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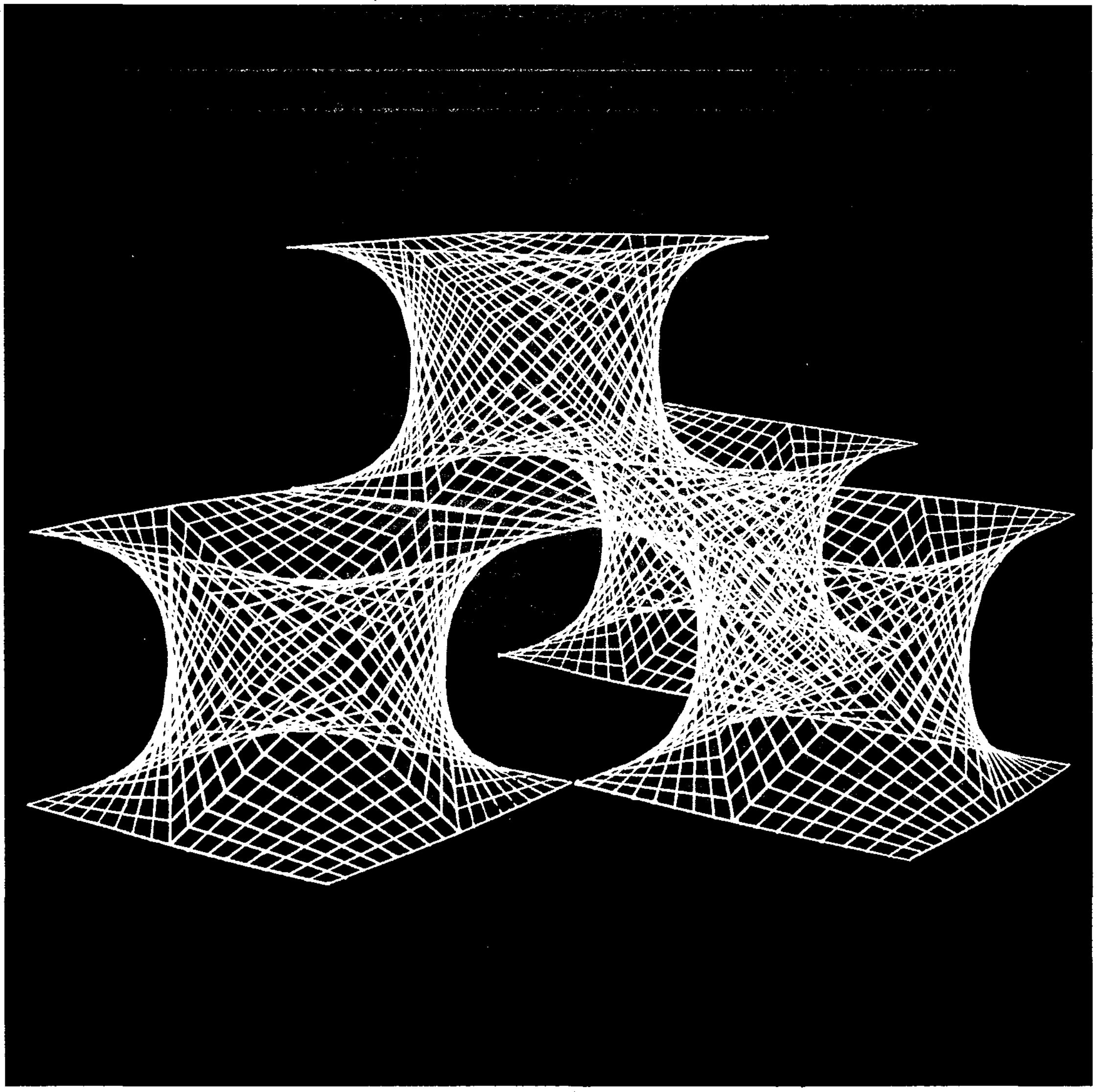

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HUMAN FLUCTUATING ASYMMETRY: WHAT DOES IT MEAN FOR PSYCHOLOGISTS?

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INTRODUCTION

In recent years researchers from diverse disciplines in the life sciences such as biology, genetics, physical anthropology, medicine, behavioral ecology, as well as several domains in psychology, have turned their focus onto the role of developmental stability of the organism. Developmental stability, sometimes referred to as developmental homeostasis, can be defined as the ability of the organism to resist or buffer the disruption of precise development by environmental and genetic stresses. When instabilityoccurs, it may be marked by relatively conspicuous morphological or behavioral errors, but more often by only minor random deviations from bilaterally symmetrical traits called fluctuating asymmetry (FA). Although the concept of FA was introduced more than 60 years ago (Ludwig 1932), it has entered into the limelight of scientific research only in the last decade.

The general assumption regarding FA, whether implicit or explicit, is that it reflects developmental stability, which is in turn correlated with Darwinian or overall fitness. Fitness here refers to the individual's own survival as well as the relative number of offspring contributed by her or him to the next generation. Sources of instability, namely environmental and genetic stresses, appear to diminish fitness since they often increase the degree to which random growth perturbations are magnified, and may further result in disruption of the developmental check mechanisms. Genomes less sensitive to such disruption are said to *canalize* development; that is, to suppress phenotypic variation (Waddington 1957). Thus, individuals better resistant to such stress may show greater fitness as well.

There are several reasons for the growing fascination with FA. First, it measures minor genetically and environmentally induced departures from a perfectly designed developmental program, and thus it provides a gauge to the organism's developmental noise, and indirectly to its viability fitness. Compared with other indices of development and fitness, FA has two important advantages: Not only it is easy to assess it, but it measures aberrations from a known morphological ideal, that is, perfect symmetry (in most organs). In addition, the study of FA provides some insights for researchers of genetics and the environment, as well as those interested in the interaction between the two. Both the likelihood for the appearance of FA in an individual and the degree to which it appears has often some heritable basis, and interestingly, it is associated with two key issues in genetics: It often decreases with protein homozygosity but increases with hybridization. In addition, studies on the change in FA due to effects of the interaction between environmental and genomic stresses may prove useful as a monitor of the disruption of developmental stability at an array of integration levels from molecular to the epigenetic. Finally and more specifically for psychology, a number of recent studies have indicated that FA is correlated with various behavioral and psychological phenomena ranging from intelligence, depression, and mating behavior. Hence, some believe, this research direction may shed light on the biological basis of human behavior and foster an integration between several research domains.

All multicellular organisms exhibit a high degree of bilateral symmetry in many of their organs. Nevertheless, many organisms, or even parts of a single organism, may show deviations from perfect symmetry. These deviations can be divided into three types of asymmetry, each characterized by a different combination of mean and variance of the distribution of differences between the right-minus-left plane (R - L) of a bilaterally symmetrical trait (Van Valen 1962). The first type, *directional asymmetry*, refers to a normally greater development of a trait on one side of the plane of symmetry than on the other side (e.g. the human heart and brain). The second type, *antisymmetry*, also refers to a normally greater development of a trait on one side of the plane of symmetry, but in contrast to the previous type it is unpredictable which side of an organism shows greater development. Thus, antisymmetry is characterized by a bimodal distribution of R - L differences, often with a mean of zero (e.g., the claws of the fiddler crab; the right and left hands in humans when measured by preference scales).

The focus of this review is on the third type of asymmetry, called *fluctuating asymmetry* (FA). FA denotes randomly produced deviations from perfect symmetry of two sides of quantitative traits in an individual for which the population mean of R - L differences is zero and their variability is near-normally distributed. This type of asymmetry arises in the course of development, and is called 'fluctuating' because its direction is not under genetic control. In fact, the subtle departure from symmetry in the individual ought not to be stimulated by genetic factors (Palmer & Strobeck 1992).

FA is basically used to measure either the effect of asymmetry per se on a certain trait or performance, or to assess the variation between either populations or individuals. Typical performance studies seek to understand the effect of asymmetry itself, whereas typical variation studies usually examine the effect of genomic or environmental causes on a number of populations or a group of individuals, using independent variables such as time span or location.

The FA found in 'normal' population, regardless of the species, is usually about 1-2% of feature size, while exposure to stress may lead to a higher levels (about 3-5%) of FA (Parsons 1990). Although humans are bilaterally symmetrical in essence, researchers have noticed the presence of small morphological asymmetries in various bilateral traits located in the body and the face. The right side has more departures from the fairly symmetrical morphology found in normal people, and this is true even when antisymmetry (handedness) is controlled (Van Dusen 1939; Garn, Mayor & Shaw 1976; Kowner 1995). In its non-pathological form, asymmetry in humans can be defined as lower than the mean $\pm$ 2 SD of a specific bilateral trait (Livshits & Kobyliansky 1991).

There is growing evidence that FA, as a marker of developmental stability, may help researchers in various domains of psychology. It may be related to plethora of psychological phenomena, and may serve as a key for future theories attempting to link a wide range of psychological themes such as mental and physical maldevelopment, behavioral variance, as well as issues concerning the interplay between environment and heredity. In the next part the relevance of FA to several psychological domains is examined.

CLINICAL PSYCHOLOGY

There is growing evidence for the importance of FA as a marker of mental health, either as an indicator of general well-being or as a predictor of severe mental disorders. The most investigated link between FA and any mental pathology concerns psychotisicm, and particularly schizophrenia. Markow and Wandler (1986) revealed that schizophrenic patients have greater dermatoglyphic FA compared with controls and that the severity of the symptoms correlates with the magnitude of the FA. In fact, schizophrenics exhibit greater FA than controls in almost any dermatoglyphic traits (see also Mellor 1992) as well as high frequency of deviance in various forms of hand morphology (Shapiro 1965). The research on FA may shed some insight on the etiology of schizophrenia. Markow (1992) proposed that schizophrenia reflects abnormal balance of symmetry and asymmetry in the brain as a result of reduced developmental buffering associated with homozygosity. The increased homozygosity may also lead to increased developmental instability in the central nervous system, which results, in turn, in deviant behavior (Markow & Gottesman 1989).

A related phenomena which may elucidate the role of FA is the development of minor physical anomalies (MPAs). Found in less than 4% of the general population, these structural features of no functional significance (e.g., wide-spaced eyes, low or malformed ears) have been used widely to infer the degree of embryonic developmental instability of the individual. (Hoyme 1993) MPAs are usually attributed to injury or atypical ectodermal differentiation during the first or second trimester of fetal life (Murphy & Owen 1996), but some may stem from slowed development of specific traits in time-locked development. (Yeo, Gangestad & Daniels 1993) There is a significant body of evidence regarding the increased prevalence of MPAs in schizophrenia (e.g., O'Callaghan, Larkin & Kinsella 1991), particularly familial schizophrenia (Waddington, O'Callaghan & Larkin 1990), and in autism (e.g., Campbell, Geller, Small, Petty & Perris 1978). In fact, there is a direct indication for the relation between FA and MPAs. Green, Bracha, Satz & Christenson (1994), for example, showed that MPAs in schizophrenia are associated with increased dermatoglyphic FA.

PERSONALITY AND SOCIAL PSYCHOLOGY

Future studies on the role of developmental stability in humans may also open a new window to the interpretation of personality, ranging from behavior, emotions, to cognitive skills. Although only a few studies have examined the role of developmental stability in these domains in humans, the strong impact which developmental instability exerts on general development suggests it may also play a role in human behavior, communication, and emotional state. Despite its limited comparative value, there is extensive evidence from studies on these aspects in non-human animals which attest the importance of developmental stability in affecting and moderating a wide range of behaviors. Multivariate analyses of courtship behavior in wild type drosophila (Markow 1987) revealed that phenodeviant males (namely, individuals suffering from sporadic occurrence of abnormal morphological deviance measured by FA) show aberrations in courtship component sequences, level of performance within each sequence, and appropriateness of courtship delivery. As for humans, Waldrop and Halverson (1971) reported greater frequency of MPAs, another manifestation of developmental instability, in children exhibiting a range of behavioral abnormalities.

One of the mechanisms which links behavior and stress was sketched by Alados, Escos & Emlen (1996) who examined changes in behavioral patterns of Spanish ibex with parasitic infection or during pregnancy. Alados et al. contended that biological structures and behavior patterns have evolved to allow the organism to explore its environment and enhance its tolerance for changes. Natural selection ought to increase complexity in behavior to maximum levels consistent with energetic constraints. Stress, however, increases metabolic rate which entails energy consumption, and consequently a reduction in behavioral complexity. Hence, as a measure of stresses, increased FA is hypothesized to predict altered behavior and increased emotional state.

FA is also related to dominance, a behavioral aspect of fitness which is associated with access to resource and ultimately with survival and reproduction. Dominant individuals among male European starlings, but not among females, were found to exhibit invariably lower levels of FA than subdominants (Witter & Swaddle 1994). Likewise, the degree of FA of antlers of the fallow dear, as well as their height, was found to be an important predictor of dominance among males (Malyon & Healy 1994). The negative relation between dominance and FA is found also in gemsboks, but in this species dominant individuals of both sexes exhibit lower FA of their horns (Møller et al. 1996). Finally, FA appears to be associated with dominance also in humans. Recent studies suggests that symmetric men are more socially dominant according to both self-report and report by romantic partners (Gangestad & Thornhill 1997a), and similarly that boys with low FA (10-15 years old) are more aggressive than their high-FA counterparts (Manning & Wood 1998).

Facial FA may also be related to one's emotional states. Shackelford and Larsen (1997) who conducted the first study regarding this association suggest facial FA may signal not only physiological stress but also psychological and emotional distress. Using multiple evaluations (e.g., self-reports, observer ratings, daily diary reports, and psychophysiological measures), they found facially asymmetric men to be more depressed, more emotionally labile, and more impulsive than relatively symmetric men. Asymmetric women experienced more muscle soreness and were also more impulsive than more symmetric women. Although the samples Shackelford and Larsen used were small and homogeneous and their findings often inconsistent, this study raises important questions regarding the etiology of emotional states and psychological stress. Critically, it moves beyond social judgments of people displaying particular facial characteristics, since subjects with lower facial FA were rated as emotionally stable not only by observers, but also rated themselves as such.

DEVELOPMENTAL PSYCHOLOGY

The research on the effect of developmental stability on human development is probably the earliest within this emerging domain. The main contribution of this research is in indicating sources of genetic and environmental stress which affect the individual during development. In contrast to other morphological phenodeviance which often occurs during a limited period of development FA occurs throughout prenatal growth and continues to alter after birth and into adulthood.

Studies show that different levels of developmental stability start to affect human development in very early stages. Babler (1978), for example, found that aborted fetuses in the second quarter of pregnancy had greater frequency of dermatoglyphic abnormalities than either older fetal abortuses or normally newborns. There is an association between certain developmental delays and high FA. Preterm newborns, for example, exhibit greater FA than term newborns, and there is an inverse correlation between the FA of infants and their gestational age as well as their health status (Livshits et al. 1988). Likewise, pre-pubertal children with delayed development show greater dermatoglyphic FA than controls (Naugler & Ludman 1996), and greater degree of FA is also associated with spinal deformity (Goldberg, Dowling, Fogarty & Moore 1996) or miscellaneous multifactorial illnesses, such as cleft lip (Woolf & Gianas 1976).

There appears to be a correlation between parents' bodily asymmetry and the level of asymmetry in their offspring, and a similar correlation between infants' body symmetry and their parents' number of infectious diseases during pregnancy (Livshits & Kobyliansky 1991). The behavior of the pregnant mother may affect the development of her postnatal infant as well, and several studies identified smoking, consumption of alcohol and obesity as maternal liabilities which have detrimental effect on the developmental stability of the newborn (see in detail in the section on environmental sources of stress). These effects notwithstanding, the socioeconomic status of parents was not found to affect the FA of Israeli infants (Livshits et al. 1988), older children in Japan (Dibennardo & Bailit 1978), or American college students (Thornhill, Gangestad & Comer 1995).

FA appears to be a useful marker of development also because it shows constant transformation throughout life span, arguably with higher points of bodily and facial FA values to emerge in a very young age, during puberty, and notably during old age. Livshits & Kobyliansky (1989) found full-term newborns in Israel to show greater bodily FA than older children (age 5-18 years), whereas two non-longitudinal studies found various levels of increase in bodily and facial FA among adolescents as compared with younger children (Wilson & Manning 1996). The increased developmental instability in puberty is probably the result of increased overall body growth as well as the development of secondary sexual traits. The appearance or growth of these traits at this period occurs under the influence of androgens and estrogens and is accompanied by temporary reduction in the immunocompetence of the individual due to the hormonal surge (e.g., Grossman 1985). Evidently, increased energy demands for body growth and immunocompetence lead to less energy for maintaining developmental stability. Still, it is possible that normal growth results in temporary FA that is of no long-term physical, psychological or clinical significance.

As a measure of the general buffering capacity of an individual's ontogenetic development, high degree of developmental instability in humans is linked to developmental abnormality. The genetic component of various multifactorial congenital anomalies not only results in malformations but also reduces resistance to adverse environmental influences. It has been repeatedly demonstrated that individuals suffering from various developmental anomalies, congenital conditions, or illness also exhibit greater FA in various traits (see Thornhill & Møller 1997). Likewise, greater dermatoglyphic and tooth FAs often characterize various genetic syndromes such as Down syndrome (e.g., Barden 1980), trisomy 14 syndrome (Fujimoto, Allanson, Crowe, Lipson & Johnson 1992), fragile X (Martin-Bell) syndrome (Peretz et al. 1988), and Goltz syndrome (Landa, Oleaga, Raton, Gardeazabal & Diaz-Perz 1993), and even mentally retarded individuals show greater anthropometric FA than normal individuals (Malina and Buschang 1984). These studies indicate that health and pathology are related to phenotypic and genetic quality, and that developmental instability may serve as a measure for this quality.

EVOLUTIONARY PSYCHOLOGY

The psychological study of human mating patterns and sexual behavior has gained much ground in recent years (e.g., Buss & Schmitt 1993; Gangestad & Simpson 1990; Sprecher, Sullivan & Hatfield 1994). The new psychological perspective on human sexuality is based on a synthesis between two interdisciplinary domains: evolutionary psychology and social cognition (for review, see Kenrick 1994). The former domain, which is the scope of this section, assumes that human mating behavior has biological roots which are found in all the evolved psychological adaptations underlying behavior in general, such as fitness (as its ultimate cause) and parental investment (as its main proximate cause), and thus we may find its fairly consistent pattern across cultures.

Evolutionary psychologists, among others, refer to the reproductive success of an individual, compared with that of all other individuals in the population, as relative fitness. This reproductive success depends importantly on access to mates, which is determined by sexual selection. This important mechanism of evolutionary change occurs because individuals of a species choose to mate with certain other individuals due to some traits. Sexual selection has two main forms: The first form is intrasexual selection (i.e., competition between males) and the second intersexual selection (i.e., female choice). FA is probably linked to sexual selection through the development of secondary sexual traits, a process which is mediated by enzyme heterozygosity and its effect on general developmental stability (Mitton 1995). It has been argued that epigamic structures and weapons of an organism should show higher levels of FA than that found in non-sexual traits, because sexual selection is essentially directional. Further, since FA is moderately heritable, reflects general fitness, and occurs in numerous features which affect reproductive success, it seems reasonable to assume that sexual selection would favor low levels of FA, and that individuals would be able to assess the level of FA of their potential mates.

To examine these assumptions, many studies investigated the relation between the degree of FA of individuals and their success in acquiring mates (see meta-analysis in Møller & Thornhill 1998). This relation was first examined in regard to female choice. Few researchers doubt such choice of males occurs in nature for access to resources or parental care. Yet, is there female choice of males who exhibit lower level of FA? A number of studies with insects (e.g., McLachlan & Cant 1995; Thornhill), and birds (e.g., Møller & Pomiankowski 1993) showed that female individuals prefer males who show lower FA in natural conditions. Forewings that differ in length by just a fraction of a millimeter, Thornhill found, may keep a male scorpion fly from finding a mate. As for birds, Swaddle and Cuthill (1994) manipulated the degree of FA in secondary sexual plumage trait in male zebra finches in order to examine the preference of birds for symmetry in non-arbitrary traits. Indeed, they revealed that females of this species prefer to perform ritualized courtship display-jumps in front of males wearing symmetrically manipulated chest plumage. This description may fit mammals as well. FA in the horns of gemsboks appear to be negatively related to the number of offspring in females and mating success of males (Møller et al. 1996).

Although there are several potential explanations for this choice, the majority of researchers seem to prefer the "good genes" model of sexual selection which posits that females choose males with the least FA because they reflect a heritable quality that affects offspring viability (for review on models of sexual selection, see Gangestad & Thornhill 1997). Inherent in this model is a close association between the indicator (FA) and fitness and that both are heritable (for criticism of the proponents of this model, see Markow & Clarke 1997). Polak (1994) offered an elaborated version of this approach, suggesting that reduced FA in males may indicate greater resistance to parasite, a trait that may pass on to their offspring. In humans, Manning, Koukourakis & Brodie (1997) found positive relation between resting metabolic rate and FA in male college students, but not in females. Viewing sexual selection as any other stress, Manning et al. suggested that high-quality males are better able to withstand the pressure of sexual selection since they are able to allocate more energy to growth and reducing FA than low-quality males.

FUTURE PROSPECTS

In spite of the many flaws and imperfections that seem to prevail in the field, the current state of research suggests that developmental instability is related to plethora of psychological phenomena. The interest in FA as the main maker of developmental instability and the consequent surge of research on this topic has brought about much expectation as well as slight disappointment. By now, researchers possess much greater data than they had a decade ago, and thus we may reasonably assess the potential of this measure.

Developmental instability, as reflected in FA, shows overall negative correlation with the overall fitness of the organism as well as various indices of health and performance in humans. Although this relation is promising, there are still some hesitations as to the widespread application of FA as a major substitute for conventional fitness measures (cf. Clarke 1996). Within humans, FA in several traits shows a relation to various disorders of both developmental and genetic etiology. However, its role as a general risk marker for pathology needs to be further clarified. This may become possible with the elimination of several methodological problems (e.g., neglect of measurement errors, lack of standardization of FA measurements, no reports of odds ratios of various morphological traits for each pathology, measurement of many traits rather than one or a few) as well as further evidence about the occurrence of FA and its relation to effects of other types of symmetries in both sexes.

With the influx of research we may expect in the coming years to know more about the advantages and limitations of FA in general and for psychological research in particular . In more practical terms, perhaps, FA can serve as a gauge of genomic (e.g., heritability, inbreeding) and environmental (e.g., nutrition, exposure to pollution, living density) stresses in human populations, and even bridge conceptually between these two clusters factors (and too often unbridgable approaches.)

The concept of FA offers additional applied outlook for future research since its assessment may become an important monitoring tool and even early-warning method for detecting individuals and populations under stress (for seminal research on non-human populations, see Sarre, Dearn & Georges 1994; Wagner 1996). Ideally, measurements of FA may enable researchers to isolate and reduce these stresses, and thus may limit developmental problems and improve developmental resistance.

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