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Androgen Levels and Body Size Are Associated with Directional as Well as Fluctuating Asymmetry Patterns in Adult !Kung San and Kavango Males from Northern Namibia

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Abstract: Fluctuating asymmetry is mainly interpreted as an indicator of developmental instability, while directional asymmetry of the upper limbs is associated with handedness. The association patterns between adult androgen levels and fluctuating as well directional asymmetry patterns are still unclear. In the present study, the association between adult androgen levels, body size and directional as well as fluctuating asymmetry pattern was tested among !Kung San and Kavango males from northern Namibia. Serum concentrations of testosterone (Tser) and 5α-dihydrotestosterone (DHT) as well as salivary testosterone (Tsal) concentrations were obtained from 114 !Kung San and 136 Kavango men aged 18–40 years. Fluctuating and directional asymmetry were determined from eight paired traits. Signed and unsigned asymmetry, composite fluctuating and directional asymmetry were calculated. !Kung San males surpassed their Kavango counterparts in the directional asymmetry but also in composite directional asymmetry (CDA) significantly. Among !Kung San males, DHT correlated significantly negatively with parameters of fluctuating asymmetry as well as with parameters of directional asymmetry. Free testosterone of the saliva correlated significantly negatively with asymmetry of hand length. Among Kavango males, DHT is negatively associated with foot breadth asymmetry, but positively associated with wrist asymmetry. Although the correlations between asymmetry patterns and androgen levels are weak, it can be concluded that among !Kung San males adult androgen levels are negatively associated with a high quality phenotype.

Keywords: directional asymmetry; fluctuating asymmetry; 5α-dihydrotestosterone; free testosterone; !Kung San; Kavango

1. Introduction

Symmetry, which is widely found in nature, is often seen as an ideal and is defined as correspondence in size, shape and relative position of parts on opposite sides of a median plane or a dividing line [1]. The body plan of *Homo sapiens*—as typical of vertebrates—is generally described as bilaterally symmetrical, this bilateral symmetry, however, is broken by consistently asymmetric placement of some internal organs such as heart, spleen, liver or gut, but also the asymmetric development of some paired organs such as lungs or the brain hemispheres [2]. Consequently, *Homo sapiens* can be described as pseudo-bilateral. Nevertheless, symmetry is interpreted as an ideal among *Homo sapiens*. This is mainly because even small deviations from perfect bilateral symmetry reflect disruptions of development homeostasis. Consequently, asymmetry of bilateral structures is highly correlated with the exposition to stress factors, such as parasitism, environmental pollution, predation risk, high population density, inbreeding, poor health, and malnutrition during individual development [3–8]. Therefore, asymmetry patterns of bilateral structures have been interpreted as indictors of developmental stress factors and were found to be associated with enamel hypoplasia and other stress parameters such as Harris lines [9–12]. Three main types of asymmetry can be distinguished: antisymmetry, directional asymmetry (DA) and fluctuating asymmetry (FA) [13,14]. Antisymmetry is defined as a pattern of bilateral variation in a sample of individuals where a statistically significant difference between sides occurs, but where the larger side varies at random among individuals [15,16]. Directional asymmetry (DA) refers to a pattern of bilateral variation in a sample of individuals where a statistically significant difference exists between sides, but the larger side is mainly the same side for all individuals of the sample [16]. Among humans a typical example of DA is found for upper limb dimensions [17–21]. In general, the right upper limbs exhibit larger dimensions than the left ones. This DA among *Homo sapiens* is mainly interpreted as a result of handedness [19,21,22].

Fluctuating asymmetry (FA)—the third variant of asymmetry—is a widespread phenomenon in nature referring to small random deviations from perfect symmetry in bilaterally-paired structures, which are symmetrical at population level [13]. Under normal conditions FA is minimal, but it is increased under stressful events. Therefore, FA is seen as an indicator of developmental instability [4,14]. Increased FA is found among people suffering from Down´s syndrome, cleft lip, Fragile X syndrome and scoliosis [4]. Furthermore, increased FA was associated with some health problems, such as toxoplasmosis, anemia, hepatitis, heart trouble, cancer and arthritis, and therefore interpreted as an indicator of some pathological conditions [23–26]. Consequently, FA is often used as a proxy to quantify developmental stress factors and analyze the effects of defective development on health, fitness and behavior [26–28]. Stress causes elevated steroid hormone levels, in particular glucocorticoid levels increase in response to stress. These elevated glucocorticoid levels help the organism to cope with the stressors immediately, but steroid hormones have also a long term impact on growth, reproduction and health [29], parameters that correlated with FA [30]. Some studies focused on the association between sex hormones—in particular androgens and estrogens—on FA patterns [31–34]. Especially the relationship between testosterone levels and patterns of FA have been examined in non-human animal studies. Studies connecting androgen levels and asymmetry patterns in humans are still rare. On the one hand, a significant association between testosterone levels and dermatoglyphic asymmetry was found [35]. On the other hand, the ratio between index finger and ring finger, the so-called 2D:4D ratio—as an indicator of fetal hormone exposure—was correlated with facial asymmetry patterns [34]. Associations between adult androgen levels and asymmetry patterns have rarely been tested. This may be due to the fact that FA patterns reflect mainly developmental instabilities which have occurred in early life. Consequently, no strong relationships between asymmetry patterns and adult sex hormone levels have been assumed. On the other hand, it is well documented that high androgen levels are costly because testosterone may suppress the immune function, and makes the organism vulnerable for parasites and pathogens [36–38]. At a first glimpse high testosterone levels may correlate positively with FA. The association between high androgen levels and reduced immune function however, does not necessarily indicate that high androgen levels are linked to a high degree of asymmetry. In contrast, it can be assumed that only symmetric males, indicating a high phenotypic quality, can afford to produce high androgen levels, which may reduce immune-competence. High phenotypic quality is also indicated by large body size. Manning [39] reported a negative association between body size as well as resting metabolic rate and FA in young males. It was concluded that high quality males had energy-thrifty phenotypes, which enabled them to allocate energy for growth and maintenance of muscle and bone [40]. Consequently, a negative association between FA and adult androgen levels can be assumed. Concerning DA patterns of the upper limb caused by handedness an association with traits indicating a high quality phenoptype can be assumed. On the one hand, left-handedness was interpreted as a marker of decreased survival fitness [41], while, on the other hand, the so-called "fighting hypothesis" plead for an evolutionary advantage of left handers in violent societies [42], although the evidence for the fighting hypothesis is not particularly strong. An association between androgen levels and handedness among adult males however was described [43]. Therefore, an association between androgen levels and patterns of DA can be assumed. Furthermore, a negative association between body size and asymmetry patterns can be predicted. The aim of the present study was to test these two hypotheses. Therefore, the association patterns between asymmetry and adult androgen levels as well as body size among traditional !Kung San and Kavango people from northern Namibia were focused on. This approach is a quite new one. Studies focusing on asymmetry patterns among traditional hunter gatherers are still rare. Jones and Hill [44] analyzed FA of the face among Ache foragers. Gray and Marlowe [5] reported FA patterns of Hadza hunter gatherers of Tanzania. Furthermore sexual dimorphism in facial asymmetry patterns of Hadza hunter gatherers were analyzed by Little et al. [45]. Among !Kung San and Kavango people the impact of sex and subsistence patterns on fluctuating and directional asymmetry has been tested [46]. Nevertheless, most studies focusing on asymmetry patterns have been conducted in developed countries such as the United States or European countries. Furthermore only few studies focused on androgen levels among adult males following a hunter gatherer subsistence [47–55]. Therefore, in the present study, for the first time, the relationship between asymmetry patterns and androgen levels during adulthood was tested among male !Kung San foragers and Kavango horticultural pastoralists.

2. Material and Methods

2.1. Study Population

Data collection took place during a field study in northern Namibia between June and September 1987. In detail field research was conducted in various locations of the Kavango district and the Nyae-Nyae area of the Bushmanland. This so called Viennese Kalahari project was carried out in close cooperation with the Department of Human Biology of the University of Hamburg. Detailed description of this project was presented in numerous publications [54–62]. Altogether, 250 subjects were enrolled in the present study. This study population consisted of two subgroups: 114 !Kung San males aged between 18 and 40 years (x = 26.5; SD = 4.9) living in an area up to 70 km around Tsumkwe, the administrative center of northern Bushmanland. At the time of data collection the !Kung San of the Nyae-Nyae area represented together with the !Kung San of northwestern Botswana the largest single division of the San surviving in the Kalahari desert. On the other hand, 136 Kavango males between the ages 18 and 40 years (x = 24.5; SD = 4.5) living in Rundu, the administrative center of the Kavango district, and the surrounding rural areas participated in the present study. All Kavango enrolled in the present study belonged to the southern Bantu speaking Kavango people which can be divided into five matrilinear tribes: Kwangali, Mbunza, Sambyu, Gciriku and Mbukshu. Members of all tribes are included in the present sample.

2.2. Subsistence Patterns

The vast majority of the !Kung San subjects followed a traditional lifestyle as hunter and gatherers to a certain extent. They lived in small more or less permanent camps consisting of 7 to 15 grass huts near waterholes. Nearly all !Kung San enrolled in the present study, however, had contact to westernized lifestyle as a result of temporary occupation of band members at cattle farms and hunting ranches.

The Kavango live north and south of the Okavango River, which forms the natural border between Angola and Namibia. As a consequence of the civil war in Angola, most Kavango settled south of the river, in Namibia at the time of data collection. The majority of inhabitants of the Namibian Kavango district practiced traditionally a mixed subsistence of cattle pastoralism and horticulture. Additionally, when they live close enough to Okavango River, they fished. Their traditional diet is characterized by vegetables and animal products, such as milk and occasionally meat, from their own plot. The majority of Kavango people enrolled in the present study lived in traditional kraals in the rural areas around Rundu. Their subsistence patterns can be characterized as horticultural pastoralists without earning a regular cash income. Only a minority of the Kavango subjects of the present study were engaged in some kind of occupation with occasionally cash income. These Kavango participants lived in Rundu, the administrative center of the Kavango district, as wage earning employees. They belonged to the minority of Kavango engaged in productive labor.

2.3. Anthropometry

For the present study beside body height and body weight, eight anthropometric measurements to assess asymmetry patterns were taken directly from the subject using a standard anthropometer, a scale and a capliper (Siber-Hegner Corp., Zurich, Switzerland). According to the methods described by Knussmann [63], right and left ear length, ear breadth, hand length, hand breadth, hand circumference, wrist breadth, foot length and foot breadth were determined. In order to avoid inter-individual measurement errors all measurements were taken by the same trained collector (E.M. Winkler, Vienna, Austria). Furthermore, to improve accuracy and control for reliability, each trait was measured twice and the average of the two repeated measures was calculated. First and second measurements correlated (Peasron correlation) with each other (all $r > 0.96$, all $p > 0.0001$). Consequently, the average values of the individual measurements were used for further analyses.

Additionally, Body mass index (BMI) was calculated by dividing body weight in kg per body height in meters (square).

2.4. Asymmetry

Signed asymmetry (SA) in each individual case was determined by calculating the difference between the right and left dimensions (R-L). In a second step unsigned right minus left side differences of trait measurements were calculated (R-L). Absolute asymmetry (AA) of each trait was calculated as follows: Unsigned asymmetry was corrected for trait size according to the formula: AA = (Iright – leftI)/[(right + left)/2] according to Palmer and Strobeck [14] and Fink et al. [28]. This method allows the direct comparison of asymmetries in dimensions of different size. Next, we calculated two different composite asymmetry indices. The appropriate use of composite asymmetry indices is discussed controversially [64–68]. Composite indices of asymmetry patterns are widely used. Gray and Marlowe [5] added the FA of all individual traits (ear length, ear breadth, elbow breadth, writs breadth, finger lengths, ankle breadth and foot breadth) to yield a person´s combined fluctuating asymmetry. Similar composite or combined asymmetry indices were calculated by Özener [16], Fink et al. [28], Flegr et al. [25] and Milne et al. [23]. In the present study, we used the composite asymmetry score according to Fink et al. [28] summarizing (unsigned) left minus right side differences of trait measurements corrected for traits size $\mathrm{IL} - \mathrm{RI}/(\mathrm{R} + \mathrm{L}) \times 0.5$. Based on this formula composite directional asymmetry and composite fluctuating asymmetry were calculated. Composite directional asymmetry (CDA) was based on traits which may be influenced by handedness (hand length, hand breadth, hand circumference, and wrist breadth). Additionally composite fluctuating asymmetry (CFA) was calculated using traits which are not influenced by handedness (ear length, ear breadth, foot length, and foot breadth). We are aware that, besides handedness, humans exhibit a kind of footedness, however only marginal bilateral differences in foot dimensions and no significant association between footedness and asymmetry patterns of foot dimensions have been described [69] Therefore, we decided to consider left right differences in foot dimensions as indicators of FA.

2.5. Hormone Levels

The following sex hormone levels were determined by specific and sensitive radioimmunoassays (RIA):

Total testosterone in the Serum (Tser);

5α-dihydrotestosterone in the serum (DHT);
Free testosterone in the saliva (Tsal).

In order to minimize the effects of diurnal endocrine fluctuations as far as possible, blood and saliva samples were taken in the morning hours about one to two hours after sun rise between 8:00 and 10:30 a.m. Blood samples were drawn through conventional venipuncture into lithiumized by trained medical personal and allowed to clot for one hour before the serum was separated through centrifugation. The participants provided a saliva sample after carefully rinsing their mouths with cold water in order to prevent a contamination of the salivary sex hormones by exogenous steroids from food or blood. In order to avoid contamination of the saliva samples with blood from oral bleeding, all saliva samples were tested using dipstick indicators designed to detect the presence of blood in the urine (Hamo dip, Merckognost, Darmstadt, Germany). Blood and saliva samples were taken at Tsumkwe (!Kung San sample) and Rundu (Kavango sample). Both saliva and serum of the !Kung San participants were immediately stored at −20 °C in an electrical deep freezer at Tsumkwe. Saliva and serum of the Kavango participants were deep frozen using a portable, battery run freezer and transported deep frozen (−20 °C) to Tsumkwe. For the transport from Namibia to the Institute of Human Biology in Hamburg, Germany, were the analysis and sex hormone determination took place, the blood and saliva samples remained deep frozen in a portable, battery-run freezer.

All samples were analyzed twice using the same assay at the Institute of Human Biology, University of Hamburg, Germany. Androgen levels of the serum and saliva were determined by means of commercial tritium marked RIA-kits (T/DHT-^{3}H-Kit, Charcoal Technique, Amersham Buchler, Braumschwaig, Germany). The standards were 12.5 to 400 pg tube for testosterone and 25 to 800 pg/tube for 5α-dihydrotestosterone. The intra- and interassay coefficients of variation were within the usual limits reported (Tser 6.6% and 11.4%; DHT 10% and 12.9%; Tsal 7.1%). Hormonal analyses have been published in previous studies [54,55].

2.6. Statistical Analysis

Statistical analysis was carried out by using SPSS for Windows Program Version 22.0 (Microsoft corp., Vienna, Austria). Pearson correlations were calculated to test the reliability of anthropometric measurements. Directional asymmetry was calculated using a one-tailed *t*-test. Two-tailed Student-*t*-tests were calculated to test group differences of the anthropometric parameters with respect to their statistical significance. The Kolmogorov–Smirnov test yielded no normal distribution for DHT levels, consequently non-parametric tests were performed to test group differences in sex hormone levels but also asymmetry-hormonal correlation patterns. Although the results of the Kolmogoroff–Smirnov test indicate that a normal distribution of all metric variables can be assumed, nonparametric tests were used to analyze percentage data according to the recommendation of Auerbach and Ruff [52]. Consequently, after calculation of descriptive statistics (means, SDs), Mann–Whitney tests were applied to test group differences with respect to their statistical significance. Spearman correlations were computed to test the relation between asymmetry of each anthropometric variable and androgen levels, body height body weight bod mass index and subject´s chronological age. Multiple regression analyses were performed in order to test the impact of body height, BMI, age, and androgen levels on asymmetry patterns. *P*-values of less than 0.05 were considered significant.

3. Results

3.1. Age and Anthropometry

Table 1 presents means and standard deviations of age, body height, body weight, body mass index and the eight bilateral anthropometric parameters according to ethnic group. !Kung San males were significantly older than Kavango males ($p < 0.001$) and—as to be expected—!Kung San males were significantly shorter and lighter than their Kavango counterparts. On the other hand, Kavango males surpassed !Kung San males highly significantly ($p < 0.0001$) in all eight bilateral anthropometric parameters.

Table 1. Age and body measurements according to ethnic groups (two-tailed student *t*-tests). x means mean value.

Measurement	!Kung San (n = 114)		Kavango (n = 136)		p-Value
	x	SD	x	SD	
Age (years)	26.5	4.9	24.5	4.5	0.001
Stature height (cm)	161.4	5.1	170.6	58.9	<0.0001
Body weight (kg)	50.4	6.2	59.2	6.9	<0.0001
Body mass index (kg/m^2)	19.31	1.89	20.34	2.09	<0.0001
Ear length right (mm)	52.2	3.9	59.7	3.9	<0.0001
Ear length left (mm)	50.8	3.4	58.5	3.4	<0.0001
Ear breadth right (mm)	29.7	2.3	34.9	2.4	<0.0001
Ear breadth left (mm)	30.6	2.3	35.6	2.6	<0.0001
Hand length right (mm)	173.7	7.8	193.6	8.3	<0.0001
Hand length left (mm)	175.0	7.2	193.8	8.3	<0.0001
Hand breadth right (mm)	76.5	3.5	86.7	3.9	<0.0001
Hand breadth left (mm)	75.1	3.2	85.3	3.8	<0.0001
Hand circumference right (mm)	188.0	8.8	211.1	9.8	<0.0001
Hand circumference left (mm)	182.4	8.3	206.4	9.8	<0.0001
Wrist breadth right (mm)	52.2	2.6	57.4	2.9	<0.0001
Wrist breadth left (mm)	50.9	2.5	56.7	3.1	<0.0001
Foot length right (mm)	241.3	9.7	266.9	11.3	<0.0001
Foot length left (mm)	241.6	9.9	267.4	10.9	<0.0001
Foot breadth right (mm)	92.3	5.1	104.8	5.7	<0.0001
Foot breadth left (mm)	93.1	5.2	105.5	5.8	<0.0001

3.2. Androgen Levels

!Kung San and Kavango males differed highly significantly in serum testosterone (Tser), serum 5α-dihydrotestosterone (DHT) and free testosterone in the saliva (Tsal). Kavango males showed significantly higher androgen levels. (see Table 2).

Table 2. Androgen levels according to ethnic groups (Mann–Whitney *u*-test).

Measurement	!Kung San (n = 114)		Kavango (n = 136)		p-Value
	x	SD	x	SD	
DHT (ng/mL)	1.35	0.67	1.80	1.13	<0.001
Tser (ng/mL)	4.73	2.09	6.03	2.59	<0.001
Tsal (pg/mL)	80.11	36.02	96.68	32.97	<0.001

3.3. Asymmetry Patterns

In a first step, signed asymmetry (SA) and absolute asymmetry (AA) were calculated. In a second step, one sample *t*-tests for each trait were performed of the whole sample in order to detect the existence of DA and FA. Table 3 demonstrates that all eight bilateral anthropometric traits showed a mean significantly different of 0, indicating FA or DA. The asymmetry of these traits however differed in direction. On average, ear breadth, hand length, foot length and foot breadth showed higher measurements on the left side, while ear length, hand breadth, hand circumference and wrist breadth showed higher measurements on the right side.

Table 3. Mean standard deviation of trait asymmetry and results of one sample *t*-tests (*t* and *p*-values).

Trait	SA			AA		
	x	**SD**	***p***	**x**	**SD**	***p***
			Total Sample			
Ear length	1.25	1.87	<0.001	0.02	0.03	<0.001
Ear breadth	−0.80	1.39	<0.001	−0.02	0.04	<0.001
Hand length	−0.76	2.71	<0.001	−0.01	0.02	<0.001
Hand breadth	1.38	1.76	<0.001	0.02	0.02	<0.001
Hand circumference	5.06	4.45	<0.001	0.03	0.02	<0.001
Wrist breadth	0.94	1.52	<0.001	0.02	0.03	<0.001
Foot length	−0.41	3.10	0.040	−0.01	0.01	0.040
Foot breadth	−0.72	2.89	<0.001	−0.01	0.03	<0.001

3.4. The Impact of Age, Body Size Ethnic Group and Androgen Levels on Asymmetry Patterns

Multiple regression analyses yielded significant impact of body height on CFA and directional asymmetry (CDA). Serum testosterone was significantly associated with CDA. In contrast, age, body mass index and DHT as well as free testosterone levels showed no significant impact on asymmetry patterns of the whole sample (see Table 4).

Table 4. Multiple regression analysis: Impact of age, body height, BMI and androgen levels on asymmetry patterns.

Trait	R^2	RC β	Significance	95% CI	R^2	RC β	Sig.	95% CI
			CFA				**CDA**	
Age	0.16	0.01	0.970	−0.01–0.01	0.27	0.01	0.852	−0.001–0.01
Body height		−0.13	**0.052**	0.00–0.00		−0.13	**0.051**	0.00–0.00
BMI		0.03	0.659	−0.01–0.01		0.04	0.542	−0.01–0.01
DHT		−0.03	0.696	−0.01–0.01		−0.11	0.105	−0.01–0.00
Tser		−0.02	0.814	−0.01–0.00		−0.15	**0.034**	−0.01–0.00
Tsal		−0.01	0.944	0.00–0.00		−0.04	0.539	0.00–0.00

Ethnic group differences in asymmetry patterns could be proved by Mann–Whitney *u*-tests of each bilateral trait and composite asymmetry patterns too. Asymmetry of ear breadth, ear length hand length, hand breadth, hand circumference and wrist breadth differed significantly between !Kung San and Kavango males. In detail, !Kung San male exhibited a higher degree of asymmetry than Kavango males. Furthermore CDA and CFA were significantly higher among !Kung San males (see Table 5).

Table 5. Asymmetry according to ethnic group (Mann–Whitney-*u*-tests).

Measurement	!Kung San		Kavango		*p*-Value
	SA	**AA**	**SA**	**AA**	
Ear length	1.82	0.04	1.53	0.03	0.006
Ear breadth	1.15	0.04	1.04	0.03	0.006
Hand length	2.16	0.01	1.44	0.00	0.001
Hand breadth	1.75	0.02	1.72	0.02	0.029
Hand circumference	6.06	0.03	5.08	0.02	0.002
Wrist breadth	1.42	0.03	1.23	0.02	0.001
Foot length	2.04	0.01	2.26	0.01	0.886
Foot breadth	1.97	0.01	2.18	0.01	0.592
CFA	-	0.08	-	0.07	0.010
CDA	-	0.09	-	0.07	0.001

3.5. Age, Body Size, Androgen Levels and Asymmetry Correlation Patterns

Spearman correlations between CDA, CFA, and absolute asymmetry of all eight bilateral traits and body height, body weight, BMI and androgen levels were performed for each ethnic group separately. Although some statistically significant correlations between asymmetry patterns and body height, BMI and DHT levels could be stated, all statistically significant correlations are very weak. All correlation coefficients are below 0.24. Consequently, no strong correlation between asymmetry patterns and androgen levels as well as body size could be documented among studied populations. In detail: correlation patterns between absolute asymmetry as well as composite asymmetry and body size as well as androgen levels differed between !Kung San and Kavango males. Body height correlated significantly negatively with CFA and foot breadth asymmetry among !Kung San males. Among Kavango males body height correlated significantly negatively with absolute asymmetry of ear breadth and wrist breadth. The body mass index correlated significantly negatively with absolute asymmetry of foot breadth and ear breadth and significantly positively with absolute asymmetry of ear length among !Kung San males, while among Kavango males body mass index correlated significantly positively with the absolute asymmetry of ear breadth only. DHT levels correlated significantly positively with absolute asymmetry of ear length, but significantly negatively with absolute asymmetry of hand breadth, wrist breadth, foot length and foot breadth and composite directional asymmetry among !Kung San males. Among Kavango males, however, DHT levels correlated significantly positively with the absolute asymmetry of wrist breadth and significantly negatively with absolute asymmetry of foot breadth. Free testosterone levels (Tsal) correlated significantly negatively with absolute asymmetry of hand length and composite directional asymmetry among !Kung San males. No significant correlations between body weight and asymmetry patterns could be observed (see Table 6).

Table 6. Asymmetry patterns and androgen levels among !Kung San and Kavango males (Spearman correlations rho) * $p < 0.05$.

Asymmetry Trait	Body Height	Body Weight	BMI	Tser	Tsal	DHT
	rho	rho	rho	rho	rho	rho
			!Kung San			
CFA	**−0.19 ***	0.08	−0.05	−0.03	0.02	0.04
CDA	0.02	0.08	0.11	−0.11	−0.17 *	**−0.19 ***
AA Ear length	−0.02	0.07	**0.23 ***	−0.01	0.09	**0.17 ***
AA Ear breadth	0.16	−0.02	**−0.19 ***	−0.03	−0.01	−0.01
AA Hand length	0.04	−0.04	−0.06	−0.16	**−0.22 ***	0.09
AA Hand breadth	0.11	0.10	0.09	0.13	0.02	**−0.19 ***
AA Hand circumference	−0.03	0.02	0.06	−0.09	−0.02	−0.09
AA Wrist breadth	0.05	0.13	0.15	−0.07	−0.03	**−0.20 ***
AA Foot length	−0.08	0.09	0.07	−0.06	−0.01	**−0.21 ***
AA Foot breadth	**−0.19 ***	**−0.19 ***	**−0.21 ***	0.05	−0.03	**−0.19 ***
			Kavango			
CFA	0.06	−0.07	−0.13	−0.07	−0.08	−0.11
CDA	0.10	−0.02	−0.02	0.05	0.08	0.11
AA Ear length	0.05	0.02	−0.03	0.01	0.02	−0.15
AA Ear breadth	**−0.17**	0.06	**0.18 ***	0.11	0.02	0.05
AA Hand length	0.04	−0.03	−0.09	0.05	0.05	0.03
AA Hand breadth	0.13	0.09	−0.03	−0.03	−0.02	0.01
AA Hand circumference	0.10	0.05	−0.01	0.01	0.03	−0.02
AA Wrist breadth	**−0.17 ***	0.06	0.11	−0.02	0.10	**0.16 ***
AA Foot length	−0.03	0.05	0.02	0.03	0.06	−0.02
AA Foot breadth	0.16	−0.01	−0.09	0.13	−0.06	**−0.18 ***

4. Discussion

The present study focuses on association patterns between fluctuating as well as directional asymmetry patterns and adult androgen levels among two traditional societies of southern Africa. In detail, the relationship between DHT, serum testosterone and free testosterone of the saliva and asymmetry patterns of eight bilateral somatic traits has been analyzed among !Kung San and Kavango males from northern Namibia.

Before starting with the detailed discussion of the present results, we have to state that this study has certain limitations. On the one hand, the age range of the participants was quite high, ranging from 18 to 40 years, and !Kung San men were older than their Kavango counterparts. Another shortcoming is the low number of anthropometric features indicating asymmetry patterns. FA was indicated by ear length, ear breadth, foot length and foot breadth. Concerning directional asymmetry, only hand breadth, hand length, hand circumference and wrist breadth could be analyzed. These limitations are mainly due to the fact that data collection of the Viennese Kalahari project took place a long time ago, in 1987. The assessment of asymmetry patterns was not the main focus of this project therefore only a low number of bilateral anthropometric measurements indicating asymmetry patterns have been collected. Nevertheless studies focusing on fluctuating and directional asymmetry patterns and/or androgen levels among traditional societies, in particular among foraging populations such as the !Kung San are extremely rare. Therefore, the present study—despite of all limitations—may be justified. Furthermore composite and combined asymmetry indices were calculated. Although there may be some doubt that composite measures reflect meaningful signals of developmental instability, composite indices have been used in the present study. This was mainly because composite indices have been used in several studies analyzing FA patterns [5,16,25,28].

The present study reveal significant differences in directional asymmetry patterns between !Kung San and Kavango males. !Kung San males surpassed their Kavango counterparts in the directional asymmetry of hand length, hand breadth, hand circumference and wrist breadth but also in CDA significantly. Concerning FA, !Kung San males surpassed their Kavango counterparts composite fluctuating asymmetry, ear breadth and ear length asymmetry statistically significantly. A high degree of FA has been reported for Hadza foragers by Gray and Marlowe [5], however, in this study, elbow breadth, wrist breadth and finger length were classified as FA. Consequently, the results of the present paper are similar to those of Gray and Marlowe [5]. Foragers such as the !Kung San and the Hadza are exposed to physical stress of all sorts such no access to regular medical care, an energetically demanding life typical of foraging societies, and living in an arid and therefore harsh habitat [5]. Consequently it can be assumed that daily life of !Kung San foragers of the present sample was clearly as stressful as that of Hadza people. Hadza people showed an extraordinary high degree of FA–even higher than other traditional populations [5]. In the present study both ethnic groups showed a right side bias which may be interpreted as a result of the dominance of right handedness [70,71]. A dominance of right handedness is found among recent humans, historic populations, fossil hominids but also nonhuman primates [72–83]. Directional asymmetry of the upper limbs is also influenced by working conditions [16,77–89], and working conditions differed between !Kung san males who followed a hunter gatherer subsistence and Kavango men who were horticultural pastoralists. On the other hand, directional asymmetry patterns triggered by handedness can also be interpreted as signs of fitness. On the one hand, decreased survival fitness among lefthanders was described [41]. In detail some studies had shown that the population percentage of left-handers steadily decreases and lefthanders are drastically underrepresented in the oldest age groups [41]. On the other side the fighting hypothesis suggested that left-handers in violent societies have a frequency dependent advantage during fights and this advantage decreases when their frequency increases [42]. In the present study, !Kung San foragers showed a significantly higher composite directional asymmetry than their Kavango counterparts. These results are in accordance with those of previous studies focusing on recent forager societies [5] but also osteological samples. These studies reveal significantly higher amounts of asymmetries and more directional biases in diaphyseal breadth dimensions among non-industrial groups than among industrial populations [72,84].

In the present study body height and body mass index were used as indicators of health. It was assumed that poor health especially during growth and development represents a major stress factor which may increase FA. FA is widely used as a bio-indicator of developmental instability caused by environmental stress factors during an individual's ontogeny. Perturbations, also named as "developmental noise", and accidents, which occur during development, cause subtle deviations from symmetry in ideally bilaterally symmetrical structures [13,14]. Increased FA patterns indicate increased stress affecting development stability negatively. In the present study the results of regression analyses showed that with increasing body height fluctuating as well as directional asymmetry decreased, while the BMI was not associated with asymmetry patterns. The regression analyses included both ethnic groups. The Spearman correlations carried out for each ethnic group separately however yielded only a weak negative association between body height and composite fluctuating asymmetry and foot breadth asymmetry among !Kung san males, and a weak negative association between body height and ear length and wrist breadth asymmetry among Kavango males. In contrast increasing BMI was associated with decreasing ear breadth asymmetry among !Kung San as well as Kavango males. Additionally, !Kung San males showed a significantly negative association between BMI as well as body weight and asymmetry of foot breadth. Ear length asymmetry, in contrast correlated significantly positively with the BMI among !Kung San participants. The negative association between body mass index and few parameters of fluctuating asymmetry among !Kung San males is in accordance with the findings of Manning [39] who reported a negative association between body mass and FA among adult males from U.K. Among adult women however Manning [39] and Milne et al. [23] found a higher degree of asymmetry with increasing body mass index Among Westernized populations a high body mass index may be interpreted as a sign of poor health, among !Kung San however, obesity is a rather unknown condition and underweight and malnutrition prevail. Body weight is condition dependent and only males with the best genes seem to be able to develop and maintain large body size [39]. Furthermore, Manning et al. [40] reported a significantly negative association between asymmetry patterns and resting metabolic rate in young men. Higher body mass index can be interpreted as a sign of health and a negative association between BMI and asymmetry patterns occur.

The main focus of the present study was the association between asymmetry patterns and androgen levels. Among !Kung San males, it could be shown, that DHT correlated significantly negatively with parameters of FA (foot length and foot breadth) as well as with parameters of DA (hand breadth, wrist breadth, and composite directional asymmetry). Only ear length asymmetry correlated positively with DHT levels. Furthermore free testosterone of the saliva correlated significantly negatively with asymmetry of hand length and composite directional asymmetry. With other words with increasing androgen levels asymmetry decreased. Among Kavango males fewer significant associations between androgen levels and asymmetry patterns occurred. DHT was negatively associated with parameters of FA such as foot breadth, but positively associated with DA such as wrist breadth. Considering the correlation coefficients, however we have to state that the correlations between body size as well as androgen levels and asymmetry patterns are very weak. Consequently there is no strong correlation between asymmetry patterns and androgen levels among studied populations. Nevertheless a trend that higher androgen levels are associated with decreased asymmetry can be described for !Kung San males but only partly for Kavango males Unfortunately only few studies analyzed the association between androgen levels and asymmetry patterns in humans and the mechanisms through which androgens exert their influence on the development of bilateral characters remain unspecified [26,27]. On the one hand, a positive association between testosterone levels and dermatoglyphic asymmetry in males was found [35]. Dermatoglyphic asymmetry was chosen because dermatoglyphic characters phenotypic plasticity is quite low, while, on the other hand, dermatoglyphics are associated with some disorders of the central nervous system. Other studies focused on the association between 2D:4D ratio, a well-known proxy of fetal testosterone levels and asymmetry patterns [33]. In detail, a high testosterone concentration, indicated by a low 2D:4D ratio, was associated with high facial asymmetry in males [34]. Other studies however, could not prove any association between 2D:4D ratio and FA [90,91]. The positive association between asymmetry and fetal testosterone levels was mainly explained by the assumption that androgens can hamper immunocompetence and thus increase asymmetry [33,36]. According to the Immunocompetence Handicap hypothesis (ICHH), testosterone suppresses immune function and thus elaborate androgen based traits represent an honest signal of male quality since only high quality males can cope with such high costs [36,92]. Consequently it was assumed that a testosterone mediated suppressed immune function increases potential stress phases such as diseases or parasite load which may result in increased FA. Recent analyses among Tsimane foragers, however, revealed that endogenous testosterone appears to be immunomodulatory rather than immunosuppressive [93]. In the present study, adult androgen levels were weakly related to patterns of asymmetry. In detail, a weak trend towards higher androgen levels and decreased asymmetry among !Kung San males was observed. With other words a high phenotypic quality—as indicated by a low degree of asymmetry—is weakly related to higher androgen levels. However, we have to distinguish between the associations between adult androgen levels and patterns of FA, which are mainly negative and the association patterns between parameters of directional asymmetry and adult androgen levels. In detail, we found a negative association between androgen levels and asymmetry of hand breath and wrist breadth among !Kung San and a positive association between adult androgen levels and wrist breadth among Kavango males. Significant differences in adult androgen level have been described between left handers and right handers [43]. In detail, left handers showed higher testosterone levels than right handers [43]. On the other hand, recent studies demonstrated that left handers show a more symmetry training of their upper limbs and less influence of handedness and consequently a reduced directional asymmetry of hand and wrist parameters [94]. The negative association between androgen levels and directional asymmetry patterns among !Kung San people observed in the present study may be due to that androgen levels are higher among left handers, but directional asymmetry of the upper limb is reduced among left handers. Furthermore, body height was negatively associated with asymmetry in the present study. The observed negative association between adult androgen levels and asymmetry can also be interpreted from the viewpoint of sexual selection and reproductive success. Sexual selection represents an enormous stress especially for males. Intrasexual selection, through male-male competition favors the evolution and development of large body size in males, while intersexual selection, through female choice strategies, favors a low degree of FA indicating developmental stability. Both large body size and low FA result in increased energy demands for somatic growth but also for maintenance of symmetry [40]. Androgens are essential for both processes. On the one hand, androgens, mainly testosterone, act anabolic and are positively associated with somatic growth. On the other hand, high androgen levels are only affordable for high quality phenotypes, characterized by a high degree of symmetry. Furthermore androgens are essential for successful reproduction in males. Testosterone—the most important androgen—is not only produced in close proximity to the sperm—producing Sertoli cells of the testes, testosterone is also essential for spermatogenesis. The positive association between adult androgen levels and symmetry described in the present study is supported by the significantly negative association between semen quality as well as semen quantity and patterns of asymmetry demonstrated in previous studies [95,96]. In this study, however, fetal androgen levels, estimated by 2D:4D ratio were related to adult ejaculate size and sperm quality [96]. Even among birds a weak association between asymmetry patterns and sperm quality could be proved [97].

From the results of the present study, it can be concluded that a high quality phenotype—indicated by a low degree of asymmetry—is weakly associated with higher adult androgen levels in !Kung San males.

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