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## Fluctuating Dental Asymmetry in Great Apes, Fossil Hominins, and Modern Humans: Implications for Changing Stressors during Human Evolution

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Fluctuating asymmetry (FA), defined by random, stress-induced deviations from perfect bilateral symmetry, is an indication of the inability to buffer against developmental disturbances, such as poor early nutrition. One method of measuring FA involves comparing individual tooth sizes on opposing sides of the mouth. In this study tooth measurements were compiled for 296 individuals from 10 species, including chimpanzees (*Pan troglodytes*), orangutans (*Pongo pygmaeus*), gorillas (*Gorilla gorilla*), modern humans (*Homo sapiens*), and a number of fossil hominins. The orangutan sample had significantly lower levels of dental FA than the gorilla, chimpanzee, *Homo erectus*, neandertal, or modern human samples. In contrast, the human and neandertal samples had significantly higher dental FA levels than any of the great ape samples. Some explanations relating to relaxed selection pressures are suggested.

**Keywords:** fluctuating asymmetry, selection pressures, fossil hominins.

### 巨猿、化石人和智人牙齿的波动不对称：人类进化中压力源变化的意义

波动不对称 (FA) 是压力的随机性引发双侧完美对称偏离的现象, 这是个体无力免受发展中不利因素 (如早期营养不良) 侵害的一个标志。比较个体口腔两侧牙齿的大小是一种测量 FA 的方法。本研究汇集了 10 个物种共 296 名个体的牙齿测量结果, 测量对象包括黑猩猩 (学名 *Pan troglodytes*)、猩猩 (学名 *Pongo pygmaeus*)、大猩猩 (学名 *Gorilla gorilla*)、智人 (学名 *Homo sapiens*), 以及许多化石人。分析发现, 猩猩样本牙齿的 FA 水平要显著低于大猩猩、黑猩猩、直立人、尼安德特人和智人样本的 FA 水平。而与之相反的是, 智人与尼安德特人样本的牙齿 FA 水平要显著高于其它任何一种巨猿样本的 FA 水平。该文提出了有关缓和的选择压力的解释。

**关键词:** 波动对称, 选择压力, 化石人。

**分类号:** B84-069

In recent years, a number of researchers have turned their attention to studying developmental instability, or the inability of an organism to buffer against genetic and environmental stresses during prenatal development. This instability can lead to deviations from perfect left-right symmetry. These slight, random deviations from bilateral symmetry can accumulate across traits; referred to as “fluctuating asymmetry”. Fluctuating asymmetry (FA) is interesting because it is negatively correlated with many indices of health and reproductive fitness (Kowner, 2001). It is also relatively easy to measure since it involves aberrations from a known physical ideal, perfect symmetry.

No one is perfectly symmetrical, but the degree of fluctuating asymmetry can vary across individuals and populations. Elevated FA in individuals is associated with vulnerability to various diseases or anomalies of development and higher levels of

morbidity (Livshits & Kobylansky, 1991). In contrast, low FA has been shown to correlate with a number of fitness indicators. Moller (1999) found that low FA values were associated with high fitness values on three dimensions: growth rate, fecundity, and survivorship, in a variety of organisms ranging from plants to humans. In humans, low FA is associated with increased genetic, physical, and mental health (Thornhill & Moller, 1997).

Low FA is also correlated with a number of measures of mating success and attractiveness in humans. Males with low FA are consistently judged by females as more attractive than males with high FA (Gangestad, Thornhill, & Yeo, 1994; Grammer & Thornhill 1994; Thornhill & Gangestad 1994). Low FA males also have more sexual partners (Thornhill & Gangestad, 1994) and more extra-pair copulations (Gangestad & Thornhill, 1997) than their less symmetrical peers. It has even been reported that women with male partners possessing low FA experience more frequent copulatory orgasms than women with male partners possessing high FA (Thornhill, Gangestad, & Comer, 1995). When women who were in the ovulatory phase of their

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menstrual cycle were asked to rate samples of male body odor for attractiveness, they preferred the scent of more symmetrical men (Thronhill & Gangestad, 1999). In women, low FA is associated with higher fertility (Manning, Kourkourakis, & Brodie, 1997; Manning, Scutt, Whitehouse, & Leinster, 1997). Facial attractiveness is negatively correlated with facial asymmetry in both men and women (Perrett, Burt, Penton-Voak, Lee, Rowland, & Edwards, 1999). Additionally, the voices of men and women with low levels of FA were rated as more attractive than the voices of individuals with high FA (Hughes, Harrison, & Gallup, 2002), suggesting that FA for one trait may be correlated with fitness of other traits. All these results are consistent with the idea that sexual selection favors symmetrical individuals because of the associated fitness benefits (Moller & Thornhill, 1998).

There is a large array of environmental and genetic stressors that can affect fluctuating asymmetry. Environmental factors can have an impact on the development of a growing organism, particularly during the embryonic stage. A number of studies have shown high FA in animal populations living in polluted areas (see Livshits & Kobyliansky, 1991), and in human subpopulations that were exposed to pollution or prenatal stresses (DiBennardo & Bailit, 1978). Parsons (1990) found that, on average, organisms living at extreme limits of species-typical environments and those exposed to pathogens or toxins show increased FA. Maternal illness or parasitism can also cause an embryo to develop less symmetrically (Parsons, 1990). It is estimated that the presence or absence of these environmental stressors accounts for at least forty percent of the total variance in fluctuating asymmetry (Livshits & Kobyliansky, 1991).

The remaining sixty percent of variance in FA is due to genetic factors: thirty percent each from additive and dominance effects (Livshits & Kobyliansky, 1991). Genotypes that are more resistant to developmental disturbances can act as a buffer against fluctuating asymmetry. Of course, since FA is associated with diminished fitness, it follows that selection should favor these FA-resistant genotypes in virtually every bilaterally symmetrical species. The degree to which FA is buffered against by genetic selection may vary across species and populations. It has been suggested that removing or weakening the stabilizing selection pressure may cause an elevation in average FA values as less resistant genotypes become more widespread in the gene pool (Livshits & Kobyliansky, 1991).

Given that fluctuating asymmetry is associated with reduced fitness, and that it varies in response to differences in environmental stress and genetic selection, it is a useful index for making comparisons

between various populations or species. One method of measuring FA in an individual involves comparing tooth sizes on the left and right sides of the mouth. This fluctuating dental asymmetry (dental FA) typically averages between 2 and 5 percent of total tooth size in various human populations, depending on the level of stress (Hershkovitz, Livshits, Moskona, Arensburg, & Kobyliansky, 1993). A number of studies have shown that dental FA is useful as an indirect measure of genetic and environmental stress in humans (Doyle & Johnston, 1977; DiBennardo & Bailit, 1978; Townsend, 1983; Townsend & Garcia-Godoy, 1984;

Kieser, Groeneveld, & Preston, 1986; Kieser, Groeneveld, & Da Silva, 1997).

Since teeth tend to be relatively well preserved in fossil specimens, dental FA can be calculated in extinct species of hominins as well. Suarez (1974) did a comparative study of cranial remains from neandertals and *Homo sapiens*, and found that the neandertals had higher levels of dental FA. However, when Doyle & Johnston (1977) attempted to replicate this finding using two additional human subpopulations, they found that both had dental FA equivalent to that of the neandertal sample in the Suarez study. In the time since these investigations, no in-depth comparative research has been conducted to examine variation in dental FA in fossil hominins. Thus, the question of how selective pressure against fluctuating dental asymmetry may have varied throughout human evolutionary history has remained unresolved. This is an interesting question. As a consequence of increased cranial capacity and the corollary development of tools and other inventions, humans have been able to generate cognitive solutions to a variety of adaptive problems (e.g., using fire to keep warm). Would the resulting relaxation of selective pressure be reflected in an increase in FA?

This study examined fluctuating dental asymmetry in fossil hominins and modern humans. Three species of living primates closely related to hominins were included for comparison with the fossils and modern humans. Six species of extinct hominins were examined, spanning early australopithecines to more recent hominin species. These were compared to a sample of modern humans from two agricultural, pre-industrial cultures. We hypothesized that dental FA varies across species when there are differences in the relative strength of stabilizing selective pressures acting on these species to minimize asymmetry.

### Methods

A total of 296 specimens from ten species were examined. Primate data were obtained from Mahler (1973). The data used in this study were buccolingual tooth diameters that Mahler measured in primate skulls from various museum collections. Buccolingual,

rather than mesiodistal measurements were used to reduce interference from wear. Thirty specimens were selected for each of three great ape species: gorillas, orangutans, and chimpanzees. Specimens with relatively incomplete dentition were omitted. The specimens were from collections at Cleveland Museum of Natural History, American Museum of Natural History, and the U.S. National Museum at the Smithsonian Institute.

Six species of fossil hominins were also examined with varying sample sizes due to limited numbers of specimens with left-right tooth pairs. Buccolingual tooth measurements were compiled for 12 *Australopithecus afarensis*, nine *Australopithecus africanus*, 17 *Paranthropus robustus*, seven *Homo habilis*, 19 *Homo erectus*, and 32 *Homo neanderthalensis*. These data were obtained from Wolpoff (1971), White (1971), Johanson, White, and Coppens (1982), and Wood (1991).

The anatomically modern human sample consisted of 110 specimens from Wolpoff (1971). As with the other species, all measurements were buccolingual tooth diameters measured in millimeters. The sample consisted of two subsets: 38 New Britain Islanders native to New Guinea and 72 Native Americans from a site called Dickson-Mound in Illinois. The Native Americans were from a late Middle Mississippian culture. These were measured by Wolpoff (1971) using skulls from the American Museum of Natural History. The sample of New Britain Islanders was also measured by Wolpoff (1971), and these skulls were from the Field Museum of Natural History in Chicago. Both subsets consisted of individuals from agricultural, pre-industrial societies. These groups were chosen because there were a large number of measurements available, and because they were from locations geographically distant from each other, thus permitting a comparison between two distinct groups of humans.

The formula used to obtain a measure of fluctuating asymmetry was one used successfully by a number of researchers (Hershkovitz, et al., 1993; Leamy, 1986; Livshits & Kobylansky, 1991; Van Valen, 1962):

$$FA = \left| \left\{ \frac{XR-XL}{.5(XR+XL)} \right\} - \left\{ \frac{1}{n} \sum \left[ \frac{XR-XL}{.5(XR+XL)} \right] \right\} \right|,$$

where XR and XL are the measurements for a particular tooth (first incisor, second incisor, etc.) on the right and left sides, respectively. The first bracketed quantity is the difference between the two teeth divided by their average size. This yields a ratio of asymmetry relative to tooth size for a particular tooth in a particular individual. The second bracketed quantity is the group average of this ratio for this tooth across individuals in the group. This is subtracted in order to remove any effects from directional asymmetry, since these are not random, and hence do not reflect fluctuating asymmetry.

Directional asymmetry was less than 0.2 percent of total tooth size in every instance. The groups used to compute this directional asymmetry were the species for the humans and primates, and the fossil hominins as a whole for the hominin specimens. This measure of FA was computed for each left-right tooth pair in the study. These values were then averaged across teeth to obtain a measure of fluctuating asymmetry for each individual. Mean values were computed for FA in each species by averaging individual scores. The average fluctuating asymmetry ratios for each species were multiplied by 100 to yield percents representing fluctuating asymmetry relative to trait size in each taxa.

### Results

A one-way ANOVA indicated significant variance in dental fluctuating asymmetry across the ten species ( $F = 5.49$ ;  $p < .001$ ). Pair-wise comparisons were performed on the mean dental FA values. Error inflation for multiple post-hoc comparisons was taken into account using Dunnett's T3 test for samples with unequal variances. Levels of fluctuating asymmetry ranged from a low of 1.64% in the orangutan sample to a high of 3.64% in the *Homo erectus* sample. TABLE 1 provides a complete list of means with their standard deviations.

Four species of fossil hominins had large margins of error on measures of dental FA: *Australopithecus afarensis*, *Australopithecus africanus*, *Paranthropus robustus*, and *Homo habilis*. Specimens from these early species of hominins were not as well preserved, and this resulted in small numbers of complete left-right tooth pairs in many of these individuals. Consequentially, these species could not be determined to have dental FA levels significantly different from any other species or each other. When the remaining six species were compared, significant pair-wise comparisons did emerge.

A one-way ANOVA revealed significant variance between these six species ( $F = 11.811$ ;  $p < .001$ ). The *Homo erectus* sample had significantly higher dental FA than the orangutans (mean difference=2.00%;  $p = .015$ ,  $d = -1.52$ ). The *Homo neanderthalensis* sample had significantly higher dental FA levels than the orangutans (mean diff. = 1.42%;  $p < .001$ ,  $d = -1.48$ ), as well as the gorillas (mean diff.=0.955%;  $p = .022$ ,  $d = -1.00$ ) and the chimpanzees (mean diff.=1.02%;  $p = .015$ ,  $d = -0.98$ ). The *Homo sapien* sample also had higher dental FA levels than orangutans (mean diff.=0.875;  $p < .001$ ,  $d = -1.29$ ), gorillas (mean diff.=0.406%;  $p = .009$ ,  $d = -0.60$ ), and chimpanzees (mean diff.=0.467%;  $p = .016$ ,  $d = -0.61$ ). The orangutans, in addition to having lower dental FA levels than these three hominin species, also had significantly lower dental FA than gorillas (mean diff. = 0.469%;  $p < .001$ ,  $d = -1.20$ ) and chimpanzees (mean diff. = 0.407%;  $p = .031$ ,  $d =$

-0.84). As an indirect test of the validity of the measurements for the living species, subsets of the primate and human samples were compared using an independent samples t-test procedure. FA levels within species did not differ significantly among primate specimens from different museum collections (all  $p$ -values  $> .920$ ). This supports the notion that the values in this study are species-typical. In the human sample, a comparison was made between the Dickson-Mound Native Americans and the New Britain Islanders. Although these two subsets were from locations on opposite sides of the globe, dental FA did not differ significantly between them ( $t = -.785$ ;  $p = .435$ ).

Table 1 Percent Fluctuating Dental Asymmetry in Great Apes, Hominins, and Humans

SPECIES	Mean	$N$	$SD$
Gorilla	2.108	30	.383
Orangutan	1.640	30	.399
Chimpanzee	2.047	30	.565
A. Afarensis	2.280	12	1.365
A. Africanus	2.547	9	1.731
P. Robustus	2.132	17	1.173
H. Habilis	2.750	7	1.733
H. Erectus	3.643	19	2.235
H. Neandertal	3.063	32	1.519
H. Sapien	2.514	110	.961
Total	2.444	296	1.215

For each of the specimens from the great ape species, gender was also provided. A one-way ANOVA revealed a significant effect of sex on levels of fluctuating dental asymmetry ( $F = 4.08$ ;  $p = .047$ ). In gorillas, chimpanzees, and orangutans, females had lower levels of FA, on average, than males. Thus, among the primates, there were main effects of species and sex on levels of FA, with the effect of species ( $F = 7.357$ ;  $p < .001$ ) being stronger than that of sex. There was no significant interaction effect between sex and species on FA ( $F = 0.225$ ;  $p = .799$ ).

### Discussion

Fluctuating dental asymmetry differed significantly across all ten species in this study. When average FA levels were considered, there appeared to be a general trend toward increasing asymmetry as one moves from great apes and early hominins to the later hominins and modern humans. Whether there is actually an increase in average dental FA over time among the fossil hominins is difficult to determine. More specimens with relatively complete dentition are needed to reduce the margin of error. Particularly in the earlier species the sample sizes are too small to make meaningful generalizations. The *Paranthropus robustus* sample, which consists of 17 specimens, is close to being of sufficient size to detect significant differences. If more specimens of this species could be included, it might prove to have lower average FA than the later hominins or humans.

Based on these data, it is clear that humans and the two species of hominins most closely related to them, *Homo erectus* and *Homo neanderthalensis*, have higher levels of fluctuating dental asymmetry, on average, than the three great ape species: gorillas, orangutans, and chimpanzees. On the basis of effect sizes, the differences ranged from moderate ( $d = -0.60$ ) to substantial ( $ds > -1.0$ ). The degree of FA was particularly large for all three species of *Homo* in comparison to the orangutan. In fact, the finding that degree of FA in the *Homo* species was more than 1 standard deviation higher than that found in the orangutan suggests considerably more relaxed pressures in *Homo* compared to the orangutan. A graph of the mean levels of dental FA together with error bars representing their 95% confidence intervals is presented in Figure 1.

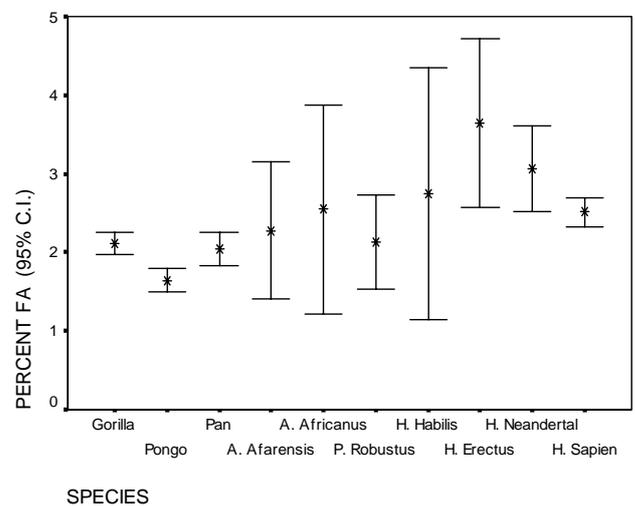


Figure 1. Plot of the average levels of fluctuating dental asymmetry across the ten species in this study. The error bars represent the 95% confidence intervals for these means. Note that the three great ape species have lower levels of dental FA, on average, than the *Homo erectus*, *Homo neanderthalensis*, and *Homo sapien* samples.

As noted previously, variation in levels of fluctuating asymmetry can be due to genetic and environmental factors. While this study was intended simply to measure variation in FA, there is reason to suspect that the differences reported here are largely due to the genetic component. Environmental stressors exert their impact on FA primarily during prenatal development. On average, however, we would not expect levels of prenatal stress to differ dramatically across these species. Most individuals would likely be from relatively stable, species-typical environments with similar levels of parasitism, exposure to pollutants, and other environmental stressors. The humans were from pre-industrial cultures, so developmental interference from industrial pollution should be minimal. Furthermore, teeth are particularly resistant to environmental

factors and their growth is largely dependent on the genome. Thus, genetic differences are probably largely responsible for the observed differences in dental FA between species. If this is the case, it raises the question of why there is variation in the degree of selection for FA-resistant genotypes.

Higher FA levels may be due to reduced selective pressures leading to less FA-resistant genes as suggested in Livshits and Kobylansky (1991). During human evolution the increase in cranial capacity, the advent of tools, and the use of fire (among other things), may have enabled hominins to gradually emancipate themselves from some of the selective pressures that would otherwise serve to maintain low levels of fluctuating asymmetry, such as food scarcity, predation, etc. This concept, known as 'ecological dominance' was developed by Richard Alexander (for review, see Flinn, et al., 2005). As selective pressures related to biotic interactions were reduced relative to those related to social competition, one consequence may have been a partial relaxation of the pressure to minimize asymmetry.

The sex difference observed in great apes, with females from each species being more symmetrical, on average, than males, is consistent with the results of Kuswandari & Nishino (2004), who reported a similar finding in humans. Their analysis of the dental casts from 160 male and 137 female Indonesian children revealed that fluctuating dental asymmetry was also significantly greater in the males. They suggest that this might be due to greater buffering conferred by the paired X chromosome in females, a model first presented by Garn & Rohmann (1963) and outlined in Garn, Lewis, & Kerewsky (1965). According to this model, an XX pair provides more buffering than an XY pair because of the larger amount of chromosomal material contained within it. While difficult to test, this hypothesis has persisted as a plausible explanation for various findings, such as the greater vulnerability to disease and mortality seen among men (e.g., Waldron, 1983). In any case, if the sex difference in fluctuating dental asymmetry in humans is caused by genetic factors, then it is likely that the same factors are responsible for the sex difference in great apes, since all four species share more than 96% of the same genes in common (Sibley & Ahlquist, 1984).

It is also important to comment on the fact that orangutans show fewer deviations from bilateral symmetry than any of the other species examined. One possible explanation for this peculiar finding relates to the unique demands of the orangutan's habitat. Unlike humans and the other great apes, orangutans spend most of their time in the trees. Although many primate species still live in the trees, Povinelli and Cant (1995) point out that the arboreal habitat poses special problems for orangutans because

of the effect their large body mass (some weigh 80kg or more) has on the fragile forest canopy substrate. As they move through the trees, orangutans carefully and methodically test and evaluate various features of the canopy to assess whether they will provide sufficient support to enable them to safely move from one branch or vine to the next without it breaking. The demands of coping with such a dangerous and unstable substrate undoubtedly put a premium on balance. Balance is probably related to bilateral symmetry. The findings of Brown et al. (2005) lend some support to this idea. They reported that human males with low FA levels were judged to be better dancers by independent raters. Perhaps the pressure to maintain balance in orangutans also acts to minimize FA in this species.

Another possible reason for the lower dental FA exhibited in orangutans may be lower levels of pathogen virulence as a consequence of limited contact between individuals. Orangutans are unique among great apes and hominins in that they are semi-solitary. Males and adolescents range alone, and adult females range only with their dependent offspring (te Boekhorst et al., 1990). Reduced contact between hosts is associated with reduced pathogen virulence (see André & Hochberg, 2005). This is because the parasite, and therefore the host, must survive longer to maximize the likelihood of transmission to another individual. Thus, low dental FA may reflect a lower level of disease virulence in orangutans because of reduced pathogen transmission. Perhaps this low disease virulence, combined with greater genotypic buffering associated with the need to maintain balance, accounts for the unusually low levels of FA observed in this species.

Finally, it is important to acknowledge three limitations implicit in this research design. First, although we suspect that genotypic variation accounts for most of the observed species differences in dental FA, there is no way to determine the relative impact of environmental factors, such as pathogen load. Second, although dental FA, like overall body FA, has been consistently shown to be a useful indirect index of developmental instability, it remains unclear whether dental FA is directly correlated with measures of FA taken from other areas of the body. Finally, since this study made use of previously published data, there was no inherent measure of inter-rater reliability. A future study measuring dental and non-dental FA using double determination procedures would allow for a quantification of measurement error, as well as a comparison between dental FA and other measures of body FA.

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