

THE IMPERFECT ORGANISM: ON THE CONCEPT OF FLUCTUATING ASYMMETRY AND ITS SIGNIFICANCE IN HUMANS, NON-HUMAN ANIMALS, AND PLANTS

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Abstract: *Fluctuating asymmetry (FA) is random, stress-induced deviations from perfect symmetry that develop during the growth of bilaterally symmetrical traits. FA may serve as a measure of 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 one important advantage: it measures aberrations from a known morphological ideal, that is, perfect symmetry. For these traits researchers in life sciences have investigated intensively the role of symmetry in the organism in the last decade. In this article we review the manifestation of FA in various organisms, its sources, and its relation to natural and sexual selection.*

1. INTRODUCTION

All multicellular organisms exhibit a high degree of bilateral symmetry in 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:

1. *Directional asymmetry* - Normally greater development of a trait on one side of the plane of symmetry than on the other side (e.g., the human heart).
2. *Antisymmetry* - Normally greater development of a trait on one side of the plane of symmetry, but in contrast to the previous type it is characterized by a broad peaked or bimodal distribution of R - L differences, often with a mean of zero (e.g., the signaling claw in male fiddler crabs).
3. *Fluctuating asymmetry* - 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.

Each of the three types of asymmetry is 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). Directional asymmetry and antisymmetry are predestined and appear at the onset of development, whereas FA arises in the course of development. FA is not under genetic control and because it tends to vary from one generation to the next it is called 'fluctuating' (Ludwig 1932; Van Valen 1962). Studies indicate that most of the bilateral morphological traits (e.g., fins, wings, eyes) show only small degrees of FA, with often a negligible absolute magnitude of asymmetry. For example, measurements of wing length of 32 different bird species revealed relative values that were most often less than 1% of the absolute size (Møller and Höglund 1991).

In recent years, numerous researchers in diverse disciplines such as biology, genetics, physical anthropology, medicine, behavioral ecology, and evolutionary psychology, have turned their attention onto the meaning and role of FA in the organism, and more than 400 articles have been published on this topic in the last decade alone (based on the Biosis database). There are several reasons for the intense 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 one important advantage: it measures aberrations from a known morphological ideal, that is, perfect symmetry.

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 it increases with hybridization. Finally, 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 homeostasis across an array of integration levels from molecular to the epigenetic (Parsons 1992).

2. THE MANIFESTATION OF FLUCTUATING ASYMMETRY IN PLANTS

Although researchers interested in FA have somewhat neglected the domain of plants, recent studies indicate that FA found in floral and foliage traits may serve as a measure of developmental stability in these organisms too (e.g., Sherry and Lord 1996a, 1996b; for review, see Freeman, Graham and Emlen 1993). One of the first studies on FA in plants was Sakai and Shimamoto's (1965) investigation of the deviation from bilateral symmetry in 11 varieties of tobacco. Although they found differences in bilateral symmetry within and between variety in both leaf width and distance between two major veins, Sakai and Shimamoto did not identify any genetic basis for the FA they observed. In another examination of the lengths of pistils and stamens in flowers of the same plant, Sakai and Shimamoto found that the variability of the lengths was positively correlated among them. They concluded that there were two independent blocks of genes, hence the existence of a genetic basis for developmental stability since some varieties were more stable than others.

Recent studies by Anders Møller suggest that FA may also be a useful indicator of resistance of individual plants to various stresses, a feature especially apparent in the development of floral traits. Møller (1995a; Møller and Eriksson 1995) found that lower petal asymmetry of *Epilobium angustifolium* was negatively related to mean lower petal length, whereas asymmetry in leaf width was positively related to mean leaf width.

As in animals, FA in plants may affect their reproduction prospects and even their survival. Bumblebees were found to show preference for symmetrical flowers over asymmetrical ones, probably because petal asymmetry is associated with lower nectar production (Møller, 1995a; Møller and Eriksson, 1995). In outcrossing plants, such as rosebay willowherb, floral FA of both donor and recipient appeared to be related to embryo abortion (Møller 1996a). As for leaves, Møller (1995b) found a positive relation between FA and prevalence of leaf-mining insects in elms.

FA at the population level may also indicate population-level performance in plants. Evans and Marshall (1996), who compared the FA of foliar and floral traits in two populations of mustard plant, found greater FA in the population with lower biomass accumulation and flower production.

3. THE MANIFESTATION OF FLUCTUATING ASYMMETRY IN ANIMALS

Until recently most studies on FA have dealt with non-human living organisms. FA is a ubiquitous phenomenon in bilaterally symmetrical traits, such as wing length in scorpionflies (e.g., Thornhill 1992a), fin width in salmon (e.g., Wagner 1996), plumage pattern in starlings (e.g., Witter and Swaddle 1994), length and width of horns in gemsboks (e.g., Møller et al. 1996), and number of antler points on the largest antler of moose (Solberg and Saether 1993).

Living organisms exhibit a remarkable variety of patterns of FA variation. Still unknown confounding factors that affect FA undoubtedly exist, which prevent us from generalizing from one population or species to another. Studies show that FA is associated with various measures of fitness in living organisms, such as survival rate and reproduction success (these topics are reviewed in detail in the following sections). As a measure of developmental stability, a high degree of FA is also strongly linked to abnormality in animals. There is a clear association, for example, between pathological failures and development of high FA. This relation has been intensively investigated in humans, but also fetuses from diabetic mothers of rhesus monkeys, for example, were found to show greater dental FA than controls (Kohn and Bennett 1986).

4. THE MANIFESTATION OF FLUCTUATING ASYMMETRY IN HUMANS

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 and Shaw 1976; Kowner 1995).

While most people exhibit moderate and unrecognizable levels of asymmetry, a high degree of FA is unequivocally linked to abnormality. The genetic component of various multifactorial congenital anomalies not only results in malformations but also reduces resistance to adverse environmental influences. An association is evident between certain developmental delays, genetic failures, and high FA. Preterm newborns, for example, exhibit greater FA than term newborns, and an inverse correlation exists between the FA of infants and their gestational age as well as their health status (Livshits et al. 1988). Developmentally delayed children show greater dermatoglyphic FA than controls (Naugler and Ludman 1996), and a greater degree of FA is also associated with spinal deformity (Goldberg et al. 1996) and miscellaneous multifactorial illnesses such as cleft lip (Woolf and Gianas 1976; Sofaer 1979).

Likewise, greater dermatoglyphic and tooth FAs often characterize various genetic syndromes such as Down syndrome (e.g., Barden 1980; Shapiro 1983), trisomy 14 syndrome (Fujimoto et al. 1992), fragile X (Martin-Bell) syndrome (Peretz et al. 1988), and Goltz syndrome (Landa et al. 1993). Mentally retarded individuals show greater anthropometric FA than normal individuals (Malina and Buschang 1984), and people suffering from schizophrenia exhibit greater FA in certain dermatoglyphic traits than healthy controls (Markow and Wandler 1986; Markow and Gottesman 1989; Mellor 1992; for a review of the human medical literature dealing with developmental instability and health, see Thornhill and Møller 1997).

FA varies considerably among normal individuals as well. In fact, progress in medical science has curtailed much of the stabilizing selection found in other species, and consequently modern-age humans exhibit greater variance in various morphological traits than in the past. In its non-pathological form, asymmetry in humans can be defined as lower than the mean ± 2 SD of a specific bilateral trait (Livshits and Kobylansky 1991).

5. SOURCES OF FLUCTUATING ASYMMETRY IN THE ORGANISM

FA in adult organisms is a trait that reflects the total environmental and genetic forces during their development (Palmer and Strobeck 1986; Parsons 1990). The effect of the interplay between genes and environment on FA is complex and requires further studies. In many cases, vulnerability to environmental factors may reflect an existing developmental instability or even genetically determined poor resistance, whereas the

process of genetic factors may be intensified by long-term environmental factors. While most studies have investigated the sources of FA in plants and non-human animals, a few suggest that FA in humans is affected by similar sources. Livshits and Kobylanski (1991), for instance, conducted analyses of family correlations between estimates of FA. They demonstrated that both genetic and environmental factors play a role in determining FA in humans.

The genomic causes of stress which affect FA include the following:

1. *Protein homozygosity*: The buffering role of heterozygosity, termed canalization, is supposed to lead to greater diversity and stability of ontogenesis (Waddington 1957). Heterozygosity in biochemical products is supposed to lead to better development under a wide range of environmental conditions. Studies show that FA relates weakly to protein homozygosity in various species (e.g., Mitton 1995; Britten 1996). There are several explanations for this. One hypothesis posits that homozygosity increases the organism's susceptibility to systematic and random sources of genetic and environmental perturbation during its development. Heterozygosity, by contrast, may enable the organism to develop properly despite genetic and environmental stresses. A second hypothesis concerns inbreeding, since it exposes deleterious recessives and increases the level of homozygosity (cf. Soule and Cuzin-Roudy 1982; Parsons 1990). Although the causes for the relation between FA and heterozygosity are still unsettled, this link seems promising since it may elucidate the overall hypothesized ties among FA, developmental stability, heterozygosity and fitness.
2. *Inbreeding*: Inbreeding may somewhat increase level of FA in various species (e.g., Clarke, Brand and Whitten 1986; Alados, Escos and Emlen 1995), have no effect in others (Fowler and Whitlock 1994), or increase prevalence of FA mainly among the more highly inbred animals in later generations (Lacy and Horner 1996). The relation between inbreeding and increased FA has been demonstrated in humans as well: Ben David et al. (1989) found among four Bedouin tribes (in which inbreeding rate is about 10 times higher than that in most European populations) higher rates of dental FA than in two large populations of whites and blacks (see also Markow and Martin 1993).
3. *Hybridization*: FA appears to be greater in between-species hybrids than in either parental species. This phenomenon occurs even though the hybrids are more heterozygous than their parents (Graham and Felley 1985; Leary, Allendorf and Knudson 1985; but see Alibert et al. 1994 for negative results).

4. *Heritability*: Thornhill and Sauer (1992) demonstrated that FA is heritable in the German scorpionfly. Møller and Thornhill (1997a), who conducted a meta-analysis of 34 studies of 17 species, calculated the overall mean effect size of heritabilities of individual FA as 0.19. It is undecided, however, if this is due to genetic variation in the machinery of development *per se*, genetic variation in resistance to disease, or other unknown aspects of viability. If, indeed, FA is heritable, sexual selection of individuals exhibiting traits with low FA ought to reduce its prevalence (cf. Møller and Eriksson 1995).
5. *Incorporation of new mutants into the genome*: Such an incorporation is supposed to cause perturbations to developmental stability and increased FA. Despite the increase in FA, Clarke and McKenzie (1987) showed that incorporation of a new, advantageous mutant in Australian blowflies resulted in greater insecticide resistance. After two decades of adaptation, the level of FA in this species returned to the level found in other flies, while the increase in fitness due to greater resistance was retained.

The environmental sources of stress which affect FA include the following:

1. *Existence of parasites, pathogens and pesticides*: Agnew and Koella (1997) found greater FA in wings of mosquitoes infected with parasites than in controls, and greater FA in horizontally transmitted parasites than in vertically transmitted, probably because vertical transmission links the reproductive interests of both parties during host-pathogen co-evolution. Similarly, treatment against parasites in naturally infected female reindeers affected the development of antlers' symmetry, but not their length (Folstad, Arneberg and Karter 1996). Plants are also susceptible to environmental effects, such as excess of fertilizer (Møller 1995b) or insect herbivory (Zvereva et al. 1997), and respond in an increase in FA.
2. *Pollution*: Aerial emission increases level of FA in plants and insects (e.g., Clarke and McKenzie 1987; Kozlov et al. 1996).
3. *Temperature*: Too low or too high temperature may affect FA during development. Zakharov (1989), for example, developed embryos of egg clutches of two species of sand lizard at four constant temperatures. The variation of scale characters as indicated by FA and number of scale disturbances was minimal at 25°C, whereas above and below this temperature it increased.

4. *Noise*: Strong or random noise appears to increase developmental stress. Litters of rats conceived and born in a condition of random noise showed greater FA in their long bones than controls (Gest, Siegel and Anistranski 1986).
5. *Density*: A positive relation was found between FA in chickens and density of their living space (Møller, Sanotra and Vestergaard 1995).
6. *Supply of food*: An increased level of nutritional or energetic stress was found to increase FA in feathers of European starlings (Swaddle and Witter 1994).

In humans, a few additional environmental sources of stress which affect FA have been demonstrated:

1. *Maternal liability*: Studies show that alcoholic consumption, smoking, or exposure to tobacco smoke, and obesity of pregnant mothers increase the dental FA of their children, probably due to prenatal stress (Kieser 1992; Kieser and Groeneveld 1994; Kieser, Groeneveld and Silva 1997).
2. *Level of acculturation*: Examination of dental asymmetries in a group of Lengua Indians showed that the old adults (40-60 years old) had greater FA than their younger cohorts (18-39 years old). Kieser, Groeneveld and Preston (1986) suggested that the older group, who experienced less acculturation (and subsequently minimal medical treatment and irregular availability of food), was subjected to higher levels of environmental stress. However, this pattern may reflect increased senescence with age as it appears that older humans have increased FA (Møller, Soler and Thornhill 1995).

6. SURVIVAL (NATURAL SELECTION) AND FLUCTUATING ASYMMETRY

The general assumption regarding FA, whether implicit or explicit, is that developmental stability, as reflected in FA, is correlated with overall fitness. Fitness here refers to the individual's own survival, as well as the survival of its own offspring, and even of its kin. Stress, a major source of instability, appears to increase the degree to which random growth perturbations are magnified, and may further result in disruption of the check mechanisms. Hence, individuals who are able to resist such stress better may show greater fitness as well.

It has long been realized that a positive relation exists between symmetry in bilateral features and survival (e.g., Beardmore 1960; review in Møller 1997). Individual domestic flies, for example, are less likely to be eaten by swallows and killed by a pathogenic fungus when they show low degree of FA in their wings and tibia (Møller 1996b). Surviving barn swallows are more symmetrical in the sexual traits of their outer tail length (both males and females) and in the non-sexual trait of their wings (males only) than non-survivors (Møller 1994). Similarly, among male and female gemsboks, lower FA in length and width of horns is related to better general condition (Møller et al. 1996).

The survival of an organism is more apparent at certain period. Rintamaki et al. (1995) examined FA in the tail of willow warblers preparing for migration. They found that females, but not males, that showed a higher degree of FA were more likely to migrate earlier. This behavior, they rationalized, resulted from the lesser ability of these females to compete for food resources in time of scarcity. The sex difference occurred because females moult later than males and thus may suffer time constraints in their moult before migration. As a partly heritable trait, FA may affect not only parents' survival but also that of their offspring. Stockley et al. (1996) found that FA of male common shrews was negatively correlated with the proportion of male offspring they fathered that survived to sexual maturity.

FA is also related to dominance and aggressiveness, evident parameters of survival. Dominant individuals among male, but not among female European starlings, were found invariably to exhibit lower levels of FA than subdominants (Witter and Swaddle 1994; Swaddle and Witter 1995). Likewise, the degree of FA of antlers of the fallow deer, as well as their height, was found to be an important predictor of dominance among males (Malyon and Healy 1994). The negative relation between dominance and FA was found also in gemsboks, but in this species dominant individuals of both sexes exhibited lower FA of their horns (Møller et al. 1996). In human as well, symmetric men were found to be more socially dominant according to both self-report and report by romantic partners (Gangestad and Thornhill 1997), and that boys with low FA (10-15 years old) were more aggressive than their high-FA counterparts (Manning and Wood 1998). FA was even found to predict men's level of violent behavior (Furlow, Gangestad and Armijo-Prewitt 1998) and sociosexual orientation during courting (Simpson, Gangestad, Christensen and Leck 1999).

7. REPRODUCTION (SEXUAL SELECTION) AND FLUCTUATING ASYMMETRY

The reproductive success of an individual, compared with that of all other individuals in the population, is referred to as relative fitness. This reproductive success depends on access to mates, which is determined by intrasexual selection (i.e., competition between males) and intrasexual selection (i.e., female choice). FA may be linked to sexual selection through the development of secondary sexual characters. This relation may be mediated by enzyme heterozygosity and its effect on general developmental stability (Mitton 1995). It has been argued that epigamic structures and weapons should show higher levels of FA than that found in non-sexual traits, because sexual selection is essentially directional. Moreover, since FA reflects general fitness and occurs in numerous features which affect reproductive success, it seems reasonable to assume that sexual selection will favor low levels of FA, and that individuals will be able to assess the level of FA of their potential mates.

A number of studies investigated the relation between the degree of FA of individuals and their success in acquiring mates (see meta-analysis in Møller and Thornhill 1997b). This relation was first examined in regard to female choice of males who exhibit lower level of FA. Concentrating on insects, Thornhill (1992a, 1992b) showed that female scorpionflies 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. Moreover, females of this species show preference for males with minimal FA even without seeing their mate: They may do so on the basis of pheromones alone. Simmons (1995) demonstrated that paired male field crickets were older, larger, and more symmetrical than non-paired males. Also the midges most successful at acquiring mates possessed wings with a lesser degree of FA; however, they had smaller bodies than non-mating midges (McLachlan and Cant 1995).

Birds appear to exhibit similar preferences. For instance, male barn swallows that acquired a mate showed lower FA in length of wings and outer tail than those that did not. Among females of this genus, those that exhibited greater tail symmetry also laid their eggs earlier (Møller 1994). Birds and insects may be able to detect differences in the degree of FA of potential mates more easily than it seems at first. In fact, some evidence exists that bilaterally symmetrical secondary sexual ornaments, among insects and birds, show far greater degree of FA than non-sexual morphological traits. Thus, the considerable size of asymmetries found in the horns of beetles and in birds' spurs (a weapon which is subjected to sexual selection), as well as in birds' ornaments, make

them more visible to members of their own species (Møller 1990, 1992; Møller and Pomiankowski 1993). Swaddle and Cuthill (1994) manipulated the degree of FA in the secondary sexual plumage trait in male zebra finches in order to examine the preference of birds for symmetry in non-arbitrary traits. Sure enough, they discovered that females of this species preferred 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 appeared to be negatively related to the number of offspring in females and mating success in males (Møller et al. 1996).

Oakes and Bernard's (1994) study is the only one to report a preference for asymmetrical sexual traits among birds, but it was criticized for confounded manipulation of symmetry (cf. Brookes and Pomiankowski 1994). Nevertheless, it is unclear whether all species show preference for symmetrical traits, sexual or non-sexual. For example, the evidence is equivocal regarding differences between the degrees of FA in various bilateral traits in mating and non-mating flies of several species (e.g., Markow, Bustoz and Pitnick 1996; Markow and Ricker 1992). Birkhead and Fletcher (1995) raised a doubt regarding the essence that underlies the signal of FA, that is, the quality it intends to represent. In a study of male zebra finches they found no relation between FA of chest band plumage and the quality of their sperm. While this finding should be clarified, Swaddle (1996) found that male zebra finches with an artificially symmetrical leg-band produced more offspring that survived beyond the period of prenatal care than males with an asymmetrical leg-band. Overall, lower degree FA in males does seem to lead, for various reasons, and probably in most species, to greater lifetime mating success (e.g., Harvey and Walsh 1993).

Still, sexual selection is associated with the level of FA not only due to females' choice or the ability of either sex to detect it. Males of the dung fly, for example, mount the female's dorsum before copulation. Only males that overcome the female's attempt to dislodge them continue to the next phase of copulation. Allen and Simmons (1996) demonstrated in this manner that males with more symmetrical foretibiae, which serve to grip the female's wing bases during mounting, are indirectly selected by female flies.

Studies on humans affirm this unmistakable relation between FA in bilateral morphological traits and mating success. Thornhill and Gangestad (1994) found a negative relation between an FA index based on seven bodily (e.g., foot breadth, ear length) traits and the number of sexual mates for both sexes. FA was also found to be a good predictor of age at first sexual intercourse, and it correlated negatively with facial attractiveness for men, but not for women (see also Gangestad, Thornhill and Yeo

1994). Recent findings suggest that the frequency of copulatory orgasm reported by women was negatively related to the degree of FA of their partners (Thornhill, Gangestad and Comer 1995).

It is still unclear how humans assess the extent of non-pathological FA or even recognize its existence. Researchers, at least, assess it using extremely subtle, and certainly invisible, differences in the pattern of dermatoglyphics, teeth size, or even foot breadth. Nonetheless, the studies cited above demonstrate an indisputable preference for mates who exhibit low FA, and consequently better developmental stability, among both animals and humans (full review in Møller and Thornhill 1997b). Obviously, the organism has good reason to do so. First, developmental stability is supposed to honestly reflect the genotypic quality of an individual due to the role genetic factors play in determining this stability. Moreover, good developmental stability suggests greater resistance to pathogens and parasites, which is an important consideration in sexual selection. Finally, one's developmental stability also suggests indirectly greater ability to care for offspring, an attribute which is related to their survival prospects.

The question remains, however, as to what are the mechanisms of sexual selection which make the organism prefer mates that display a greater degree of developmental stability. Most of the studies mentioned revealed the level of FA ad hoc, whereas only a few studies have demonstrated the ability of the organism to recognize FA *per se*, and outside the laboratory. It is evident that in cases of extremely high FA it serves as a detrimental cue *per se* in sexual selection. In the case of non-pathological FA, however, we are still in need of more evidence regarding the role of FA and the cue it may provide.

8. ASSESSMENT AND PROGNOSIS

The burgeoning interest in FA and the consequent surge of research on this topic has brought about much expectation as well as criticism (e.g., Gangestad and Thornhill 1997; Palmer 1999; Whitlock and Fowler 1997; for discussion see Kowner 2001). By now we have acquired much data about this measure, to the extent that we may attempt to assess its potential. It is evident that FA, as a reflection of developmental instability, shows an overall negative correlation with the overall fitness of the organism. Nonetheless, the evidence still seems inadequate to support the widespread application of FA as a substitute for conventional fitness measurement (cf. Clarke 1996).

In humans, FA in several traits shows an indisputable relation to various disorders of both developmental and genetic etiology. However, its role as a risk marker for pathology needs to be further clarified. This may become possible with the elimination of several methodological problems such as lack of standardization of FA measurements, measurement of many traits rather than one, and neglect of measurement errors.

The intensity of research in this field suggests that within a few years we may find out about the spectrum of applications that FA can provide. One promising line of research concerns the still unclear association between FA and canalization. Differences in the level of FA may be used to infer relative differences in genetic variability between closely related populations in the past or present. Moreover, FA could measure the evolution of increased canalizing ability within taxa (Palmer and Strobeck 1986). In more practical terms, perhaps, FA can serve as a gauge of genomic (e.g., inbreeding) and environmental (e.g., exposure to pollution, living density) stresses. Its assessment may become an important monitoring tool and early-warning method for detecting individuals and populations under stress.

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