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INFLUENCE OF SELECTIVE PRESSURES RESULTING FROM MORTALITY ON MORPHOLOGICAL VARIABILITY IN HUMAN POPULATIONS

Intraspecies differentiation of mankind is conditioned by the same mechanisms which regulate variability of gene pools in other species. These mechanism can be observed only in the succession of generations, hence for their investigation we ought to have a suitable time depth, with regard to man — a historical perspective.

Although the mechanisms for man and other species are the same, it is obvious that for human populations there is a special factor regulating their adaptive value — culture. Natural selection is the main mechanism responsible for the origin and maintenance of inter- and intrapopulational variability of man for usualy there is a considerable exchange of genes between populations which diminishes results of genetic drift. Isolation of human breeding populations is mostly relative and due to distances separating local groups.

In a separate paper (Henneberg and Piontek 1975) we have presented a method for measuring, on the grounds of demographic data, intensity of selective pressures acting through mortality in earlier and modern human populations (it is the so-called Biological State Index — I_{bs}). On the basis of investigations carried out with the use of this method we have found that average intensity of selective pressures has consequently dropped from paleolithic up to modern times; simultaneously interpopulational divergence of intensity of natural selection operation increased.

On these observations we have based two hypotheses concerning changes in within- and interpopulational variability under varying selection intensity. The first hypothesis states that decreasing intensity of natural selection operation results in increasing within-group variability of polygenic characters in human populations. The second hypothesis concerns interpopulational variability. Along with the decrease of selective pressures, accompanied by advancing similarity of cultural demands and conditions, during the history of our species interpopulational differences should decrease. In other words: we may expect that relaxation of selective forces results in the decrease of intergroup variability expressed by variance of groups' averages of characters with polygenic mode of inheritance.

We have attempted to corroborate the above hypotheses on published data taken from 57 series originating from Europe and its neighbourhood, covering time span from Neolithic up to modern times. (For the list of series and more details see: Henneberg et al. 1976). As cranial measurements are the most commonly published representations of polygenic characters in earlier human groups, wa have chosen for the analysis their set listed in *table 3*. Since the first hypothesis seems to be corroborated satisfactorily by our previous work (Henneberg et al. 1976) we would like to outline here briefly only main points of the analysis. To test whether there is a significant increase in within-group variability with the decrease of selective pressures resulting from mortality we have observed correlations between standard deviations of cranial measurements in the series with time of their origin. For regulation of selective forces in man is mostly cultural it is advisable to take stages of technological and organizational advance as units of time scale instead of absolute time units (i.e. years). Moreover, application of such "cultural"

time scale enables one to calculate moment-product correlation coefficients instead of parameters for curvilinear interdependence.

In order to express jointly variability of ten cranial measurements in each series we have used average standardized value of standard deviations — $m_{(s)}$:

$$m_{(s)j} = \frac{1}{k} \sum^{k} \frac{s_{ij} - s_i}{\sigma_{si}} \qquad (1)$$

where: k — number of characters in a series j, separately for males and females, s_{ij} — standard deviation of the i-th character j-th series, s_i — mean standard deviation of the i-th character in whole sample of series, σ_{si} — standard deviation of s_{ij} values. Correlation of $m_{(s)}$ values with "cultural" time is very clear: $r = +0.452$ (significant at the 0.01 level) and, as we had expected positive. Obviously, also mean $m_{(s)}$ values increase with cultural progres in concordance with the statement of the first hypothesis (tab. 1).

TAB. 1.

Period	N series	Mean m_s
Neolithic	13	−0.29
Bronze + Early Iron Age	6	−0.07
Early Middle Ages	18	+0.04
XV—XVIII c.A.D.	11	+0.09
XX c.A.D.	9	+0.30

In the paper mentioned above we have dealt with the second hypothesis as follows. The hypothesis states that interpopulational variability decreases with the decrease of selective pressures i.e. with advancing cultural development. Hence variation of mean values of cranial characters within the samples of series from analysed periods should decrease in order: Neolithic-Early Iron Age → Early Middle Ages → XV-XVIII c. → XX c. For the purpose of analysis we have used arithmetic means of cranial measurements from separate series as individual data and computed, for each period, standard deviations s_A:

$$s_{A(p)} = \sqrt{\frac{\sum^{N_p}(A_i - \bar{A})^2}{N_p}} \qquad (2)$$

where: A_i — mean value of a given character in an i-th series, $\bar{A}$ — crude (unweighted) arithmetic mean of A_i-s in the sample of N_p series belonging to the period "p".

These values were corrected for possible influence of random error variance resulting from the sizes of the series. After due corrections we have found statistically significant drop of intergroup variance from Neolithic up to modern times in following characters: g-op, n-pr, zy-zy, breadth of ap. pir., ba-b and ft-ft in males, g-op, zy-zy, n-ns,

breadth of ap.pir., height of orbits, and ba-b in females. None of other characters showed opposite trend in intergroup variance. Hence, in accordance with our second hypothesis intergroup variability, at least in several cranial characters, is decreasing with time. But, as always in the researches on differentiation of human populations, there is still existing doubt as to the source of this differentiation. It may be due as well to the operation of natural selection as to interpopulation gene exchange — migration. In our previous work (Henneberg et al. 1976) this problem was not solved satisfactorily, so in the present paper we attempt to analyse the intergroup variability decrease with respect to possible effects of interpopulational gene exchange.

TAB. 2. *Mean and average square distances between series in each period (in thousands of kms)*

Period	N distances	$\sum d/N$ (1000 kms)	$\sqrt{\sum d^2/N}$ (1000 kms)
Neolithic to Early Iron Age	93	1.77	2.27
Early Middle Ages	153	1.28	1.70
XV—XVIII c.A.D.	55	1.05	1.23
XX c.A.D.	36	1.02	1.18

As may be seen in *table 2* mean square geographical distances, and mean distances too, between series representing various periods are different, showing tendency to decrease with time. In such a situation the decrease of intergroup variance of polygenic characters group averages can be contributed not to the natural selection itself, but to the increasing genetic correlation between observed populations. To exclude the influence of gene pools correlation on interpopulational variability of morphological characters and to enable us to observe the variation resulting solely from natural selection operation we have to chose for analysis only series from populations practically isolated. On a continuously settled continent, as Europe, in long periods geographical distance is the main isolating factor. Similarity of gene pools of populations isolated by distance may be conveniently expressed by the coefficient of genetic correlation, which according to Malécot may be computed from following formula (Cavalli-Sforza and Bodmer 1971):

$$\varrho_{(x)} = e^{-x\sqrt{\frac{2b}{m}}} \qquad (3)$$

where: $\rho_{(x)}$ — coefficient of genetic correlation between populations separated by distance x, b — coefficient of recall to equilibrium, m — migration rate. Assuming that exchange of genes among populations was intense (50 % exogamy) from the above equation we obtain coefficient of genetic correlation at a distance 500 kms equal to 0.0008 with arbitrarily taken $b = 0.00005$. Such a correlation is negligible. Hence for further analysis we may

think of populations separated by the distance 500 kms or more as about strongly isolated with minimal influence of mutual gene exchange on morphological similarities.

From the samples for each period we have excluded all series originating from localities separated by less than 500 kms distance as crow flies. For the remaining series interpopulational variance was estimated by the same way as previously (see equation 2) with the slight change — sum of square differences was divided not by number of series but by degrees of freedom ($N_v - 1$). Such a change is necessary for estimation of variance when dealing with small samples. Results are presented in *table 3*. For females, after reduction of modern

TAB. 3.

Character	Neolithic to Early Iron.		Early Med.		XV to XVIII c.		XX c.	
	s_A	i_s	s_A	i_s	s_A	i_s	s_A	i_s
	males							
g—op	4.2	0.61	3.8	0.39	3.1	0.00	4.9	1.00
eu—eu	2.1	0.00	3.8	1.00	2.9	0.47	3.7	0.94
n—pr	2.3	0.60	2.5	1.00	2.0	0.00	—	—
zy—zy	4.6	1.00	2.3	0.26	1.7	0.06	1.5	0.00
n—ns	1.35	0.67	1.83	1.00	1.00	0.44	0.36	0.00
B.A.P.	0.92	1.00	0.37	0.08	0.32	0.00	—	—
H.O.	1.01	1.00	0.98	0.91	0.68	0.00	—	—
mf—ek	1.35	1.00	0.71	0.00	1.01	0.47	—	—
ba—b	1.91	0.37	1.78	0.00	2.13	1.00	—	—
ft—ft	2.14	1.00	2.04	0.92	1.50	0.47	0.93	0.00
mean i_s		0.73		0.56		0.29		0.39
	females							
g—op	3.7	1.00	3.1	0.45	2.6	0.00		
eu—eu	2.9	0.00	3.0	0.25	3.3	1.00		
n—pr	3.1	1.00	2.1	0.00	2.2	0.10		
zy—zy	4.2	1.00	2.1	0.16	1.7	0.00		
n—ns	1.91	1.00	1.82	0.94	0.42	0.00		
B.A.P.	0.82	1.00	0.79	0.91	0.49	0.00		
H.O.	1.27	1.00	0.80	0.55	0.22	0.00		
mf—ek	1.37	1.00	0.92	0.00	0.94	0.04		
ba—b	2.56	1.00	1.43	0.00	1.92	0.43		
ft—ft	2.14	0.30	2.44	1.00	1.43	0.00		
mean i_s		0.83		0.43		0.16		

B.A.P. — *breadth of the apertura piriformis*
H.O. — *height of orbits*

populations sample with the geographical distance criterion number of series fell below 5, so we have had to exclude this sample from further considerations as not reliable.

In order to join the results for all characters standarized increase was computed for each measurement:

$$i_{s(p)} = \frac{S_{A(p)} - S_{A(min)}}{\Delta S_A} \quad (4)$$

where: $i_{(s)p}$ — standarized increase of $S_{A(p)}$ for a given P, $S_{A(min)}$ — the smallest S_A observed, ΔS_A — difference between the smallest and the largest

S_A values for a given character. Afterwards, for each period arithmetic mean of i_s values over all characters was computed. It is clear from table 3 that, after correction for possible permanent migration effect, the decrease of intergroup variability is still significant. This change in variability can be, with high degree of probability contributed to the decrease of selective forces intensity. Hence our second hypothesis seems corroborated.

The indirect method applied for corroboration of the two hypotheses permit us to draw conclusions with a certain degree of probability only. Although we have tried to avoid the influence of permanent migration on observed trends there is still some doubt existing as to the changes of breeding populations sizes with time and resulting from them inbreeding effects. We may argue that isolation of any human group is only relative and not existing for long periods (say 500 years or more) so inbreeding effects on polygenic characters are scarcely probable. Also some long-range sporadic migrations can be responsible for part of the changes found in variability, but as yet it seems rather to be not the case in our material. Nonetheless in the present state of our knowledge concerning skeletal material from earlier human populations there is no possibility to analyse effects of these two factors and we must rely almost totally on indirect argumentation only.

In conclusion it may be said that natural selection is the main, but obviously not the sole, force influencing morphological within- and intergroup variability in human populations during the history of Homo sapiens sapiens. It may be also said that described trends in variability, regardless their causes, have to be taken into account in future works in which intergroup comparisons between sets of skeletal material measurements are made for microtaxonomic purposes. For instance, it is of practical importance, that it will be easier to define a number of clearly distinguishable neolithic „races" or „racial types" than the modern ones.

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