

Possible Cases of Relaxed Selection in Civilized Populations

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Summary. Genetic traits which are disadvantageous or deleterious in “primitive” cultures, of hunters and food gatherers, have very low frequencies in almost all cases. There are a few special exceptions, such as the sickle cell trait. Some deleterious traits under genetic control are rare in “primitive” populations but have fairly high frequencies in populations with long histories or prehistories of “civilization”, such as Chinese, Japanese or European populations. The Darwinist might suggest that these traits have less selective disadvantage, that is, lower rates of selective elimination, in “civilized” habitats; i.e. that the various changes in habitat accompanying “civilization” have caused the rigor of natural selection to relax, in part or perhaps completely.

Several cases are discussed of traits under genetic control or genetic influence which demonstrate this phenomenal contrast, between low frequencies among “primitive” populations and high frequencies among “civilized” populations. Population data are presented for 4 such cases: colorblindness, myopia, abnormality of the nasal septum and abnormally small external opening of the tear duct.

Zusammenfassung. Mit einigen bekannten Ausnahmen, z. B. Sichelzellanämie, kommen genetische Merkmale, die bei den Urvölkern von Jägern und Sammlern ungünstig oder sogar schädlich wirkten, mit niedriger Häufigkeit vor. Genetisch bedingte schädliche Merkmale, die selten unter Urvölkern gefunden werden, kommen jedoch häufiger vor bei Bevölkerungen, die eine lange Geschichte bzw. Vorgeschichte der „Zivilisation“ besitzen, wie z. B. in China, Japan oder Europa. Ein Darwinist würde behaupten, daß bei „zivilisierten“ Wohnorten solche Merkmale selektiv weniger nachteilig wirken, d. h., daß die selektive Ausscheidung langsamer vorgeht. Anders gesagt: der mit der „Zivilisation“ verbundene Wechsel des Wohnortes bildet einen Grund für eine Milderung der Strenge der natürlichen Auslese.

Es werden einige genetisch bestimmte oder genetisch beeinflusste Merkmale besprochen, die den Unterschied zwischen den Häufigkeiten (niedrig bei Urvölkern, hoch bei „zivilisierten“ Völkern) aufzeigen. Für 4 solcher Fälle: Farbensinnstörungen, Kurzsichtigkeit, Nasenscheidenwand-Deformitäten und anomale kleine Außenöffnungen der Tränenwege werden die Befunde aus den Bevölkerungen dargestellt.

I. Introduction

The substance of Darwin's thesis of evolution by natural selection has been accepted by virtually all biologists. Papers honoring the centennial of “The Origin of Species by Natural Selection” (1859) referred to Darwinism as no longer a theory, but a fact. Fortified first by Mendelism, then by experimental evolution, population genetics and other developments of recent decades, the mechanism of organic evolution is based solidly on natural selection and properly called Neo-Darwinism.

Variation in the intensity or rigor of natural selection has been investigated extensively and intensively. It reflects changes in ecological habitats throughout nature with time and locality. Experimental breeders have produced maximal rates of artificial selection, resulting in demonstrations of most rapid evolutionary change. In contrast, paleontologists have described ancient forms, particularly fossil insects, which are almost indistinguishable from contemporary species, indicating minimal, almost negligible rates of evolution. Selection rates of both experimental and natural populations have been described under the most widely differing circumstances and analysed by refined statistical methods.

In natural populations the immediate response to relaxed selection is an increase in phenotypic variation. Hereditary impulses are permitted wider expression in less rigorous environments. Genes which were eliminated from the former environments gradually accumulate in successive generations. A growing proportion of the increased phenotypic variation becomes genetic.

Domestication

“As a consequence of continued variability and more especially of reversion, all highly improved races, if neglected or not subject to constant selection, soon degenerate . . . In all races the degeneration will be proportional to the neglect with which they are treated” (Darwin, 1876, vol. 2, p. 225).

Darwin recorded a wealth of information about evolutionary changes in animals and plants under domestication, some of which might be attributed to the effects of relaxed selection. Among common barnyard animals he was impressed by such changes as losses in protective coloration, diminished keenness of all the senses, imperfection in various instinctive behaviors, and less skill in various aptitudes in contrast with those of a species' wild forebears. Reduction in the wing size of Muscovy domestic ducks, unable to fly since the earliest records, struck him particularly, having been previously impressed by the flightless condition of wild birds which became adapted to running, such as the Ostrich and Apteryx, or the giant Dodo. Darwin pointed out the typically drooping external ears of most breeds of dogs contrasted with the erect ears of wild ancestral stocks. Without human aid, considerable numbers of domestic animals and fowl would die at birth or hatching, fail at first to feed easily, fall prey to vermin or predators throughout their lives, and in extreme cases even fail to mate. If returned to their natural wild habitats, where they would have to feed and fend for themselves, it would seem doubtful that many domestic varieties would survive.

In commenting on this situation, Fisher wrote (1958, p. 12): “Many of our domesticated varieties are evidently ill-fitted to survive in the wild condition. The mutations by which they arose may have been occurring for an indefinite period prior to domestication without establishing themselves, or appreciably affecting the variance of the wild species. In domestication, however, not only is the rigour of Natural Selection relaxed so that mutant types can survive, and each such survival add something to the store of heritable variance, but novelties of form or colour, even if semi-monstrous, do undoubtedly attract human attention and interest, and are valued by man for their peculiarity. The rapidity with which new variance is accumulated will thus be enhanced. Without postulating any change in the mutation rates due to domestication, we should necessarily

infer from what is known of the conditions of domestication that the variation of domesticated species should be greater than that of similar wild species, and that this contrast should be greatest with those species most anciently domesticated." The final clause may be noted particularly.

It might be questioned whether domesticated animals are actually maladapted to their new, "unnatural" habitats, since the traits of their wild ancestors which were lost may have little or no "survival value" in the protected environments furnished by man. The answer is complicated. Some of the losses represent no maladaptations, such as mild declines in acuity of hearing, vision, or sense of smell. In many respects domestic breeds of animals and plants are indeed obviously better adapted genetically to their new habitats than their wild ancestors would be. They are less apt to fight or stampede or escape, are more resistant to diseases, more productive of meat or hides or whatnot, and more fecund. These changes have resulted partly from the artificial selection practiced by man and partly from natural selection in the new habitats of domestication. At the same time most breeds have undergone a second type of evolutionary change, which earlier writers described with words such as "retrogressive" and "degenerative". They have accumulated larger frequencies than their wild ancestors of genes which are undesirable to their human owners even under domestication. Parturition difficulties of sheep; straying of newborn calves from their mothers; inability of chicks to peck themselves out of their eggs; high frequencies of inadequate vision, and hearing — several defects in the dog are described by Scott and Fuller (1965, p. 389, et seq) — these and many similar situations are well known to experienced breeders.

Since man changed his own environment through cultural developments long before he domesticated plants and animals, it might be said that the earliest domesticated animal was man himself. But a clear distinction should be made between the two. Man never practiced artificial selection within his own species, with minor exceptions, whereas in animal domestication the selection has been special, deliberate and purposeful. Man is a domestic animal only in the narrow sense that he changed his environment profoundly and radically. The further question, whether or not these changes were greater and more abrupt in man than in certain domestic animals — whether or not genetic and therefore evolutionary changes were more rapid in man — is almost always answered negatively.

Cave Environments

A second theatre of specialized evolution is offered in the wide variety of life which has become adapted through many centuries to cave habitats, resulting in profound genetic changes. Among the most striking has been blindness, with extreme reduction of the entire ophthalmic system. In hundreds of species, particularly of insects and fish, the eyes have become diminutive, as rudimentary as the radius and fibula of modern ungulates (horses) and the pelvis and hind limbs of many cetaceans (whales).

It has been contended that these changes illustrate essentially progressive adaptation to darkness and other specialized conditions of cave habitats, rather than the effects of selection relaxation. Obviously, there is a selective advantage to small eyes or absent eyes in such an environment, since more space, nutrition,

energy, etc. is thereby available for other organs and parts, such as tactile and olfactory organs. But there seems no reason to exclude the phenomenon of degeneration completely while giving priority to that of progressive adaptation. Evolutionary forces are sufficiently vast and complex to include several completely different processes or mechanisms, all operating simultaneously.

A similar statement might apply to and hopefully may satisfy some of the more sweeping criticisms of the classical evolutionary concept or mechanism, that of genetic balance between mutation and selection. Some of the comments have appeared to be skeptical of the effects of relaxed selection, attributing evolutionary change almost entirely to selection, together with the mechanism of balanced adaptive polymorphy. While this phenomenon has been demonstrated brilliantly and explained with conviction, it need not discount the classical concept. There is room for both processes, and for others as yet undiscovered.

Selection in Man

Human evolution is the more impressive on consideration of its rapidity. Brain capacity increased from some 100 cm³ to 1500—1800 cm³ in less than 1 million years. No other species of mammal has approached this record. But the rate halted abruptly with the development of human culture. Attempts to explain such speed and its sudden cessation have led to interesting speculation. The only firm statement which seems possible is the trite one that selection rates must have changed dramatically (Haldane, 1949; Mayr, 1963, pp. 634—635).

Relatively few studies or observations of changes in selection rate have been reported. Almost all have concerned increases of rate, resulting in progressive adaptation. Examples include the marked resistance of Negroes to yellow fever (Lewis, 1942, p. 210); the decreased skin pigmentation throughout northwestern Europe, producing blondness, a relatively recent adaptation to the minimal sunshine in this part of the world (Coon, 1965, pp. 8, 213, 229—234); the immunity of American Indians of northeastern U.S.A. to poison ivy, poison oak and poison sumac, three plants which are unique to the area and which afflict most individuals of all other races; these Indians' freedom from all allergic reactions to North American plants; the greater resistance of populations with the longest histories of civilization to a number of infectious and contagious diseases, in contrast with the susceptibility of primitive people throughout the world to the diseases of Asians and Europeans, as far as any specific resistance has a genetic component. For example, Ashkenazi Jews are unusually resistant to tuberculosis (Rakower, 1953). This "has been tentatively explained by the suggestion that the Jews in the ghettos of the Middle Ages were severely crowded for many generations. They contracted more tuberculosis, with death of the susceptible genotypes, so that today we are dealing with a population that is more resistant . . ." (Motulsky, 1961).

Examples of decreased selection rates are more rare. Yet they include cases of dramatically rapid evolutionary change, some of which it is the purpose of the present paper to summarize.

The prehistory of the human species offers ample evidence of the genetic effects of relaxation. Each of us is burdened with a long list of vestigial organs and parts — the vermiform appendix, oversized colon and chin, third molar teeth,

tiny and useless fifth toe and toenail, remnants of body hair, etc. These are degenerate survivors from radically different habitats of the remote past, which have not yet been eliminated completely by evolutionary processes including relaxed selection, and which suggest eloquently the vast array of human traits which have already been eliminated (Glass, 1966, p. 45). Indeed, were it not for relaxed selection our bodies would be monstrous freaks. As it is they are veritable museums of natural history, exhibiting countless cases — with extremely wide variation in size, shape, plan, etc. — of what might be called “evolutionary nonsense”. All these vestigial structures have minimal degrees of adaptive advantage to current environments. The fact that they may also reveal the effects of progressive adaptation, such as for example a reduction in size, does not detract from the significance of the observation that they represent maladaptation.

Akin to vestiges are atavisms, rare cases of reversion of structures in a few chance individual cases, such as an enlarged coccyx, underdeveloped regions in the front of the neck (relics of ancient gill slits), multiple pairs of breasts (polymastia), well developed scalp muscles, long tactile hairs, unusual flexibility of the great toe. Most atavisms (or reversions) are flotsam and jetsam, occasional remnants which are still in process of being removed by relaxed selection, in combination with progressive adaptation, operating over very long periods of time.

Probably the most widely known case of rapid evolutionary change caused by a single locus mutation is that of the greatly increased frequency of the sickle cell gene among West African Negroes. The protection against plasmodial malaria which this gene confers to heterozygote carriers gives it high selective values in endemic areas, despite the biological cost of the sickle cell anemia suffered by homozygotes, almost all of whom die unless hospitalized. Hardly less well known is the rapid decrease in the frequencies of the sickle cell gene among descendants of West African Negroes who have lived for a few generations in a non-malarial habitat. Selection for the gene is thus relaxed and the frequency steadily declines through the elimination of homozygotes. Documentation of both these changes is impressive.

Cases are recorded of deliberate artificial relaxation of selection against deleterious traits through social convention. In an isolated area of New Brunswick (Canada) where aniridia is frequent the sufferers are treated with unusual charity by their neighbors. Unable to support themselves unaided, they nevertheless produce large families as recipients of local beneficence and generosity. The author has observed a similar situation among poor subsistence farmers in the Berkshire Hills of western Massachusetts where gross mental retardation (feeble-mindedness) is frequent. An extraordinarily high rate of albinism occurs among certain populations of American Indians, including the Hopi of Arizona and the Cuna on the Islands of Darien off the east coast of Panama. Affected individuals are almost totally dependent for support on normal persons. Since albinos in these cultures are regarded with high respect, bordering on religious awe and veneration, generous support is freely given, and apparently has been given for generations (Woolf *et al.*, 1969).

It would seem reasonable to expect that a wide variety of hereditary imperfections and abnormalities in man have increased in frequency among long “civilized” populations, beginning perhaps in Upper Paleolithic cultures with specialization

of labor and increasing among the earliest agriculturists. It would seem reasonable to attribute this increase to a relaxation in selection rates resulting from the many forms of protection from the rigors of outdoor life consequent upon a denser population, more stable food supply, village settlements in more robust huts, wider opportunities of occupation, etc. The resulting "spread of harmful autosomal recessive genes" has been described by Haldane in a paper under this title as follows:

"As a consequence of civilization these small communities (typical of all "uncivilized" populations) are merged in larger towns and states. The frequency of homozygotes falls sharply. But mutation is no longer balanced by selection and the gene frequency increases slowly. This process is now going on . . . we may expect therefore a slow increase for some thousands of years in the frequencies of rarer recessive conditions" (Haldane, 1939, p. 235).

With similar reference Mayr writes (1963, pp. 654—655): "A rise in the frequency of such (deleterious) genes will have no drastic effect on the future of mankind as long as adequate medical facilities are available." He continues: "The increase in frequency of such genes in the human species indicates a relaxation of normal selection which has exceedingly little to do with man's phyletic evolution (i.e. genetic differences between man and other primates, between races, and between other population groupings). The futility of eugenics based on endeavors to eliminate such "bad" genes has been brilliantly demonstrated by Dunn and Dobzhansky (1946). Such genes will become a real problem for mankind only if sufferers should occur in large numbers . . ."

Habitat Contrasts

As a first step towards making a study of the effects of relaxed selection, data have been compiled among samples of two groups of populations, designated crudely but briefly "primitive" and "civilized", for genetically controlled or genetically influenced traits which are presumed to be non-adaptive or deleterious in habitats of the former cultures but not in habitats of the latter. Assuming that the genetic backgrounds or constitutions of the two groups of populations are fairly much alike for traits other than those under consideration, the changes in gene frequency after several scores of generations since the civilized populations quit their primitive habitats can be considered by making such comparisons. The ideal trait should have a high or fairly high genetic component, simple genetic mechanism, facile diagnosis, early onset, high penetrance, irreversibility, and population frequencies of at least 1 or 2% in the "civilized" group of populations.

The largest and earliest body of data of relevance concerns the results of physical examinations of United States Army conscripts during World War I (Love and Davenport, 1920). In every State having sufficient numbers of "red" Indians to warrant separate reporting, conscripts of the white race showed significantly higher rates of several attributes. Most frequent were, in order, 1. refractive disorders of the eye, principally myopia; 2. mild hearing losses; 3. flat feet, hallux valgus and pronated feet. These and other differences between American Indian and white conscripts in U.S.A. have been reported subsequently (U.S. Selective Service System, 1946; Karpinos, 1962). Although the reliability of military examinations and reports may be open to question it is of some signif-

icance that consistently similar results have been obtained from large samples in many States during four periods: (1917—1919, 1941—1945, 1950—1951, 1959—1960).

II. Colorblindness

Perhaps the best trait for investigating relaxed selection is sexlinked color vision deficiency. 4 chief types, each controlled by a single X-linked mutant gene, are called deuteranopia and deuteranomaly, severe and mild green blindness, respectively; protanopia and protanomaly, severe and mild red blindness. Extreme anomalies have been identified (Adam *et al.*, 1969 a, b) and there may be 6 types, perhaps more. Diagnosis is fairly quick and easy by standardized color plates. For greater accuracy and differential diagnosis of the milder forms, testing by anomaloscope is preferable, after rapid screening by color plates. The deficiencies are manifest from early childhood, are irreversible and resistant to environmental influences. A wealth of population data has been published. Gene frequency estimates are equivalent to sample rates among males, since the genes are X-linked.

The argument for relaxed selection is based on the low rates prevailing among primitives, essentially hunters and food gatherers, in sharp contrast with higher rates among long civilized people. In a 1962 review, among 13 samples of "full-blooded" primitives aggregating 7712 the pooled rate is 2%, in sharp contrast with about 5% for 99 samples of civilized aggregating 436853. Rates of Chinese centered at about 5.5%, ranging from 5 to 6.9%; of Japanese from 3.6 to 5%, with a few exceeding. Most British rates fall between 5 and 9%. Populations somewhat removed from hunters and gatherers in time or in habitat are apt to have intermediary rates, as are populations descended from mixtures of primitives and civilized (Post, 1962a). Subsequent reports based on color plate (Ishihara) tests are noted in Table 1.

From such data Kalmus (1965) observed that "sex-linked defective color vision provides the only clear example of a simple inherited defect, the frequency of which is significantly increased with the advent of civilization".

It may be reasoned that the pre-agricultural ancestors of civilized populations once had the low colorblindness rates which characterize contemporary hunting populations, and that the various protections conferred by successive cultural advances — better housing, more dependable food supply, etc., resulting from pastoral animal culture, agriculture, settled village habitat, etc. — caused a decrease in the intensity of selection against colorblindness. This hypothesis is based on a number of assumptions which have not yet been tested, but which seem plausible.

The argument is refined by noting the significantly lower rates in Japan contrasted with those in China, where culture has been generally more advanced at every period since the earliest archaeological horizons. China was the first to develop or receive each successive cultural advance from earliest Paleolithic through the last of the Metal Ages.

A similar cultural lag occurred on the larger islands off the coast of Korea, where Kang *et al.* (1967) found colorblindness in 3.9% of a sample of 4290, contrasted with 5.5% among 1231 in Seoul. Again, the population with the longer history of "higher" culture has the higher rate of colorblindness.

Table 1. *Rates of red-green color vision deficiency in selected samples*

	N	Color- blind (%)	Deuter- anoma- lous (%)	Reference (senior author only)
<i>By anomaloscope</i>				
Belgium	9540	7.5	—	De Laet (1935)
Britain	1338	8.8	5.1	Nelson (1938)
France	517	7.2	4.6	Hébert (1957)
France	1243	8.6	4.9	François (1957)
Germany	6863	7.7	4.0	Schmidt (1936)
Netherlands	3168	8.0	4.7	Crone (1968)
Norway	9047	8.0	5.1	Waalder (1927)
Russia	1343	9.2	—	Flekkel (1955)
Switzerland	2000	8.0	4.3	von Planta (1928)
Switzerland	1036	8.2	5.1	Wieland (1933)
Switzerland	1000	9.0	4.7	Bally (1954)
			4.7	
<i>By color plates</i>				
Hausa, Nigeria	380	2.1		Roberts (1967)
Miao tribesmen, Thailand	312	2.2		Flatz (1967)
Eskimo „fullbloods“	297	2.5		Skeller (1954)
Eskimo „half-bloods“	132	6.6		Skeller (1954)
Maoris, New Zealand	571	2.6		Grosvenor (1970)
Chomorros, Mariana Is.	246	3.3		Plato (1964)
Iran, Tabriz	949	4.5		Plattner (1959)
Tibetans	241	5.0		Tiwari (1969)
Thailand, northern	2128	5.2		Flatz (1967)
Turkey	1686	5.2		Ökte (1960)
British naval recruits				Vernon (1943)
E Scotland	6236	4.9		
E coast England	43278	6.7		
NW England, S Wales	52797	7.4		
Central England	14455	8.6		
SW England	6648	9.3		
Total, recruits	123414	7.5		
France	6635	9.0		Kherumian (1959)
<i>By anomaloscope</i>				
Papuans, New Guinea	4820	4.7	1.8	Adam (1969 a)
Bantus, Uganda	1294	3.9	0.7	Adam (1970)

British data provide a third case. Colorblindness rates of 123414 naval recruits tested at 77 stations show a progressive decrease northwards and eastwards, from highest rates in Cornwall and along the English Channel, all above 10%, to lowest rates in the east of Scotland, averaging 4.9%, while Edinburgh has but 3.55%. Kherumian and Pickford (1959) have described the situation nicely, showing the extreme heterogeneity of the 77 recruiting station rates and arranging them into geographical areas which are homogeneous each within its area but again hetero-

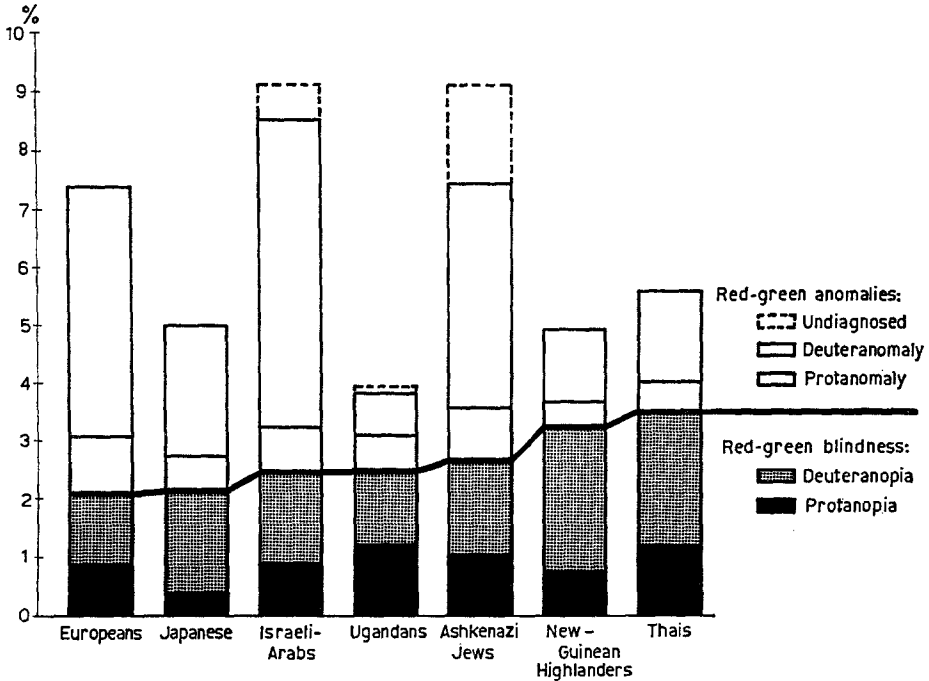


Fig. 1. Red-green blindness and red-green anomalies among 7 population samples in which the number of anomaloscopically diagnosed colorblinds exceeds 50. The defects are arranged from bottom to top in a tentative order of decreasing severity with a possible exception of the rare trichromatic extreme anomalies: the latter are included with the commoner "simple" anomalies, protanomaly and deuteranomaly, since most population data do not differentiate the two categories in each of the two series. Reproduced from Adam *et al.* (1970, p. 63) with the kind permission of the author and the American Journal of Physical Anthropology

geneous amongst themselves. A decreasing cline northwards is consistent with the pattern of successive cultural invasions of southern Britain from earliest Neolithic times onward. A second cline, decreasing eastwards, is less clear but also statistically significant (Post, 1963) and is consistent under the relaxation hypothesis with the successive invasions of the east coast by Saxons, Jutes and others who had shorter cultural histories than the older inhabitants. These were pushed ever westwards by each wave of invaders. Finally, the colorblindness rates of Britain's 10 areas average (unweighted) 7.5%, contrasted with 9.0% in France among 6635 students also tested with color plates (Kherumian and Pickford, 1959).

Since testing by anomaloscope reveals many colorblind who might escape positive diagnosis by testing with color plates, rates based on plates must be considered minimal estimates and treated with caution. Unfortunately almost all reports of primitives are based on color plate testing.

Two samples of primitives tested by anomaloscope are included in Table 1 and represented in Fig. 1 (Adam *et al.*, 1970) together with comparative data of Europeans, Japanese, Israeli-Arabs (Palestinians), Ashkenazi Jews in Israel and Thais. The rates of colorblindness in each group roughly reflects the antiquity of its civilization, except for the Japanese and Thais.

The authors comment on the relatively uniform and low rates of protanopia and protanomaly in these populations, and throughout the world, noting that "the gene which seems so far to be responsible for most of the highly significant world variations in the rates of "colorblindness" is that of deuteranomaly (mild green deficiency). Its frequencies range from 0.7% in indigenous Ugandans to 5.1% among several European samples (Kherumian and Pickford, 1959) and 5.3% among some Israeli Arabs" (Adam *et al.*, 1970).

The low rate of deuteranomaly in Japan contrasted with Europe and the Middle East appears inconsistent with the relaxation hypothesis (Adam, 1969). China, India, Turkey and Iran also have lower rates than Europe (Table 1). Explanation may lie in the recurrent invasions of these ancient centers of civilization by less acculturated people through the centuries. China for example has received invaders from the north and west; Indian centers have absorbed primitives from surrounding hills and mountains; modern Turks and Persians are descended only in part from the ancient populations, most of whom were slaughtered by nomadic invaders from central Asia. Because of its relative isolation, Europe did not receive such influxes.

Further explanation may be found in the differences in genetic background between Asians and Europeans, which might affect genetic expression and therefore selection.

Anomaloscope data increase the temptation to make very rough estimates of mutation and selection rates. The simplest model might be to assume that selection against colorblindness in European populations ceased completely 4000 years ago. Considering deuteranomaly alone and allowing 25 years per generation, the responsible mutant gene would have been accumulating for 160 generations. Its frequency in 2000 B.C. may be taken at 1.25%, midway between the 0.7% of Bantus in Uganda (Adam *et al.*, 1970) and the 1.8% of Papuans in New Guinea (Adam *et al.*, 1969b), the only 2 large samples of primitives we have who were tested by anomaloscope. The 9 European samples in Table 1 similarly tested, average (unweighted) 4.72%.

If then the gene for deuteranomaly has increased from 1.25 to 4.72% in European populations in 160 generations, and if this increase of 3.46% has been due solely to the accumulation of new mutations, or to net mutation after subtracting possible reverse mutation, then the rate of mutation has been about $0.0346 \div 160$ or 0.00022 per generation (22×10^{-5}). Employing data partly from

	Increase of gene frequency		Time (yrs.)	Approximate number of generations	Net mutation rate, per gene per generation
	from	to			
Protan genes	0.005	0.020	3000	120	12.5×10^{-5}
			4000	160	9.375×10^{-5}
			5000	200	7.5×10^{-5}
Deutan genes	0.015	0.060	3000	120	37.5×10^{-5}
			4000	160	28.13×10^{-5}
			5000	200	22.5×10^{-5}

Ishihara testing, Kalmus (1965) obtained similar figures, neatly summarized in his Table 11, page 91 for all 4 types of X-linked colorblindness:

These rates are high. The range of human mutation rates between "high and low" suggested by Penrose (1961) is from 0.000005 to 0.00005 ($1/2$ to 5×10^{-5}). If there are 2 independent loci for deuteranomaly then the rate for each locus would be halved, if they were equal. Assuming that relaxation commenced 8000 years ago, or even more, through changes in culture or habitat not yet understood, the rate might be halved again, but it would still be high.

This is discouraging for the further indulgence of estimating the rate of selection among primitives. Employing the formula for sex-linked recessive traits $s = 3u/q$ (Li, 1955, p. 287) where s is selection rate, u is mutation rate and q is the gene frequency, the equation would become $s = 3(0.00022)/0.0125$ or $s = 0.0528$. This seems also high. It is difficult to imagine 528 among every 10000 colorblind male primitives dying or failing to leave offspring simply because of having slightly defective green color vision. Presumably additional numbers of males were simultaneously succumbing to genetic deaths through other types of colorblindness.

Explanation of such high rates may lie in multiple loci, or in greater antiquity of critical changes in habitat than even 8000 years. Possibly colorblindness has been favored by positive selection under special circumstances. For example in transitional cultures of hunters and primitive cultivators, presenting a broader choice of occupation than the pure Paleolithic, men who failed in tracking and trailing through the handicaps of colorblindness, even if ignorant of these conditions, might have sought other pursuits, less hazardous and more conducive to leaving larger families (Neel and Post, 1963). Or, perhaps selection and mutation for colorblindness is much higher than for other human traits.

Unfortunately, little is known about the disadvantages of colorblindness in primitive habitats. Survival in any wilderness is dependent on accurately observing and memorizing a vast number of details of landscapes and vistas. Their colors vary with clouds, especially at dawn and twilight. A series of color fotos of "nature's signposts" from one static viewpoint under various conditions of lighting, projected before large audiences, will differentiate colorblind persons almost as well as standard tests. It is said that some colorblind observers distinguish camouflaged objects better than normal observers, but this has never been investigated carefully and is believed true only under rare conditions of lighting. Normal color vision is required universally for qualification of airplane pilots, army and navy officers, military observers of various types, and in a long list of civilian occupations. Endurance tests of airplane pilots and observers have shown that colorblind candidates are more subject to fatigue. Colorblind hunters are more prone to shooting accidents. Since primitive cultures often require movement alone or in small groups for long distances over unknown and unmarked wilderness, it seems reasonable to assume that colorblind persons would be eliminated more rapidly than normals, especially at younger ages (Berens *et al.*, 1953; Caanitz, 1935; Judd, 1943; Hendley *et al.*, 1949; Hollier-Larusse, 1958; Neel *et al.*, 1963; Poppen, 1941; Velhagen, 1936; Wright, 1953). There is much evidence that colorblindness in general imposes grave handicaps in Paleolithic and early Neolithic cultures and habitats, but we have no information on the differential selectivity of the various types. The relatively slight differences between primitives and civilized in the

frequencies of severe colorblindness, protanopia and deuteranopia, have not been explained. Has selection relaxed against deuteranomaly alone?

III. Myopia

After colorblindness the most rewarding field for studying relaxed selection in long civilized populations is probably the complex of traits composing distant vision acuity, of which the most frequent element is myopia, or "nearsightedness" (Miller, 1961). Refraction can be measured quantitatively, with tolerable accuracy. It is fairly stable with age and environmental influences, although increasing somewhat with "close work", excessive reading, etc. (Goldschmidt, 1968, pp. 118—121). The genetic component is high, its basis polygenic. Heritability has been estimated from studies of twins. Population data are available which permit rough estimates of the survival or selection value and significance of myopia to individuals and groups — its role in evolution.

A number of twin studies show higher concordance between monozygotic than dizygotic pairs. A pooling of twin data from 5 authors (Table 2) shows significantly higher concordance at 5 levels of inter-pair difference, combining positive with negative refractions of matched eyes: (Huber, 1931; Jablonski, 1922; Jancke and Holste, 1941; Van Rötth, 1937; Waardenburg, 1950). In a later study coefficients of correlation were computed from refractions of 78 monozygotic twin pairs, 40 dizygotic twin pairs and 48 unrelated pairs matched in age and sex as controls (Sorsby and Fraser, 1964). The 3 coefficients are close to unity, 0.5, and zero, respectively. This result produces a heritability estimate of almost 100% ($H = M - D/100 - D$), and supports the hypothesis of additive effect of a number of genes without dominance.

Heritability has been demonstrated also by analysis of rates of vision defect among the offspring of parents of various degrees of consanguinity. Children of 4 such classes of Japanese parents have been investigated: a) 1st cousins, b) 1—1/2 cousins, c) 2nd cousins, and d) unrelated controls. The progressively descending rates of vision defects from a) through d) are presented in Table 3 (data from Miller, 1961). They give strong evidence for the role of "recessive genes" which produce vision deficiency, since homozygosity at all loci is increased among the offspring of more closely related parents.

Table 2

Concordance of monozygotic and dizygotic twin pairs in spherical refraction, classified as "not different" (concordant) by 5 definitions or levels, based on pooled data of 5 authors cited in text

Definition of "different" (D = diopters)	596 Monozygotic pairs		467 Dizygotic pairs		χ^2
	Not different	%	Not different	%	
Under $\frac{1}{2}$ D	371	62	207	44	33
Under $\frac{3}{4}$ D	458	77	262	56	51
Under 1 D	488	81	286	61	55
Under $1\frac{1}{2}$ D	526	88	353	76	29
Under 2 D	564	94	388	83	36

Table 3. Rates of vision defects of Japanese children in 4 classes of parental relationship

Acuity	Relationship of parents			
	1st cousins	1½ cousins	2nd cousins	unrelated
Snellen 20/70 or worse	0.0836	0.0736	0.0560	0.0645
Snellen 20/40—50 or worse	0.0610	0.0544	0.0465 ^a	0.0433 ^a
Congenital blindness	0.0039	(too few cases)	0.0014	0.0006

^a Note: All differences are highly significant excepting the difference between these two rates.

A wealth of population data is available for both primitives and civilized. Although some studies are less thorough and dependable than others, all show a sharp contrast between the two groups. (This is not true for contagious diseases of the eye.) The world distribution of myopia is summarized by Mann (1966, p. 544). 6 groups of populations in which myopia is rare or absent are: African Bushmen, African Negroes, American Indians, Australian aborigines, certain natives of India (except Jews and Parsis), Melanesians and Polynesians. Myopia is reportedly common in 8 groups: China, Japan, Korea, Egypt and Morocco, Iran, Thailand and all the countries of Europe, particularly Malta and Holland.

Four particular statements of Mann (1966) are relevant here; "The myopia of the Chinese . . . occurs in all social classes" (p. 35). It is obviously "racial" or hereditary, since it becomes manifest at early ages (p. 254). Natural selection may have favored myopia (in China) to judge by the excessively long hours children are forced to spend reading and writing, where in contrast "among nonliterate hunting and nomadic people myopia would be a great disadvantage. We find it extremely rare among the Australian aborigines and the New Guinea peoples" (p. 255).

A number of studies of contrasts in the frequency of myopia between pairs of population samples which differ sharply in cultural history, and differ correspondingly in rates of myopia, are summarized and critically reviewed by Post (1962b) and by Av-Shalom *et al.* (1967). Brahmans in India are shown to have rates almost as high as Europeans and significantly higher than other castes, in two studies. Several samples of Indian "Hill Tribes" have low rates, such as "primitives" elsewhere. Among the 3 principal racial groups in Mexico and the United States, the American Indian and Negro consistently demonstrate lower rates of myopia than Caucasians (Karpinos, 1960). Unfortunately, most of these studies are of adults and fail to specify the degree of myopia. Selected rates of school children, of greater significance, are listed as follows by Av-Shalom *et al.* (1967, p. 1730). The last two samples are of African Negroes.

	Myopia (%)
Sweden	17
Germany	27
Japan	27
Tanzania	11—28
Sweden (secondary school only)	19—25
Japan (secondary school only)	46
Egypt	70
Monrovia (present authors)	1.96
Dar-es-Salaam (present authors)	1.38

Egyptian Copts (Christians), descended from long civilized populations, have higher frequencies than neighboring Muslims, relatively recent invaders of Egypt from nomadic desert tribes (Meyerhof, 1914):

	N	Over —10 D	Under —10 D	Sum	%
<i>Illiterates</i>					
♂ Muslims	284	26	69	93	33
♂ Copts	109	14	28	42	39
	$\chi^2 = 0.93 \ p > 0.20$				
♀ Muslims	424	12	36	48	11
♀ Copts	356	19	55	74	21
	$\chi^2 = 12.4 \ p < 0.001$				
<i>Literates</i> (♀ too few for comparison)					
♂ Muslims	820	50	164	214	26
♂ Copts	1105	91	302	393	36
	$\chi^2 = 19.1 \ p < 0.001$				
♂ Nubians	178	0	0	0	0

Furthermore the proportion of extreme myopes is greater among Copts. The same author reported myopia rates higher among Copts and Muslims pooled (32% of 2591 males) than among either the Europeans (20% of 750 males) or the Middle Eastern people (22% of 282 males) whom he examined in Cairo (Meyerhof, 1914).

Ashkenazi Jews have frequently been shown to have higher rates of myopia than Gentiles, although no study is known in which the control group had similar backgrounds of "close work". Pearson and Moul (1927, p. 114) reported myopia in 13.3% of 900 Jewish schoolboys, compared with 2.3% among 10415 English schoolboys of the same ages tested under similar conditions. Sourasky (1928) obtained results of 43 and 22%, respectively, subdivided in age group as follows:

Age	Jewish		Gentile	
	N	% defective	N	% defective
6	48	40		
7	138	44		
8	162	41	100	14
9	270	42	100	21
10	298	45	100	25
11	325	38	100	23
12	319	46	100	19
13	89	51	100	28
Total	1649	43	600	22

Sorsby (1934, 1938, 1951) refracted 772 "unselected" Jewish and 672 non-Jewish children in London, aged 4 through 8, finding the incidence of myopia about double among the former at corresponding ages. He attributed the difference to

Table 4. *Spherical refractions of young adult males in 4 population samples, adapting the data of 4 authors*

Population	Eskimos Green- land	"Bush" Negroes illiterates	Swedes con- scripts	British recruits
Author	Skeller	Holm	Strom- berg	Sorsby
Year	1954	1937	1936	1960
Pages	176—177	96	288	1396
No. eyes	227	1154	5122	2066
Age	15—19	18—37	20	17—27
Mean Refraction	+0.24	+0.27	+0.53	+0.92
Average Deviation ^a	0.46	0.37	0.89	1.42
Diopters				
> +4			0.003	0.028
+4	0.009		0.002	0.017
+3	0.013		0.004	0.040
+2	0.049	0.013	0.017	0.064
+1	0.057	0.125	0.238	0.334
0 ± fractions	0.863	0.854	0.680	0.446
-1	0.009	0.003	0.022	0.027
-2		0.001	0.014	0.016
> -2		0.004	0.020	0.028
	1.000	1.000	1.000	1.000

^a Average of the deviations from "0" (emmetropia), in diopters, not observing sign, viz. hyperopia (+) and myopia (-).

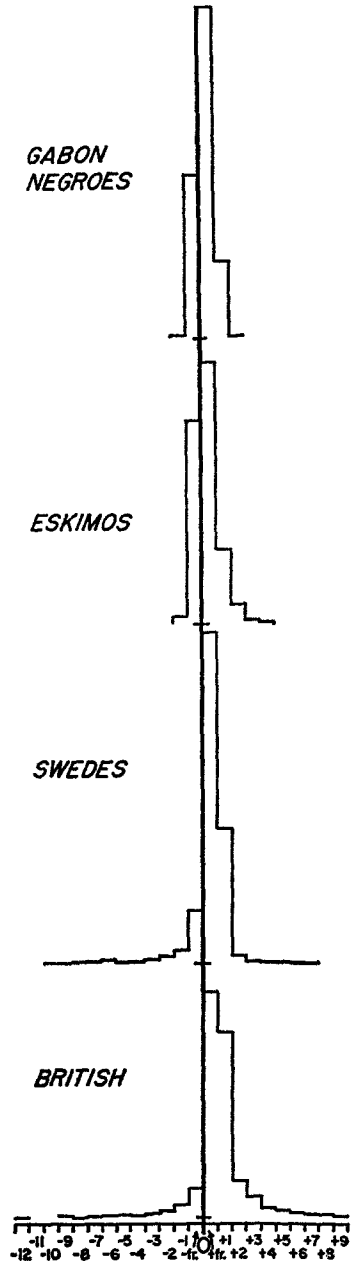


Fig. 2. Frequency distributions of refractions in 2 population samples of primitives and 2 of long civilized, on the same dioptric scale. Data from Table 4. (Emmetropia is represented by a heavy line.) Note the longer tails on both sides of the civilized samples

heredity since the influences of environment could not have been great at these tender ages, adding: "These curves of frequency during childhood bring out clearly the reason for the greater incidence of myopia in the adult Jewish population: the curve for Jewish children is decidedly flatter, i.e. the mode of refraction is on a lower hypermetropic level, and the whole curve is tilted towards the myopic side" (Sorsby, 1938, p. 396).

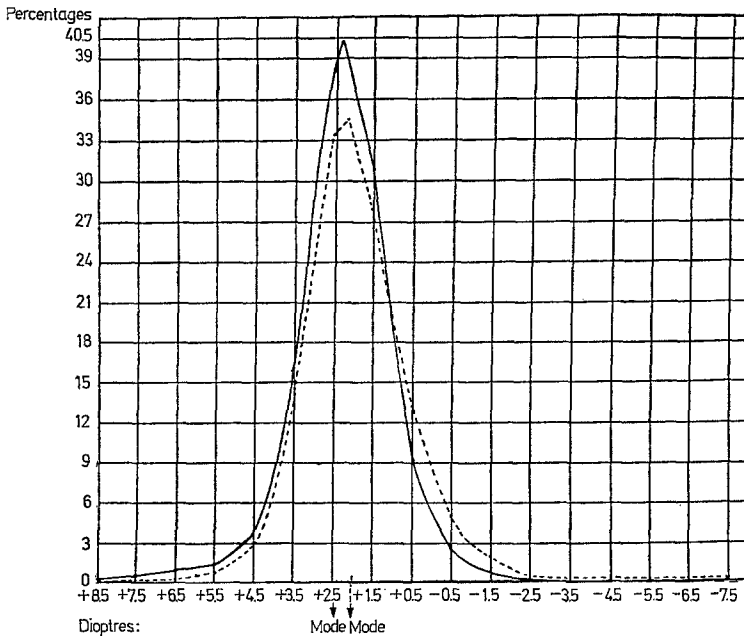


Fig. 3. Refractions of 772 Jewish and 672 non-Jewish children aged 4 to 8 years in London (from Arnold Sorsby, 1938, Transactions of the Ophthalmological Society of the United Kingdom, LVII, 394, with the kind permission of Professor Sorsby and the publishers). Refractions under atropine cycloplegia. — Non-Jewish children; - - - - - Jewish children. (Taken from Eugen. Quart. 9, 201 (1962) with permission; all rights reserved)

Civilized populations also present a slight but significant increase in frequency of hyperopia ("farsightedness"). Since relaxed selection tends to increase genetic variation, this should not be surprising. The typical frequency distribution curve of spherical refraction for any population is far from normal, being highly leptokurtic with an exceedingly large modal class of emmetropes and short tails of myopes and hyperopes. The distribution curves of civilized populations depart in three ways from those of primitives. They are somewhat flatter, and have longer and thicker tails on both sides, due to larger frequencies of both myopes and hyperopes of all degrees, with consequently fewer emmetropes. They are less symmetrical, since marked myopes greatly outnumber marked hyperopes. Thirdly, their means are slightly more on the hyperope side, because of higher frequencies of mild hyperopes. These features are represented in Table 4 and illustrated in Fig. 2, based upon 4 careful and thorough population studies. Summaries are given in Post (1962b).

Unusual care should be taken before making comparisons in the frequencies of refraction groups between populations. Samples should be drawn on the same basis, particularly of age, and examinations should be made by the same technical methods. These should be as objective as possible and, of course, preferably made by the same investigator. Most important, environmental influences should be thoughtfully evaluated and discounted. The general conclusion that a population's

frequency of myopia reflects the antiquity of its history or prehistory would hardly be justified from a few sample comparisons, but it does seem reasonable on the whole from the large number of comparative studies which consistently point in this direction.

Furthermore, it does not seem unreasonable to suppose that early man was subject to the most rigorous selection for distant vision acuity. In his constant movements, quest for food by whatever means, particularly in the avoiding of enemies, defective vision would have led to speedy death. Unmarked wildlands cannot be traversed efficiently, whether they are well known or not, even under conditions of leisure, without excellent eyesight. Under conditions of stress such as hunger, storms, warfare, etc. selection pressures must have been intense. Obviously they varied with culture, ecological conditions, terrain and other factors. Persons doubting the high selection pressures on primitive man of vision acuity should experiment with bow-and-arrow shooting and animal tracking and bird watching, etc. — without glasses, and in company with persons of normal acuity.

One may conjecture logically that throughout the long dawn of man's cultural beginnings a slowly growing proportion of individuals may have occasionally found relief. Occupations such as flint chipping and working with wood, fiber, skins, etc. do not demand the highest standards of distance vision. Culture-habitats which supported specialists in such industries were probably more tolerant of persons with slight refractive aberrations, particularly those who also possessed compensatory abilities. Some cultures may have even favored a mild myopia. This escape may have been rare until the cultures developed sufficiently to support full-time artisans as well as agriculturists. Relaxation may have increased following the domestication of animals, insofar as hunting may have been given up. With further developments of the Neolithic revolution, the trend towards relaxation probably proceeded more rapidly. Cultures which deliberately protected large classes of the population or provided support for them must have lowered the selection standard for vision acuity even further.

IV. Nasal Septum Deformities of the Skull

“Deviated nasal septum” has been corrected surgically on a large scale for decades and has generated a large literature, yet no explanation of its high frequency among Caucasians has received general acceptance, and its rarity among other races appears ignored. The present endeavor responds to both queries.

Skulls were chosen for population comparisons since they are more easily available (and more docile) than living subjects; repetition of examinations are facile; and modern Europeans can be contrasted with their neolithic forebears. Most of the abnormalities are lateral outgrowths of bony tissue of the vomer. Occasionally the ethmoid is also involved. A “spur” or “shelf” intrudes into the nasal passage on one side or the other, with approximately equal frequencies, restricting the free flow of air. Ossification of the lamellae is asymmetrical, through unilateral hypertrophy, producing a second type of “deviation” — a bowing or warping or buckling of the septum. Variation in the form and location of the abnormal bony outgrowths is almost infinite, as is the variation in the pattern of bowing. Bowing is more severe in the living since it is exaggerated in the cartilag-

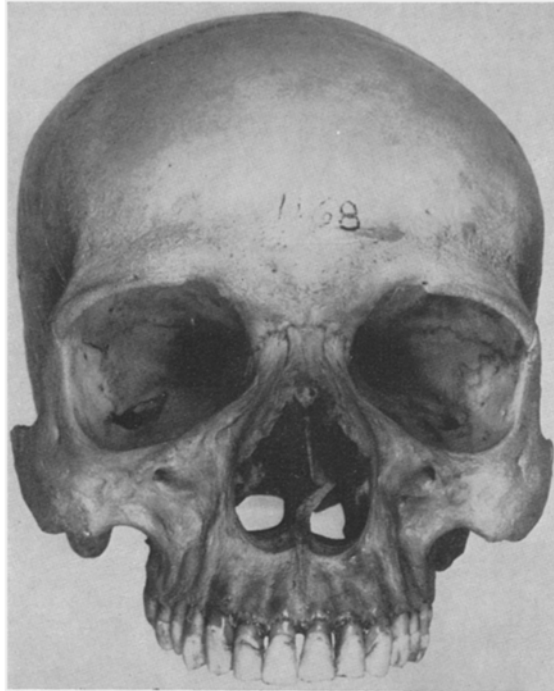


Fig. 4. Marked septal deviation to the left. Top of margin of vomer intrudes far into the left nasal passage. No indication of trauma or disease. American colored male, macerated. Terry Collection in U.S. National Museum. Courtesy of Professor Mildred Trotter. (From Soc. Biol. **16**, 180 (1969). Copyright (1969) by the American Eugenics Society, Inc. All rights reserved)

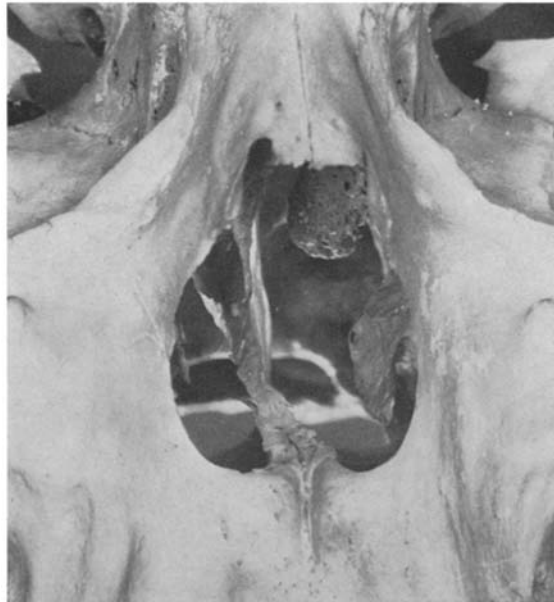


Fig. 5. Marked septal deviation to the right, with "bowing" into the right nasal aperture. Note bi-laminar structure of nasal spine and septum; enlargement of left conchae; absence of signs of trauma. European male, U.S. National Museum. Photo by Don Ortner, Smithsonian Institution. (From Soc. Biol. **16**, 181 (1969). Copyright (1969) by the American Eugenics Society, Inc. All rights reserved)

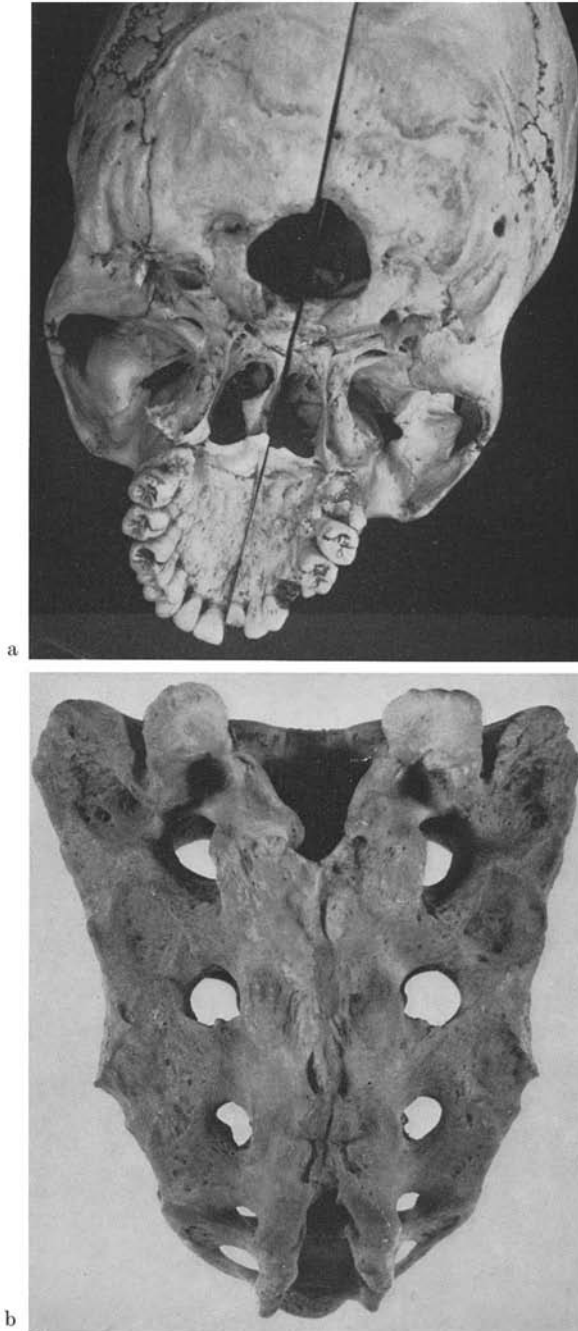


Fig. 6. a Inferior margin of "spur" into left nasal passage, from nasal septum, visible just above hard palate. Photo by Department of Anatomy, Western Reserve University Medical School, Cleveland. (From *Soc. Biol.* 16, 184 (1969). Copyright (1969) by the American Eugenics Society, Inc. All rights reserved.) b Abnormalities in the sacrum of a male Caucasian. U.S. National Museum, Photo by Don Ortner



Fig. 7. Abnormally small and misplaced nasolachrymal canal, mascerated skull of Hawaiian "pureblood" male, U.S. National Museum No. 225 524, gift of Naval surgeon, 19th Century, photographed by Professor J. L. Angel

inous portion of the septum, which is rarely preserved in skulls. Bowing occludes the nares on the convex side even more than the bony outgrowths, curtailing the free flow of air on the convex side, while the concave side suffers from over-ventilation. Both types of "deviation" are of course maladaptive, as expected in cases of relaxed selection.

Etiology

Gray (1965, 1967) reported septal abnormalities in 2.2% of a sample of 882 white babies after vaginal delivery. Many authors have attributed deviated septum to exogenous factors such as trauma or pressure on the fetus. Therefore several samples of Caucasoid skulls have been examined and scored for a number of factors which might be suspected of contributing to, or being associated with, deviated septum. Their frequencies in pairs of subsamples, one with and one without septal abnormality, were then compared. In 180 such paired comparisons the results were all negative, with high levels of statistical significance in all cases but one (Post, 1966b, 1969a). The factors are:

Trauma — of any bone of the face.

Asymmetry — of nasal bones, nasal sill or aperture, and of premaxillary bone.

Size of nasal aperture — length; breadth.

Tear ducts — size and normalcy of form of external opening.

Length of face, excluding mandible.

Height of nasal bridge.

Height of palate.

Development of palatine torus.

Dental occlusion: a) Articulation of upper and lower first molars; b) overbite; c) overjet; d) crossbite; e) crowding of anterior teeth.

Thickness of septum.

The only factors associated with deviated septum are age (at death) and sex. Deviations are more frequent in older skulls of both sexes, and more frequent among males than females.

Some authors have invoked hereditary factors, but only one study of family histories is known. Leicher (1929) compared 100 pairs of parents with their 288 offspring over age 16 in type and degree of deviation. He reported that 90% of the offspring of 2 normal parents were also normal; 45% of the offspring of 1 normal and 1 abnormal parent were normal; 20% of the offspring of 2 abnormal parents were normal. Several twin studies have been published, 2 of which permit heritability estimates, which are 0.39 and 0.62. Schwarz (1923) classified monozygotic (MZ) and dizygotic (DZ) pairs in 3 categories as to type and degree of resemblance: "same; similar; and different". Consolidating the first 2 classes, his results are:

	MZ	DZ
Same or similar	28 (52.8%)	7 (22.6%)
Different	25	24
	53	31

Since the rates of resemblance are significantly distinct in both studies, estimates of heritability are justified:

$$\frac{M - D}{100 - D} = \frac{52.8 - 22.6}{100 - 22.6} = 0.39.$$

Twin data of Schnitzler (1933) may be treated likewise:

	MZ	DZ
Same or similar	25 (73.5%)	8 (29.6%)
Different	9	19
	34	27

Heritability is estimated: $\frac{73.5 - 29.6}{100 - 29.6} = 0.62.$

Population Comparisons

Frequencies of septal abnormalities have been reported in 29 population samples, 18 primitive, 9 civilized and 2 Neolithic (here considered apart) as well as in several samples of mixed descent (Post, 1966b, 1969a).

Skulls were graded subjectively as to degree of occlusion of the nares. Three grades of abnormality were employed: slight, marked and very marked. Subjective grading is unsatisfactory, being arbitrary and ill defined, but it offers the only way of making a study of this sort. Standards were established in the mind of the investigator by grading 100 European skulls several times. Errors approxi-

Table 5
Rates of normal and abnormal nasal septa (vomer). sl = slight, m = marked, vm = very marked

Population	N	Normal (%)	Abnormal		
			sl (%)	m (%)	vm (%)
Group A — <i>Hunters and food gatherers</i>					
Dakota Indians ^a	72	64	25	9	1
Pueblo Indians	86	72	16	11	1
Illinois Indians ^a	77	73	12	15	0
Australian aborigines	27	74	15	11	0
West Africans (1969)	37	73	27	0	0
Hawaiians ^a	109	82	14	4	0
California Indians ^a	100	82	12	6	0
Kwakiutl Indians	45	89	0	11	0
Montana Indians	48	90	4	6	0
Eskimo	271	90	8	2	0
Eskimo ^a	30	90	10	0	0
E. Algonkian Indians	63	90	5	3	2
Papuan-Melanesians	153	91	6	3	0
Aleuts	36	92	5	3	0
Aleuts ^a	213	92	7	1	0
Eskimo (1969)	85	96	4	0	0
Alaskan Indians	27	96	0	4	0
Bushmen, SW Africa	12	100	0	0	0
Unweighted mean	1491	85	10	5	0
Group B — “ <i>Civilized</i> ”					
Europeans, northwestern	42	36	36	16	12
Czechoslovaks (1969)	86	42	28	20	10
U.S. whites ^a (1969)	263	44	25	23	8
Egyptians, Ptolmaic	204	56	16	22	6
Egyptians, Ptolmaic ^a	102	63	30	9	0
Europeans, mixed	437	68	14	18	1
Chinese	37	70	8	19	3
Mongols ^a	112	70	15	5	10
Chinese ^a	62	73	21	6	0
Unweighted mean	1336	59	22	14	5
Group C — <i>Neolithic</i>					
Northwestern Europe	192	70	22	7	1
Egypt	56	86	5	9	0

^a Examined in U.S. National Museum, Washington. The other contemporary skulls are in the Museum of Natural History, New York. The Egyptian neolithic skulls are in the Department of Anatomy, Medical School, Cairo; the European neolithic skulls in various museums in Europe.

mated 6% the first time, less on each succeeding test. Particular care was taken to distinguish post-mortem shrinking and warping from growth abnormalities, to identify cases of trauma and to avoid bias in omitting severely damaged skulls. Since age differences are important (Ali, 1965) no adolescent skull was included. Trial comparisons between subsamples of skulls aged 15—40 and subsamples over

60 from the same population showed no significant differences in the rates of abnormality. Although male rates are considerably higher than female rates the sexes are pooled in population comparisons since in many cases no note was made of sex, and the noted cases indicate that the two sexes are represented fairly equally in most samples. Further discussion of these and other questions of procedure have been published, with complete results (Post, 1966b, 1969a).

The contrast between higher frequencies among civilized and lower frequencies among primitives is marked (Table 5). Frequencies of normal septa of the 9 samples of civilized populations aggregating 1336 skulls range from 36 to 73%, those of the 18 primitives aggregating 1491 skulls, from 64 to 100%, viz:

% Normal	35+	40+	45+	50+	55+	60+	65+	70+	75+	80+	85+	90+	95+	T
Primitive						1		4		2	1	7	3	18
Civilized	1	2			1	1	1	3						9
Neolithic								1			1			2

A sample of 192 neolithic skulls from northwestern Europe with 70% normal stands between the frequencies of primitives and of civilized, which average (unweighted) respectively 84 and 59%. A sample of Egyptian neolithic skulls with 86% normal is within the range of primitives.

Although no estimate of statistical significance of population differences is justified by data obtained in this way, overall difference between the two groups of populations would appear to overshadow errors of subjective grading, of age and sex and fortuitous variation. To a person who has examined a few septa of skulls of both groups, no statistics would be necessary for representing the magnitude and depth of the contrast. The "normal" septa in samples of primitives with low frequencies of abnormality are impressively regular and symmetrical, to the point of monotony, with few borderline cases. But in all European samples a large proportion of "normals" are close to being classed as abnormal, and a high proportion of the abnormal are graded "marked" or "very marked", as shown in Table 5. No statistic could reflect the extreme variety of the deformities in European skulls, all bizarre and grotesque, yet each case unique, all obviously without function.

The selective disadvantages of abnormal septa are high beyond controversy. Deviation produces over-ventilation on one side, with consequent drying of the mucous membrane and diminished activity of the cilia. Under-ventilation is produced on the other side. Both conditions encourage infection and mouth breathing, with increased risk of serious complications (Riggs, 1961; Gill, 1963; Gray, 1965, 1967). Under-ventilation at the opening of the eustacian tube may lead to tinnitis, deafness, or sinusitis (Coakley, 1930). Marked deformity of the septa lead to frequent head colds and increase the risk of otitis media, loss of hearing and loss of sense of balance. Mouth breathing produces recurrent infections of the throat and sinuses, with diminished acuity in taste and smell (Heatley, 1937). The penalties of mouth breathing to stone-age man are reviewed by Post (1966b, 1969a).

V. Small Tear Ducts; Breast Cancer; Mild Hearing Loss; Spina Bifida Occulta

No additional "trait" with similar advantages for appraising the effects of relaxed selection has been studied in detail, but four others which offer tempting possibilities for investigation have been considered briefly.

Abnormally small lumen of the tear duct (nasolachrymal canal) is often associated with dacryocystitis, infection and inflammation of the duct (Schaeffer, 1920), which afflicts about 3% of white adults in large clinic samples in Britain (Traquair, 1941; Foster, 1956; Dalglish, 1964) but is almost unknown among negroes (Santos-Fernandez, 1921; Garfin, 1942). The lumen of the negro tear duct is said to have larger diameter, shorter and more straight course than that of whites (Martin, 1928, vol. 1, p. 970), but no measurements have been published. No other reference to racial comparison is known. Family histories of dacryocystitis among Caucasians have been reported (Schnyder, 1920; Sorsby, 1951, p. 196; 1953, p. 367; Viers, 1955, p. 73; Waardenburg *et al.*, 1961, pp. 295—297). One might therefore speculate that relaxed selection among Caucasians has occasioned an accumulation of genes which produce under-sized tear ducts, from centuries of greater protection against the stresses of life in post-paleolithic cultures, and greater protection of afflicted individuals.

This hypothesis was approached by measuring the size of the external opening of the tear duct in 48 samples of skulls (Post, 1969b, c), viz: males and females, lefts and rights in 12 populations in the following numbers:

	Females	Males
Eskimo and Aleuts	246	246
Paleolithic Indians, etc.	57	91
African Negroes	127	99
Peruvian Indians	102	121
Papuan-Melanesians	104	98
Hawaiians	105	83
Pueblo Indians	92	76
Australian aborigines	53	53
Chinese	41	152
American colored	42	438
Caucasians, modern	312	551
Caucasians, neolithic	102	156

Samples were compared, not in mean size and variance but in the frequencies which fall below the threshold of any particular size category. The Caucasian samples have excessive numbers of "abnormally" small lumen, defining "abnormal" at every possible threshold. In 2×2 tables the differences are significant at high levels by Chi square tests. For example, comparing males in left tear duct size at category number 7:

	Size 7 and smaller	Larger than size 7	T
Africans	13	37	50
Caucasians	190	81	271
<i>T</i>	203	118	321

$\chi^2_{(1)}$ is 33.5.

American colored and Chinese are intermediary between Caucasians and primitives. Eskimo and Aleuts have the largest ducts.

Males have larger ducts than females in all population samples, but the differences are not statistically significant. This may be a function of the overall excess in size of the male skull rather than being associated with lachrymal function, since there is no significant sex difference in orbital size and therefore presumably none in the volume of tear flow. Subsamples of "older" skulls (over 60) have smaller duct openings than "younger" skulls (under 50) in Caucasian samples of both sexes, and American colored male samples, which may be attributed to bone absorption with age.

Explanation of the excess of smaller sized duct openings among modern Caucasians has been sought in every possible direction. Ecological adaptation is discounted by the wide variety of environments represented by the samples — arctic, temperate, subtropical desert, tropical desert and tropical humid. No sample is distinguishable from another except the Caucasian, and to a lesser extent the American colored, which may be attributed to their partially Caucasian ancestry. The neolithic Caucasian openings are classed with the primitive, although the sample sizes are too small to have significance. The only explanation which is apparent is that of relaxed selection.

Carcinoma of the breast causes more deaths than carcinoma at any other site among white women in the United States. Worldwide morbidity and mortality rates among Caucasians are higher than in any other race. The closest approach is by American colored women, which may be due to their partially Caucasian ancestry. East Asians have notably low rates, as have their descendants in other lands. The genetic component in breast cancer is substantial (Wainwright, 1931; Martynova, 1937; Jacobsen, 1947; Busk, 1948; Penrose *et al.*, 1948, 1953; Smithers, 1948; Macklin, 1952, 1959a, b; Woolf, 1955; Anderson *et al.*, 1958; Oliver, 1958; Murphy *et al.*, 1959; Bonser *et al.*, 1961). Therefore the hypothesis arises of attributing the high rates among Caucasians to racial factors. Although breast cancer among males is rare, both the clinical picture and the racial distribution resemble those for females (Newill, 1961; Schottenfeld and Lilienfeld, 1963).

A special feature in the culture-habitat of Caucasians which is lacking in other long-civilized populations is the artificial feeding of goats' milk to infants. Goats were domesticated in earliest neolithic times somewhere in the Middle East. Evidence is abundant that their milk was utilized almost universally at the earliest neolithic horizons by Caucasians, particularly for infants and children, but apparently milk culture did not diffuse very far among non-Caucasians.

This situation may explain the high frequency of mothers' milk failure which is noted among Caucasian populations everywhere today, by invoking the relaxed selection hypothesis (Levin, 1963). Genetic factors in hypolactation are widely recognized (Hughes, 1948; Pfändler, 1949; Hytten, 1954; Wickes and Curwen, 1957; Gans, 1958; Ingold, 1960; Meyer, 1960). The frequency of "genetic hypolactators" has been estimated at about 5 to 6% of British mothers who desired to nurse and who received encouragement and instruction in nursing (Spence, 1938; Dummer, 1949; Hytten, 1958). Failure to nurse is almost unknown among non-Caucasians.



Fig. 8. Bifid spines of thoracic vertebra of Caucasian female, U.S. National Museum. Photographed by Don Ortner, Smithsonian Institution

These situations are discussed in Post (1966a), with consideration of a possible genetic relationship (pleiotropy) between hypolactation and breast cancer, under the hypothesis of relaxed selection in the Caucasian race resulting from ancient utilization of domestic animal milk for baby feeding.

High frequencies of genetic types of deafness have been reported in isolated populations of Caucasians, notably in mountain valleys and on small oceanic islands, but they represent recent phenomena and illustrate rather special cases of relaxed selection. Race differences in mild losses have been investigated, occasionally in anticipation of demonstrating higher levels of sensitivity among "savages" and "primitives" than civilized populations. Results have not been impressively reliable. 5 large and careful investigations of hearing acuity among Negroes and whites are critically reviewed by Post (1964). They may be summarized as follows: a) Mild hearing losses of Negroes are more frequent than those of whites at 3 lower pitches (tonal frequencies of 440, 880 and 1760 cycles per second) for four age groups: to very slight degrees in the youngest (10—19),

maximally in the oldest (40—49), and in both sexes, although the race differences are less pronounced among females; b) At the highest pitch the reverse situation is found, with mild hearing losses of whites more frequent than those of Negroes (7040 cps.). Results are mixed at the intermediary pitch (3520 cps.). The testing of conscripts by the whispered voice at very high pitches has amply confirmed this finding; c) Among African Negroes tested in their own culture where noise exposure has been minimal, the mild hearing losses at all tonal frequencies were phenomenally rare. The implications of these results under hypotheses of relaxed selection are matters for conjecture.

Spina bifida occulta presents a fourth "trait" opportune for investigating and comparing the frequencies of genetically conditioned abnormalities of the skeleton among civilized and primitive populations, including neolithic samples. Vertebral spines remain bifid or cleft, through failure of left and right lamellae to fuse during ossification, in sufficiently high frequencies to permit population contrasts. Relevant publications are critically reviewed and new data reported by Post (1966c), with comments having particular significance for relaxed selection. In general summary: a) Cervical spines are cleft to mild degrees more frequently in Negro than in white samples, but to marked and very marked degrees more frequently in white than in Negro samples; b) Lower thoracic and lumbar spines present the reverse situation, with excesses among Negroes of marked clefts contrasted with whites; c) Sacral hiatus, or marked bifurcation of the fifth sacral vertebra, often involving the fourth and perhaps even the third sacral vertebra, is more frequent in populations with long histories of civilization than among various samples of primitives; d) Hernia of the first sacral vertebra, independently of hiatus of the fifth, presents this same contrast between samples of civilized and primitive populations. Although museum collections of skeletal remains provoke questions of sampling bias, the above observations are perhaps the more credible for having been reported by several different authors.

Evolutionary changes in teeth and jaws have been investigated more frequently than any "trait" mentioned above. The subject is well reviewed with a generous bibliography by Wolpoff (1968), who also discusses relaxed selection in general.

In conclusion the hope is expressed that more extensive and more thorough investigations may be made of possible cases of relaxed selection in civilized populations. Particularly rewarding would be investigations of the many genetically influenced anomalies, disorders and diseases which are susceptible to modern therapy. Examples include hare lip and/or cleft palate, congenital dislocation of the hip (orthopedic or plastic surgery); congenital pyloric stenosis, megacolon, Fallot's tetralogy (major operations); schizophrenia (a variety of treatments). All cases of relaxed selection — the First Corollary of Darwinism — are examples of rapid evolution. Cases arising from modern therapy and preventive medicine demonstrate the most rapid changes.

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