

allosteric molecules, the conformation of which is regulated by the hormones (26). Direct binding studies (40) suggest that some of these receptors are located in the nucleus. Since the repressor appears to function in the cytoplasm to inhibit synthesis of the aminotransferase, it seems unlikely at first glance that the nuclear receptors themselves are the labile repressor.

Therefore, the mechanism by which the steroid-receptor complex influences repressor activity might well be indirect, for example either inhibiting repressor synthesis or transport, or else promoting its degradation.

Alternatively, the inducers might interact directly with the cytoplasmic repressor causing its translocation to the nucleus, where it could no longer inhibit aminotransferase synthesis. If this were true, the nuclear receptors would represent only an inactive form of the repressor. This possibility might be consistent with the presence, in the uterus, of cytoplasmic receptors which migrate to the nucleus after complexing with estradiol (41).

Relatively few results are available at this time which actually exclude conceivable mechanisms of hormone action. One set of such experiments (26, 40) shows that steroid metabolism is not required for binding to the specific corticosteroid receptors in HTC cells; and another study (42) has shown that neither cyclic adenosine monophosphate nor adenylyl cyclase are present in these cells.

References

1. F. Jacob and J. Monod, *J. Mol. Biol.* **3**, 318 (1961).
2. M. Ptashne, *Nature* **214**, 232 (1967); W. Gilbert and B. Muller-Hill, *Proc. Nat. Acad. Sci. U.S.* **56**, 1891 (1966); *ibid.* **58**, 2415 (1967).
3. R. E. Marshall, C. T. Caskey, M. Nirenberg, *Science* **155**, 820 (1967).
4. H. Harris, in *Progress in Nucleic Acid Research*, J. N. Davidson and W. E. Cohn, Eds. (Academic Press, New York, 1963), vol. 2, p. 19; K. Scherrer, L. Marraud, F. Zajdela, I. London, F. Gros, *Proc. Nat. Acad. Sci. U.S.* **56**, 1571 (1966); J. F. Housais and G. Attardi, *ibid.*, p. 616; R. Shearer and B. McCarthy, *Biochemistry* **6**, 283 (1967).
5. G. Tomkins and B. N. Ames, *Nat. Cancer Inst. Monogr.* **27**, 221 (1967).
6. D. F. Summers and J. V. Maizel, *Proc. Nat. Acad. Sci. U.S.* **59**, 966 (1968).
7. M. Jacobson and D. Baltimore, *ibid.* **61**, 77 (1968).
8. R. T. Schimke, E. W. Sweeny, C. M. Berlin, *J. Biol. Chem.* **240**, 322 (1965).
9. E. C. C. Lin and W. E. Knox, *ibid.* **233**, 1186 (1958).
10. E. B. Thompson, G. M. Tomkins, J. F. Curran, *Proc. Nat. Acad. Sci. U.S.* **56**, 296 (1966).
11. G. M. Tomkins, E. B. Thompson, S. Hayashi, T. D. Gelehrter, D. K. Granner, B. Peterkofsky, *Cold Spring Harbor Symp. Quant. Biol.* **31**, 349 (1966).
12. D. K. Granner, S. Hayashi, E. B. Thompson, G. M. Tomkins, *J. Mol. Biol.* **35**, 291 (1968).
13. S. Hayashi, D. K. Granner, G. M. Tomkins, *J. Biol. Chem.* **242**, 3998 (1967).
14. F. Valeriote, F. Auricchio, G. M. Tomkins, D. F. Riley, *ibid.* **244**, 3618 (1969).
15. F. T. Kenney, *ibid.* **237**, 3495 (1962).
16. B. Peterkofsky and G. M. Tomkins, *J. Mol. Biol.* **30**, 49 (1967).
17. F. T. Kenney, *Science* **156**, 525 (1967).
18. A. Grossman and C. Mavrides, *J. Biol. Chem.* **242**, 1398 (1967).
19. J. Reel and F. T. Kenney, *Proc. Nat. Acad. Sci. U.S.* **61**, 200 (1968).
20. F. Auricchio, D. Martin, Jr., G. M. Tomkins, *Nature*, in press.
21. D. Martin, Jr., G. M. Tomkins, M. Bresler, *Proc. Nat. Acad. Sci. U.S.* **63**, 842 (1969).
22. D. Martin, Jr., G. M. Tomkins, D. K. Granner, *ibid.* **62**, 248 (1969).
23. L. D. Garren, R. R. Howell, G. M. Tomkins, R. M. Crocco, *ibid.* **52**, 1121 (1964).
24. G. M. Tomkins, T. D. Gelehrter, D. K. Granner, B. Peterkofsky, E. B. Thompson, *Exploitable Molecular Mechanisms and Neoplasia* (Williams and Wilkins, Baltimore, 1969), p. 229.
25. B. Peterkofsky and G. M. Tomkins, *Proc. Nat. Acad. Sci. U.S.* **60**, 222 (1968).
26. H. H. Samuels and G. M. Tomkins, *J. Mol. Biol.*, in press.
27. T. D. Gelehrter and G. M. Tomkins, *ibid.* **29**, 59 (1967).
28. B. R. McAuslan, *Virology* **21**, 383 (1963); E. Scarano, D. de Petrocellis, G. Augusti-Tocco, *Biochim. Biophys. Acta* **87**, 174 (1964); T. Noguchi, *J. Fac. Sci. Univ. Tokyo, Sect. IV Zool.* **11**, 255 (1967); B. W. O'Malley, *Biochemistry* **6**, 2546 (1967); E. Eliasson, *Exp. Cell Res.* **48**, 1 (1967); *Biochem. Biophys. Res. Commun.* **27**, 661 (1967); J. R. Whittaker, *J. Exp. Zool.* **169**, 143 (1968); D. R. Wing and D. S. Robinson, *Biochem. J.* **106**, 667 (1968); D. W. Stubbs and D. B. Haufrect, *Arch. Biochem. Biophys.* **124**, 365 (1968); D. Nebert and H. V. Gelboin, *J. Biol. Chem.* **243**, 6250 (1968); A. A. Moscona, M. H. Moscona, N. Saenz, *Proc. Nat. Acad. Sci. U.S.* **61**, 160 (1968); R. L. McCarl and R. C. Shaler, *J. Cell Biol.* **40**, 850 (1969); J. Vilcek, T. G. Rossman, F. Varacalli, *Nature* **222**, 682 (1969).
29. H. H. Samuels and G. M. Tomkins, in preparation.
30. P. R. Gross, L. I. Malkin, W. A. Moyer, *Proc. Nat. Acad. Sci. U.S.* **51**, 407 (1964).
31. L. D. Hodge, E. Robbins, M. D. Scharff, *J. Cell Biol.* **40**, 497 (1969).
32. J. J. Castles and M. F. Singer, *J. Mol. Biol.* **40**, 1 (1969).
33. T. D. Gelehrter and G. M. Tomkins, *Proc. Nat. Acad. Sci. U.S.*, in press.
34. W. Beerman, in *Developmental Cytology*, D. Rudnick, Ed. (Ronald Press, New York, 1959), p. 83.
35. D. D. Brown and E. Littna, *J. Mol. Biol.* **8**, 669 (1964).
36. J. Bonner, M. E. Dahmus, D. Faimbrough, R. C. Huang, K. Marushige, Y. H. Tuan, *Science* **159**, 47 (1968).
37. J. Paul and R. S. Gilmour, *J. Mol. Biol.* **34**, 305 (1968).
38. R. R. Burgess, A. A. Travers, J. J. Dunn, E. K. F. Bautz, *Nature* **221**, 43 (1969).
39. R. J. Britten and E. H. Davidson, *Science* **165**, 349 (1969).
40. J. Baxter and G. M. Tomkins, *Proc. Nat. Acad. Sci. U.S.*, in press.
41. E. V. Jensen, T. Suzuki, T. Kawashima, W. E. Stumpf, T. W. Jungblut, E. R. De Sombre, *ibid.* **59**, 632 (1968).
42. D. K. Granner, L. R. Chase, G. D. Aurbach, G. M. Tomkins, *Science* **162**, 1018 (1968).

Human Biological Adaptability

The ecological approach in physical anthropology.

Gabriel W. Lasker

The theme of the U.S. effort in the International Biological Program is listed as "Man's survival in a changing world," and the whole of the International Biological Program has been described as focusing on ecology, especially human ecology.

The Human Adaptability Project is

one of the principal aspects of the International Biological Program. Internationally about 50 nations are participating in the Human Adaptability Project studies of adaptation of many different peoples to a wide variety of environments. Of the integrated research programs constituting the U.S. contri-

bution to the International Biological Program, five studies form the Human Adaptability group while eight constitute the environmental management group (I). The former consist of (i) the "International Study of Circumpolar Peoples Including Eskimos" involving adaptations to cold; (ii) the "Population Genetics of the American Indian" emphasizing adaptations to life under primitive conditions on the tributaries of the Amazon and Orinoco rivers; (iii) the "Biology of Human Populations at High Altitudes" in the Andes of Peru and in the Rockies but coordinated with studies in the Ethiopian highlands, and in the Himalayan and Tien Shan mountains; (iv) "Nutritional Adaptation to the Environment"; and (v) the "Ecology of Migrant Peoples." A sixth program in chronobiology is being prepared.

Because adaptation has a variety of connotations that are different in different disciplines, this surge of activity and the participation of so many physical anthropologists in it warrant an attempt to explain a physical anthropologist's view of human adaptation. I shall not attempt to review here man's adaptation to infectious diseases, man's cultural adaptations, the story of the evolution of man, or the abundant physiological literature on various homeostatic adaptations.

Adaptation is the change by which organisms surmount the challenges to life. In the broadest sense biological adaptation encompasses every necessary biological process: biochemical, physiological, and genetic. Adaptation can therefore be involved in (i) major evolutionary events, (ii) growth of the individual, and (iii) behavioral and physiological changes lasting only hours or minutes. Human adaptation covers both functional processes and the structures on which they depend. It differs from human biology as a whole chiefly by its limitation to the concern with how the organism relates to the circumstances it must meet to live.

Adaptation implies its antithesis: if one way of functioning is adaptive, another is less adaptive or disadaptive under comparable circumstances. From this springs the idea of adaptive selection, the central theme of the Darwinian theory of evolution—the natural selection of better-adapted organisms and the extinction of the less well adapted through reduced fertility or earlier death. In this sense adaptation is a modification in structure or function that enables an organism to survive and reproduce. The term can apply to a particular organ or the whole individual and to entire populations or whole species. The more different the individuals or species are, the more able we are to identify the relation of the anatomical differences to different behavior and different adaptation to the environment. Conversely, the peoples of the world today are so similar that it is often difficult to relate specific structural differences to the specific environmental differences man encounters throughout the world. Adaptation occurs at three levels: (i) selection of genotype, (ii) ontogenetic modification, and (iii) physiological and behavioral response. As one goes from interspe-

cific differences to individual differences within the human species, the chief emphasis shifts from the first level to the second and third. This can be exemplified by anthropological studies of human adaptation to altitude, cold, heat, migration, and other circumstances.

Altitude Adaptation

Adaptation of man to high altitudes involves numerically a relatively small problem. Only about 25 million people (that is, less than 1 in 100) of the world's people live in high mountains. But high altitudes, with their low atmospheric oxygen tension, present an environmental problem that could not be modified by human inventions until the present century when bottled oxygen and other such therapies were available for treating mountain sickness. Men living in the mountains use drugs such as alcohol and coca (the plant that yields the narcotic cocaine) to lessen their psychological burden, and this may alter the nature of their response and hence the impact of the conditions. However, the extent to which these drugs ameliorate the physiological burden of the altitude seems to be slight although consumption of alcohol can raise the foot temperature of the highland Indian and increase his comfort during the cold of night (2).

When individuals climb from sea level to an elevation of 4000 meters or more, there are large differences in the extent of the response and some individuals may even die of pulmonary edema. However, a usual response is an increased rate of breathing and an increased pulse rate under comparable work loads. After a few days at that altitude there is some short-run "adaptation," including increase in hemoglobin concentrations, but there still are difficulties in working. Families who continue to live there incur increased risks of miscarriages, birth defects, and infant deaths. Individuals reared at these elevations achieve more adequate adaptation and the risks are lower. Those born into populations genetically adapted to the altitude apparently do better still. Newman and Collazos and, more recently, Baker (3) report that in the Peruvian Andes growth and skeletal maturation is retarded; the consequent relative stunting is possibly an advantage. Chest measurements do not follow this trend toward small dimensions, however; Indian boys in the high moun-

tains of Peru, while developing more slowly than coastal dwellers in other respects, develop a larger thorax and greater lung capacity (4).

Mountain dwellers thus show the three chief modalities of adaptation: (i) short-run physiological changes; (ii) modifications during growth and development; and (iii) modification of the gene pool of the population. It is probable that the well-adapted mountain dweller suffers some relative shortcomings when at sea level, but since the Indians who migrate from the Andes to the cities on the coast suffer some of the same kinds of social disabilities as Appalachian Mountain folk do in the core cities of the United States, analysis of purely biological status is complicated by the concomitants of social status, and the results of studies of such people are difficult to interpret. One example of the fact that good genetic adaptation at one elevation may be bad at another is the case of sickle-cell and thalassemia traits. Heterozygosis confers a degree of immunity to endemic malaria in low-lying areas; but at very high elevations even the heterozygotes may have hemolytic crises.

Cold Adaptation

Man in the arctic provides another example of adaptations. In the arctic, however, people build houses, wear clothes, and light fires. These cultural traits constitute the predominant adaptations, and they are available for anyone to borrow. Thus the Eskimos have designed fine arctic clothing, and European and American explorers have copied their parkas and mukluks. Furthermore, Eskimos have developed behavioral patterns to meet crises. William Laughlin, F. A. Milan, and others are contributing much to our knowledge of Eskimo adaptations. If one Eskimo falls into the water, a companion will immediately share half his dry clothing—enough to get both men home, cold but alive.

Despite cultural adaptations there are times when biological differences count. Baker (5) gives an example of the Yahgan at the cold, southern tip of South America: we should not envision one native dying of exposure in a snow-storm while a better-adapted companion survives; instead, cultural modes ordinarily modify the biological conditions; the family of the ill-adapted individual dies of starvation huddled at

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their campfire while the well-adapted counterparts comfortably collect shellfish in the frigid water. To study cold-adaptation in man one must take account of indoor as well as outdoor temperatures, and also of activities, clothing, and shelter.

For life, man must maintain a core temperature close to 37°C. In the cold he does this by reducing circulation to the extremities (which therefore drop to lower temperatures than the trunk). But the vessels of the extremities periodically dilate; this cold-induced "cycling" is a widespread phenomenon among mammals and must be adaptive in some way (perhaps through decreased chance of frostbite) although it costs loss of stored heat. Body heat is generated by metabolizing food, burning it up as fuel. Shivering is an involuntary activity that increases the production of heat. All peoples of all places respond to cold in much the same ways. However, some people from cold climates (notably the Central Australian aborigines) have been reported to meet cold sleeping conditions by having the extremities cool off more relative to the trunk, and also by lowering core temperatures; but the subjects of these studies chewed tobacco and the leaves of *Duboisia* which contains an alkaloid poison. This cultural practice rather than genetic constitution may account for the difference in response (6). The short-run adaptations differ somewhat in those inured to the cold and in those new to it, but it is not definitely known how much genetic capacity for acclimatization, if any, differs among peoples.

In other species of animals, arctic forms tend to differ in predictable ways from those found in more southerly areas. One of the differences, fur, has no counterpart in man. The Eskimos, for instance, are relatively devoid of body hair. Arctic forms have small body-surface area relative to body mass. Some heat is lost in breathing, but most heat loss is through the skin; therefore the surface area of the skin (and hence the size of the individual, which largely determines surface area) relates to dissipation of heat. Body mass consists of metabolizing tissues (which produce heat) and fat (much of it just beneath the skin where it may help to insulate); hence increases in weight cause increased heat production and retention. Newman applies to man the two rules (or laws) which express these

relations between body size and form with temperature (7). Bergmann's rule (7) states that, in bodies of the same shape, the larger one has relatively smaller surface area; cold-adapted animals therefore tend to be large. Allen's rule (7) states that short extremities further increase the ratio of mass to surface area and that cold-adapted forms have relatively short limbs. In man, general body size as measured by weight or stature is, on the average, positively correlated with climate—especially the temperature in the coldest month. In continuous populations of large land areas of the Northern Hemisphere, including China, Europe, and the contiguous states of the United States, there is a gradient from larger average size in the north to smaller in the south (8). Nevertheless these dimensions vary considerably in any one place, and there are numerous exceptions to Bergmann's rule. For instance, Eskimos are small but squat and have relatively short limbs. Some people of East Africa provide an instructive example; they are very tall, but slim, and their limbs are exceptionally long (9). In any case, Roberts showed that the relation of weight to climate applies on a world scale, Schreider extended this to the ratio of surface area to weight, and Newman concluded that temperature accounts for almost 80 percent of the variance in average body mass of different populations throughout the world, when an appropriate allowance for stature is included (10). In mankind in general, tall stature is achieved primarily by growth of the limbs (trunk length being much less variable). The real test of the applicability of the rules of Bergmann and Allen to man should, therefore, come in genetically determined tendencies to depart from this nutritionally determined pattern, and to find large size with short limbs in the arctic and short stature with long limbs in the tropics.

Other details of morphology may also relate to heat balance. Nose form seems to be adapted to the degree of need to moisten the air one inhales. Noses are narrower in colder zones. Although correlations of nasal dimensions with degree of prognathism and shape of the dental arch complicate interpretation, the average ratio of the width to the length of the nose (nasal index) of populations throughout the world is highly correlated with climate—especially with vapor pressure, the amount

of moisture in a given amount of air (11). Of the various Mongoloid peoples, Eskimos have the narrowest noses. But it is unwise to assume that every morphological feature found in Eskimos is directly a protection against cold. For instance, the large, broad Mongoloid face of the Eskimo is more exposed to cold than the smaller face of the European, but frostbite of the face is rarely serious in either people (12).

High altitudes are also cold, and altitude studies must deal with the influence of both altitude and temperature. Some individuals adapted to altitude and cold maintain warmer hands and feet than nonadapted controls. This may serve to maintain more oxygen in these tissues as well as meet the challenge of low temperature (13).

Heat Adaptation

The regulation of human responses to excessive heat involves at least two distinct types of environment—dry heat and humid heat. In a hot place when a person works hard, the temperature is extreme, the humidity is high, or the sunlight is excessive, it puts a strain on the temperature-regulation system of the body. After about a week of acclimatization to repeated heat stress a subject will improve his tolerance for these conditions through increased sweating and decreased cardiovascular strain (14).

Most species of primates live in tropical forest environments. In the view of many, man's ancestors at one stage also lived in a hot, humid zone with little movement of air and with little direct sunlight. Under those circumstances the heat is well tolerated during rest but hard work produces heat stress.

In drier and more open country at low latitudes, where it is possible that, at a later stage, man's progenitors evolved their upright posture and a hunting-gathering economy, sweat evaporates more readily but sunlight on man and on the objects about him add a severe radiant heat load to the problems of heat adaptation. Sweating remains important. The upright posture reduces the surface area exposed to direct sunlight compared to that of a quadruped. Whether hair, at least long, straight hair could be an added protection against heat is problematical. In any case nakedness, far from being an advantage, as some anthropologists

have mistakenly claimed, would have prevented man from adapting to life under desert-like conditions until he achieved ready access to water through use of vessels or learned to wear loose clothing of some sort (15). Man cannot drink very much water at one time but can sweat more per hour than any other mammal so far tested. Before man learned how to carry water with him, human occupation of open plains and savanna therefore required behavior that would make it easy to reach drinking water frequently.

Although man is unique in his heat-adaptive mechanisms, there is little innate difference between human groups in their ability to respond to heat stress. Short-term acclimatization aside, there is little evidence of population differences. Since heat absorption and dissipation are surface phenomena, the search for possible population differences is logically concentrated on the area of the skin and the nature of its structures: pigment granules, hair, and sweat glands. Groups inhabiting the tropics are, as already noted, generally composed of small individuals. This increases the surface area relative to mass so that heat produced by activity can be more readily dissipated. Although even moderate activity in a hot environment normally results in some heat storage, excess heat must be dissipated sooner or later and this is more significant than the somewhat greater capacity for heat storage of larger individuals. In hot deserts the people are generally lean, another way of increasing the relative surface area and facilitating heat dissipation.

Pigment is not a simple question. Inhabitants of equatorial zones are dark. This is true of Melanesia, Australia, South India, and Africa, although in other respects the peoples of these areas are very different. Common adaptive modification rather than close common origins therefore accounts for the similarity in skin color. Numerous theories have been advanced to explain why dark skin color is adaptive in hot climates, and there is still no general agreement. Although light skin reflects more radiant heat, dark skin must protect the body better. Among other things dark skin inhibits sunburn, and sunburn interferes with the sweating response. Dark skin is also less susceptible to skin cancer, and it prevents the synthesis of too much vitamin D. In zones with much sun in summer, and

little in the winter, the ability to tan in summer would therefore be an advantage. Marjorie Lee and I (16) subjected individuals of various groups to measured amounts of ultraviolet light and we measured changes in the amount of light of different wavelengths reflected from the skin. We found that the capacity to tan varies considerably between individuals—even those with similar initial pigmentation.

The chief pigment of skin is melanin, and control of its production is evidently polygenic but based on few alleles at few loci. Livingstone (17) shows by computer simulation that on these assumptions one can easily account for the sort of skin color distributions one encounters in going from north to south in Europe, the Near East, and Africa, if there is a small differential advantage of presence of dark color in tropical Africa and vice versa in Europe. His calculations include a variety of assumptions, including migrations between populations. They do not explain its basis, but they do show that adaptative natural selection for skin color reasonably accounts for the known skin color distribution. Low rates of selection and recent migration are consistent with the facts that after some hundreds of years Europeans in the tropics are still light and Negroes in the United States are still dark. After several thousand years, however, American Indians in the tropics are slightly darker than those of North America to about the extent Livingstone's calculations would predict. Furthermore, the selective advantages postulated in the model are of a relatively low order so it is hardly surprising that we still lack direct evidence of the nature and amount of selection that takes place.

The role of human differences in hair with respect to heat tolerance is hard to calculate. Sheep with thick wool can thereby stand very heavy exposure to direct sunlight. Perhaps the retention of head hair in human beings is related to the crown of the head being the most exposed part in the noonday sun, but the influence of hair of different color and form remains to be established experimentally. Essentially nothing is known concerning when man's progenitors began to have such bald bodies or whether this antedated the invention of cloaks and hats.

It was once believed that Negroes had more or more efficient sweat glands than whites. Careful counts of areas of

skin show no such thing. The only known difference is that obese individuals have fewer sweat glands per given area of skin than thinner individuals. Persons of different body build seem to have approximately the same total number of sweat glands, however (18). After all, ability to maintain body temperature at a constant level is as important to an Eskimo trotting beside his sled dogs as to a caravaneer astride his camel.

Nutritional Adaptation

Nutritional adaptation not only depends on the resources available but also on the mode and degree of utilization. The utilization of food resources is a culturally-determined matter. Hunters, fishermen, and food collectors select only certain of the available foodstuffs. Agriculture and animal husbandry in any one place is limited to a very small number of edible species by the knowledge and culturally determined technology of the group. We still know relatively little about differences in nutritional requirements between populations. There do seem to be some inherent differences of this kind. Size itself is the most significant variable. Furthermore basal metabolic rate seems to be inherently high in populations which have always had a diet of good quality and low in some poorly nourished populations. Thus in one region in South China where a meager diet, 90 percent of which was from grain (mostly polished rice), has been reported, basal metabolic rates are also low. Neither the immediate diet nor that usual in the population explain all the variability in metabolic rates, however (19). Newman, in considering human bodily adjustments to nutrition, reports several instances where ingestion of necessary nutrients is a very small fraction of the supposed minimum requirements (7). He concludes that tolerances must vary over the world and that some human populations have adapted to levels of intake that would be fatal in others. On the other hand, ability to get by on less food may be more general. Throughout history most populations of the world have been subjected to repeated famines, and mankind must therefore share adaptive mechanisms to meet food shortages.

In addition, time apparently has been adequate for some special adaptations

in subpopulations. For instance, difficulty in digesting milk sugar (lactose) has been reported as occurring more frequently in some populations than in others, and the Chinese, whose cultural practices do not include use of milk from domestic animals, have a high rate of lactose intolerance; symptoms from ingesting monosodium glutamate, on the other hand, were reported not in those who have used this cooking powder for many generations but in Americans who call it "the Chinese restaurant syndrome" (20). One takes it for granted, on theoretical grounds at least, that where specific nutrients are scarce, populations with lower natural requirements for them would thrive, but this must be a minor advantage compared with the possession of adaptive cultural practices for acquiring such nutrients.

Lack of much food (hypocaloric diet) often occurs in the very environments, the tropics, where soils are leached of minerals and foods of animal origin are scarce. Furthermore, the food ingested must often feed parasites as well as the person. Thus the increase in body weight, from tropics to frigid zones, noted earlier under consideration of Bergmann's rule, may be a response to nutritional stress as well as to cold and heat stresses.

Plasticity

The adaptations discussed so far are mostly of two kinds; those genetically entrenched in the population by repeated natural selection and those dependent on a capacity to acclimatize in the short run (whether the capacity is equally shared by all subpopulations of the species or not). There is also a third intermediate type of alteration, modification of an individual during his growth and development. It may be thought of as a special case of acclimatization, but, since the process is essentially irreversible after adulthood, it deserves separate consideration and it may be separately designated as plasticity.

Early in the present century some anthropologists first asked whether the traits that were being used to characterize races could be influenced directly by environmental factors. They did not mean Lamarck's theory of inheritance of acquired characteristics, which had already been discredited; nor did they mean Darwin's description of the selectivity of the natural environment. The

question was: Would people grow up to be physically different if they lived differently? In 1905, Walcher, a German obstetrician, showed that, when babies are regularly placed on the backs of their heads, they become broader-headed than do babies who are customarily placed on their sides (21). In the same year, Fishberg compared measurements of the cephalic index and stature of Jews in various parts of Europe and in the United States and found that the two groups differed in these respects from each other (22). If cephalic index and stature could change in immigrants of at least one European group, how could these measurements be used as major criteria of race?

At this time many Americans were concerned with the assimilation of immigrants. Franz Boas exploited this concern in getting support from the United States Immigration Commission for a survey of the physical measurements of immigrants (23). Whatever may have been the expectations of the commission, Boas characteristically set himself a concrete problem and defined it operationally. Are the American-born children of European immigrants significantly different from their parents in such characteristics as cephalic index and stature? If so, do they also differ in the same respects from their immigrant brothers and sisters? Of the various groups Boas studied, his largest samples were of Central European Jews and Italians from Sicily. In both groups the offspring born in America tended to be taller than their parents; but in the Jews the cephalic index decreased, and in the Sicilians it increased. The measurements of the immigrant brothers and sisters, correlation with the length of the time the parents had been in the United States, and smaller studies of other nationalities led to the conclusion that the changes were the result of some aspect of the American environment that tends to bring about an American type with tall stature and medium cephalic index.

Some anthropologists attempted to explain Boas' findings on the basis of some selection, perhaps a self-selection of immigrants. To examine the possibility of such selection of immigrants, as well as the possibility of changes in the offspring of immigrants, Shapiro, in collaboration with Hulse and Lessa, undertook studies of two national groups in Hawaii, the Chinese and Japanese. Besides migrants and persons born in Hawaii, his study included

nonmigrants in the Orient, for whom Shapiro coined the word "sedentes." Of the Chinese study only a brief preliminary report ever appeared; the Japanese study, however, has been fully presented (24). The Japanese born in Hawaii were taller and broader-headed, and they differed significantly from Japanese immigrants in this and numerous other respects. However the immigrants were also different from the sedentes in many dimensions—including many in which those born in Hawaii differed from the immigrants. Shapiro explained the difference between sedentes and migrants on the basis of selection, and that between migrants and Hawaiian-born persons on the basis of factors in the environment during the growth period. The general findings of Boas and Shapiro have been confirmed by a number of studies (25).

Nevertheless, a number of problems remained. In the various studies, the immigrants measured were older than the subjects born in America, and to some extent this fact might explain the differences. There is a tendency for individuals to decrease somewhat in height after the age of 30 or so, and, in addition, people have been getting taller from generation to generation all over the world; both in Japan and the United States, for example, adult sons are taller than their fathers (and also taller than their fathers were at the same age). Such increases have been going on for 100 years and possibly for 200 or more years. Bowles has shown that Harvard sons of Harvard fathers were taller than their fathers were at the same age. The sons are larger in most other bodily measurements also, markedly so in the length of their thighs and forearms. Damon has followed some of these same families for four generations and finds no further increase in stature in the last generations, however, and he suggests that it is a straw in the wind that the secular increase in height has ended for economically favored American men (26).

To take account of secular trends as well as the effects of migration, Goldstein undertook a study in Mexico of Mexican parents and their adult children and a parallel study of Mexican immigrants to the United States and their adult children born in America (27). He found that the immigrants were larger in the usual respects than the sedentes, that the younger adults in Mexico were larger than their like-sexed parents, and that those born in

the United States were larger than their parents. The last difference was the most pronounced, however, and seemed to indicate a growth factor that is especially strong in the United States.

Subsequent studies of Mexicans have confirmed that Mexicans who grow up in the United States are taller and larger in other ways than those brought up in Mexico and that this is not the result of initial differences between those who migrate and those who do not (28).

On the other hand, studies of Italian Swiss in Italy and California demonstrate three factors leading to increased dimensions in the United States: (i) A selective migration of larger individuals; (ii) a tendency for those whose parents come from different communities to be larger than offspring of endogamous marriages, a finding confirmed in some but not in all other studies of the question; and (iii) plasticity in response to environmental conditions that are different in the two locations (29).

What is there in the environment of the United States that accounts for the greater growth here? The pattern of plastic changes is constant in all the studies of migrants, but such studies do not isolate specific causes (30). Nevertheless there is little evidence of significant influences of variation in temperature, altitude, or hygiene. The biggest single factor is diet, and the most significant aspect of diet is not the quality nor the vitamin content but simply the quantity of food. In the United States hypercaloric diets (too much food) are apparently more of a problem for health than any shortage or dietary deficiency. Coronary heart disease and other circulatory disorders are one of the chief causes of death, and the life insurance companies have found that, on the average, persons of normal weight for height live longer than the overweight and that underweight individuals live still longer.

Large body size would seem to be an advantage in the face of hypercaloric diets; the extra size achieved during growth would provide a larger frame and more metabolizing tissue to consume high caloric diets in adulthood without creating an excess that can only turn to fat. This may be as important as a small size achieved through the growth period is to an adult who must survive on a diet of very few calories per day. But there are other factors in the equation. Individuals adjust their food intake, and even in times of scarcity individuals of different size may

have different abilities to acquire food. Cultural factors are important, too, through the enforcement of various modes of food distribution and norms of rationing during shortages.

Growth

The adaptation of organisms is not only to adult form—important as viability of adults is to the survival of the population. Each developmental stage must also be viable, of course. In man growth itself requires considerable nutrients and is therefore part of the nutrient-energy economy. Tanner has surveyed the influence of environments on the growth process itself (31). During a period of starvation, a child slows down his growth, thereby conserving food energy. But he also tends to delay his maturation, thereby preserving the possibility of making up most of the loss if the period of deprivation is not too long and adequate food again becomes available. These temporary interruptions of growth in size with age may have little effect on body form. In virtually every country studied, growth of children was retarded as a result of the wartime food shortages of 1944–1945, but the characteristic population norms in proportion and eventual adult size were much less, if at all, affected.

Adverse conditions tend to retard growth, but not equally in all respects. Weight is, of course, immediately affected and height somewhat more slowly. As already noted, there is a general stunting and retardation of bony development in children in the Andes, but early and marked chest development occurs. Greulich found that in Japan children of all ages are, on the average, smaller than American white children in standing height, sitting height, and weight. The Japanese children are also slower in the ossification and maturation of specific bones. In these respects, however, North American-born children and also Brazilian-born Japanese children approach American standards (32).

Different criteria of maturation show different degrees of influence by nutrition and disease. Eruption of the teeth seems more resistant to modification than skeletal development (usually assessed on x-rays of the wrist). Sexual development, especially menarche (the age at which girls have their first menstruation) is retarded about 2 years in populations of lower social status or

who for other reasons have poor nutrition; menarche occurs earlier as conditions ameliorate (33). There is always a positive correlation between different signs of growth and development, however. Growth is thus channelized by genetic factors—no doubt slightly different in different populations—and adaptation is achieved by retardation within the channel in the face of acute stresses on the growth process. When the stress is chronic there may also be some change in the channels.

Some individuals, viewing the way racial differences have been used in the past as an excuse to enslave or even to annihilate whole populations, try to deny the existence in man of any adaptive differences. But differences exist both between individuals within the population and, on the average, between populations. Adaptive variability is a great asset to the species, hence, at least potentially, to future generations of every population. Throughout evolutionary history, however, adaptive traits which were inherent in certain genotypes and differently distributed in various subpopulations have probably given way to species-wide plasticity—an adaptive capacity available to any member of the species if he is subjected to certain conditions during development. Plasticity in turn must tend to be supplanted by the capacity to ever more rapid adaptation and acclimatization. The ready reversibility of acclimatization in the individual and of plastic traits in the subpopulation permit adaptation of genetically similar individuals in diverse environments. This must have been a necessity for man as he became one of the most widely distributed species and as he frequently changed his environments with ever-increasing rapidity.

The three modes of adaptation (selection, plasticity, and acclimatization) overlap and intergrade in populations and in individuals. The increasing importance of ready response does not eliminate selective pressures. All three modes are still operating and, in this day of rapidly changing conditions, provide a safeguard for the species. At a time when human genetic engineering is discussed and may be implemented, it is well to understand the significance of human variability and human adaptability. Social and political policies that provide opportunities for all will best accommodate varying individuals according to their biological capacities and needs.

Summary

Adaptation is an aspect of virtually all questions of human biology. Besides their interest in evolution through adaptive selection of the primates, including man, physical anthropologists are concerned with biological adaptability as a human attribute. In this sense adaptation has been examined at three overlapping levels: (i) those represented by differences in the extent of inherent capacities in subpopulations long exposed to different conditions, such as differences in the inherited determinants of body form and skin pigment in peoples in different climatic zones; (ii) adaptations acquired during the growth period of the individual such as residual stunting and reduced caloric needs in individuals receiving low caloric diets throughout childhood; and (iii) reversible acclimatization to the immediate conditions such as the changes which make it easier to work at high altitudes after the first few days there. Greater resilience to change is achieved if adaptations are reversible in each generation or within a lifetime. This implies an evolutionary tendency to shift human adaptability from genetic selection to ontogenetic plasticity to reversible adaptability.

References and Notes

1. Research Studies Constituting the U.S. Contribution to the International Biological Program (National Academy of Sciences, Washington, D.C., 1968), part 2.
2. R. B. Mazess, E. Picon-Reategui, R. B. Thomas, M. A. Little, *Aerosp. Med.* **39**, 403 (1968); J. M. Hanna, "The effects of coca chewing on exercise in the Quechua of Peru," *Hum. Biol.*, in press; M. A. Little, "Effects of alcohol and coca on foot temperature responses of highland Peruvians during a localized cold exposure," *Amer. J. Phys. Anthropol.*, in press.
3. M. T. Newman and C. Collazos, *Amer. J. Phys. Anthropol.* **15**, 431 (1957); P. Baker, *Science* **163**, 1149 (1969).
4. A. R. Frisancho, "Human growth and pulmonary function of a high altitude Peruvian Quechua population," *Hum. Biol.*, in press.
5. P. T. Baker, *ibid.* **32**, 3 (1960).
6. P. F. Scholander, H. T. Hammel, J. S. Hart, D. H. LeMessurier, J. Stem, *J. Appl. Physiol.* **13**, 211 (1958); C. S. Hicks, *Perspect. Biol. Med.* **7**, 39 (1963); R. W. Newman, personal communication; *J. Appl. Physiol.* **25**, 277 (1968).
7. M. T. Newman, *Ann. N.Y. Acad. Sci.* **91**, 617 (1961).
8. G. W. Lasker, *Anthropol. J. Inst. His. Phil. (Chungking)* **2**, parts I and II, 58 (1941); C. S. Coon, *Races of Europe* (Macmillan, New York, 1939); R. W. Newman and Ella Munro, *Amer. J. Phys. Anthropol.* **13**, 1 (1955).
9. The great size of the Watusi is a notable exception to Bergmann's rule which Baker (5) thinks may be due to their having been a ruling caste—hence perhaps less subject to the stress of work in the heat. In any case, these and other data from Africans show the complexity of the interaction between different ecological principles and quite unknown factors which must be integrated in the determination of physique, and which leads to many exceptions in the application of any one explanation. D. F. Roberts and D. R. Bainbridge, *Amer. J. Phys. Anthropol.* **21**, 341 (1963); J. Hiernaux, *La Diversité Humaine en Afrique Subsaharienne* (Inst. Sociol. Univ. Libre, Bruxelles, 1968).
10. D. F. Roberts, *Amer. J. Phys. Anthropol.* **11**, 533 (1953); E. Schreider, *Nature* **165**, 286 (1950); E. Schreider, *ibid.* **167**, 823 (1951); M. T. Newman, *Ann. N.Y. Acad. Sci.* **91**, 617 (1961).
11. J. S. Weiner, *Amer. J. Phys. Anthropol.* **12**, 615 (1954); M. H. Wolpoff, *ibid.* **29**, 405 (1968); E. V. Glanville, *ibid.* **30**, 29 (1969).
12. A. T. Steegmann, Jr., *Hum. Biol.* **39**, 131 (1967); "Thermal responses to cold in Hawaii," *Amer. J. Phys. Anthropol.*, in press.
13. P. Baker, *Science* **163**, 1149 (1969).
14. J. S. Weiner, *J. Roy. Anthropol. Inst. Gt. Brit. Ireland* **94**, 230 (1964).
15. R. W. Newman, "Why man is such a sweaty and thirsty naked animal: A speculative review," *Hum. Biol.*, in press.
16. M. M. C. Lee and G. W. Lasker, *ibid.* **31**, 252 (1959).
17. F. B. Livingstone, "Polygenic models for the evolution of human skin color differences," *ibid.*, in press.
18. A. S. Kip, "Measurement and regional distribution of functioning eccrine sweat glands in male and female Caucasians," *ibid.*, in press.
19. Reviews of the anthropological significance of basal metabolic rates by E. A. Wilson [*Amer. J. Phys. Anthropol.* **3**, 1 (1945)], N. A. Barnicot [*Sci. Progr. London* **153**, 124 (1951)], and D. F. Roberts [*J. Roy. Anthropol. Inst. Gt. Brit. Ireland* **82**, 169 (1952)] indicate that the world distribution of basal metabolic rates is inversely related to mean annual temperature even when due allowance is made for differences in stature and weight; there remains some doubt concerning what fraction of this adaptation is inherent, because rates change in migrants.
20. Among asymptomatic subjects, A. E. Davis and T. Bolin [*Nature* **216**, 1244 (1967)] report that all 15 Chinese, 4 of 5 individuals from the Indian subcontinent, and 2 of 12 Caucasians had abdominal pain and diarrhea after ingesting 80 grams of lactose. The Chinese restaurant syndrome was described by H. H. Schaumburg, R. Byck, R. Gerstl, and J. H. Mashman [*Science* **163**, 826 (1969)].
21. G. Walcher, *Zentralb. Gynaekol.* **29**, 193 (1905).
22. M. Fishberg, *Ann. N.Y. Acad. Sci.* **16**, 155 (1905).
23. F. Boas, *Changes in Bodily Form of Descendants of Immigrants*. Senate document 208, 61st Congress, 2nd Session. Washington, D.C. (1910).
24. H. L. Shapiro, "The Chinese population in Hawaii." Preliminary paper prepared for the 4th general session of the Institute of Pacific Relations, New York (1931), pp. 3-29; *Migration and Environment* (Oxford Univ. Press, New York, 1939).
25. P. K. Ito, *Hum. Biol.* **14**, 279 (1942); G. W. Lasker, *Amer. J. Phys. Anthropol.* **4**, 273 (1946); F. P. Thieme, *Pap. Mich. Acad. Sci. Arts Lett.* **42**, 249 (1957).
26. G. T. Bowles, *New Types of Old Americans at Harvard and at Eastern Women's Colleges* (Harvard Univ. Press, Cambridge, 1932); A. Damon, *Amer. J. Phys. Anthropol.* **29**, 45 (1968).
27. M. S. Goldstein, *Demographic and Bodily Changes in Descendants of Mexican Immigrants* (Univ. of Texas, Inst. of Latin Amer. Studies, Austin, 1943).
28. G. W. Lasker, *Hum. Biol.* **24**, 262 (1952); *ibid.* **26**, 52 (1954); ——— and F. G. Evans, *Amer. J. Phys. Anthropol.* **19**, 203 (1961).
29. F. S. Hulse, *Arch. Suisses Anthropol. Gén.* **22**, 103 (1957).
30. B. A. Kaplan, *Amer. Anthropol.* **56**, 780 (1954).
31. J. M. Tanner, in *The Biology of Human Adaptation*, P. T. Baker and J. S. Weiner, Eds. (Clarendon Press, Oxford, 1966), pp. 45-66.
32. W. W. Greulich, *Amer. J. Phys. Anthropol.* **15**, 489 (1957); P. B. Eveleth and J. A. de Souza, *Hum. Biol.* **41**, 176 (1969).
33. R. J. W. Burrell, M. J. R. Healy, J. M. Tanner, *Hum. Biol.* **33**, 250 (1961); K. P. Sabharwal, S. Morales, J. Méndez, *ibid.* **38**, 131 (1966); V. G. Vlastovsky, *ibid.* **38**, 218 (1966); K. Bojlén and M. W. Bentzon, *ibid.* **40**, 69 (1968); L. A. Malcolm, "The growth and development of the Bundi child of the New Guinea highlands," *ibid.*, in press.