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Maximum genetic proportion of metric traits from different regions of the skull in ancient human populations of Northwestern Argentina

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SUMMARY

In order to explain the evolutionary process of ancient human populations that inhabited a specific geographical region from quantitative skull traits, it is advisable to know the evolutionary potential of metric characters. For this reason, the proportion of the maximum genetic variance or maximum heritability (h^2_m) of the variables studied was estimated. In addition, it was evaluated whether h^2_m changes between regions of the skull (face, base and vault) and the degree of association between the phenotypic variance and the maximum genetic variance. Twenty-one symmetrical variables on the left and right sides of the skull were measured in 245 skulls from five prehistoric samples from northwestern Argentina. The upper limit of heritability was estimated using the repeated measurement method. To test whether there are differences between the h^2_m of each group, the Kruskal-Wallis test was used. The maximum genetic values of each variable were obtained through a regression analysis (right measure on left measure). The relationship between phenotypic and maximum genetic values was evaluated by correlation analysis. Significant bilateral difference is demonstrated in six of 21 characters. The average h^2_m is 0.77 and ranges between 0.58 and 0.93. The average correlation between phenotypic values and maximum genotypic values was 0.8 (R^2=0.65), suggesting that it is possible to make inferences of the genetic structure of the population from phenotypic information. The high proportion of maximum observed genetic variance indicates an important evolutionary potential of the craniofacial complex in ancient populations of northwestern Argentina.

Key words: Prehistoric populations – Craniometric traits – Bilateral measures – Maximum genetic variance – Repeatability – Evolutionary potential

INTRODUCTION

The metric variables of the human skull, as any phenotypic character, are determined by a genetic component and an environmental component. One of the objectives of population genetics is to estimate the proportion of the phenotypic variance (V_P) explained by the genetic variance (V_G) or heritability (h^2) of the quantitative characters. This allows us to know the genetic structure within and between populations and to make inferences about the evolutionary process. The articles that have estimated the h^2 of quantitative characters (Clark, 1956; Vandenberg, 1962; Hiernaux, 1963;

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da Rocha et al., 1972; Morton and Green, 1972; Nakata et al., 1974; Susanne, 1975, 1977; Devor et al., 1986; Devor, 1987; Sharma, 1987; Abney et al., 2001; Sparks and Jantz, 2002; Badaruddoza and Patharia, 2012, among others) indicate that the values of h^2, in particular of the head, present an important proportion of genetic variance. For example, Devor (1987) observed that phenotypic variation in 11 craniofacial traits in living individuals is determined by genetic and non-genetic factors in approximately equal proportions, and Nakata et al. (1974) estimated an average h^2 of 0.59 for 34 variables studied. Other authors evaluated the evolutionary potential of metric or non- metric characters of the human skull by partitioning V_P into its genetic and environmental components (Sjøvold, 1984; Varela and Cocilovo, 1999, 2007; Carson, 2006a, 2006b; Cocilovo et al., 2006; Medeot et al., 2008; Martínez-Abadías et al., 2009; Varela et al., 2009; Fuchs et al., 2014; Ŝeŝelj et al., 2015).

Knowing the genetic component underlying the phenotype of the skull allows us to verify the correlation between phenotypic and genetic variation and to make inferences about the genetic structure of populations from phenotypic information (Cheverud, 1988; Konigsberg and Ousley, 1995; Marroig and Cheverud, 2001; Relethford, 2002; González-José et al., 2004; Varela and Cocilovo, 2007). In addition, since the skull is an anatomo-functional unit, which protects the brain and some sense organs, it is expected that the metric characters of the cranium contain a variable heritability within limits, allowing an adaptation to possible genetic and environmental changes. Martínez-Abadías et al. (2009) and Ŝeŝelj et al. (2015) observed, in different samples, that there are no differences in the h^2 of the metric characters among the main regions of the skull.

In the ancient Azapa population on the northern coast of Chile, it was demonstrated that the maximum genetic variance of craneometric characters remains constant among geographic subareas and cultural periods (Varela and Cocilovo, 2007).

Partition of the phenotypic variance in quantitative characteristics of the skull

The studies that have estimated the genetic variation of the human skull are scarce. Sjøvold (1984) studied the h^2 in metric and nonmetric characters of the skull in a collection of known pedigree of the locality of Hallstatt (Austria). To estimate heritability, he used the progenitor-progeny regression method (father-son, father-daughter, mother-son, mother-daughter). Their results indicate that higher heritabilities are associated with measurements of different regions of the skull: malar size, zygomaxillary width, subtense and subtense fraction, occipital chord and subtense, and transmeatal axis radii (bregma, vertex, nasion, subspinale, dacryon, zygoorbitale, zygomaxillare).

With the same Hallstatt sample, Carson (2006a) estimates the heritability for 33 skull metric characters using the of maximum likelihood variance components method. In general, h^2 values are low and moderate; in three traits the value of h^2 is zero; in 11 traits the values ranged between 0.2 and 0.26; in another 11 cases between 0.28 and 0.40, and in eight cases between 0.46 and 0.87. The average h^2 for all variables was 0.32 and the variables with the highest h^2 are basion-nasion length, orbital height, basion-bregma height, basion-prosthion length, nasion-prosthion height, bimaxillar breadth, nasal height, and external alveolar breadth. These h^2 values are similar or less than those obtained by Sjøvold (1984).

In a reanalysis of the skulls from Hallstatt's sample (Martínez-Abadías et al., 2009), h^2 was calculated for a total of 58 measurements from different regions of the skull. The results indicate that there are no differences between the h^2 of the facial, neurocranial and basal dimensions and that the proportion of genetic variation is low to moderate. The highest h^2 are observed in the orbital, nasal and zygomatic region. These authors also observe a significant correlation between phenotypic and genetic matrices. Similarly, Varela and Cocilovo (2007), using metric characters of the skull, showed a correlation of 0.94 between phenotypic distances and maximum genetic distances in prehistoric human groups on the north coast of Chile. These results support the use of phenotypic data to interpret the evolutionary history of human populations, and agree with the observations made by Cheverud (1988), Marroig and Cheverud (2001), Relethford (2002) and González-José et al. (2004). The three papers that used the Hallstatt sample agree that h^2 are moderate-low and that standard errors are high, probably as a consequence of sample size (Martínez-Abadías et al., 2009).

Ŝeŝelj et al. (2015) estimated the heritability of 76 measurements from different regions of the craniofacial complex, recorded from 1379 cephalographs of participants in the Fels Longitudinal Study with known pedigree. Heritability estimates ranged from 0.10 to 0.60, with the majority being moderate. In addition, they observed similar ranges of heritability in the different craniofacial components (splacneocranial, basicranial and neurocranial).

Similarly, in the ancient population of Punta Teatinos in the semi-arid north of Chile, it was observed that the proportion of the maximum genetic variance of tooth measurements, particularly molars, is smaller than those of the skull (Varela et al., 2009).

In natural populations, and in particular in ancient human groups, h^2 cannot be estimated because there is no information on the biological relationships among individuals in the population. In these cases, it is possible to estimate the maximum heritability (h^2_m) or repeatability (r) measuring the same character on the right and left side in organ-

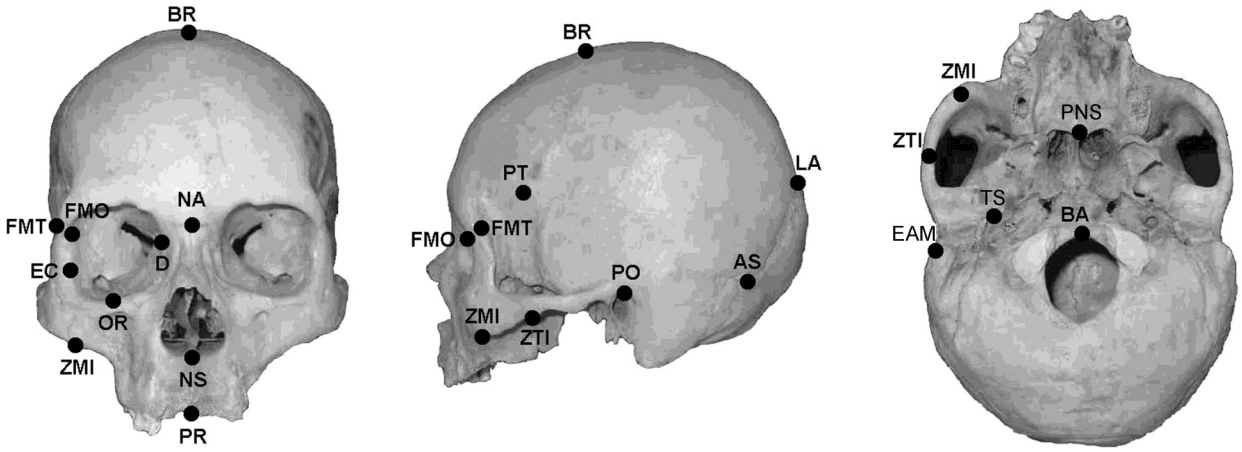

Fig 1. Skull landmarks in frontal, lateral and basal views.

isms with bilateral symmetry. In Bedouin populations, the estimate of r in bilateral skull variables ranged from 0.64 to 0.93 (Hershkovitz et al., 1990). In different ancient populations of northern Chile and northwestern Argentina the h^2_m in metric skull traits ranged from 0.48 to 0.94 (Varela and Cocilovo, 1999, 2007; Cocilovo et al., 2006; Medeot et al., 2008; Varela et al., 2009; Fuchs et al., 2014).

To know the proportion of the genetic and environmental variance of the metric traits of the craniofacial complex is relevant for making evolutionary inferences of the prehistoric human populations that inhabited the South Central Andean area.

These antecedents in prehistoric human populations allow us to propose the following hypotheses: a) the maximum heritability of skull should be moderate (between 0.3 and 0.6) or high (greater than 0.6) and similar between sexes and among populations in a given region; b) if the h^2_m of skull metric characters is within a range of moderate-high values, differences in the h^2_m between skull variables can be expected; c) if phenotypic variation reflects genotypic variation, an important correlation between phenotypic and genetic matrices and a low association between phenotypic and environmental matrices should be observed.

According to the above, in the present work it is proposed to estimate, in ancient populations of the northwest of Argentina, the proportion of the maximum genetic component or h^2_m of the metric traits of the main regions of the skull (face, base and vault); to examine if the repeatability differs between sexes and between artificially deformed and undeformed skulls; to evaluate the degree of similarity of the maximum heritability among the traits of the three regions of the craniofacial complex; and to analyze the correlation between the phenotypic and maximum genetic information.

MATERIALS AND METHODS

The material used consists of 245 skulls of both sexes (176 male and 69 female) belonging to five samples from northwestern Argentina (NOA): Agua Caliente (AC, n=48) of the Late period with dates between 1020 and 1497 AD (Fuchs and Varela, 2013) of the Puna de Jujuy subregion; La Poma (LP, n=91); Valles (VA, n=48, represented by Calchaquí, Santa María, Hualfin and Belén sites) and Santa Rosa de Tastil (TA, n=15) of the period of Regional Development-Inca (1000-1550 AD) (Marcelino and Ringuelet, 1973; Baldini, 1980; Baffi and Cocilovo, 1989-1990; D'Altroy et al., 2000; DeMarrais, 2001) of the Valliserrana subregion; and Las Pirguas (PI, n=43) of the Middle period (650-861 AD) (Carnese et al., 2010; Varela and Cocilovo, 2019) of the Selvas Occidentales subregion.

The material studied is housed in the Museo Etnográfico Juan B. Ambrosetti of the Universidad de Buenos Aires and in the Museo de Ciencias Naturales of the Universidad Nacional de La Plata, Argentina. Sex was determined based on Acsádi and Nemeskeri (1970) and Bass (1981) for individuals in postreproductive age (Monlar, 1971; Bass, 1981; Lovejoy, 1985). The skulls were classified as artificially deformed (tabular) and not deformed (Dembo and Imbelloni, 1938).

The same observer measured 21 symmetrical variables on the left and right sides of the three skull regions (face, vault and base). Table 1 defines each of the variables and Fig. 1 shows the location of the points on the skull. Measurements were taken with a fine-tipped caliper with vernier scale (Mitutoyo, 0.02 mm accuracy) and with curved branch compass (GPM, 0.5 accuracy).

The measurement of the same character of the right and left sides of the skull allows partitioning the environmental variance (V_E) into a special environmental variance (V_{Es}) that represents the variance within the individual (between both sides) produced mainly by localized environmental effects acting during ontogenetic development or by measurement errors, and the general environmental variance (V_{Eg}) that explains the variance be-

Table 1. Bilateral traits of the skull

Region	Definition	Abbreviation
FACE	Distance from Prosthion to Frontomalar orbital [3]	PR-FMO
	Distance from Nasion to Frontomalar orbital [2]	NA-FMO
	Distance from Zygomaxillare inferior to Frontomalar temporal [3].	ZMI-FMT
	Distance from Nasosespinale to Zygomaxillare inferior [1,3]	NS-ZMI
	Cheek bone height, minimal distance from the inferior orbital edge to the inferior maxillar edge [4]	CBH
	Orbital breadth, from dacrion to ectoconchion [1]	OBB
	Orbital height, maximum distance between the upper and lower edges of the orbit, perpendicular to the orbital bredth [1]	OBH
	Orbito-alveolar height, the least distance between the lower edge of the orbit and the alveolar edge [1]	OBA
VAULT	Distance from Pterion to Frontomalare Temporale [3]	PT-FMT
	Distance from Pterion to Asterion[2]	PT-AS
	Distance from Pterion to Tempero-sphenoidal junction at petrous [2]	PT-TS
	Distance from Bregma to Pterion[2]	BR-PT
	Distance from Bregma to Asterion[5]	BR-AS
	Distance from Bregma to Porion[5]	BR-PO
	Distance from Lambda to Asterion[5]	LA-AS
BASE	Distance from Anterior external auditory meatus to Zygomaxillare inferior [2]	EAM-ZMI
	Distance from Asterion to Tempero-sphenoidal junction at petrous [2]	AS-TS
	Distance from Basion to Anterior external auditory meatus [2]	BA-EAM
	Distance from Posterior nasal spine to Tempero-sphenoidal junction at petrous [3]	PNS-TS
	Distance from Zygotemporale inferior to Posterior nasal spine [3]	ZTI-PNS
	Distance from Zygomaxillare inferior to Asterion[3]	ZMI-AS

[1] Wilder (1920), Comas (1966), Bass (1981); [2] Hutchison and Cheverud (1995); [3] Medeot et al. (2008); [4] Howells (1973), [5] Hershkovitz et al. (1990).

tween individuals and arising from permanent or non-localized circumstances. In this way it is possible to estimate the maximum heritability (h^2_m) or repeatability (r) of a character as $h^2_m = (V_G+V_{Eg})/(V_G+V_{Eg}+V_{Es})$, where V_G is the genetic variance. Since V_G+V_{Eg} is equal to the maximum genetic variance (V_{Gm}), and $V_G+V_{Eg}+V_{Es}$ is equal to the total or phenotypic variance (V_P), it turns out that $h^2_m=V_{Gm}/V_P$.

Since V_G+V_{Eg} represents the variance between individuals (V_B) and V_{Es} represents the variance within individuals (V_W), h^2_m was estimated as $h^2_m=V_B/(V_B+V_W)$ (Becker, 1975; Falconer and Mackay, 1996; Lynch and Walsh, 1998), and its standard error as:

se = $\sqrt{\{2[1+(n-1)r]^2(1-r)^2\}/[n(n-1)(N-1)]}$ (Fisher, 1954), where N=number of individuals and n=number of repetitions per individual.

Non-parametric analysis (Kruskal-Wallis and Mann-Whitney tests) was used to evaluate whether the h^2_m of metric traits is different between groups (total sample, male, female, male undeformed, female undeformed, male deformed and female deformed). Previously it was verified that the h^2_m of the skull variables are equal between NOA samples (AC, LP, VA, TA and PI). Then it was tested whether there are differences between the h^2_m of the traits of the three regions of the skull (face, vault and base) and between the 21 metric variables of the skull, using the same statistical analysis mentioned above.

Through a regression between repetitions (right over left) for each variable, the predicted values or maximum genetic values (Gm) and the residual values or special environmental values (Es) were obtained. The degree of association between phenotypic (P), maximum genetic and special environmental values was evaluated by means of a regression analysis (P vs. Gm and P vs. Es). This information allows us to evaluate the degree of dependence of the phenotype with respect to the genetic and environmental components.

To evaluate intra-observer error, in 48 individuals each variable was measured twice on the right side and twice on the left side. In this way, the variation between the measurements on both sides of the skull (laterality) and the variation between the first and second measurements made on the same side of the skull (repetition or intra-observer error) were analyzed by means of an analysis of the variance of two factors.

Table 2. Mean and standard error (SE) of the right (R) and left (L) sides, difference between the right and left sides (R-L) of each variable and p-value

Region	Trait	Mean_R (mm)	SE_R	Mean_L (mm)	SE_L	R-L (mm)	p-value
FACE	PR-FMO	82.95	0.28	83.37	0.29	-0.43	0.2627
	NA-FMO	51.70	0.17	50.71	0.15	0.99	**0.0000**
	ZMI-FMT	47.76	0.20	48.10	0.21	-0.34	0.2113
	NS-ZMI	55.31	0.22	55.20	0.22	0.12	0.7051
	CBH	22.60	0.15	22.44	0.16	0.16	0.4380
	OBB	39.57	0.11	39.22	0.11	0.35	**0.0252**
	OBH	35.54	0.12	35.94	0.12	-0.39	**0.0223**
	OBA	37.76	0.25	38.26	0.27	-0.50	0.1571
VAULT	PT-FMT	27.61	0.20	26.72	0.20	0.90	**0.0015**
	PT-AS	93.50	0.32	93.24	0.30	0.26	0.5191
	PT-TS	60.97	0.23	60.78	0.24	0.19	0.5556
	BR-PT	94.55	0.31	95.16	0.33	-0.62	0.1649
	BR-AS	131.06	0.42	129.72	0.39	1.33	**0.0103**
	BR-PO	131.01	0.37	130.35	0.38	0.66	0.1990
	LA-AS	82.55	0.38	82.04	0.36	0.51	0.3062
BASE	EAM-ZMI	61.07	0.22	60.87	0.22	0.20	0.4980
	AS-TS	64.62	0.21	64.69	0.20	-0.07	0.8084
	BA-EAM	56.16	0.18	56.02	0.18	0.13	0.5816
	PNS-TS	50.86	0.19	50.26	0.19	0.60	**0.0231**
	ZTI-PNS	65.58	0.21	65.51	0.17	0.08	0.8953
	ZMI-AS	114.27	0.34	114.03	0.53	0.27	0.2824

RESULTS

Table 2 shows the mean and standard error of each character of the skull (right and left) and test of equality between the two sides for the total sample (N=245). Of 21 characters studied, six showed statistically significant differences between the right and left side, three of them are from the face region (NA-FMO, OBB, OBH), two from the vault (PT-FMT, BR-AS) and one from the base (PNS-TS). In five variables (NA-FMO, OBB, PT-FMT, BR -AS, PNS-TS) the dimensions were larger on the right side, and in one trait (OBH) the opposite occurred. The three variables with the greatest difference between both sides of the skull were BR-AS (1.33), NA-FMO (0.99) and PT-FMT (0.90), and the three with the smallest difference were AS-TS (-0.07), ZTI-PNS (0.08) and NS-ZMI (0.12). Table 3 shows repeatability and standard error for each trait by skull region for the following groups: total sample (T), male (M), female (F), male not deformed (MND), male deformed (MD), female not deformed (FND), female deformed (FD). The results of Kruskal-Wallis ANOVA by Ranks show that there are no differences between the repeatability of the seven groups mentioned above ($H_{(6, N=147)}$ =5.19; p=0.520) (Fig. 2).

Observing the Total group of Table 3, it is verified that the three variables with greater repeatability are PR-FMO (0.93), CBH (0.90) and BR-PO (0.87) and the three characters with lower proportion of maximum genetic variance are NA-FMO (0.60), BR-AS (0.64) and PT- FMT (0.65). The rest of the variables have a repeatability that varies between 0.70 and 0.86. The standard errors of these estimates are low and fluctuate between 0.01 and

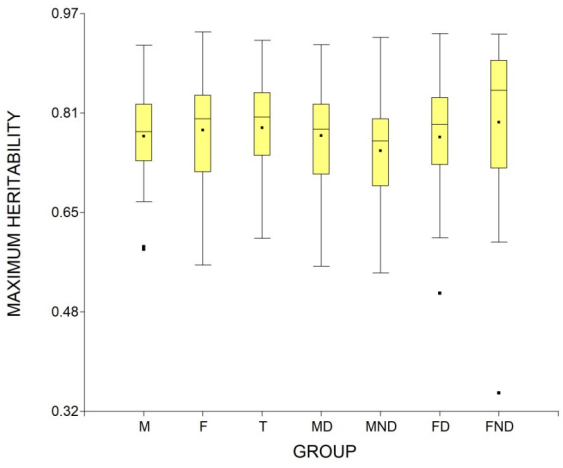

Fig 2. Box-plot of repeatability of skull metric variables for each group. T: total, M: male, F: female, MND: male not deformed, MD: male deformed, FND: female not deformed, FD: female deformed. Dot: mean, horizontal line: median.

Table 3. Maximum heritability (h^2_m) and standard error (SE) for total sample-T, male-M, female-F, male not deformed-MND, male deformed-MD, female not deformed FND, female deformed FD

		T		M		F		MND		MD		FND		FD		Average	
Region	Trait	h^2_m	SE	h^2_m	SE	h^2_m	SE	h^2_m	SE	h^2_m	SE	h^2_m	SE	h^2_m	SE	h^2_m	SE
FACE	PR-FMO	0.93	0.01	0.92	0.01	0.94	0.01	0.91	0.03	0.92	0.01	0.94	0.03	0.94	0.02	0.93	0.02
	NA-FMO	0.60	0.04	0.58	0.05	0.56	0.08	0.55	0.12	0.60	0.06	0.66	0.15	0.51	0.10	0.58	0.11
	ZMI-FMT	0.84	0.02	0.82	0.03	0.88	0.03	0.83	0.05	0.81	0.03	0.90	0.05	0.87	0.03	0.85	0.04
	NS-ZMI	0.86	0.02	0.86	0.02	0.82	0.04	0.93	0.02	0.82	0.03	0.92	0.04	0.79	0.05	0.86	0.04
	CBH	0.90	0.01	0.90	0.01	0.86	0.03	0.78	0.06	0.92	0.01	0.88	0.06	0.86	0.04	0.86	0.04
	OBB	0.81	0.02	0.80	0.03	0.79	0.05	0.80	0.06	0.80	0.03	0.89	0.06	0.74	0.06	0.81	0.05
	OBH	0.84	0.02	0.82	0.02	0.88	0.03	0.69	0.09	0.86	0.02	0.90	0.05	0.85	0.04	0.83	0.05
	OBA	0.73	0.03	0.71	0.04	0.76	0.05	0.77	0.07	0.69	0.05	0.88	0.06	0.71	0.07	0.76	0.06
	Average	0.81	0.02	0.80	0.03	0.81	0.04	0.78	0.06	0.80	0.02	0.87	0.06	0.78	0.05	0.81	0.05
VAULT	PT-FMT	0.65	0.04	0.66	0.04	0.61	0.08	0.63	0.10	0.67	0.05	0.35	0.23	0.66	0.08	0.58	0.11
	PT-AS	0.81	0.02	0.79	0.03	0.83	0.04	0.69	0.09	0.79	0.03	0.74	0.12	0.83	0.04	0.76	0.07
	PT-TS	0.75	0.03	0.75	0.03	0.71	0.06	0.73	0.08	0.76	0.04	0.65	0.15	0.73	0.06	0.72	0.08
	BR-PT	0.77	0.03	0.73	0.04	0.82	0.04	0.63	0.10	0.75	0.04	0.82	0.09	0.83	0.04	0.76	0.07
	BR-AS	0.64	0.04	0.59	0.05	0.65	0.07	0.68	0.09	0.56	0.06	0.72	0.13	0.60	0.09	0.64	0.09
	BR-PO	0.87	0.02	0.85	0.02	0.89	0.03	0.79	0.06	0.87	0.02	0.91	0.05	0.88	0.03	0.86	0.04
	LA-AS	0.78	0.03	0.78	0.03	0.79	0.05	0.76	0.07	0.77	0.03	0.74	0.12	0.81	0.05	0.77	0.07
	Average	0.75	0.03	0.74	0.03	0.76	0.05	0.70	0.08	0.74	0.04	0.70	0.13	0.76	0.06	0.73	0.08
BASE	EAM-ZMI	0.83	0.02	0.81	0.03	0.83	0.04	0.75	0.07	0.82	0.03	0.89	0.05	0.80	0.05	0.81	0.05
	AS-TS	0.70	0.03	0.69	0.04	0.70	0.06	0.60	0.11	0.70	0.04	0.60	0.17	0.72	0.07	0.66	0.10
	BA-EAM	0.79	0.02	0.77	0.03	0.75	0.05	0.73	0.08	0.78	0.03	0.82	0.09	0.73	0.06	0.77	0.06
	PNS-TS	0.74	0.03	0.74	0.03	0.69	0.06	0.83	0.05	0.71	0.04	0.71	0.13	0.69	0.07	0.73	0.07
	ZTI-PNS	0.80	0.02	0.78	0.03	0.80	0.04	0.77	0.07	0.78	0.03	0.91	0.04	0.75	0.06	0.80	0.05
	ZMI-AS	0.85	0.02	0.82	0.02	0.84	0.04	0.82	0.05	0.82	0.03	0.85	0.08	0.83	0.04	0.83	0.05
	Average	0.78	0.02	0.77	0.03	0.77	0.05	0.75	0.07	0.77	0.03	0.80	0.09	0.75	0.06	0.77	0.06
	Total Average	0.78	0.02	0.77	0.03	0.78	0.05	0.75	0.07	0.77	0.03	0.79	0.10	0.77	0.06	0.77	0.06

0.04. In the case of the repeatability of some variables of the FND group, the standard errors are larger because the sample size is smaller. A posteriori non-parametric test shows differences between the repeatabilities of the face and the vault, with a probability of 0.004 (Table 4). No difference could be demonstrated in the maximum genetic component between the face and the base, and between the vault and the base. It was also shown that there are statistically significant differences among the repeatabilities of the 21 skull metric traits (Kruskal-Wallis test: $H_{(20,N=84)}$=58.17, p=0.000). A posteriori non-parametric test shows that statistical differences occur between the following pairs of variables: PR-FMO vs. NA-FMO (p=0.002), PR-FMO vs. PT-FMT (p=0.006), PR-FMO vs. BR-AS (p=0.014), PR-FMO vs. AS-TS (p=0.022), that is, when variables with high (PR-FMO) and low repeatability (NA-FMO, PT- FMT, BR-AS and AS-TS) are involved in the comparison.

The results of the regression between phenotypic values and maximum genetic values, and between phenotypic values and special environmental values (Table 5), show that, on average, the maximum genetic variance explains 64.7% of the total phenotypic variance of skull traits, and the remaining 35.3% is explained by the special environmen-

Table 4. Non-parametric comparison of maximum heritability among the three regions of the skull and probability between pairs of groups

Kruskal-Wallis test: $H_{(2, N= 84)}$ =10.52, p =0.0052			
post-hoc comparisons (p-values)			
Region	Face	Vault	Base
Face	-------	0.0041	0.1719
Vault		--------	0.7723
Base			-------

Table 5. Correlation (R), regression (R^2), probability (p) and standard error (SE) between the phenotypic component (P) versus the maximum genetic (Gm) and special environmental (Es) components, for each metric variable of the skull

		P vs Gm				P vs Es			
Region	Traits	R	R²	p	SE	R	R²	p	SE
FACE	PR-FMO	0.932	0.868	<0.001	1.618	0.363	0.132	<0.001	4.156
	NA-FMO	0.667	0.446	<0.001	1.960	0.745	0.554	<0.001	1.757
	ZMI-FMT	0.847	0.718	<0.001	1.662	0.531	0.282	<0.001	2.650
	NS-ZMI	0.857	0.735	<0.001	1.753	0.515	0.265	<0.001	2.920
	CBH	0.898	0.807	<0.001	1.025	0.439	0.193	<0.001	2.096
	OBB	0.823	0.677	<0.001	1.017	0.568	0.323	<0.001	1.473
	OBH	0.857	0.734	<0.001	0.988	0.515	0.266	<0.001	1.643
	OBA	0.732	0.537	<0.001	2.646	0.681	0.463	<0.001	2.847
	Average	0.827	0.690		1.584	0.545	0.310		2.443
VAULT	PT-FMT	0.684	0.467	<0.001	2.344	0.730	0.533	<0.001	2.196
	PT-AS	0.812	0.659	<0.001	2.898	0.584	0.341	<0.001	4.025
	PT-TS	0.754	0.568	<0.001	2.382	0.657	0.432	<0.001	2.733
	BR-PT	0.774	0.600	<0.001	3.053	0.633	0.400	<0.001	3.736
	BR-AS	0.655	0.429	<0.001	4.973	0.755	0.571	<0.001	4.314
	BR-PO	0.879	0.772	<0.001	2.751	0.478	0.228	<0.001	5.061
	LA-AS	0.782	0.612	<0.001	3.675	0.623	0.388	<0.001	4.618
	Average	0.763	0.587		3.154	0.637	0.413		3.812
BASE	EAM-ZMI	0.830	0.688	<0.001	1.967	0.558	0.312	<0.001	2.924
	AS-TS	0.705	0.497	<0.001	2.354	0.709	0.503	<0.001	2.342
	BA-EAM	0.791	0.625	<0.001	1.722	0.612	0.375	<0.001	2.226
	PNS-TS	0.756	0.571	<0.001	1.957	0.655	0.429	<0.001	2.258
	ZTI-PNS	0.801	0.642	<0.001	1.597	0.598	0.358	<0.001	2.138
	ZMI-AS	0.848	0.719	<0.001	2.859	0.530	0.281	<0.001	4.570
	Average	0.789	0.624		2.076	0.610	0.376		2.743
	Total Average	0.801	0.647		2.111	0.586	0.353		2.918

F-values are distributed with 1 and 243 df

tal variance. Most of the variables of the face present a high proportion of the maximum genetic component (between 67% and 86.8%), with the exception of the OBA and in particular the NA-FMO distance (the proportion explained by this component is lower, 53.7% and 44.6% respectively). The average percentage of V_P explained by the V_{Gm} of the vault variables represents 58.7%, ranging from a minimum of 42.9% (BR-AS) to a maximum of 77.2% (BR- PO). In the skull base traits this percentage varies between 49.7% (AS-TS) and 71.9% (ZMI- AS), with an average of 62.4%. The variables with the greatest environmental effect are NA- FMO (face), BR-AS (vault), PT-FMT (vault), AS-TS (base) and the least influenced by the special environment are PR-FMO (face) and CBH (face).

With respect to intra-observer error, no significant differences were demonstrated between the first and second measurement made on each side of the same individual. Furthermore, no interaction between laterality and repetition was found, which ensures independence of both factors and a more objective estimate of repeatability (see Appendix and Medeot et al., 2008).

DISCUSSION

The results of the differences between the average right and left values of each variable of the skull allow us to notice a bilateral asymmetry produced by localized environmental effects during the development of the individuals. Statistically significant differences between both sides were demonstrated in six variables (29%) (Table 2). Five of them have a greater development towards the right side, of which three are of the face (NA-FMO, OBB, CBH), two of the vault (PT-FMT, BR-AS) and one of the base of the skull (PNS-TS). In addition, a face variable (OBH) has a higher mean value on the left side of the skull. Considering all the characters studied, it is observed that there is a predominance of the growth of the variables to-

wards the right side. It is likely that the tendency towards one side or the other of the variables is related to the anatomy and function of the organs associated with the traits of the different regions of the skull, and with alterations of the normal process of growth and development of individuals.

In the prehistoric population of Las Pirguas in northwestern Argentina, Medeot et al. (2008) worked with 60 skulls and the same 21 traits as in the present investigation. They demonstrated differences in four variables (NA-FMO, PT-FMT, BR-AS and BR-PO) between the right and left sides of the skull, with asymmetry to the right. In the ancient group of Punta de Teatinos of the northern Semiarid of Chile (N = 54), of a total of six variables of the skull and three of the jaw, a bilateral difference was observed in the BR-PO with predominance towards the right side (Cocilovo et al., 2006). In a sample of 235 individuals from the prehistoric population of the Puna de Jujuy in Argentina, Fuchs et al. (2014) determined that of a total of 11 bilateral metric variables of the skull, five (45 %) showed differences between the measurement of the right and left sides of the skull. Of these five variables, three were greater on the right side (OBA, NA-FMO, BAS-PO=Length Basion-Porion) and two on the left side (OBH, PR-FMO). The results mentioned in these three articles are consistent with what we observed (Table 2).

In a sample of 266 adult Bedouin skulls (Hershkovitz et al., 1992), a general trend of growth of the variables was observed towards the right side. Of the 34 skull variables analyzed by these authors, 23 (68%) showed differences between the left and right sides, a markedly higher percentage than that observed in the sample analyzed in this study (Table 2). These last results allow to propose that the proportion of variables that differ statistically between the measurement of both sides of the skull depends at least on the population, the number of variables and the size of the sample.

Table 2 shows that the main differences between right and left occur in vault and face variables, coinciding with Hershkovitz et al. (1992). This result suggests a more important localized environmental effect in these two regions than at the base, probably as a consequence of faster development and less temporary exposure to environmental noise during development at the skull base.

The results in Table 3 and Fig. 2 show the similarity between the repeatability values of the total, male, female, male undeformed, male deformed, female undeformed and female deformed groups. Statistical tests showed that there are no significant differences between the repeatabilities of these groups, indicating equal proportion of maximum genetic variance or equal proportion of special environmental variance within individuals. In the population of Punta Teatinos and Las Pirguas,

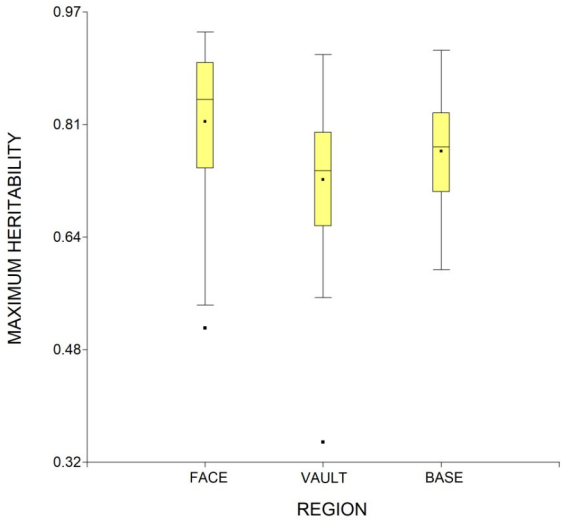

Fig 3. Box-plot of the repeatability of skull metric variables in the three regions of the skull (face, vault and base). Dot: mean, horizontal line: median.

it was demonstrated that the proportion of maximum genetic variance is distributed independently of sex (Medeot et al., 2008; Varela et al., 2009), and in the Azapa valley it was observed that repeatability does not change between cultural periods and between sub-regions (Varela and Cocilovo, 2007).

The average estimate of the repeatability of the 21 skull variables for the total sample was 0.78 (Table 3), i.e. the special environmental component, produced by localized environmental effects during development, represents 22% of the total phenotypic variation. The average repeatability taking into account six variables (CBH, OBB, OBH, OBA, ZMI- AS, BR-PO) in common with other prehistoric populations of northwestern Argentina and northern Chile was 0.83, this value is comparable with the estimated repeatability in Las Pirguas (0.78), Puna de Jujuy (0.82), San Pedro de Atacama (0.79), Punta de Teatinos (0.90), Valle de Azapa (0.83) (Varela and Cocilovo, 1999, 2007; Medeot et al., 2008; Varela et al., 2009; Fuchs et al., 2014).

Although the h^2_m depends on the character and population, some variables such as cheekbone height (CBH) and orbit height (OBH) (Table 3) have high repeatability values, as observed in the populations of San Pedro de Atacama (Varela and Cocilovo, 1999), Arica (Varela and Cocilovo, 2007), Las Pirguas (Medeot et al., 2008), Punta Teatinos (Varela et al., 2009) and Puna de Jujuy (Fuchs et al., 2014). The high repeatability value of the orbital frontomalar prosthion distance (FMO-PR) (Table 3) coincides with that observed in Las Pirguas (Medeot et al., 2008) and Puna de Jujuy (Fuchs et al., 2014). Similarly, there are variables such as NA- FMO, BR-AS and OBA that shows low repeatability (Table 3), a particularity that is repeated in the populations of Las Pirguas

(Medeot et al., 2008) and Puna de Jujuy (Fuchs et al., 2014). This information suggests that there are traits in different populations that systematically present a higher proportion of phenotypic variance explained by the maximum genetic variance (h^2_m) compared to other traits. This characteristic is likely to represent a property of populations that share a nearby common ancestral population and similar non-genetic conditions. Also, it is observed that when comparing the repeatability of Table 3 with those obtained by Hershkovitz et al. (1990) in Bedouin populations, it is verified that in both studies the distance bregma-porion (BR-PO) and height of orbit (OBH) have a high h^2_m value.

The results presented in Table 4 and Fig. 3 show that there are differences among the h^2_m values of the regions of the skull considered (face, vault, base), and in particular this difference occurs between the face and the vault. This means that the variables involved in the face region have, on average, a greater proportion of maximum genetic variance than the variables involved in the vault region. In addition, it was observed that there are differences between the h^2_m values of characters of the same region and between characters of different regions. These differences are explained by the high proportion of maximum genetic variance of the PR-FMO variable compared to those characters that have the lowest proportion of V_{Gm}. Differences can be inferred by observing in Table 3 the range of variation of the average repeatability, between 0.58 for NA-FMO and 0.93 for PR-FMO, both characters belonging to the face region. For the vault region the range is between 0.58 (PT-FMT) and 0.87 (BR-PO), and for the base region between 0.66 (AS-TS) and 0.83 (ZMI-AS). Similar repeatability ranges have been verified in other prehistoric groups in Argentina and Chile, such as San Pedro de Atacama (Varela and Cocilovo, 1999), Punta de Teatinos (Cocilovo et al., 2006; Varela et al., 2009), Azapa (Varela and Cocilovo, 2007), Las Pirguas (Medeot et al., 2008), and Puna de Jujuy (Fuchs et al., 2014), but it was not analyzed if there is a difference in h^2_m among skull variables. In the Bedouin population studied by Hershkovitz et al. (1990), a similar range of variation is also observed, but it was also not tested if there are differences between the repeatability of skull characters.

Carson (2006a) analyzes the heritability of skull traits in Hallstatt's sample, and expresses that variables such as widths and facials have less heritability than lengths and neurocranials, respectively. However, without considering variables criticized by the author such as external alveolar breadth (MAB) and Nasion-prosthion height (NPH), it is observed that the two variables with the highest h^2 are nasal height (NLH) and Bimaxillary breadth (ZMB), i.e. characters related to the face.

Martínez-Abadías et al. (2009), also in the Hallstatt skull sample, estimated a range of h^2 in skull metric traits between zero and 0.43, and did not demonstrate differences in the proportion of the genetic component between regions of the skull. In the sample analyzed by Ŝeŝelj et al. (2015), a range of h^2 variation between 0.10 and 0.60 was estimated. Also, a higher average genetic proportion was observed in the traits of the neurocranium than in the variables of the base and face of the skull. In these last two articles it is verified that the value of higher h^2 corresponds with variables of the facial region.

It is important to note that the accuracy of heritability depends on factors that are often not properly taken into account. Different methods are used to calculate h^2 based on the type of relationship between individuals in a sample, and in some of these methods it is not possible to separate the effect of the common environment or the effect of the maternal environment. Another factor that can cause deviations from the heritability estimate is the interaction between alleles at the same locus (dominance) or between alleles at different locus (epistasis) in quantitative traits. In some experiences, as in our case, this last effect is assumed to be negligible. These issues have been adequately addressed by Falconer and Mackay, 1996; Lynch and Walsh, 1998; Guo, 1999; Harris, 2008; among others.

The results obtained in this study show differences in the proportion of the maximum genetic component between regions and between skull variables (Table 4), which is reflected in the variation range of the repeatability estimate (Table 3). This characteristic coincides with the studies previously analyzed, where it is emphasized that the heritability and repeatability of the skull metric variables have an important range of variation. In addition, when observing the different results discussed, it is verified that high or low r or h^2_m values of skull variables are not a characteristic of a region of the skull. This means that in the same region it is possible to observe traits with a high proportion of the genetic component and other variables with a low proportion of the genetic component. For this reason, the statistical differences between the proportion of V_{Gm} of the regions of the skull depends on the population studied, the selection criteria of the variables, the number of characters of each region of the skull, and the methodology used to test the equality of repeatability between regions.

The high proportion of maximum genetic variance observed in the metric characters of the skull of the populations studied show an important evolutionary potential, within the limits established by the range of variation of h^2_m and the anatomical-functional integration of the craniofacial complex.

The results derived from the regression between the phenotypic component (P) in relation to the maximum genetic component (Gm) and the spe-

cial environmental component (Es) of each variable indicate that phenotypic information can be used as a genetic indicator in quantitative population genetics models to make evolutionary inferences. Similar results were obtained by other authors (Cheverud, 1988; Marroig and Cheverud, 2001; Relethford, 2002; Gonzalez- José et al., 2004; Varela and Cocilovo, 2007; Martínez-Abadías et al., 2009). Particularly in the prehistoric population of Arica (northern Chile), a strong correlation between the maximum genetic kinship model and the phenotypic kinship model was found (Varela and Cocilovo, 2007). It is also verified that h^2_m is an indicator of the degree of correlation between phenotypic and maximum genetic values: i.e., characters with high and low h^2_m correspond to high and low correlations respectively (Tables 3 and 5). This coincides with that expressed by Cheverud (1988).

The bilateral asymmetry observed in this study occurs within individuals, and is produced by localized environmental conditions that occur during the development of individuals. This special environmental effect is somewhat greater on the face and the vault of the skull, probably attributable to a longer time of environmental exposure during the growth and development of these two regions compared to the base of the skull.

We demonstrated that in the populations studied, h^2_m is independent of sex and artificial deformation. In addition, repeatability does not vary between the different samples from northwestern Argentina, suggesting a common pattern of variation of the maximum genetic component of the skull in the ancient populations of the region.

The analysis carried out allows us to confirm the hypothesis that the proportion of V_{Gm} or r of the skull of the populations of northwestern Argentina is moderate-high, representing, on average, a 78% of the total phenotypic variation, with a minimum of 58% (NA-FMO) and a maximum of 93% (PR-FMO) in face variables. This evidence indicates a remarkable evolutionary capacity of the craniofacial complex, offering the concrete possibility of genetic changes within and between populations through the action of different evolutionary factors on genetic variability.

Our analysis shows that the pattern of variation of the maximum genetic component of the skull is similar to that of other prehistoric populations in northwestern Argentina and northern Chile. Backing up the second hypothesis, the results show significant statistical differences between the h^2_m of traits from different regions and from the same region of the skull, evincing a range of variation of the proportion of the genetic component of the metric characters of the skull. Finally, as the third hypothesis proposes, a high correlation between phenotypic values and maximum genetic values was demonstrated, indicating that it is possible to make evolutionary predictions from the phenotypic information of the skull.

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Appendix. Two-way ANOVA. Difference between the right and left sides, between the first and second repetition and interaction between side and repetition

Region	Trait		SS	Degr. of	MS	F	p
FACE	PR-FMO	Side	2.3411	1	2.3411	0.0871	0.7682
		Repetition	0.0107	1	0.0107	0.0004	0.9841
		Side*Repetitio	0.0522	1	0.0522	0.0019	0.9649
		Error	4892.4575	182	26.8816		
	NA_FMO	Side	64.3625	1	64.3625	9.1533	0.0028
		Repetition	0.0268	1	0.0268	0.0038	0.9509
		Side*Repetitio	0.0008	1	0.0008	0.0001	0.9914
		Error	1307.8804	186	7.0316		
	ZMI-FMT	Side	10.0559	1	10.0559	1.0262	0.3124
		Repetition	0.0010	1	0.0010	0.0001	0.9918
		Side*Repetitio	0.0012	1	0.0012	0.0001	0.9911
		Error	1802.9887	184	9.7989		
	NS-ZMI	Side	4.9883	1	4.9883	0.3782	0.5393
		Repetition	0.0005	1	0.0005	0.0000	0.9950
		Side*Repetitio	0.0624	1	0.0624	0.0047	0.9452
		Error	2453.3445	186	13.1900		
	CBH	Side	7.2385	1	7.2385	1.8850	0.1714
		Repetition	0.0225	1	0.0225	0.0059	0.9390
		Side*Repetitio	0.0003	1	0.0003	0.0001	0.9930
		Error	721.9282	188	3.8400		
	OBB	Side	3.4402	1	3.4402	0.7650	0.3829
		Repetition	0.0272	1	0.0272	0.0061	0.9380
		Side*Repetitio	0.0292	1	0.0292	0.0065	0.9358
		Error	836.4493	186	4.4970		
	OBH	Side	5.0073	1	5.0073	1.9375	0.1656
		Repetition	0.0013	1	0.0013	0.0005	0.9824
		Side*Repetitio	0.0385	1	0.0385	0.0149	0.9030
		Error	480.6948	186	2.5844		
	OBA	Side	0.0000	1	0.0000	0.0000	1.0000
		Repetition	0.0004	1	0.0004	0.0000	0.9963
		Side*Repetitio	0.0048	1	0.0048	0.0003	0.9873
		Error	3528.0618	188	18.7663		
VAULT	PT-FMT	Side	53.4553	1	53.4553	5.9370	0.0158
		Repetition	0.0058	1	0.0058	0.0006	0.9798
		Side*Repetitio	0.0050	1	0.0050	0.0006	0.9813
		Error	1674.7089	186	9.0038		
	PT-AS	Side	5.1811	1	5.1811	0.4027	0.5265
		Repetition	0.4544	1	0.4544	0.0353	0.8511
		Side*Repetitio	0.5699	1	0.5699	0.0443	0.8335
		Error	2418.6855	188	12.8653		
	PT-TS	Side	3.0856	1	3.0856	0.2626	0.6089
		Repetition	0.0221	1	0.0221	0.0019	0.9655
		Side*Repetitio	0.0009	1	0.0009	0.0001	0.9930
		Error	2208.9177	188	11.7496		

Appendix. Two-way ANOVA. Difference between the right and left sides, between the first and second repetition and interaction between side and repetition

Region	Trait		SS	Degr. of	MS	F	p
	BR-PT	Side	1.0591	1	1.0591	0.0624	0.8029
		Repetition	0.0020	1	0.0020	0.0001	0.9913
		Side*Repetitio	0.0000	1	0.0000	0.0000	1.0000
		Error	3188.6543	188	16.9609		
	BR-AS	Side	263.297	1	263.297	11.564	0.0008
		Repetition	0.024	1	0.024	0.001	0.9740
		Side*Repetitio	0.000	1	0.000	0.000	1.0000
		Error	4280.3448	188	22.768		
	BR-PO	Side	111.2110	1	111.2110	5.5721	0.0193
		Repetition	0.0066	1	0.0066	0.0003	0.9855
		Side*Repetitio	0.0431	1	0.0431	0.0022	0.9630
		Error	3752.2236	188	19.9586		
	LA-AS	Side	21.1117	1	21.1117	0.6039	0.4381
		Repetition	0.0000	1	0.0000	0.0000	1.0000
		Side*Repetitio	0.0000	1	0.0000	0.0000	1.0000
		Error	6432.8959	184	34.9614		
BASE	EAM-ZMI	Side	0.2473	1	0.2473	0.0218	0.8828
		Repetition	0.0400	1	0.0400	0.0035	0.9527
		Side*Repetitio	0.0130	1	0.0130	0.0011	0.9731
		Error	2110.8081	186	11.3484		
	AS-TS	Side	5.5216	1	5.5216	0.9019	0.3435
		Repetition	0.0200	1	0.0200	0.0033	0.9545
		Side*Repetitio	0.0169	1	0.0169	0.0028	0.9582
		Error	1150.9307	188	6.1220		
	BA-EAM	Side	0.0426	1	0.0426	0.0042	0.9486
		Repetition	0.0099	1	0.0099	0.0010	0.9752
		Side*Repetitio	0.0023	1	0.0023	0.0002	0.9881
		Error	1924.3713	188	10.2360		
	PNS-TS	Side	22.3587	1	22.3587	2.8623	0.0923
		Repetition	0.0048	1	0.0048	0.0006	0.9802
		Side*Repetitio	0.0008	1	0.0008	0.0001	0.9918
		Error	1468.5519	188	7.8114		
	ZTI-PNS	Side	4.6294	1	4.6294	0.4214	0.5171
		Repetition	0.0091	1	0.0091	0.0008	0.9771
		Side*Repetitio	0.0471	1	0.0471	0.0043	0.9479
		Error	1911.6143	174	10.9863		
	ZMI-AS	Side	2.1828	1	2.1828	0.1050	0.7463
		Repetition	0.0137	1	0.0137	0.0007	0.9795
		Side*Repetitio	0.0022	1	0.0022	0.0001	0.9918
		Error	3866.0320	186	20.7851		