NATURAL SELECTION AND ASYMMETRY:
THE POINTS OF INTERSECTION

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INTRODUCTION

The vast majority of contemporary scientists resolve Wienner's dilemma "to know nothing about everything or to know everything about nothing" in favour of the second possibility. Avalanche-like increase of scientific knowledge urges scientists to operate with an enormous amount of information concentrated in such a narrow field that its area really tends to zero. Sadly as it may sound, the hyperbole "nothing about anything" is often relevant to all branches of their own discipline in whose investigation scientists are not directly engaged.

In this respect Biology does not make any exception. Several decades ago, it seemed that scientists who study the action of the natural selection and those dealing with cell biology have very little to tell to each other. Fortunately, trends appear in the last decades which permit to throw bridges between these areas. The application of DNA-sequencies in examination of phylogenetic relationships is an example in this respect. We believe that asymmetry in man could be another example. Both the symmetry and its "alter ego", asymmetry, are undoubtedly results of the natural selection. On the other hand, the ontogenetic pathways towards bilateral symmetry and the extent of deviations from it are genetically determined at cell and molecular levels. Though complicated, this relationship is so regular that one kind of asymmetry became a measure for the intensity and effectiveness of one of the forms of natural selection.

FORMS OF THE NATURAL SELECTION

In our century Darwin's theory of natural selection (1) has been substantially enlarged and enriched in two main directions.

First, some of the mechanisms of the selection have been better understood. The "differential survival" of the fittest and the "differential mortality" of the individuals who perish in the struggle for existence were enriched with the concept of "differential reproduction". Besides, from a genetical point of view, the survival of the fittest is a "differential reproduction of genotypes" (for bibliography see 3,4,5).

The second direction in which Darwin's theory developed, concerns the forms of natural selection. As far as the living beings tend to concentrate around the most advantageous (for the given environment) adaptive norm, in the vast majority of cases they show normal distributions of the traits subjected to natural selection. When the environmental conditions change, the whole distribution, including the adaptive mean, is removed towards the more appropriate values. This is the well known moving selection; in most of the cases Darwinian selection is a moving one. The issue has been further developed by Schmallhausen (6,7,8) and Simpson (9,10,11). When the adaptive mean becomes disadvantageous and deviations from it are tolerated by selection, the normal distribution becomes biomodal and is later disrupted into two separate distributions (disruptive selection). Unlike the "flat" graphic presentations of the distributions of traits subjected to different forms of selection (e.g.,12), Simpson's figures present transversal sections of these distributions, whose levels are presented by concentric circumferences. If the pressure of the selection is one-directed, these circumferences are initially concentrated and then displaced in that direction (moving selection). If the forces of the selection could be presented by two or more vectors, the rings are initially deformed and then disrupted (disrupting selection). Thus, Simpson's "centrifugal selection" includes both moving and disrupting forms of the natural selection.
However, the main contribution of Schmalhausen and Simpson (6,7,8,9,10,11) is the conception of stabilizing natural selection. It has long been considered that if the traits remain unchanged, that means that the underlying genes have remained unchanged - the well known "conservatism of the heredity". When the mutation rates have come to light, it became clear that such is not the case and that the persistence of phenotypic traits is only possible on condition that certain selection forces maintain it (stabilizing selection). This selection tends to make the distribution narrower, enhancing its excess and preserving its symmetry. It is thereby an counteraction to the mutation variability, which enlarges the range and diminishes the excess of the distribution. The main result of stabilizing selection, the remarkable conservatism of the successful evolutionary gains, is seen at all the levels of organization of living beings. At molecular level the structure of the haem in the hemoglobin molecule and the universality of the genetic code are good examples. At anatomical level, the stabilizing selection has kept a constant number of the eyes, two, in all vertebrates during all the time of their existence from the Ordovic period of the paleozoic era up to now. Also, since the appearance of vertebrates adapted to land life 320 million years ago, the pentadactilous limb has persisted despite that mutations have arisen all the time, which have produced limbs with either more than five or less than five axes. At taxonomic level stabilizing selection caused the persistence of "Living fossils", e.g., the trilobite-like arthropod Limulus, which has persisted as a species from the Silur up to nowadays (13).

After the category of stabilizing selection being established, the next most important step was its subdividing by Waddington (14) into two forms. The first of them, named normalizing selection, includes all the mentioned effects of the stabilizing selection on the places and shapes of the distributions. The second (and from a lot points of view, the more important) form of stabilizing selection is the canalizing one. Waddington (14) considered that if a part of embryonic material is forced out of the favoured path of development, it will exhibit regressive behavior, tending to return it to the normal course of development. If, e.g., some chemical factor disturbs the embryogenesis, and the presumptive tissue still succeeds in developing into a normal tissue of the given kind, we must conclude that it was able to compensate for the initial abnormality caused by the disturbing factor and to return to the normal path of histogenesis. Also, dominance of a genetic factor over its recessive allelomorph can be regarded as indicating that the developmental processes affected by it are able to compensate for the initial abnormality caused by the presence of the recessive allele and to assure the normal dominant and result. Waddington (14,15,16) named such paths canalized or buffered. Second essential point is that the degree of canalization is under genetic control. In other words, individuals of some genotypes will show a more powerful tendency to return to the normal canalized paths of development than others (14). In the example mentioned above, it is well known that the degree of dominance can be controlled by the remainder of the genotype.

If individuals differ in their degree of canalization, which is under genetic control, it is only logical that selection forces will act on populations and will tend to increase the degree of the canalization. This form of stabilizing selection was named canalizing selection (14,15,16,17). It tolerates and establishes in populations those beings, whose genotypes exceed the others in their capability to compensate for the affecting factors and to return quickly and effectively to the normal paths of development. At this higher extent of "differential reproduction of genotypes", the canalizing selection is responsible for arising, supporting and perfecting of genetically determined mechanisms (regulatory, compensatory, feedback, etc.), able to assure normal ontogenesis in subnormal or even abnormal conditions.

At this point one line of development of biological knowledge, this dealing with the forms of the natural selection, has been crossed by another line, which concerns the different kinds of symmetry in Biology.

**KINDS OF ASYMMETRY**

- Van Valen (18) defined three main kinds of asymmetry, and most of the contemporary investigators accept them, although some contradictions exist concerning the exact limits between these kinds of asymmetry.

  1. Directional asymmetry, when there is normally a greater development of the character on one side of the plane of symmetry than on the other; the mean values of the character differ systematically between the two sides. In other words, the mean of the signed right minus left differences is always significantly different from zero; its positive value shows a right side preponderance and vice versa.

Many investigators described directional asymmetry of the human body dimensions, skeletal maturation, etc. In most of the studies (19,20,21), right upper but not lower extremity shows larger dimensions. An absence of upper limb asymmetry is observed in the non-right handed subsamples. Sometimes, the asymmetry among non-right handed subjects favours the right side in some dimensions but the right minus left differences are not statistically significant (for bibliography, see 21). Out of the three kinds of asymmetry, directional is the most closely related to human laterality. The morphological and physiological right-left differences in the use of the extremities, in visual, auditory and other cognitive functions is an immense topic in Human Biology, which the present short review is not
concerned with. In the last decade special attention has been paid to the hormonal (for bibliography, see 22), genetic (for bibliography see 23,24) and evolutionary (for bibliography see 25,26) respects of the human laterality. And yet, the relationships between functional laterality and the quantitative values of morphological symmetry are far from clear.

2. Antisymmetry is regarded as a situation, where asymmetry is normally present, but, unlike the directional asymmetry, it is variable which side has greater development. There is a negative correlation between the measures of the character on the two sides of the plan of symmetry, and the negative correlation usually implies a negative interaction. Also, the presence of antisymmetry is indicated by a bimodal distribution of the signed differences between the sides, or, at least, by a tendency toward platykurtosis as compared with the normal distribution. Interesting experimental works appeared on this kind of asymmetry (27). However, it seems that it is much easier to define it than to separate "pure" asymmetry or to eliminate entirely antisymmetry when other kinds of asymmetry have to be concerned. That is why, although it is present in some cases, antisymmetry is rarely studied in recent investigations.

3. Fluctuating asymmetry is a term involved by Ludvig (28). It is usually defined as asymmetry that is a result of the inability of the organism to develop in precisely determined paths. The distribution of the signed differences between the two sides is normal (or bimodal); the mean development of the character of each side is, as a whole, equal. This results in a mean of the signed differences equal to (or near) zero, and this is the most prominent difference from directional asymmetry. Soule (29) says that "Asymmetry is fluctuating if the signed differences between paired structures are normally distributed with mean zero".

One of the main Van Valen's findings is that in two out of three investigated species, mean correlations of 0 were found between fluctuating asymmetries of different characters; a low positive correlation was found in the third species, but the author considered that this exception could be only apparent. In other words, Van Valen shows the lack of general buffering capacity, at least in the three species investigated (18).

Fluctuating asymmetry has been investigated in widely different species, from Drosophila melanogaster (30) to several felid species, especially Cheetah (31,32). Also, fluctuating asymmetry of the dentition has been studied in a number of experimental animals subjected to thermal, audiogenic, dietary and chemical stress (for bibliography, see 33 and 34). The work by Siegel and Mooney (33) is especially important, as far as authors find significantly increased fluctuating asymmetry of dental calcium levels in audiogenic noise stressed rats. While the majority of works deal with metric anatomical traits, the paper in question tends to reveal stress induced changes in fluctuating asymmetry in biochemical processes, such as calcium transport.

In man, the magnitude if fluctuating odontometric asymmetry has been reported in relation to consanguinity (35,36,37), to chromosomal aneuploidies (38,39), to cleft lip and palate (40,41,42), to general environmental stress (43,44,45), to schizophrenia (46), etc.

Besides, it was reported that fluctuating asymmetry of the dentition is a measure of canalization in man, and populations differ in their fluctuating dental asymmetry, depending on the stress to which they have been subjected. When a population is subjected to evaluated levels of stress, the number of less-well canalized individuals increases significantly (34). Similarly, Jantz and Webb involved dermatoglyphic asymmetry as a measure of canalization (47,48).

While directional asymmetry and antisymmetry are developmentally controlled and are normally adaptive asymmetries, fluctuating asymmetry is reduced by natural selection (21). It is regarded as a residuum after the developing organism has done its best to become as symmetrical as possible, after allowance for directional asymmetry and antisymmetry (18). The temperature effect, arousing differences in the number of early cells, going to one side or the other, was discussed as a possible cause of fluctuating asymmetry (14,22). Also, many other parameters could be considered: position of the egg, distribution and interactions of subcellular materials, microtemperature gradients, etc. (18). All of them could be subjected to different endogenous or exogenous stressful factors. In terms used in information theory these factors are analogous to the "noise" causing random disturbances of the patterns. Therefore, fluctuating asymmetry has been referred to as a result of developmental noise. On its turn, resistance to developmental noise is closely related to canalization of development. That is why, the term "buffering" is used to refer to both canalization and resistance to developmental noise. (18).

THE POINTS OF INTERSECTION

• No matter how closely related to each other the canalizing selection, canalization, buffering capacity and resistance to developmental noise are, it is our opinion that they are not synonyms. What is more, these terms have their well expressed hierarchy. The fundamental process is canalizing selection and its result is usually named canalization. The central event in canalization, i.e., the most important result of canalizing selection, is development of genetically determined mechanisms, able to assure development of the organism along the established developmental pathways, despite the action of disturbing
environmental factors, metaphorically named developmental noise. These mechanisms exercise buffering action and their entity determines the buffering capacity of the organism. As for the noise resistance, this term is yet somewhat wider than buffering capacity, since it might include causes for resistance other than buffering mechanisms developed by canalizing selection. And yet, buffering capacity is undoubtedly the “active”, and therefore the most important part of the noise resistance.

There are several areas of investigation, whose results could give us information concerning the action of canalizing selection. One of them, and, we do believe, the most promising of them, is dermatoglyphic asymmetry which provides excellent possibilities for quantitative analysis of all kinds of bilateral asymmetry.

If we summarize the main findings presented in the two previous parts of the present review, it will become clear that there are two lines of increasing knowledge in Biology, which seem to be too far from each other. The first of them concerns the forms of natural selection and the second is that part of "antropological chauvinism", along with the obstacles presented above, determined the author's desire to see Bulgarians not only among peoples with well known general dermatoglyphic characteristics, but also among those with well studied dermatoglyphic asymmetry.

After giving the full picture of digital dermatoglyphics of Bulgarians (49) and applying some new methodological concerns (50,51,52), the general conception about relative asymmetry was accepted. It says that finger pattern asymmetry could only be investigated if we bear in mind (and if we include in formulas) the frequencies of the pattern types in the population under study. Similarly, the asymmetry of the ridge counts is more much more informative if the absolute right minus left differences are related to the pattern sizes. If, e.g., two homologous fingers display corresponding values of 10 and 14, and another finger pair displays values of 1 and 3, all existing methods consider the first of these finger pair more asymmetrical, whereas our formula solves the problem in favour of the second pair; the logical basis for such a decision is evident.

Further, dermatoglyphic asymmetry in Bulgarians was worked out in detail (53,54). Four kinds of asymmetry - directional, ambidirectional, relative and fluctuating - have been investigated in a large sample of 2130 healthy Bulgarians, 1065 of either sex.

Each sex and each finger pair have been separately investigated and presented. Relative finger pattern asymmetry was found to be somewhat higher in males, the same being relevant to the ridge-count asymmetry and intraindividual diversity. However, the more the analysis of ridge-count asymmetry is worked out in detail, the more it becomes evident that both sexes are asymmetrical not so much to a different degree than in a different manner. In our case, very important sex differences were revealed in the structure and finger distribution of directional and fluctuating asymmetries.

As mentioned in one of the previous parts of the present review, Van Valen (18) found that fluctuating asymmetries of different characters of the same species are not correlated to each other, and interpreted this fact as a lack of general buffering capacity. Our results have clearly shown that fluctuating asymmetries are not correlated not only in widely different traits but also among different sexes.
by Van Valen, but even in such correlated traits as the ridge-counts on different fingers (54). This reinforces considerably the lack of general buffering capacity.

Also, when dermatoglyphic patterns are concerned, it seems that special attention should be paid to the symmetry and asymmetry of certain particular dermatoglyphic patterns. Thus, the symmetry of the hypothenar radial arch exceeds appreciably that of the remaining hypothenar pattern types (55).

As mentioned above, one may have the courage to interpret data concerning particular (e.g., pathological) contingents only if he has stable population data on different kinds of dermatoglyphic asymmetry. In this respect, our investigations on dermatoglyphic asymmetry in congenital inferiority of connective tissue (56) and the comparison of right and left hand claspers and arm folders in their dermatoglyphic asymmetry (57) gave more than promising results.

**FINAL NOTES**

- The perspectives of further investigation in the points of intersection of natural selection and asymmetry could be briefly sketched in several directions:
  1. Revealing cellular mechanisms which govern the asymmetry at higher levels of life. In this respect, the brilliant work by Wood (58) is a good example. The author succeeded to accomplish reversal of embryonic handedness by micromanipulation at the 6-cell stage of the Nematode C. Elegans embryos, and to make important conclusions concerning the cell interactions during the early embryogenesis.
  2. Investigating the detailed picture of the normal asymmetries, including dermatoglyphic one, in large samples of different populations.
  3. Using data from point 2, to compare populations to each other in their asymmetries and to relate the obtained results to their ethnohistorical and socioeconomic background.
  4. Using data from point 2, to compare groups of patients with different medical disorders to the average norm of asymmetry in their own populations.
  5. Studying dermatoglyphic asymmetry as related to human laterality. As a working hypothesis, decreased or even inverted directional and increased fluctuating asymmetry could be expected in left handers.

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**REFERENCES**


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