

Fluctuating Asymmetry and Canalization: An Appraisal Based on a-b Ridge Counts Among Indian Populations With Diverse Backgrounds

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ABSTRACT The relationship between fluctuating asymmetry, measured as the absolute difference between the right and left a-b ridge counts, and total a-b (R + L) ridge count was studied in an assortment of Indian population samples representing a wide spectrum of socioeconomic and occupational backgrounds. They included marine fishermen, inland and estuarine fishermen as well as migrants and their parental counterparts, tribes, and castes of different hierarchy- lower, middle, and upper. The samples together numbered a total of 3,239 subjects, 2,240 males and 999 females. The results failed to support Jantz and Webb's (1980) hypothesis of a quadratic relationship between fluctuating asymmetry of a-b ridge count and its phenotypic value. Only 3 of 22 samples (about 13%) showed a significant fit with a reasonable degree of consistency over a set of independent random subsamples; even initially only 7 of 22 (about 30%) samples showed a significant fit, or nearly so. Supplementary evidence drawn from these populations with reference to the relationship between fluctuating asymmetry and heterozygosity levels and inbreeding coefficients was also consistent with the interference that fluctuating asymmetry of a-b as it is measured and examined at the population level does not reflect canalization. *Am. J. Hum. Biol.* 11:367-381, 1999.

Fluctuating asymmetry (FA) is generally considered a useful measure of developmental homeostasis or canalization. It has been studied in a number of organisms, including humans (see Livshits and Kobylansky, 1991, for a review). A high level of FA is thought to indicate that the organism has low capacity for buffering adverse environmental effects that could deflect the course of its genetically determined program of development (Van Valen, 1962). Both exogenous and endogenous stresses appear to determine the degree of asymmetry. For example, high levels of asymmetry have been found in fish populations inhabiting waters around industrial centers and in ponds containing unusually high concentrations of mercury and low pH (Leary and Allendorf, 1989). Similar results were obtained among rats and other animals under laboratory conditions. Dental asymmetry in some human populations is also attributed to environmental influences (Doyle and Johnston,

1977). On the other hand, the levels of heterozygosity, inbreeding, and other endogenous stresses like chromosomal abnormalities and polygenic morbidity were also associated with an increased FA in humans (Livshits and Kobylansky, 1991) and in other animal species.

Although the initial emphasis among humans had been on the study of dental asymmetry, dermatoglyphic traits were more frequently studied recently and are considered suitable markers for the study of developmental homeostasis. This is because dermatoglyphic features are formed before the 19th week of gestation (Penrose and Ohara, 1973) and are not amenable to change

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thereafter due to age and/or environmental factors. Consequently, they may preserve an earlier stage of fetal development than most characters that are examined post-natally. The local disruptions occurring early in fetal development may have more general consequences for the organism (Jantz and Webb, 1980).

Different but somewhat related approaches were used in the study of dermatoglyphics, particularly the FA of a-b ridge count and canalization. Most of the studies support the notion that FA reflects a degree of developmental noise. For example, individuals with congenital abnormalities like cleft lip who manifest decreased heterozygosity exhibit elevated levels of FA in the a-b ridge count, compared to the normal controls (Adam and Niswander, 1967; Wolf and Gianas, 1976, 1977). Similarly, evidence for increased a-b asymmetry is consistently found in schizophrenics compared to normals (Markow and Wandler, 1986; Markow and Gottesman, 1989; Mellor, 1992). Further, Rose et al. (1987) observed that MZ twin pairs asymmetric for a-b ridge count were significantly less similar in the performance on many psychological tests. At the population level, Markow and Martin (1993) studied an inbred isolate and found a significantly greater FA of a-b ridge count compared to non-inbred groups. While Malhotra (1987) observed racial funds in finger ridge counts among 69 populations from different parts of the world, Jantz and Webb (1982) observed such patterns in a-b ridge count asymmetry.

On the other hand, Jantz and Webb (1980) examined the relationship between FA and the phenotypic value of a-b ridge count, the fit was quadratic with an U-shaped curve, implying that the extreme phenotypic values were associated with greater asymmetry compared to those near the mean. The authors hypothesized that this reflected the effectiveness of the canalizing system during development. Implicit in the hypothesis is the assumption that, if asymmetry bears no relationship to canalization, it is expected to occur randomly throughout the range of phenotypic values. On the other hand, if the extreme values, result from poor canalization, and if asymmetry provides a measure of canalization, extreme phenotypic values should be more asymmetric than values close to the mean. It is also assumed that the individuals

around the population mean are more heterozygous, hence less asymmetric than the others. This hypothesis has been tested in only two other samples (Jantz and Brehme, 1993; Arrieta et al., 1995). Jantz and Brehme (1993) found results consistent with the hypothesis in a large sample of Germans, while Arrieta et al. (1995) did not find convincing evidence in a Basque population in which only females, not males, showed a quadratic fit. However, Livshits and Kobylansky (1987), using an operationally different yet implicitly similar approach, obtained results supporting the Jantz and Webb (1980) hypothesis. FA of different dermatoglyphic traits was greater in anthropometrically polyextreme individuals compared to polymodal ones. The two approaches were similar in the assumption that the phenotypic values around the mean are more heterozygous and less asymmetric compared to the extremes.

This positive evidence naturally tempts one to conclude that dermatoglyphic asymmetry, and particularly that of the a-b ridge count, can be used as a measure of the degree of developmental homeostasis. Of particular interest and relevance to the present paper is the Jantz and Webb (1980) hypothesis, the biological significance of which was questioned by Chakraborty and Jin (1991). It may be pertinent to note that Jantz and Webb (1980) recognized the preliminary nature of their study and suggested further studies among populations with diverse backgrounds, genetic, and environmental, to test if the observed relationship is universal. The present paper attempts to test the relationship between FA and the phenotypic value of the a-b ridge count among 15 male and 7 female Indian population samples from diverse socioeconomic and occupational backgrounds: migrant fishermen, their parental counterparts, inland and estuarine fishermen, middle and upper ranking caste groups, and the tribals. The universal applicability, and hence biological significance of the hypothesis of Jantz and Webb (1980) was tested. Although the samples represent only one geographical region of the world, they encompass populations covering the entire spectrum of socioeconomic and ethnic backgrounds within India. Average heterozygosity at 11 biochemical loci and average inbreeding coefficients were available for some of the popula-

TABLE 1. *Geographical and socioeconomic backgrounds of the populations along with inbreeding coefficients and sample sizes**

Population	Sex	Sample size	Geographic background	Occupation	Inbreeding coefficient
Migrant Fishermen					
Vadabaliya of Penticotta (VP)	M	101	Puri, Orissa	Marine fishermen	0.032
	F	97			
Vadabaliya of Vadapeta (VV)	M	90	Puri, Orissa	Marine fisherman	0.023
	F	137			
Jalary (J)	M	111	Puri, Orissa	Marine & lake fishermen	0.020
	F	50			
Parental Fishermen ¹					
VPP	M	148	Coastal Andhra & Orissa	Marine fishermen	0.026
VVP	M	141	Coastal Andhra & Orissa	Marine fisherman	0.015
JP	M	139	Coastal Andhra & Orissa	Marine & estuarine fishermen	0.017
Estuarine and Inland Fishermen and Agriculturists					
Palle	M	152	Coastal Andhra	Marine & estuarine fishermen	0.018
Vadde	M	317	Kolleru, A.P.	Inland Fishermen	0.022
	F	387			
Reddy	M	160	Chittoor, A.P.	Agriculturists	0.028
Tribes					
Raj Gond	M	328	Gadchiroli dist. Maharashtra	Hunter-gatherers turned to terrace & settled agriculturists	0.005
	F	197			
Maria Gond	M	233	Gadchiroli dist. Maharashtra	Hunter-gatherers turned to terrace & settled agriculturists	0.006
	F	94			
Pardhan	M	56	Gadchiroli dist. Maharashtra	Hunter-gatherers turned to terrace & settled agriculturists	0.007
	F	37			
Upper Castes					
Rajputs	M	113	Kumaon region	Warriors & agriculturists	—
Kumaon Brahmins	M	91	in U.P.	Service	—
Ayengar Brahmins	M	60	Villiputtur, T.N.	Service	—

*AP, Andhra Pradesh; UP, Uttar Pradesh; TN, Tamilnadu.

¹VPP, VVP, and JP are parental populations, respectively, of the VP, VV, and J migrants.

tions; they were also examined for a possible relationship with asymmetry.

MATERIALS AND METHODS

The 22 samples (15 male and 7 female) consisted of a total of 3,239 subjects (2,240 males and 999 females) drawn from 15 endogamous caste populations. The names of the populations, socioeconomic, occupational and geographical backgrounds, and sample sizes are furnished in Table 1. Sample sizes in most cases are reasonably large, being close to 100 or larger. Eight populations are fishermen, although of different kinds: deep sea fishermen, shallow water fishermen, and inland fishermen, all from the Eastern coast of India, specifically from the Andhra and Orissa coasts. There are also migrant and parental fishermen. Most of these populations had been pursu-

ing the traditional mode of fishing until very recently. Out of the remaining seven, three populations belong to the scheduled tribal populations of Gadchiroli district in Maharashtra. Although traditionally hunter-gatherers, they have now largely taken up settled and terrace cultivation. The Reddies are land-owning agriculturists and are middle ranking in the traditional social hierarchy. They are from chittoor district of Andhra Pradesh. The remaining three belong to the upper castes. The Ayengar Brahmins are from Tamilnadu, while the Rajputs and the other Brahmin group reside in the Kumaon region of Uttar Pradesh in India. The Rajputs, who were warriors traditionally, currently engage in agriculture and salaried jobs; the members of two Brahmin groups mostly depend on sedentary occupations like salaried jobs.

The populations in the present study provide a wide spectrum of socioeconomic, occupational, and other lifestyle backgrounds. The three migrant populations, having migrated to Puri at different points of time, not only provide contrasts in relative levels of adaptation to the local environment but also to their parental counterparts, who have lived in their native areas for generations. The migrant populations also show certain striking differences in mode of occupations, although all of them are primarily marine fishermen. While the VP fish in deep sea, the other two groups fish in the shallow waters. Jalaris also fish in the nearby Chilka lake in the lean season. In comparison, the Palle fish mostly in the Godavary estuary and the Vadde are inland fishermen from Kolleru lake near Vijayawada. While the samples for the three migrant groups were drawn from Puri, their parental counterparts were sampled from about 40 villages along the 300 mile long coast of Ganjam district in Orissa and Srikakulam, Visakapatnam, and East and West Godavari districts of Andhra Pradesh. All of these groups practice close consanguineous marriages, rank low in caste hierarchy, and have poor socioeconomic status. The sanitary and health conditions are poor with very high infant mortality rate (Reddy, 1984; Reddy et al., 1987) and little access to modern medical amenities. The three tribal groups, on the other hand, are socioeconomically quite similar yet present a contrasting ecological milieu, being part of the forest ecology. The practice of consanguineous marriages is restricted and thus the inbreeding coefficients are relatively low compared to the fishermen and middle ranking Reddies (Table 1).

The middle ranking Reddies and the upper castes provide a socioeconomic contrast to the fishermen and tribal populations. They are, on average, significantly more literate and economically stronger with better access to modern medical amenities. Infant mortality rates are expected to be low among them, especially compared to the other groups in the study. While the Reddies and Ayengar Brahmins from the south practice close consanguineous marriages, the Aryan kinship system prohibits the two Kumaon groups from doing so.

The dermal prints which form basis for the present study were collected and analyzed mostly by the present investigator over a period of about 20 years, sometimes with the help of colleagues. The a-b ridge

counts were made following Holt (1968). Fluctuating asymmetry was taken as the absolute difference between a-b counts of the right and left hands and was designated as $|R - L|$. With the help of the SPSS package, the $|R - L|$ values were regressed on the $R + L$ values of a-b ridge count; the linear and quadratic terms were entered.

RESULTS

Means and SDs of total a-b ridge count and directional and absolute asymmetries

The means and SDs of the total a-b count and directional ($R - L$) and absolute ($|R - L|$) asymmetries for the different categories of populations are presented in Table 2. The mean values of total a-b ridge count are consistently smaller for males and females of each of the tribal populations compared to the castes, irrespective of the hierarchy—lower, middle, or upper. The castes show relative homogeneity with a few exceptions. While the directional asymmetry seems to favor the left hand in the dozen caste populations, it favors the right hand in the three groups of tribals in both sexes. Whereas it averages to slightly less than minus one ridge in the three upper castes, the middle caste, and the inland and marine-indigenous fishermen, it is much larger in the tribes (+1.7 ridges in males and +2 in case of females) and the three groups of migrant fishermen at Puri (-1.7 ridges). The directional asymmetry is statistically significant at least in some populations among the tribes and migrant groups of fishermen. Nevertheless, except in one of the 22 samples (VV females), it is not significantly related to the total a-b count; hence, correction for this was not attempted in the absolute asymmetry prior to the regression analyses.

For absolute asymmetry, the tribal groups also show the largest values, although the middle ranking Reddies, two of the three upper castes and a couple of samples of fishermen show relatively large values. On the average, the fisherfolk, migrant and parental, show the smallest mean value for FA. Contrary to expectations, the parental counterpart of each migrant group of fishermen at Puri show larger mean FA. The three tribal groups show not only the reversed pattern of asymmetry compared to the other groups, but the phenotypic values ($R + L$) are also much smaller, which may suggest a different developmental schedule in these populations.

TABLE 2. Means and standard deviations of the total a-b ridge count, and directional and fluctuating asymmetries

Population	Sex	Total a-b (R + L)		Directional (R - L)		Fluctuating (R - L)	
		Mean	SD	Mean	SD	Mean	SD
Migrant Fishermen							
VP	M	73.98	17.00	-1.51	3.39	2.87	2.34
	F	73.73	12.48	-1.18	3.08	2.60	2.02
VV	M	79.18	11.33	-1.93	3.31	2.98	2.41
	F	76.92	14.03	-2.35	3.74	3.45	2.75
J	M	78.44	9.75	-1.90	3.62	3.25	2.47
	F	78.66	11.15	-2.18	4.28	3.62	3.13
Parental Fishermen							
VPP	M	73.01	9.15	-1.01	3.98	2.93	2.87
VVP	M	71.60	10.11	-1.52	4.18	3.43	2.82
JP	M	69.87	10.01	-0.27	4.33	3.40	2.69
Estuarine and Inland Fishermen and Agriculturists							
Palle	M	75.53	9.09	-0.69	3.93	3.06	2.54
Vadde	M	73.21	10.27	-1.02	4.17	3.25	2.92
	F	71.75	9.52	-0.54	5.08	3.91	3.28
Reddy	M	72.17	10.07	-1.46	4.93	3.78	3.48
Tribes							
Raj Gond	M	67.30	9.00	1.62	4.30	3.50	2.97
	F	66.16	9.69	1.08	4.96	3.75	3.41
Maria Gond	M	67.51	8.45	1.89	4.16	3.50	2.94
	F	68.31	9.55	1.56	4.33	3.73	2.67
Pardhan	M	66.73	8.10	1.45	4.22	3.70	2.46
	F	67.49	8.22	3.65	4.19	4.57	3.13
Upper Castes							
Rajputs	M	76.58	11.81	-0.71	4.79	3.45	3.38
Kumaon Brahm	M	73.35	9.55	-0.98	4.59	3.51	3.09
Ayengar Brahm	M	78.63	9.01	-1.03	3.86	3.03	2.58

Sex differences in the three variables are not significant in any of the populations. However, while the heterogeneity in mean total a-b count is significant among both the migrant ($F = 4.62$, $P = 0.011$) and parental ($F = 9.01$, $P = 0.000$) populations in males, such a heterogeneity is apparent in the mean values of directional ($F = 3.09$, $P = 0.047$) and fluctuating ($F = 3.86$, $P = 0.022$) asymmetries among the migrant females of the fishermen. The mean directional asymmetry is also significantly heterogeneous among the tribal females ($F = 4.67$, $P = 0.01$), mainly because of the unusually high mean value in the small sample of Pardhans.

RELATIONSHIP BETWEEN THE
FLUCTUATING ASYMMETRY AND TOTAL
a-b RIDGE COUNT:
REGRESSION ANALYSES

Migrant and parental fishermen

The quadratic regression equations of R - L on R + L for the six male and three female samples of fishermen are presented below.

$$\text{VP (males) } |R - L| = 0.06783*(R + L) - 0.000384*(R + L)^2 + 0.067.$$

$$\text{VP (females) } |R - L| = 0.04887*(R + L) - 0.000270*(R + L)^2 + 0.506.$$

$$\text{VV (males) } |R - L| = 0.12683*(R + L) - 0.000849*(R + L)^2 + 1.632.$$

$$\text{VV (females) } |R - L| = 0.04361*(R + L) - 0.000039*(R + L)^2 + 0.334.$$

$$\text{J (males) } |R - L| = -0.66190*(R + L) + 0.004036*(R + L)^2 + 29.96.$$

$$\text{J (females) } |R - L| = -0.65742*(R + L) + 0.004339*(R + L)^2 + 27.95.$$

$$\text{VPP (males) } |R - L| = 0.15535*(R + L) - 0.000968*(R + L)^2 - 3.18.$$

$$\text{VVP (males) } |R - L| = -0.30861*(R + L) + 0.002220*(R + L)^2 - 13.91.$$

$$\text{JP (males) } |R - L| = 0.03173*(R + L) + 0.000052*(R + L)^2 + 0.92.$$

Analyses of variance of the regressions suggest that, of the 9 samples, only Jalary

TABLE 3. Results of ANOVA of the quadratic regression of $|R - L|$ $a-b$ on the total $a-b$ ($R + L$) ridge count among Jalary males, a migrant group

Source of variation	D.F.	Total sum of squares	Mean squares	F-value	P
Linear	1	2.46	2.46	0.40	0.530
Residual	109	666.48	6.12		
Quadratic	2	35.95	17.97	3.07	0.051
Residual	108	632.99	5.86		
Reduction in SS due to quadratic	1	33.49	33.49	5.71	0.019

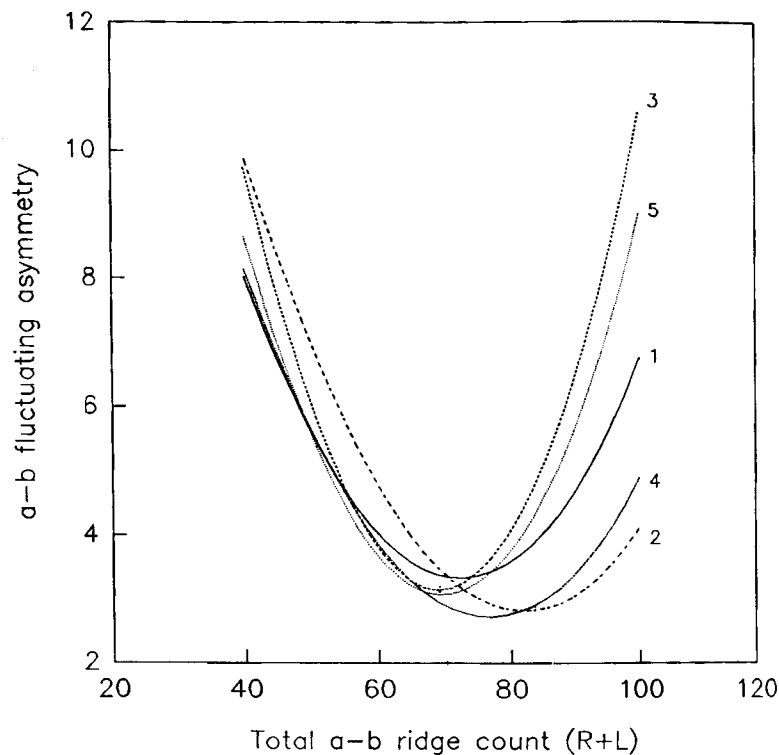


Fig. 1. Fitted quadratic regression curves for the 5 groups that show significant fits. Numbers 1-4 denote Reddy, Jalary, Vadde and Palle males, respectively, and 5 Raj Gond females.

males (Table 3) show a marginally significant ($P = 0.051$) fit. Although the linear regression in this sample is not significant, the reduction in the sum of squares due to the quadratic regression is significant ($P = 0.019$). The fitted regression curve for this sample is shown in Figure 1. The minimum asymmetry occurs just about 5 ridges above the observed mean.

Inland and estuarine fishermen and agriculturists

The quadratic regression equations for Vadde males and females and for Palle and Reddy males are presented below.

$$\text{Palle (males) } |R - L| = -0.61646*(R + L) + 0.004015*(R + L)^2 + 26.39.$$

$$\text{Vadde (males) } |R - L| = -1.07660*(R + L) + 0.007786*(R + L)^2 + 40.37.$$

$$\text{Vadde (females) } |R - L| = -0.05905*(R + L) + 0.000486*(R + L)^2 + 5.60.$$

$$\text{Reddy (males) } |R - L| = -0.64841*(R + L) + 0.004479*(R + L)^2 + 26.80.$$

The results of ANOVA suggest that all three male samples (Vadde, Palle and Reddy) in this category show a significant quadratic

TABLE 4. Results of ANOVA of the quadratic regression of $|R - L|$ a-b on the total a-b (R + L) ridge count among Palle males, an estuarine group of fishermen living in contiguous and overlapping areas of the parental groups of fishermen in the present study

Source of variation	D.F.	Total sum of squares	Mean squares	F-value	P
Linear	1	0.65	0.65	1.00	0.752
Residual	150	975.82	6.51		
Quadratic	2	44.67	22.33	3.57	0.031
Residual	149	931.80	6.25		
Reduction in SS due to quadratic	1	44.01	44.01	7.04	0.009

TABLE 5. Results of ANOVA of the quadratic regression of $|R - L|$ a-b on the total a-b (R + L) ridge count among Vadde males, an inland fishermen group of Kolleru lake in Andhra Pradesh, India

Source of variation	D.F.	Total sum of squares	Mean squares	F-value	P
Linear	1	87.42	87.42	6.89	0.009
Residual	316	4012.19	12.70		
Quadratic	2	468.45	234.22	20.32	0.000
Residual	315	3631.17	11.53		
Reduction in SS due to quadratic	1	381.02	381.02	33.05	0.000

TABLE 6. Results of ANOVA of the quadratic regression of $|R - L|$ a-b on the total a-b (R + L) ridge count among land-owning agriculturists

Source of variation	D.F.	Total sum of squares	Mean squares	F-value	P
Linear	1	8.00	8.00	0.66	0.418
Residual	158	1913.35	12.11		
Quadratic	2	67.09	33.55	2.84	0.061
Residual	157	1854.25	11.81		
Reduction in SS due to quadratic	1	59.10	59.10	5.00	0.027

fit (Tables 4, 5, 6). The linear regression is not significant in the Palle and Reddy. Nevertheless, the reduction in the sum of squares due to the quadratic regression is significant in each of the three samples. The fitted regression curves for the three populations are also shown in Figure 1. In each of the three cases, the minimum asymmetry corresponds closely with the observed mean a-b count, within two ridges above the mean value. The fit is not significant in case of Vadde females.

Tribal populations

The regression equations for the six tribal populations, three male, and three female, are given below.

$$\text{Raj Gond (males)} |R - L| = -0.21146*(R + L) + 0.001681*(R + L)^2 + 9.98.$$

$$\text{Raj Gond (females)} |R - L| = -0.89004*(R + L) + 0.006393*(R + L)^2 + 34.05.$$

$$\text{Maria Gond (males)} |R - L| = 0.16862*(R + L) - 0.001017*(R + L)^2 - 3.18.$$

$$\text{Maria Gond (females)} |R - L| = 0.08945*(R + L) - 0.000593*(R + L)^2 + 0.45.$$

$$\text{Pardhan (males)} |R - L| = -0.37847*(R + L) + 0.002809*(R + L)^2 + 16.26.$$

$$\text{Pardhan (females)} |R - L| = 0.73226*(R + L) - 0.005698*(R + L)^2 - 18.53.$$

The ANOVA of the regressions suggests that the quadratic fit as well as the reduction in the sum of squares due to the quadratic regression is significant only in Raj Gond females (Table 7). The fitted regression curve for this population (no. 5) is included in Figure 1. As expected, the minimum asymmetry occurs just 2 ridges above the observed mean.

The upper castes

The quadratic regression equations for the three upper caste male samples are presented below.

TABLE 7. Results of ANOVA of the quadratic regression of $|R - L|$ a-b on the total a-b (R + L) ridge count among Raj Gond females, a traditional tribe in India

Source of variation	D.F.	Total sum of squares	Mean squares	F-value	P
Linear	1	47.41	47.41	4.15	0.043
Residual	195	2227.90	11.43		
Quadratic	2	224.54	112.27	10.62	0.000
Residual	194	2050.77	10.57		
Reduction in SS due to quadratic	1	177.13	177.13	16.76	0.000

TABLE 8. Results of ANOVA of the quadratic regression of $|R - L|$ a-b on the total a-b (R + L) ridge count among Rajput males, an upper caste-warrior group of Northern India

Source of variation	D.F.	Total sum of squares	Mean squares	F-value	P
Linear	1	103.68	103.68	9.82	0.002
Residual	111	1172.31	10.56		
Quadratic	2	191.98	95.99	9.74	0.000
Residual	110	1084.01	9.85		
Reduction in SS due to quadratic	1	88.30	88.30	8.96	0.003

TABLE 9. Results of ANOVA of the quadratic regression of $|R - L|$ a-b on the total a-b (R + L) ridge count among the upper caste Brahmin group of the Kumaon region in India

Source of variation	D.F.	Total sum of squares	Mean squares	F-value	P
Linear	1	26.93	26.93	2.88	0.094
Residual	89	833.82	9.37		
Quadratic	2	197.80	98.90	13.13	0.000
Residual	88	662.95	7.53		
Reduction in SS due to quadratic	1	170.87	170.87	22.68	0.000

Rajputs (males) $|R - L| = -0.44653*(R + L) + 0.003277*(R + L)^2 + 17.97$.

Kumaon Brahmins (males) $|R - L| = -1.70925*(R + L) + 0.011315*(R + L)^2 + 66.98$.

Ayengar Brahmins (males) $|R - L| = -0.18344*(R + L) + 0.001453*(R + L)^2 + 8.36$.

The ANOVA of regressions suggests that in the two Kumaon groups, the Rajputs and Brahmins, the quadratic fit (Tables 8 and 9) as well as the reduction in the sum of squares due to the quadratic regression are significant ($P < 0.01$). The fitted regression curves are shown in Figure 2. It is apparent that the minimum FA corresponds very closely with the observed phenotypic mean, conforming to the expectations of the hypothesis. The R^2 values are the largest among the groups that show significant fits so far. While R^2 ranges between 2% and 8% among the others, it is as high as 13% among the Rajputs and 23% among the Ku-

maon Brahmins. However, in one of the most socioeconomically advanced Ayengar Brahmins of Southern India, FA fails to show a quadratic fit with the phenotypic value of total a-b ridge count, and the amount of variance as indicated by R^2 is very low.

The good fits observed among the two Kumaon groups suggested a need to look at the raw data more closely. In the process, several values (4 of 113 in Rajputs and 2 of 91 in the Brahmins) were identified as outliers. For example, in some cases, the right a-b or left a-b ridge counts were so high that they were almost equal to the population mean of the right + left a-b ridge count. These two samples were re-analyzed after excluding these cases. In the Rajputs the quadratic fit totally disappears (Figure 2), bringing R^2 to a low value of 0.5%; in the Brahmins, the reduction in the sum of squares due to the quadratic regression, is marginally significant. However, the R^2 decreases to 4.5% from an initial value of 23%.

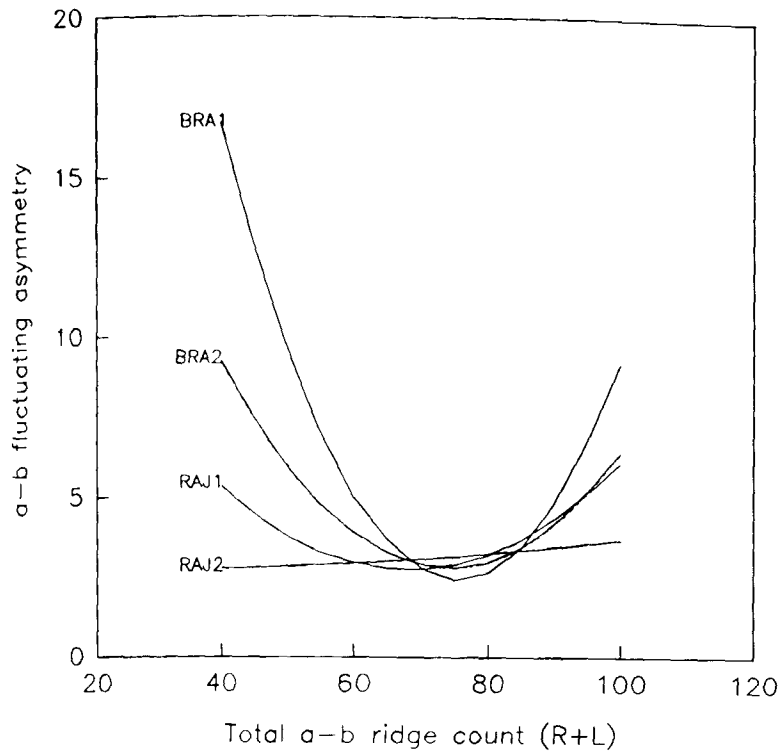


Fig. 2. Fitted quadratic regression curves for the two upper caste groups, Rajput and Brahmin males, before (1) and after (2) removing the outliers.

DISCUSSION

The analysis of FA in such a wide array of populations provides a means to critically evaluate results and examine the problem in a wider perspective. First and foremost, however, the analysis permits assessment of how well or how poorly the observed results conform to the expectations of the Jantz and Webb (1980) hypothesis of a quadratic relationship between a-b FA and its phenotypic value. The overall agreement is rather poor. In only seven of the 22 samples is the quadratic fit significant ($P < 0.05$) or nearly so. One of the implications of this finding is that if such studies are conducted in isolated individual populations, the probability of not obtaining a significant quadratic fit is at least 70%. As noted earlier, the exclusion of outliers from the two Kumaon groups reduced the good fit down to relatively nonsignificant levels. In two of the seven samples (the Jalary and Reddy males), although the reduction in the sum of squares due to the quadratic regression is

significant, the quadratic regression itself fails marginally to reach significant levels. An attempt to test the consistency in the observed fits through a 70%, 60%, and 50% independent random subsamples of each of the seven successful samples suggests a high degree of uncertainty in obtaining such a fit, except in the Kumaon Brahmin and Vadde males and Raj Gond females. This leads to the inference that there may be little biological reality in the observed pattern of quadratic fits. Given that the proportion of variance in $|R-L|$ explained by the total a-b ridge count is rather low, a relatively larger size of the sample for some of the populations would have enhanced the degree of confidence in this inference. The quadratic fit seems to be more consistently observed in two European populations studied thus far. Presumably, therefore, this inference has to be limited to Indian populations until more data from other regions become available.

How can the reasonably good fit in at least some populations be explained? One of

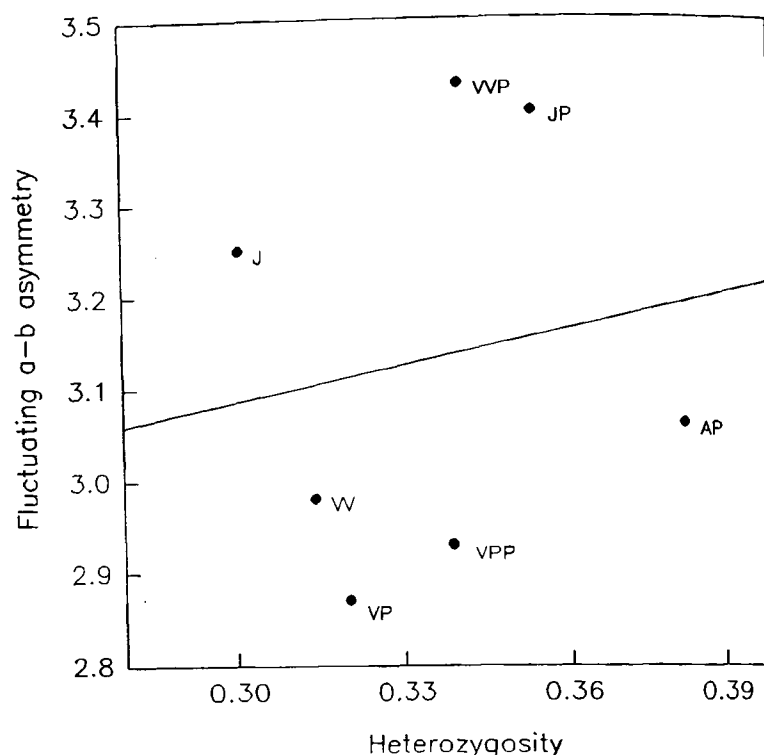


Fig. 3. Bivariate plot of mean fluctuating a-b asymmetry and average heterozygosity at the 11 biochemical blood groups, redcell enzymes and serum proteins-loci for the 7 populations.

the plausible hypotheses can be that certain populations are better canalized than others; hence, they show a good fit. It is suggested that, due to revolutionary progress in medicine, the present generation of westernized/urbanized populations must have preserved many deleterious genotypes due to relaxation of stabilizing selection (Terrenato et al., 1981; Ulizzi et al., 1981) and this might lead to greater degree of FA among such populations (Livshits and Kobylansky, 1991). There is, however, no pattern observed in the nature of the populations that showed significant fit. For example, among the seven populations that showed a significant fit, there are marine fishermen like the Jalary, inland fishermen, tribals, and middle and high ranking groups, representing the socioeconomic spectrum in India. These populations also show different levels of modernization and access to modern medical amenities. While the fishermen and tribal populations live under most natural conditions, the Brahmins and Rajputs are

relatively more urbanized. Similarly, this range of socioeconomic variety is apparent even among the populations that did not show a significant fit. There is also no pattern apparent in the mean FA among these populations, pertaining to socioeconomic, occupational, or migrational backgrounds to substantiate the earlier hypotheses of increased FA among modernized populations due to relaxation of selection (Livshits and Kobylansky, 1991), or of greater FA among populations undergoing higher levels of stress (Niswander and Chung, 1965; Perzigian, 1977; Doyle and Johnston, 1977; Leary and Allendorf, 1989), although the precise nature of stress and its mode of operation in human embryonic development is not clear. Several earlier attempts also failed to detect any pattern in finger ridge count asymmetry among populations presumably undergoing different levels of stress (Jantz, 1975; Malhotra, 1987). Nevertheless, environmental and prenatal factors may be acting longer on the a-b ridge count compared to

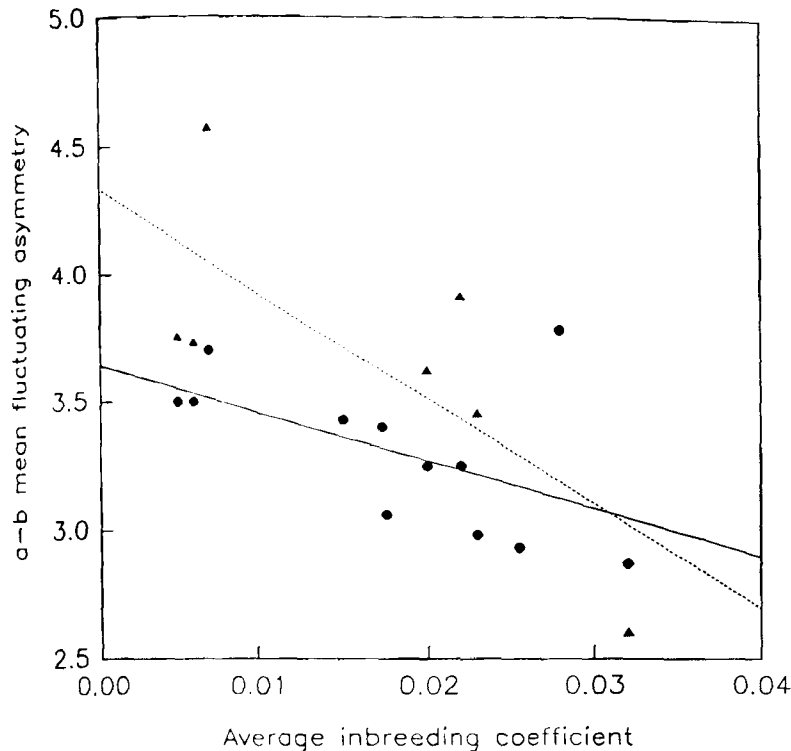


Fig. 4. Bivariate plot of mean fluctuating a-b asymmetry and mean inbreeding coefficient in the 12 male and 7 female samples. While the filled circles represent males, the triangles represent female samples. While the solid regression line is of males, the dotted line is of females.

the fingers (Samandari, 1973; Hale, 1952), and therefore, a-b area may be more asymmetric (Reddy et al., 1991a). That the a-b count is sensitive to certain aspects of development has been indicated by its relationship to paternal age and parity (Oliveira, 1978). The genetic component in asymmetry is observed to be low (Arrieta et al., 1993).

There is also a high degree of sex-consistency in the populations that did not show a quadratic fit, but not in those that showed it. Of the seven populations that showed significant fit, data were available for both sexes in three samples. Of these, the Jalary and the Vadde fishermen showed good fits in males, but not in females. Similarly, Raj Gond females, but not males, showed a significant fit. On the other hand, of the 15 populations that did not show quadratic fit, four samples included males and females and none showed a significant fit. Further, only one of the seven female samples showed significant results, dis-

counting the inference of Micle and Kobylansky (1986) on the greater homeostasis among females due to two sex chromosomes against hemizygous males. The relatively larger mean FA of females compared to their male counterparts also questions the inference as empirically inconsistent.

The central assumption underlying the Jantz and Webb (1980) hypothesis and of others dealing with asymmetry of quantitative traits in humans (Livshits and Kobylansky, 1987; Kobylansky and Livshits, 1986) is that the morphometric centrality of quantitative traits is associated with greater levels of heterozygosity causing less asymmetry and, conversely, the extremes with the greater proportion of homozygosity and greater levels of asymmetry (Soule and Cuzin-Roudy, 1982). This is plausible especially because there is ample evidence to support the view that heterozygotes are developmentally more stable (Livshits and Kobylansky, 1985) and hence better adapted (Chakraborty and Rayman, 1983).

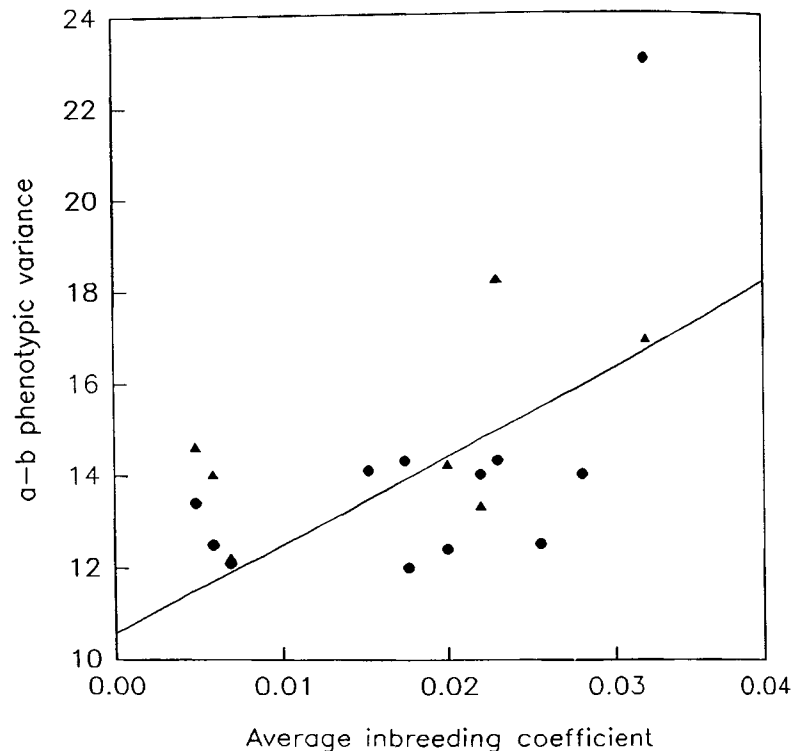


Fig. 5. Bivariate plot of inbreeding coefficient and the phenotypic variance of the total (R + L) a-b ridge count; circles represent males, and the triangles females.

There is also evidence for FA to increase with increasing inbreeding or homozygosity in humans, although most of it pertains to dental morphology (Niswander and Chung, 1965; Perzigian, 1977; Markow and Martin, 1993). However, Chakraborty (1987) has shown that modal types do not always show highest heterozygosity, while Comuzzie and Crawford (1990), with appropriate protection for multiple comparisons, failed to find adequate evidence to support the negative association between heterozygosity and morphological variability in the Mennonites. In fact, Kobylansky and Livshits (1986) failed to find finger dermatoglyphic asymmetry to be consistent with this theory in the sense that they observed greater finger ridge count asymmetry among the biochemically most heterozygous individuals. Considering finger ridge count asymmetry as a marker of fitness (Jones, 1987; Clarke and McKenzie, 1987), Reddy et al. (1991b) studied age variation (including youngest to the oldest individuals possible in the population) among the Vadde fishermen in-

cluded in the present study. The underlying hypothesis was that people with greater asymmetry should have been selected out with advancing age and, therefore, on average one should find people with relatively less average asymmetry with increasing age. This hypothesis had a conceptual affinity with stabilizing selection proposed by Waddington (1957). The results failed to show any trend in FA over the age groups and the authors concluded that the process of stabilizing selection might have been active only at the prenatal and neonatal periods, and even if it had implications to dermatoglyphic asymmetry, its operation during the postnatal period may not be to the perceptible levels to reflect systematic changes over age groups in a population.

Soule and Cuzin-Roudy (1982) provide a theoretical treatise of why and under what circumstances one would expect a quadratic relationship between asymmetry and the phenotypic value. As per the hypothesis, this pattern is typical of traits that are more complex genetically, highly heritable and

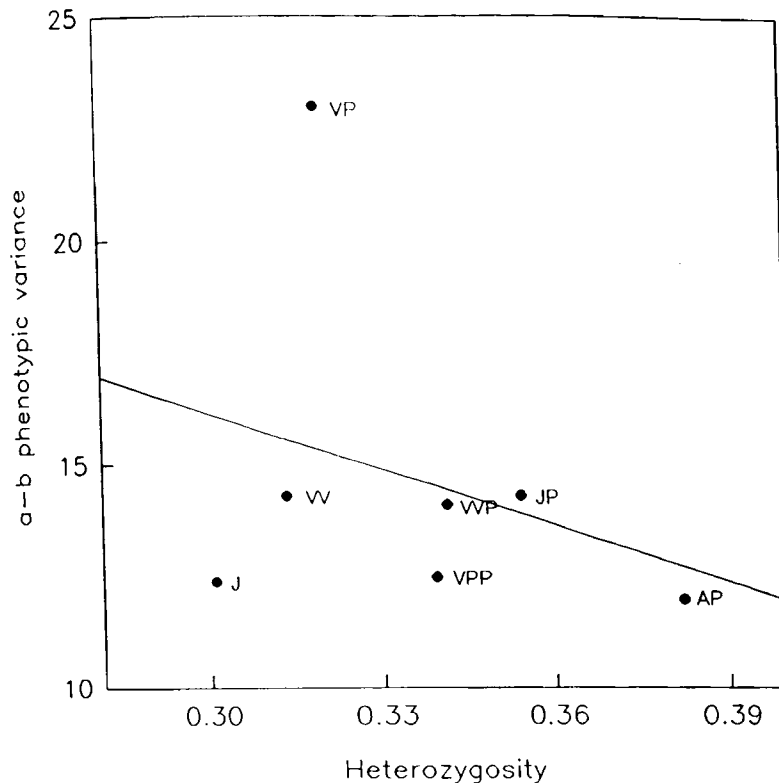


Fig. 6. Bivariate plot of mean heterozygosity and phenotypic variance of the total a-b ridge count (R + L) in the 7 samples of fishermen.

least variable. Paradoxically, while the authors found evidence for the hypothesis in a variety of lower organisms and traits, the evidence was contrary in case of the highly heritable finger ridge counts of a human population, in that putatively homozygous extreme phenotypes were no more asymmetrical than the individuals near the mean. This was interpreted as due to the relatively small number genes that may determine the pattern ridge counts; hence, the resultant homozygosity had no perceptible effect on the developmental stability and on FA.

It may be pertinent to look for other lines of evidence that can be drawn from the studied populations and that can be used in support or against the hypothesis being tested. For seven of the 15 populations in the study, data on heterozygosity levels at 11 biochemical loci were available (Reddy et al., 1989, 1995) and could be used to test if there was an association with average FA. A plot of mean FA against the average heterozy-

gosity of these populations (Fig. 3) suggests wide scatter and no clear relationship. The correlation is positive ($r = 0.16$), but not significant. The regression line, however, inclines positively against the theoretically expected negative dependency. A similar attempt to plot mean values of FA against the mean inbreeding coefficient was possible for 12 of the 15 populations (Fig. 4). It suggests a negative and significant association between the variables but, again, inconsistent with theoretical expectations. The correlations are significant for males ($r = -0.54$; 11 d.f., $P < 0.05$) and females ($r = -0.71$; d.f. 6, $P < 0.05$) and in the pooled sample ($r = -0.61$; d.f. 18, $P < 0.01$). These two lines of evidence are consistent with each other in their inconsistency with the theoretical expectation and in turn with the hypothesis under study. However, in conformity to quantitative genetic theory, there is a significant positive association (Fig. 5) between inbreeding and phenotypic variance of the total a-b ridge count among these

populations ($r = 0.54$; d.f. 18, $P < 0.01$). Although similarly consistent with theory, the negative association observed (Fig. 6) between the mean heterozygosity and phenotypic variance ($r = -0.29$; d.f. 6, $P > 0.05$) is not significant.

There is thus very little evidence in the foregoing analysis to support/substantiate the Jantz and Webb (1980) hypothesis, or to support that dermatoglyphic asymmetry that can be used as a marker for early disruption in development as suggested by Livshits and Kobylansky (1987, 1991). Livshits and Smouse (1993), using a multivariate approach and proper scaling of the asymmetry measures, conclude that the asymmetry is related with nothing, and has no association with morphometric centrality, in particular. Because FA represents so little of the phenotypic variance, any pattern it might show with other variables could well rise or fall on details of measurement technique. A very small proportion of the 22 samples that show the expected quadratic fit, the extremely low proportion (averaging to <5%) of variance explained, the lack of internal consistency, and the very low genetic component observed in a-b asymmetry all substantiate this conclusion. It may be recalled that Waddington (1957), who was a proponent of the theory of stabilizing selection/canalization, did not think that FA was related to canalization (Waddington, 1960), and Van Valen (1962) and Reeve (1960) did not find evidence for such a relationship in the experimental situation.

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