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Asymmetry patterns are associated with body size and somatic robustness among adult !Kung San and Kavango people

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ABSTRACT: Asymmetry of bilateral anatomical structures is widely found in nature. Fluctuating asymmetry, i.e. mostly tiny random deviations from perfect symmetry in bilateral structures, is mainly interpreted within the framework of developmental instability. This interpretation is mainly due to the fact, that higher fluctuating asymmetry is often found in association with various pathological conditions but also from increased stress during somatic development. Directional asymmetry, in contrast, describes a distinct pattern of bilateral variation in a group of individuals, characterized by the tendency to find the larger side mainly at the same side for all individuals. This kind of asymmetry is mostly caused by behavioral lateralization. Somatic stress during development affect not only asymmetry patterns, it is has also an adverse effect on somatic growth. Therefore, the present study tested the hypothesis, that increased asymmetry is associated with decreased body height as well as postcranial length and robustness dimensions. The association patterns between fluctuating as well as directional asymmetry and parameters of somatic growth and robustness are analyzed among 236 !Kung San and 248 Kavango people of Namibia between the ages of 18 and 65 years. Fluctuating asymmetry was determined by ear length and ear breadth. Directional asymmetry was determined by hand length and hand breadth dimensions. Fluctuating as well as directional asymmetry correlated significantly negatively with body height and length dimensions, the correlations however, were weak. The results are interpreted as a corroboration of the theory that developmental stress may increase fluctuating asymmetry but on the other hand may decrease body size.

KEY WORDS: directional asymmetry, fluctuating asymmetry, adult body height, somatic robustness, growth, !Kung San, Kavango

Introduction

As typical of vertebrates, the body of *Homo sapiens* appears symmetrical along the midline. Nevertheless, dimensions of paired organs and paired soft tissue elements as well as paired skeletal elements may differ markedly (Van Valen 1962). Asymmetry patterns of bilateral structures can be distinguished into three different types: antisymmetry, fluctuating asymmetry (FA) and directional asymmetry (DA) (Van Valen 1962; Palmer and Storbeck 1986). Antisymmetry describes

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the bilateral variation among individuals of the same species, the direction of asymmetry, however varies randomly among individuals (Palmer and Strobeck 2003) Fluctuating asymmetry is a widely found in nature. In this case bilaterally paired structures showed small deviations from perfect symmetry (Van Valen 1962). The third kind of asymmetry patterns is directional asymmetry (DA). DA means the occurrence of typical deviations from symmetry in a sample of individuals, in which the same side is mostly larger than the other (Özener 2010).

Although slight asymmetries of bilateral structures are common among of *Homo sapiens,* symmetry is widely interpreted as an ideal, a sign of attractiveness indicating health and reproductive fitness (Manning et al. 1997, 1998; Prieto et al. 2011; Zaidi 2011). These associations between symmetry and health as well as fitness are mainly due to the fact, that fluctuating asymmetry correlates impaired health (Thornhill and Moller 1998), but also with reduced reproductive success (Milne et al. 2003, Moller 2006; Flegr et al. 2005). Fluctuating asymmetry is mainly seen as the result of several minimal developmental perturbations that occur independently on both sides (Klingenberg 2003; Van Dongen 2018). Consequently, some authors associate fluctuating asymmetry and periods of developmental instability (Thornhill and Moller 1998). Under optimal conditions, fluctuating asymmetry is minimal, but stressful events during development seem to increase fluctuating asymmetry. Numerous studies have clearly shown, the strong positive association between the exposure to environmental, as well as intrinsic stress factors and increased fluctuating asymmetry (Moller et al. 1995; Schäfer et al. 2006, Hoover and Matsumura 2008; Özener and Graham 2014). Therefore, increased fluctuating asymmetry is seen as a result, of pathological conditions and stress factors during development (Milne et al. 2003; Flegr et al. 2005; Moller 2006). Consequently, fluctuating asymmetry is widely used as a proxy to identify stressful periods during development, which may affects health, growth, fitness and behavior (Benderlioglu et al. 2004; Fink et al. 2004, 2014; Manning et al. 2009).

Other important indicators of stress during development are growth patterns (Deaton 2007). Human growth is significantly affected by stress factors during subadult phase and it is well documented that psychic as well as somatic stress factors may result in impaired growth and consequently decreased adult body height and decreased skeletal robustness even during adulthood (Ruel et al. 1995; Karlberg and Luo 2000). Consequently, it might be assumed that stress factors enhancing fluctuating asymmetry may also affect growth patterns and therefore a negative association between fluctuating asymmetry and somatometric parameters may be observable. Up to now, only few studies focused on the relationship between body height, weight, physical strength as well as somatometric parameters and asymmetry patterns among humans (Manning 1995; Milne et al. 2003; Wells et al. 2006; Özener and Ertugrul 2011; Özener and Graham 2014: Fink et al. 2014). Associations between fluctuating asymmetry and weight status as well as physical strength could be proved (Manning 1995; Fink et al. 2014) Özener and Etrugul (2011) showed a significant association between lower body height and increased fluctuating asymmetry, indicating a significant effect of developmental instability on growth patterns as well as fluctuating asymmetry. Nearly all of the studies mentioned above however, have been carried out among probands from Western societies who suffer seldom from poor living conditions resulting in severe developmental instability.

Another problem of investigations focusing on developmental instability estimated by fluctuating asymmetry in general and in particular its associations with health as well as growth parameters do not separate between fluctuating asymmetry and directional asymmetry. Directional asymmetry is predominantly due to behavioral lateralization and is found among many different species from invertebrate up to *Homo sapiens*. Among *Homo sapiens* directional asymmetry is typically found for upper limb dimensions (Livshits et al. 1998; Lazenby 2002; Battles 2009; Jaskulska 2009; Weiss 2009). In detail, the dimensions of the right upper limbs surpass mainly those of the left ones. This directional asymmetry is mainly interpreted as a result of handedness (Steele and Mays 1995; Steele 2000; Jaskulska 2009; Weiss 2009). Some activities focus heavily on one upper limb and lead therefore to unilateral loading of the dominant limb. These differences in mechanical loading caused asymmetric bone and muscle development on the right and the left arm, such as seen among elite tennis players (Krahl et al. 1994; Haapasalo et al. 2000; Bass et al. 2002; Irleland et al. 2014; Kontulainen et al. 2003). These differences in behavioral lateralization however are not only found among upper limbs only. There is also some evidence that in addition to handedness footedness exists, which might result in asymmetry patterns of foot and leg dimensions too. Van Dongen (2018) pointed out the importance of behavioral lateralization for somatic asymmetry patterns. Consequently, asymmetries of upper and lower limb dimensions should be seen within the framework of directional asymmetry.

In the present study associations between asymmetry patterns and parameters of growth and robustness among two non-western societies, was analyzed. In particular, male as well as female !Kung San and Kavango people from northern Namibia were focused on. A negative association between fluctuating asymmetry and length, height and robustness dimensions during adulthood is predicted.

Material and methods

The Viennese Kalahari project

The so called Viennese Kalahari project was part of a project cooperation between the Institute of Human Biology of University of Vienna and the Department of Human Biology of the University of Hamburg during the late 1980s. Field research and data collection for the present part of the project took place in northern Namibia from June to September 1987. In detail, data collection took place at the Nyae-Nyae area up to 70 km around Tsumkwe, the administrative centre of northern Bushmanland and in Rundu, the administrative centre of the Kavango district, as well as in the surrounding rural areas near Rundu. Figure 1 presents the area of field research. The field research included the collection of anthropometric data, blood and saliva samples for the determination of sex hormone levels and behavioural as well as psychological data. The results of these investigations have been published in numerous papers (Christiansen 1991, 1992; Christiansen and Winkler 1992; Winkler and Christiansen 1991,

Fig. 1. Area of research in Namibia

1993; Winkler and Kirchengast 1994; Kirchengast and Winkler 1995, 1996, a,b; Kirchengast 2017; Kirchengast and Christiansen 2018). These papers provide a detailed description of data collection and research area.

Study population

The study population comprised 484 healthy adult subjects. In detail, 91 !Kung San females ageing between 18 and 65 years (Mean=30.7, SD =11.6), 145 !Kung San males ageing between 18 and 65 years (Mean=31.5, SD=11.5), 87 Kavango females ageing between 18 and 60 years (Mean=28.2, SD=9.7) and 161 Kavango males ageing between 18 and 60 years (Mean=25.4, SD=4.5) were enrolled in the analysis. A more detailed description of the !Kung San and Kavango people enrolled in the present study can be found in several previous publications focusing on the results of the Viennese Kalahari project (Christiansen 1991, 1992; Christiansen and Winkler 1992; Winkler and Christiansen 1991, 1993; Winkler and Kirchengast 1994; Kirchengast and Winkler 1995, 1996, a,b; Kirchengast 2017; Kirchengast and Christiansen 2018).

Lifestyle characteristics of !Kung and Kavango people

During the late 1980s many traditional tribes experienced some modernization, the majority of the !Kung San study population however, followed still a typical forager lifestyle characterized by small group size, high mobility and semi permanent camps consisting of 7 to 15 grass huts during the late 1980s. Nevertheless, nearly all !Kung San participants had some experience with westernised lifestyle patterns because some band members had worked temporarily at cattle farms and hunting ranches.

Originally, the Kavango settled in various areas of southern Angola and northern Nambia near the Okavango River. During the late 1980s the civil war in Angola, forced many Kavango to migrate to northern Namibia. At the time of field research, the Kavango participants of the present study living in rural areas around Rundu followed still a non-westernized life style. As typical of the inhabitants of the rural parts of the Namibian Kavango district, they lived in typical kraals and their subsistence was based on cattle pastoralism and horticulture. None of them had access to a regular cash income. Only few of the Kavango participants lived in the small city of Rundu and worked as wage earning employees.

Body size and somatic robustness

Body size and somatic robustness were estimated by several somatometric parameters. All measurements were taken directly from the subject, based on the standardized methods published by Knussmann (1988). The technical equipment comprised an anthropometer, a scale, and a sliding caliper (Siber-Hegner Corp. Switzerland). Facial robustness was assessed by three cranial measurements (frontal breadth, bizygomatic breadth and bigonial breadth). Body size and postcranial robustness were determined by body height and eight further postcranial measurements (chin height, acromial height, and navel height, sitting height, span, biacromial breadth, pelvic breadth and body weight). In order to assess asymmetry patterns, ear length, ear breadth, hand length, hand breadth, foot length and foot breadth were measured. In order to ensure accuracy and reliability of the somatometric analysis, all measurements of the somatometric parameters mentioned above, were taken twice by the same trained person (E.M.Winkler†). The reliability of the two measurements the weighted Cohen´s kappa test was used. For the 12 somatometric parameters kappa values between 0.91 and 0.93, indicating a high reliability were observed. Therefore, for the further statistical analyses, the average of the two repeated measures was used. This high reliability of the somatometric measurements according to kappa values was corroborated by the Cronbach alpha analysis. All Cronbach alpha were >0.91, indicating a high reliability. In a next step, the Body Mass Index (BMI) was calculated (body weight in kg)/ (body height in m)^2 in order to obtain information regarding weight status. To get more information about robustness and body proportion, the acromial-cristal index (acromial breadth/ pelvic breadth), relative acromial breadth (acromial breadth/ body height) and relative pelvic breadth (pelvic breadth/ body height) were calculated.

Asymmetry

In a first step, signed asymmetry and unsigned asymmetry were calculated. Signed asymmetry was defined as the difference between the right and left dimensions (R–L), unsigned asymmetry was determined as follows (IR–LI). In a next step, unsigned asymmetry was corrected for trait size using the formula: (Iright – leftI)/[(right + left)/2] according to Palmer and Strobeck (1986) and Fink et al. (2014). In order to reduce the number of bilateral traits, three different composite asymmetry indices were calculated, although the use of this kind of indices is discussed controversially (Leung et al. 2000, Graham et al. 2010; Van Dongen 2000, 2006, 2015). Nevertheless, composite indices of asymmetry patterns have been used by Özener (2010) Fink and colleagues (2014), Flegr and colleagues (2005), Milne and colleagues (2003) and Gray and Marlowe (2002).

In the present study, the composite asymmetry score was calculated according to Fink et al. (2014), who summarized (unsigned) left minus right side differences of trait measurements corrected for traits size IL – RI/(R + L)/2. In detail, composite directional asymmetry and composite fluctuating asymmetry were calculated. In order to test the presence of directional asymmetry a two way mixed model ANOVA was used for the factors hand length and hand breadth. Since the factor side was statistically significantly (p <0.001), directional asymmetry was assumed for hand measurements. Composite directional asymmetry (CDAhand) was based on traits, which might be influenced by handedness (hand length and, hand breadth). Beside handedness, humans exhibit a kind of footedness (Peters 1988). In literature, only marginal bilateral differences in foot dimensions and no significant association between footedness and asymmetry patterns of foot dimensions have been described (Datta Banik et al. 2015). A two way mixed model ANOVA to test the existence of directional asymmetry of foot dimensions indicated no directional asymmetry of the foot. According to these results, in the present study asymmetry patterns of the feet are considered as fluctuating asymmetry. Consequently, a composite fluctuating asymmetry index of foot dimensions (CFAfoot) including foot length and foot breadth was calculated. Composite fluctuating asymmetry (CFAear) was described by ear length and ear breadth.

Statistical analysis

For statistical analysis, SPSS program version 22.0 (Microsoft corp.) was used. In order to ensure the reliability of somatometric measurements the Cronbachs alpha was calculated. After the calculation of descriptive statistics (means, SDs), factor analyses with varimax rotation were computed to reduce the number of somatometric variables. A one-tailed t-test was applied to calculate the direction of asymmetry. The expected value of the one-tailed t-test was 0. Auerbach and Ruff (2006) recommended the use of non-parametric tests for the analysis of asymmetry patterns. Consequently, for the analysis of group differences non-parametric Mann-Whitney tests were used. Spearman rank correlations were computed to test the association patterns between asymmetry parameters and body size as well as somatic robustness. P-values of less than 0.05 were considered significant.

Results

Sex and ethnic differences in body size and robustness

Means and standard deviations of age, body size and the six bilateral somatometric parameters for each sex and ethnic group separately are reported in Table 1. As to be expected, males were significantly taller and more robust ($p<0.001$) than females. Females in contrast, surpassed males in relative pelvic breadth only. This was true of both ethnic groups. Among !Kung San however, body mass index and pelvic breadth differed only insignificantly between the two sexes. Kavango males and females showed no significant differences in body mass index, ear length and ear breadth. Concerning ethnic differences, !Kung San people were significantly shorter, lighter and more gracile than Kavango people. This was true of both sexes.

To reduce the number of somatometric variables and to analyze the structure of the somatometric data, a factor analysis of all 12 anthropometric variables (frontal breadth, bizygomatic breadth, bigonial breadth, body height, chin, height, acromial height, navel height, sitting height, span, biacromial breadth, pelvic breadth and body weight) was computed. The six bilateral measurements (hand length, hand breadth, ear length, ear breadth, foot length, foot breadth) were excluded from the analysis. After varimax rotation two factors with an Eigenvalue above 1.0 could be identified. Factor 1 (Eigenvalue 8.23) can be interpreted as a “height and postcra-

Table 1. Age and body measurements according to sex and ethnic group (Mann-Whitney-U tests)

Variable	!Kung San Males (n=145) Mean±SD	!Kung San Females (n=93) Mean±SD	SexΔ !Kung *p*-value	Kavango Males (n=161) Mean±SD	Kavango Females (n=85) Mean±SD	SexΔ Kavango *p*-value	EthnicΔ Males *p*-value	EthnicΔ Females *p*-value
Age (years)	31.5±11.5	30.7±11.6	0.618	25.8±6.8	29.3±9.6	0.003	0.001	0.372
Frontal breadth (cm)	10.6±0.4	10.2±0.4	<0.0001	11.1±0.6	10.5±0.4	<0.0001	<0.0001	<0.0001
Bizygomatic breadth (cm)	13.2±0.4	12.3±0.4	<0.0001	14.0±0.5	13.1±0.4	<0.0001	<0.0001	<0.0001
Bigonial breadth (cm)	10.1±0.5	9.5±0.5	<0.0001	10.7±0.5	9.9±0.4	<0.0001	<0.0001	<0.0001
Body height (cm)	160.7±5.6	149.3±5.3	<0.0001	171.0±5.9	159.7±4.8	<0.0001	<0.0001	<0.0001
Chin height (mm?)	139.6±5.3	128.6±5.1	<0.0001	148.9±5.8	138.3±4.8	<0.0001	<0.0001	<0.0001
Navel height (cm)	96.7±4.5	90.3±4.5	<0.0001	103.7±4.5	98.0±4.0	<0.0001	<0.0001	<0.0001
Sitting height 9cm)	84.2±2.8	78.5±2.6	<0.0001	88.3±3.1	82.8±2.1	<0.0001	<0.0001	<0.0001
Acromial height (cm?)	132.7±5.2	122.6±5.0	<0.0001	141.1±5.7	132.3±4.5	<0.0001	<0.0001	<0.0001
Span (cm?)	168.1±7.4	153.1±6.1	<0.0001	183.7±7.5	171.2±6.9	<0.0001	<0.0001	<0.0001
Acromial breadth (cm)	34.8±1.8	30.7±1.6	<0.0001	37.8±2.0	33.7±1.7	<0.0001	<0.0001	<0.0001
Pelvic breadth (cm)	23.1±1.3	22.7±1.6	0.068	25.8±1.3	25.2±1.3	<0.0001	<0.0001	<0.0001
Body weight (kg)	49.6±6.5	42.6±6.5	<0.0001	59.3±6.9	50.4±6.3	<0.0001	<0.0001	<0.0001
Body mass index (kg/m^2)	19.16±1.88	19.08±2.61	0.765	20.28±2.09	19.74±2.30	0.071	<0.0001	0.074
Rel. acromial breadth (cm)	21.7±0.9	20.5±0.9	<0.0001	22.1±1.1	21.1±0.9	<0.0001	<0.0001	<0.0001
Rel. pelvic breadth (cm)	14.4±0.7	15.2±0.8	<0.0001	15.1±0.9	15.8±0.7	<0.0001	0.01	<0.0001
Acromial-pelvic index	15.1±0.8	13.5±1.0	<0.0001	14.7±0.4	13.4±0.7	<0.0001	<0.0001	0.214
Ear length right (cm)	5.3±0.5	5.2±0.4	0.042	6.0±0.4	5.9±0.5	0.072	0.001	0.001
Ear length left (cm)	5.2±0.4	5.1±0.4	0.022	5.9±0.4	5.8±0.4	0.069	0.001	0.001
Ear breadth right (cm)	3.0±0.2	2.9±0.2	0.010	3.5±0.3	3.4±0.3	0.001	0.001	0.001
Ear breadth left (cm)	3.1±0.2	2.9±0. 2	0.001	3.6±0.3	3.4±0.2	0.001	0.001	0.001
Hand length right (cm)	17.3±0.8	15.9±0.7	0.001	19.5±0.9	18.3±0.9	0.001	0.001	0.001
Hand length left (cm)	17.4±0.8	15.9±0.5	0.001	19.4±0.8	18.3±0.8	0.001	0.001	0.001
Hand breadth right (cm)	7.6±0.4	6.9±0.3	0.001	8.7±0 4	7.9±0.4	0.001	0.001	0.001
Hand breadth left (cm)	7.5±0.3	6.7±0.3	0.001	8.6±0.4	7.9±0.4	0.001	0.001	0.001
Foot length right (cm)	24.1±1.1	22.1±0.9	0.001	26.8±1.2	24.7±1.2	0.001	0.001	0.001
Foot length left (cm)	24.1±1.1	22.0±0.9	0.001	26.8±1.1	24.7±1.2	0.001	0.001	0.001
Foot breadth right (cm)	9.2±0.4	8.4±0.4	0.001	10.5±0.6	9.5±0.6	0.001	0.001	0.001
Foot breadth left (cm)	9.3±0.5	8.3±0.4	0.001	10.6±0.6	9.5±0.5	0.001	0.001	0.001

nial robustness factor", higher loadings (0.55–0.95) were found for body height, chin, height, acromial height, navel height, sitting height, span, biacromial breadth, pelvic breadth and body weight. Factor 2 (Eigenvalue 1.18) can be classified as "facial factor" with higher loadings (0.67–0.81) for frontal breadth, bizygomatic breadth, bigonial breadth.

Asymmetry patterns

The analysis of asymmetry patterns starts with an one tailed t-tests for each bilateral parameter for each sex and ethnicity separately, in order to identify asymmetry patterns. The means of ear length, ear breadth, and hand length and hand breadth were significantly different from 0 (see Table 2). These results may be interpreted as a typical pattern of fluctuating or directional asymmetry. Ear length, hand length and hand breadth tended to exhibit higher values at the right side, while ear breadth showed a significant tendency to the left side. These patterns are found among both sexes and both ethnic group. Foot length however, differed not significantly from 0. This was true of both sexes and both ethnic groups. Foot breadth showed a significant tendency to the left side among !Kung San and Ka-

Table 2. Mean standard deviation of trait asymmetry and results of one sample t-tests

Variable	!Kung San				Kavango			
	Males		Females		Males		Females	
	Mean±SD	*p*-value	Mean±SD	*p*-value	Mean±SD	*p*-value	Mean±SD	*p*-value
Ear length	1.33±2.05	<0.001	1.33±2.04	<0.001	1.08±1.69	<0.001	1.34±1.96	<0.001
Ear breadth	−1.01±1.33	<0.001	2.93±1.26	0.010	−0.72±1.39	<0.001	−0.40±0.87	<0.001
Hand length	1.07±2.93	<0.001	1.97±2.58	0.027	−0.24±2.29	0.197	0.36±2.13	0.118
Hand breadth	1.41±1.97	<0.001	3.11±1.49	<0.001	1.40±1.61	<0.001	1.54±1.84	<0.001
Foot length	−0.20±3.11	0.440	2.93±2.27	0.496	−0.46±3.21	0.075	0.14±2.71	0.633
Foot breadth	−0.51±2.93	0.040	0.05±2.24	0.068	−0.57±2.96	0.017	0.09±2.57	0.737
CFAEar	0.07±0.05	<0.001	0.03±0.05	<0.001	0.05±0.05	<0.001	0.05±0.04	<0.001
CDAHand	0.04±0.03	<0.001	0.03±0.03	<0.001	0.03±0.02	<0.001	0.03±0.02	<0.001
CFAFoot	0.03±0.03	<0.001	1.33±0.02	<0.001	0.03±0.02	<0.001	0.03±0.02	<0.001

Table 3. Asymmetry patterns according to sex and ethnic group (Mann-Whitney- u-tests)

Variable	!Kung San			Kavango			ethnicΔ Males	ethnicΔ Females
	Males	Females	*p*-value	Males	Females	*p*-value		
	Mean±SD	Mean±SD		Mean±SD	Mean±SD		*p*-value	*p*-value
Ear length	0.034±0.030	0.035±0.033	NS	0.024±0.024	0.027±0.029	NS	0.001	NS
Ear breadth	0.039±0.037	0.029±0.031	0.041	0.029±0.037	0.018±0.022	0.014	0.021	0.006
Hand length	0.012±0.014	0.011±0.012	NS	0.007±0.009	0.008±0.009	NS	0.001	0.031
Hand breadth	0.023±0.022	0.031±0.022	0.004	0.019±0.015	0.024±0.019	NS	NS	0.012
Foot length	0.009±0.009	0.007±0.007	NS	0.009±0.008	0.007±0.085	NS	NS	NS
Foot breadth	0.023±0.023	0.019±0.019	NS	0.020±0.019	0.019±0.010	NS	NS	NS
CFAEar	0.073±0.050	0.065±0.049	NS	0.053±0.045	0.045±0.039	NS	0.001	0.002
CDAHand	0.035±0.026	0.043±0.027	0.035	0.027±0.018	0.031±0.020	NS	NS	NS
CFAFoot	0.031±0.027	0.027±0.021	NS	0.029±0.022	0.025±0.024	NS	0.001	0.004

NS – not significant.

Table 4. Asymmetry patterns and anthropometric parameters among !Kung San people (Spearman rank correlations)

Variable	AS Ear length		AS Ear breadth		As Hand length		As Hand breadth		AS Foot length		As Foot breadth		CFA Ear		CDA Hand		CFA Foot	
	R	*Sig.*	R	*Sig.*	R	*Sig.*	R	*Sig.*	R	*Sig.*	R	*Sig.*	R	*Sig.*	R	*Sig.*	R	*Sig.*
Males																		
Frontal breadth	−.03	NS	−.01	NS	.09	NS	−.16	*	.02	NS	−.04	NS	−.01	NS	−.01	NS	.01	NS
Bizygomatic breadth	.01	NS	.05	NS	−.07	NS	.06	NS	.07	NS	−.07	NS	.07	NS	.06	NS	−.02	NS
Bigonial breadth	.04	NS	−.12	NS	−.08	NS	.03	NS	.03	NS	−.08	NS	−.04	NS	−.01	NS	−.04	NS
Body height	−.02	NS	.09	NS	.04	NS	−.04	NS	−.07	NS	.06	NS	.06	NS	.08	NS	.11	NS
Chin height	−.01	NS	.09	NS	.02	NS	−.03	NS	−.07	NS	.04	NS	.06	NS	.08	NS	.08	NS
Navel height	−001	NS	.12	NS	.01	NS	−.06	NS	−.01	NS	.01	NS	.09	NS	.04	NS	.09	NS
Acromial height	.01	NS	.10	NS	.03	NS	−.04	NS	−.05	NS	.09	NS	.08	NS	.07	NS	.15	*
Sitting height	.04	NS	.06	NS	.07	NS	−.09	NS	−.03	NS	.03	NS	.07	NS	.04	NS	.08	NS
Span	−.01	NS	.07	NS	.02	NS	−.02	NS	−.11	NS	−.02	NS	.05	NS	.08	NS	.01	NS
Biacromial breath	.03	NS	.05	NS	−.09	NS	−.07	NS	−013	NS	−.06	NS	.07	NS	−.03	NS	−.02	NS
Pelvic breadth	−.07	NS	−.01	NS	.06	NS	−.12	NS	.01	NS	.05	NS	−.03	NS	.01	NS	.11	NS
Body weight	.02	NS	−.04	NS	−.03	NS	−.11	NS	−.01	NS	−.04	NS	−.02	NS	−.01	NS	.02	NS
Body mass index	.08	NS	−.13	NS	−.06	NS	−.07	NS	.04	NS	−.04	NS	−.05	NS	−.03	NS	.01	NS
Acromial-cristal index	.07	NS	.06	NS	−.13	NS	.07	NS	−.10	NS	−.09	NS	.08	NS	−.03	NS	−.09	NS
Rel. acromial breadth	.04	NS	.03	NS	−.12	NS	−.02	NS	−.09	NS	−.14	*	.06	NS	−.06	NS	−.12	NS
Rel. pelvic breadth	−.06	NS	−.06	NS	.02	NS	−.08	NS	.05	NS	−.02	NS	−.07	NS	−.03	NS	.01	NS
Postcranial factor	−.01	NS	.09	NS	.06	NS	−.05	NS	−.07	NS	.06	NS	.07	NS	.08	NS	.10	NS
Head factor	.02	NS	−.07	NS	−.05	NS	−.02	NS	.06	NS	−.09	NS	−.02	NS	−.01	NS	−.05	NS

Sig. – statistically significant at $^{*}p \le 0.05$, $^{**}p \le 0.01$, $^{***}p \le 0.001$, NS – not significant.

Table 4. continued

Variable	AS Ear length		AS Ear breadth		As Hand length		As Hand breadth		AS Foot length		As Foot breadth		CFA Ear		CDA Hand		CFA Foot	
	R	*Sig.*	R	*Sig.*	R	*Sig.*	R	*Sig.*	R	*Sig.*	R	*Sig.*	R	*Sig.*	R	*Sig.*	R	*Sig.*
Females																		
Frontal breadth	.01	NS	.02	NS	.18	*	−.06	NS	.01	NS	.15	NS	.06	NS	.02	NS	.15	NS
Bizygomatic breadth	−002	NS	.01	NS	.04	NS	−.09	NS	−.01	NS	.05	NS	.02	NS	−.04	NS	.09	NS
Bigonial breadth	−005	NS	−.04	NS	−.09	NS	.08	NS	.08	NS	−.15	NS	−.04	NS	.06	NS	−.11	NS
Body height	−.16	*	−.09	NS	−.01	NS	−.19	*	−.01	NS	−.01	NS	.06	NS	−.08	NS	.05	n.s
Chin height	−.16	*	−.08	NS	.02	NS	−.12	NS	.01	NS	.01	NS	.07	NS	−.03	NS	.07	NS
Navel height	−014	NS	−.08	NS	.12	NS	−.19	*	−.02	NS	.05	NS	.07	NS	−.09	NS	.08	NS
Acromial height	−.14	NS	−.08	NS	.03	NS	−.18	*	−.01	NS	.04	NS	.06	NS	−.05	NS	.09	NS
Sitting height	−.16	*	.07	NS	.11	NS	−.27	**	.02	NS	.10	NS	.14	NS	−.14	NS	.15	NS
Span	.09	NS	−.12	NS	−.13	NS	−.26	**	−.07	NS	−.01	NS	−.01	NS	−.19	*	.04	NS
Biacromial breath	.02	NS	−.15	NS	−.12	NS	−.24	*	−.21	*	−.13	NS	−.09	NS	−.23	*	−.16	NS
Pelvic breadth	.08	NS	.01	NS	.07	NS	−.09	NS	−.03	NS	.10	NS	.09	NS	−.02	NS	.12	NS
Body weight	−.08	NS	−.05	NS	−.10	NS	−.18	*	−.03	NS	−.01	NS	−.06	NS	−.14	NS	.02	NS
Body mass index	−.17	*	−.06	NS	−.08	NS	−.08	NS	.01	−NS	−.01	NS	−.12	NS	−.08	NS	.01	NS
Acromial-cristal index	.12	NS	−.12	NS	−.12	NS	−.09	NS	−.13	NS	−.14	NS	−.20	*	−.13	NS	−.18	*
Rel. acromial breadth	−.15	NS	−.13	NS	−.11	NS	−.09	NS	−.25	**	−.15	NS	−.19	*	−.16	NS	−.24	*
Rel.pelvic breadth	.01	NS	.01	NS	.08	NS	.01	NS	−.03	NS	.09	NS	.05	NS	.03	NS	.07	NS
Postcranial factor	−.18	*	−.09	NS	−.03	NS	−.19	*	−.01	NS	−.04	NS	−.01	NS	.07	NS	.03	NS
Head factor	−.09	NS	−.01	NS	.02	NS	.01	NS	.01	NS	.01	NS	−.02	NS	.01	NS	.03	NS

Sig. – statistically significant at *$p \leq 0.05$, **$p \leq 0.01$, ***$p \leq 0.001$, NS – not significant.

Table 5. Asymmetry patterns and anthropometric parameters among Kavango people (Spearman rank correlations)

Variable	AS Ear length		AS Ear breadth		As Hand length		As Hand breadth		AS Foot length		As Foot breadth		CFA Ear		CDA Hand		CDA Foot	
	R	*Sig.*	R	*Sig.*	R	*Sig.*	R	*Sig.*	R	*Sig.*	R	*Sig.*	R	*Sig.*	R	*Sig.*	R	*Sig.*
Males																		
Frontal breadth	.01	NS	.06	NS	−.09	NS	−.13	NS	−.04	NS	−.11	NS	.07	NS	−.09	NS	−.06	NS
Bizygomatic breadth	.09	NS	.01	NS	−.07	NS	−.06	NS	−.07	NS	−.03	NS	.09	NS	−.03	NS	−.01	NS
Bigonial breadth	.17	.023	.03	NS	−.06	NS	.01	NS	.15	*	.08	NS	.15	*	−.01	NS	.15	.042
Body height	−.01	NS	−.16	.024	.01	NS	.01	NS	−.09	NS	.09	NS	−.11	NS	.06	NS	.13	NS
Chin height	.02	NS	−.14	.041	−.01	NS	.02	NS	−.12	NS	.09	NS	−.09	NS	.07	NS	.12	NS
Navel height	−.05	NS	−.14	.044	.01	NS	.01	NS	−.06	NS	.10	NS	−.11	NS	.07	NS	.14	*
Acromial height	−.04	NS	−.19	.008	.04	NS	.02	NS	−.08	NS	.12	NS	−.16	*	.08	NS	.15	*
34Sitting height	.05	NS	−.12	NS	.05	NS	−.05	NS	−.09	NS	.06	NS	−.04	NS	.01	NS	.07	NS
Span	−.04	NS	−.04	NS	−.02	NS	.04	NS	−.07	NS	.10	NS	−.03	NS	.08	NS	.09	NS
Biacromial breath	.04	NS	.13	NS	−.04	NS	−.07	NS	.09	NS	−.02	NS	.15	.030	−.04	NS	.02	NS
Pelvic breadth	.02	NS	−.05	NS	−.03	NS	−.02	NS	−.04	NS	−.04	NS	−.01	NS	−.01	NS	.05	NS
Body weight	.01	NS	.08	NS	−.07	NS	−.09	NS	.01	NS	−.01	NS	.08	NS	−.08	NS	−.02	NS
Body mass index	.01	NS	.21	.006	−.09	NS	−.15	*	.04	NS	−.07	NS	.17	*	−.16	*	−.03	NS
Acromial-cristal index	−.01	NS	.16	.025	−.01	NS	−.02	NS	.05	NS	.02	NS	.11	NS	−.02	NS	.03	NS
Rel. acromial breadth	.01	NS	.25	**	−.05	NS	−.02	NS	.16	*	−.06	NS	.21	**	−.05	NS	.01	NS
Rel.pelvic breadth	.01	NS	.04	NS	−.09	NS	−.07	NS	−.01	NS	−.16	*	.06	NS	−.12	NS	−.12	NS
Postcranial factor	−.05	NS	−.16	*	.06	NS	.03	NS	−.10	NS	.11	NS	−.13	NS	.09	NS	.13	NS
Head factor	.11	NS	.10	NS	−.13	NS	−.11	NS	.06	NS	−.09	NS	.17	*	−.13	NS	−.04	NS

Sig. - statistically significant at *$p \le 0.05$, **$p \le 0.01$, ***$p \le 0.001$, NS – not significant.

Table 5. continued

Variable	AS Ear length		AS Ear breadth		As Hand length		As Hand breadth		AS Foot length		As Foot breadth		CFA Ear		CDA Hand		CDA Foot	
	R	*Sig.*	R	*Sig.*	R	*Sig.*	R	*Sig.*	R	*Sig.*	R	*Sig.*	R	*Sig.*	R	*Sig.*	R	*Sig.*
Females																		
Frontal breadth	.03	NS	.02	NS	−.23	.019	−.07	NS	−.03	NS	.02	NS	.09	NS	−.09	NS	.01	NS
Bizygomatic breadth	.09	NS	−.01	NS	−.11	NS	−.09	NS	−.03	NS	.02	NS	.11	NS	−.09	NS	.01	NS
Bigonial breadth	.01	NS	−.05	NS	.10	NS	−.05	NS	−.19	.048	−.03	NS	−.05	NS	−.03	NS	−.09	NS
Body height	.08	NS	.06	NS	−.18	*	−.04	NS	.08	NS	.11	NS	.09	NS	−.06	NS	.19	*
Chin height	.05	NS.	.01	NS	−.19	*	−.20	NS	.09	NS	.10	NS	.06	NS	−.06	NS	.17	NS
Navel height	.04	NS	−.03	NS	−.19	*	−.06	NS	.14	NS	.16	NS	.01	NS	−.09	NS	.27	**
Acromial height	.02	NS	−.02	NS	−.20	*	−.05	NS	.10	NS	.16	NS	−.01	NS	−.07	NS	.24	*
Sitting height	.05	NS	−.02	NS	−.13	NS	−.06	NS	−.06	NS	−.04	NS	.04	NS	−.07	NS	−.01	NS
Span	.14	NS	.03	NS	−.16	NS	−.05	NS	.04	NS	.04	NS	.13	NS	−.06	NS	.11	NS
Biacromial breath	.02	NS	.05	NS	.02	NS	−.15	NS	.09	NS	−.08	NS	.06	NS	−.10	NS	−.01	NS
Pelvic breadth	.17	NS	−.08	NS	−.07	NS	−.12	NS	−.08	NS	−.04	NS	.11	NS	.10	NS	−.01	NS
Body weight	.04	NS	.03	NS	−.16	NS	.04	NS	.04	NS	.07	NS	.07	NS	.03	NS	.13	NS
Body mass index	.02	NS	−.01	NS	−.08	NS	.09	NS	−.01	NS	−.01	NS	.04	NS	.08	NS	.02	NS
Acromial-cristal index	−.08	NS	.11	NS	.11	NS	−.06	NS	.16	NS	−.04	NS	−.02	NS	−.03	NS	.01	NS
Rel. acromial breadth	.01	NS	.04	NS	.18	NS	−.12	NS	.07	NS	−.12	NS	.04	NS	−.05	NS	−.09	NS
Rel.pelvic breadth	.12	NS	−.12	NS	.11	NS	−.09	NS	−.12	NS	−.08	NS	.05	NS	−.03	NS	−.09	NS
Postcranial factor	.07	NS	.01	NS	−.14	NS	−001	NS	.11	NS	.11	NS	.05	NS	−.03	NS	.21	*
Head factor	.03	NS	−.04	NS	−.03	NS	−.07	NS	−.12	NS	−.09	NS	.03	NS	−.07	NS	−.14	NS

Sig. - statistically significant at *$p \le 0.05$, **$p \le 0.01$, ***$p \le 0.001$, NS – not significant.

vango males, among females however, an insignificant tendency toward higher measurement values of the right side were found. All three composite indices differed significantly from 0.

Furthermore, ethnic groups as well as both sexes differed in asymmetry patterns. !Kung San people showed significant sex differences in unsigned asymmetry of ear breadth, hand breadth and composite asymmetry of the hand. Especially asymmetry of the hand was significantly higher among !Kung San females. In contrast, significant sex differences among Kavango people were found for unsigned asymmetry of ear breadth only. Additionally, ethnic differences in asymmetry patterns could be observed: !Kung people showed a significantly lower asymmetry in ear and hand dimensions than Kavango people. This was true of both sexes (see Table 3).

Body size and asymmetry correlation patterns

Spearman rank correlations between unsigned asymmetry of ear, hand and foot dimensions as well as composite indexes and all twelve absolute anthropometric parameters, four indices and the facial as well as postcranial height and robustness factor were calculated.

While !Kung San males showed only three significant correlations, i.e. between frontal breadth and unsigned asymmetry of hand breath, relative acromial breadth and unsigned asymmetry of foot breadth and acromial height and composite asymmetry of the foot, !Kung San females exhibited several statistically significant correlations between unsigned asymmetry patterns and mainly postcranial body dimensions. The majority of these correlations were negative indicating a significant association between higher asymmetry and shorter and more gracile body dimensions (see Table 4).

Table 5 presents the asymmetry –body size correlation patterns among male and female Kavangos. Kavango males showed several significantly negatively correlations between unsigned asymmetry of ear breadth and body height as well as parameters of postcranial length and height parameters, but significantly positive associations between unsigned asymmetry of ear breadth and weight status and indices indicating somatic robustness. Among Kavango females unsigned asymmetry of hand length and foot length correlated significantly negatively with facial dimensions as well as body height and postcranial length and height dimensions.

Discussion

This study deals with associations between asymmetry patterns and somatometric parameters indicating growth and robustness among female and male !Kung San and Kavango peoples from northern Namibia. Body size and robustness were determined by 12 absolute somatometric parameters, describing height, length and robustness and four indices describing body proportions. These somatometric traits were correlated with asymmetry patterns of six bilateral somatic traits. Up to now, associations between asymmetry patterns and developmental instability have been mostly analyzed among population of First World or highly westernized countries. This is especially true of the analysis of associations between fluctuating asymmetry and growth patterns. In this case, probands from highly developed countries may be problematic however, because it is difficult to find participants that are shorter or suffer from developmental instabilities because of poor living condition (Özener and Ertugrul 2011). Unfortunately, only few studies included people living in traditional societies for such analyzes. Jones and Hill (1993) worked among Ache foragers, Gray and Marlowe (2002) and Little and colleagues (2008) included Hadza hunter gatherers of Tanzania in their studies. The impact of sex and subsistence patterns on fluctuating and directional asymmetry, but also the association between asymmetry and sex hormones has been tested for the present !Kung San and Kavango sample in previous studies (Kirchengast 2017, Kirchengast and Christiansen 2018). Therefore, studies focusing on the developmental situation among people from traditional or non-western societies are especially valuable.

Before discussing the results of the present study in detail, it is necessary to focus on its limitations. On shortcoming is high age range of the participants from 18 years up to 65 years. Another important problem is the low number of somatometric traits indicating asymmetry patterns. Fluctuating asymmetry was determined by ear length and ear breadth only. Directional asymmetry was assessed by hand breadth and hand length. According to the mixed ANOVA model foot length and foot breadth were interpreted as fluctuating asymmetry markers, although foot length and foot breadth may also be influenced by behavioural lateralization (Datta Banik 2015). Furthermore, it is really a shortcoming that finger length were not collected in 1987. These various problems emerge mainly from the fact that, that data collection took place a more than thirty ago, in 1987. Furthermore, the aim of the Viennese Kalahari project was not the assessment of asymmetry patterns. Despite of these limitations, the recent study is justified by the fact, that associations between asymmetry patterns and growth and robustness among non-western populations, in particular among foragers such as the !Kung San, are extremely rare.

In a first step, the associations between asymmetry patterns and sex as well as ethnicity were tested. As demonstrated in a previous study, sex as well as ethnicity was related significantly not only with absolute and relative body dimensions but also with asymmetry patterns (Kirchengast 2017). !Kung San males as well as females showed a significant higher degree of asymmetry than their Kavango counterparts. This was especially true of ear dimensions and hand dimensions, indicating differences in fluctuating as well as directional asymmetry. These results are in accordance with those of Gray and Marlowe (2002), who reported a high degree of fluctuating asymmetry among Hadza foragers, although Gray and Marlowe used elbow breadth, wrist breadth and finger length to determine fluctuating asymmetry. It can be assumed, that hunter gatherer populations such as the !Kung San and the Hadza are exposed to many kinds of somatic stress during early development but also throughout subadult and adult phase of life which might affect fluctuating but also directional asymmetry (Gray and Marlowe 2002). Furthermore, asymmetry patterns differed markedly between male and female !Kung San, while Kavango people showed only for ear breadth asymmetry a significant sex difference. !Kung San females, in contrast, showed a higher degree in directional asymmetry, while !Kung San males showed a higher degree in fluctuating symmetry. This finding may be one the one hand interpreted as an indicator of sex differences in subsistence activities, which might result in increased directional asymmetry of female hands. On the other hand, the higher degree of fluctuating asymmetry among males may be interpreted as increased male sensitivity to environmental stress factors and developmental instability.

Based on these results, the correlations between asymmetry and somatometric parameters were analysed for each sex and ethnic group separately. Furthermore, asymmetry patterns of the ear were considered as fluctuating asymmetry, asymmetry patterns of the hand were considered as directional asymmetry, maybe influenced by behavioural lateralization.

Considering the association between asymmetry patterns and parameters of growth and robustness, it turned out that facial or cranial parameters showed no significant association with asymmetry patterns. Significant correlations with fluctuating as well as directional asymmetry were found for body height and postcranial parameters of length, height and robustness. Considering both ethnic groups and sexes separately, marked differences in the correlations patterns occurred between the ethnic groups and the two sexes. While !Kung San males showed only extremely few significant correlations between asymmetry patterns and somatometric dimensions, !Kung San females showed several statistically significant correlations between fluctuating as well as directional asymmetry patterns and height and length dimensions. In detail, asymmetry of ear length, foot length and hand breadth correlated significantly negatively with body height but also some other length and height dimensions as well as body mass index and indices of postcranial robustness. With other words, with increasing fluctuating as well as directional asymmetry !Kung San females are shorter and more gracile. Among Kavango people significant negative correlations between body height as well as postcranial length and height dimensions and fluctuating asymmetry were found for males, however fluctuating asymmetry correlated significantly positively with body mass index and postcranial robustness indices. Among Kavango females some significantly negative correlations between height and length dimensions and hand length, which was interpreted as a directional asymmetry pattern, could be observed. These findings however have to be interpreted with caution. On the one hand from the total 648 correlations only 58 were of statistical significance. Furthermore, considering the correlation coefficients, the correlations between asymmetry parameters and body size parameters are very weak. The correlation coefficients – even among statistically significant correlations – are quite low ranging from 0.15 to 0.24. Considering p-value 0.01 and below, only 11 correlations remain statistically significant. Consequently, the present study yielded no strong correlation between asymmetry patterns and adult body dimensions. Nevertheless, a typical trend of an association between increased asymmetry and decreased body size could be observed. These findings verify the hypothesis predicted for this study, namely a negative association between asymmetry and body size, growth parameters and somatic robustness.

To sum up, among !Kung San females, and Kavango males and females, increased asymmetry was associated with decreased body height, decreased postcranial length dimensions and, among !Kung San, with decreased robustness. As pointed out before, fluctuating asymmetry is mainly seen as an indicator of stress causing developmental instability. Stress however, may not only be associated with developmental instability and consequently increased fluctuating asymmetry, stress effects also somatic growth (Deaton 2007). During early life and subadult phase, increased psychic as well as somatic stress may reduce somatic growths and may result in shortness or reduced length and height dimensions (Ruel et al. 1995, Karlberg 2000). Consequently, it may be assumed that adult body height but also other length and height dimensions but also parameters of postcranial robustness might be interpreted as indicators of optimal life circumstances an developmental stability during growth period. On the other hand, it is well documented, that individuals experiencing developmentally stability during early life and growth period are more resistant to stress factors during this phase of life and, consequently, these individuals show a lower degree of asymmetry (Thornhill and Moller 1998). Since asymmetry as well as decreased growth may be interpreted as indicators of developmental instability, it can be assumed that asymmetry and height and length dimensions are two sides of the same coin. Somatic growth and the development of fluctuating asymmetry pattern take place mainly during subadult phase of life. Unfortunately, only few studies focused on these association patterns during subadult phase. Wilson and Manning (1996) described the influencing factors and effects of developmental stability during the growth period. Their study revealed significant changes in fluctuating asymmetry over the subadult period from age 2 to18 years. The high degree of asymmetry during infancy and early childhood decreases in both sexes from the age of 2 until the age of 11. During puberty and early adolescence, asymmetry rises again in males at the age of 13 and in females at the age of 14. During later adolescence, at about the age of 15, asymmetry decreases once more. According to Wilson and Manning [65], this typical change of fluctuating asymmetry patterns pattern during subadult phase is mainly due to the effects of growth rate and metabolic rate. In detail, body asymmetry increases during periods in which growth rate and metabolic rate are high. This association between high growth rate and increased asymmetry is mainly due to the high metabolic energy demands during growth phase, which might result in a decrease in developmental stability. On the other hand, growth rate and metabolic rate are lower in individuals who experience limited growth (Spur et al. 1986; Udani 1992), which may cause a decrease in stress on the body symmetry. Increased growth rate may represent a stress factor, which may cause increased fluctuating asymmetry. Wells et al. (2006) reported an association between a faster growth rate in post-natal life (but not in foetal life) and increased asymmetry at the age of 9 years. The author interpreted these findings within the framework of the ‘good development’ hypothesis. According to this hypothesis, symmetry status at the age of 9 may be interpreted as a signal of growth rate in an early window of development (Wells et al. 2006). Considering the studies mentioned above, it is not easy to distinguish between stress factors and developmental instability caused by growth/metabolic rate and that caused by poor life circumstances.

Only few studies focused on the situation among adults. Manning (1995) reported a negative relationship between body symmetry and both weight and height. Brown et al. (2008) presented similar results. The results of the present study however, corresponded to those of Özener and Ertugrul (2011), who reported a significant increase in asymmetry associated with decreased body height among young Turkish males.

In contrast, to height and length dimensions, weight status and postcranial breadth dimensions correlated significantly negatively with asymmetry patterns among !Kung San females only. Positive correlations between fluctuating asymmetry and weight and robustness indicators were found among Kavango males exclusively. These findings are in contrast to those of Milne et al (2003) who described an increasing asymmetry with increasing body mass index for women only. Little et al. (2002) analyzed asymmetry patterns of six somatometric traits among chronically under-nourished and well-nourished schoolchildren in South Mexico. It turned out, that, contrary to expectations, well-nourished children tended to be more asymmetrical than mild- to moderately under-nourished ones. These results are in accordance with the observations of Hardman (2004) who reported lower levels of fluctuating asymmetry than expected in highly malnourished children in rural areas of Northern Thailand. Consequently, the association between body weight, weight status and asymmetry patterns remains unclear.

In the present study, beside fluctuating asymmetry caused by perturbations, also named as “developmental noise”, and environmental stress factors during an individual´s ontogeny (Wilson and Manning 1996), directional asymmetry caused by behavioral lateralization was analyzed. Directional asymmetry may be interpreted as an indicator of heavy unilateral mechanical forces, which may affect somatic development and growth too (Pickering et al. 2008). Asymmetry of hand breadth and hand length, which are typical indicators of directional asymmetry were negatively associated with height and length dimensions in !Kung San and Kavango females but not in !Kung San and Kavango males. Both ethnic groups showed a typical right side bias, which may be interpreted within the framework of the dominance of right handedness (Faurie et al 2005). Right handedness, is widely found among *Homo sapiens*, his ancestors and non-human primates. In detail, about 90% of recent humans, historic populations, fossil hominids and nonhuman primates are right handed (Steele and Mays 1995; Steele 2000; Cuk et al. 2001; Sarringhaus et al. 2005; Pickering et al. 2008; Uomini 2009; Lozano et al. 2009; McManus et al. 2010; Reeves et al. 2016). This kind of directional asymmetry of is also influenced by daily workload and working conditions (Haapasalo et al. 2000; Bass et al. 2002; Krahl et al. 1994; Özener 2010; Waidhofer and Kirchengast 2015). It is well described that working conditions differed between male and females in traditional societies. !Kung San females showed the highest asymmetry of hand breadth of all four sub group considered in this study. Heavy manual working may increase hand asymmetry. Among !Kung San females, heavy working during growth phase may be interpreted as a n indicator of heavy work in subsistence since young age. These working patterns, which may be energetically exhausting may increase somatic stress and may resulted in decreased body height but also decreased postcranial length and height dimensions. Similar patterns of hard work from young age onwards may also be assumed for Kavango females resulting in increased stress during growth phase, which might enhance asymmetry of the hand dimensions and decreased body height. On the other hand, decreased body height may be interpreted as an indicator of lower social status and consequently increased physical workload, which may resulted in a higher degree of directional asymmetry of hand dimensions among females.

In conclusion, the results of the present study plead for a typical association between adult body dimensions such as body height as well as other postcranial length and height dimensions and asymmetry patterns in !Kung San and Kavango people. The associations however, are weak.

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Conflict of interest

The author declares that there is no conflicts of interest.

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