southern United States, and later, the Great Depression. Such fluctuations throughout history likely account for the nonlinear relationship between year of birth and asymmetry. Though this study is preliminary, it suggests some interesting patterns in cranial asymmetry. We look forward to seeing if the observed patterns continue and/or become better resolved as new data are added from modern cases.

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REFERENCES

Auffray, J., Ailbert, P., Renaud, A., Orth, A., and Bonhomme, F., 1996, Fluctuating asymmetry in *Mus musculus* subspecific hybridization: Traditional and Procrustes comparative approach, in: *Advances in Morphometrics*, L. F. Marcus, M. Corti, A. Loy, G. J. P. Naylor, and D. E. Slice, eds., Plenum Press, New York.

Bookstein, F. L., 1991, *Morphometric Tools for Landmark Data*, University of Cambridge Press, London.

Farkas, L. G., and Cheung, G., 1981, Facial asymmetry in healthy North American Caucasians: An anthropometrical study, *Angle Orthod.* 51:70–77.

Gower, J. C., 1985, Generalized Procrustes analysis, *Pschometrika* 40:33–50.

Hershkovitz, I., Livshits, G., Moskona, D., Arensburg, B., and Kobyliansky, E., 1993, Variables affecting dental fluctuating asymmetry in human isolates, *AJPA* 91:349–365.

Howells, W. W., 1973, *Cranial Variation in Man: A Study by Multivariate Analysis of Patterns of Difference among Recent Human Populations*, Papers of the Peabody Museum No. 67, Peabody Museum, Harvard Museum, Cambridge, MA.

Jantz, R. L. and Brehme, H., 1993, Directional and fluctuating asymmetry in the palmar interdigital ridge-counts, *Anthrop. Anz.* 51:59–67.

Jantz, R. L. and Meadows Jantz, L., 2000, Secular change in craniofacial morphology, *Am. J. Hum. Biol.* 12:327–338.

Klingenberg, C. P., Badyaev, A. V., Sowry, S. M., and Beckwith, N. J., 2001, Inferring developmental modularity from morphological integration: Analysis of individual variation and asymmetry in bumblebee wings, *Am. Nat.* 157(1):11–23.

Klingenberg, C. P. and McIntyre, G. S., 1998, Geometric morphometrics of developmental instability: Analyzing patterns of fluctuating asymmetry with Procrustes methods, *Evolution* 52(5):1361–1375.

Leamy, L. J., Routman, E. J., and Cheverud, J. M., 2002, An epistatic genetic basis for fluctuating asymmetry of mandible size in mice, *Evolution* 56(3):642–653.

Mardia, K. V., Bookstein, F. L., and Moreton, I. J., 2000, Statistical assessment of bilateral symmetry of shapes, *Biometrika* 87(2):285–300.

Palmer, A. R. and Strobeck, C., 1986, Fluctuating asymmetry: Measurement, analysis, Patterns, *Annu. Rev. Ecol. Syst.* 17:391–421.

Palmer, A. R. and Strobeck, C., 1992, Fluctuating asymmetry as a measure of developmental stability: implications of non-normal distributions and power of statistical tests, *Acta Zool. Fenn.* 191:57–72.

Peck, S., Peck, L., and Kataja, M., 1991, Skeletal asymmetry in esthetically pleasing faces, *Angle Orthod.* 61:43–47.

Richtsmeier, J., 1987, A comparative study of normal, Crouzon and Apert craniofacial morphology using finite-element scaling analysis, *AJPA* 74:473–493.

Rutherford, S. L., 2000, From genotype to phenotype: Buffering mechanisms and the storage of genetic Information, *Bioessays* 22:1095–1105.

Sciulli, P. W., Doyle, W. J., Kelley, C., Siegel, P., and Siegel, M. I., 1979, The interaction of stressors in the induction of increased levels of fluctuating asymmetry in the laboratory rat, *AJPA* 50:279–284.

Siegel, M. I., Doyle, W. J., and Kelley, C., 1977, Heat stress, fluctuating asymmetry and prenatal selection in the laboratory rat, *AJPA* 46:121–126.

Slice, D., 2001, Landmark coordinates aligned by Procrustes analysis do not lie in Kendall's shape space, *Sys. Biol.* 50(1):141–149.

Slice, D. C., 1998, *Morpheus* et al.: *Software for Morphometric Research*, Revision 01-31-00. Department of Evolution and Ecology, State University of New York, Stony Brook, NY.

Slice, D., Bookstein, F. L., Marcus, L. F., and Rohlf, F., 1996, A glossary for geometric morphometrics, in: *Advances in Morphometrics*, L. F. Marcus, M. Corti, A. Loy, G. J. P. Naylor, and D. E. Slice, eds., Plenum Press, New York, pp. 531–551.

SPSS, Inc., 1998, SYSTAT Statistics, SPSS, Inc., Chicago.

Waddington, C. H., 1957, *The Strategy of Genes*, MacMillan Co, New York.