Evolution and Human Behavior 33 (2012) 708 – 714

Evolution and Human Behavior

Original Article

Cues to fertility: perceived attractiveness and facial shape predict reproductive success

Lena S. Pflüger[a,*], Elisabeth Oberzaucher[a], Stanislav Katina[b,c], Iris J. Holzleitner[a], Karl Grammer[a]

[a]Department of Anthropology, University of Vienna, Althanstrasse 14, A-1090, Vienna, Austria
[b]School of Mathematics and Statistics, University of Glasgow
[c]Department of Applied Mathematics and Statistics, Faculty of Mathematics, Physics and Informatics, Comenius University, Bratislava

Initial receipt 19 April 2011; final revision received 23 May 2012

Abstract

Attractive facial features in women are assumed to signal fertility, but whether facial attractiveness predicts reproductive success in women is still a matter of debate. We investigated the association between facial attractiveness at young adulthood and reproductive life history—number of children and pregnancies—in women of a rural community. For the analysis of reproductive success, we divided the sample into women who used contraceptives and women who did not. Introducing two-dimensional geometric morphometric methodology, we analysed which specific characteristics in facial shape drive the assessment of attractiveness and covary with lifetime reproductive success. A set of 93 (semi)landmarks was digitized as two-dimensional coordinates in postmenopausal faces. We calculated the degree of fluctuating asymmetry and regressed facial shape on facial attractiveness at youth and reproductive success. Among women who never used hormonal contraceptives, we found attractive women to have more biological offspring than less attractive women. These findings are not affected by sociodemographic variables. Postmenopausal faces corresponding to high reproductive success show more feminine features—facial characteristics previously assumed to be honest cues to fertility. Our findings support the notion that facial attractiveness at the age of mate choice predicts reproductive success and that facial attractiveness is based on facial characteristics, which seem to remain stable until postmenopausal age.

Keywords: Facial attractiveness; Facial shape; Reproductive success; Fluctuating asymmetry; Geometric morphometrics

1. Introduction

Female faces are assumed to display honest cues to fertility by means of facial attractiveness (Grammer, Fink, Møller, & Thornhill, 2003). Previous studies support the notion that the perception of women's facial attractiveness is based on morphological indicators of physiological and developmental condition. For instance, small random deviations from perfect bilateral symmetry (Van Valen, 1962), so-called fluctuating asymmetries (FAs), are known to negatively affect ratings on facial attractiveness (Grammer & Thornhill, 1994; Rhodes, Proffitt, Grady, & Sumich, 1998; Mealey, Bridgstock, & Townsend, 1999). As these small morphological deviations develop early during embryogenesis as an outcome of genomic and environmental stress, a low level of FA has been linked to developmental stability (Parsons, 1992; Gangestad, Thornhill, & Yeo, 1994; Thornhill & Møller, 1997) and health (see meta-analysis of Van Dongen & Gangestad, 2011). Other anthropometric indicators are so-called hormone markers. In humans, the basic facial proportions are affected by prenatal sex steroides. For instance, the influence of oestrogene leads to 'typically female' features (e.g., less robust jaws, high eybrows, and fuller lips), which are known to positively affect ratings on female attractiveness and are supposed to serve as reliable indicators of fecundity (Johnston & Franklin, 1993; Fink et al., 2005).

Even though the impact of facial attractiveness on human mate choice is well documented and theoretically discussed, no distinctive facial characteristics, which

* Corresponding author.
E-mail address: lena.pflueger@univie.ac.at (L.S. Pflüger).

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http://dx.doi.org/10.1016/j.evolhumbehav.2012.05.005

covary with female reproductive success, have been identified so far. Three previous studies investigated the relation between *perceived* facial attractiveness at the age of young adulthood and final number of children. Hill and Hurtado (1996) showed that facial attractiveness correlates with the number of children in a hunter and gatherer society. Pawlowski, Boothroyd, Perrett, and Kluska (2008) and Jokela (2009) investigated the association between facial attractiveness at youth and postmenopausal number of children in samples of contemporary women. Jokela's findings indicate that, for women living in industrialized settings, physical attractiveness is related to the number of children, while Pawlowski et al. (2008) failed to show any association.

The aim of the present study was to shed light on the signalling value of female facial attractiveness in terms of reproductive success. In contrast to previous research, we applied a new approach of landmark-based geometric morphometric methodology (GMM) in order to analyse female facial shape corresponding to reproductive success. We hypothesized that if perceived attractiveness at the age of young adulthood predicts female reproductive success, faces must possess anthropometric measurable indicators, which have driven the perception at young age.

2. Materials and methods

2.1. Data collection

Questionnaire data and facial photographs were collected from 88 women of a rural community of 1868 inhabitants in Carinthia (Austria). All women were at postmenopausal age (mean±S.D.=61.04±8.70 years) and in a long-term relationship with their current partner (mean age at the start of the partnership±S.D.=20.07±4.01 years). Subjects were interviewed about their total number of children. Besides the biological offspring, reproductive success was measured by estimating number of pregnancies, taking (induced) abortions into account.

In order to control for potentially confounding variables, we collected the following information: age of participants, years of marriage to their husband (father of their children), education of subject and corresponding husband, income of subject and corresponding husband before pension, family contact of subject while raising children, and religiosity of subject. Additionally, women were asked about the use of hormonal contraceptives (HC) during their fertile years.

We collected facial portraits showing participants at young adulthood (aged 19–23 years). Images were mostly wedding pictures taken by the same photographer. Additionally, we took standardized frontal pictures (constant in lightning condition, camera-to-subject distance, and focal length) of women's present-day faces while participants showed neutral expressions (i.e., having mandible relaxed with teeth not touching and lips closed freely).

2.1.1. Sample subdivision

For the analysis of facial shape, portraits which were not exactly frontally imaged (N=10) were excluded (e.g., when heads were rotated vertically or horizontally). This resulted in a total of 78 women used for the assessment of the relation between FA and facial attractiveness. Two women had to be excluded in the analyses considering reproductive success due to missing data (husbands did not fill out the questionnaire). For the analysis considering facial attractiveness and reproductive success, the sample was divided into women who used HCs (N=46) and women who never used HCs (N=40) during their fertile years.

2.2. Attractiveness rating

Facial pictures showing participants at young adulthood were aligned in colour, size, tonal value, and contrast. Hair and accessories were masked with an oval frame. One hundred twenty-five male students (mean age±S.D.=23.47±3.90 years) of the University of Vienna evaluated the female faces on the items 'attractive' and 'sexy' with sliders ranging from 1 (*not attractive/sexy*) to 100 (*highly attractive/sexy*). From past experience, we expected that the evaluation of 88 stimuli easily overtaxes participants and leads to exhaustion. In order to prevent such bias, each male participant was requested to evaluate a subset of 20 randomly chosen faces. The rating study resulted in at least 20 ratings per woman.

2.3. Statistical analyses

Statistical analyses were performed in *R* (R Development Core Team, 2010). All univariate two-variable associations were estimated by Spearman correlation coefficient r_s, and the test of zero correlation (9999 permutations) was used to test this association. We controlled for the confounding effect of age, years of marriage, income of husband, and own income while estimating the association between facial attractiveness and number of children by Spearman partial correlation coefficient r_s. The test of zero partial correlation (9999 permutations) was used to test this association. The mean levels of facial attractiveness (attractiveness/sexy) between women who used HCs and women who did not were compared by the two-sample Wilcoxon test (9999 permutations). The effect of family contact, education of subject, education of husband, and religiosity (church appendance) on number of children was tested by the Kruskal–Wallis test (9999 permutations).

2.4. Landmark-based GMM

Landmark-based GMM deals with the analysis of geometrical information about the form (also called geometric morphometrics; Bookstein, 1991). Digitizing (semi)landmarks on facial representations [two-dimensional (2D) portraits] provides individual geometric information of each specimen based on (semi)landmark coordinates. The main idea of GMM analysis is to adjust Cartesian coordinates of (semi)landmarks with respect to position, orientation (rotation), and scale (size) using *Procrustes superimposition* [Generalized Procrustes Analysis (GPA), Bookstein, 1991]. The resulting centred Procrustes shape coordinates (centred PSCs; Procrustes tangent coordinates) capture shape information only and can be used for subsequent multivariate statistical analyses. One major advantage of using GMM is that statistical results (e.g., multivariate linear regression) emerge in terms of estimated (semi)landmark coordinates and findings can be visualized (Schaefer et al., 2006).

2.4.1. Landmark setup and Procrustes superimposition

The shape of women's present-day faces was determined by digitizing 2D coordinates of 35 anatomical landmarks, which were based on biologically homologous facial traits. Fifty-eight semilandmarks (slidings; Gunz, Mitteroecker, & Bookstein, 2005) on curves (eyebrows, pupils, lips, and chin) were added to improve the shape description of the faces (see supplementary material, available on the journal's website at www.ehbonline.org). With respect to a reference face, the semilandmarks on the target faces were iteratively slid along the particular curves until bending energy is minimized (Slice, 2005). (Semi)landmarks were digitized by one person only. In order to assess the intraobserver error, a randomly selected face was digitized repeatedly 10 times (with at least 24-h time lapse). This resulted in a median intraobserver error of 1.44% per (semi)landmark with respect to the whole sample median variance.

In order to transform Cartesian coordinates into shape coordinates, a GPA was performed. First, the centroid of each form was computed, and all (semi)landmark configurations were translated to the same origin. Next, landmark configurations were scaled to the same size (centroid size) and finally rotated around the origin in order to minimize the sum of squared distances between corresponding (semi) landmarks (Rohlf & Slice, 1990). This resulted in PSCs, i.e., coordinates that are invariant to change in location, rotation, and scale (Slice, Bookstein, Marcus, & Rohlf, 1996).

2.4.2. Measuring FA

To analyse facial FA, we quantified the dissimilarities in shape (deviations of PSCs) between the original configurations and their relabelled reflections (RRs; Mardia, Bookstein, & Moreton, 2000).

The original (semi)landmarks and their RR counterparts were jointly submitted to GPA in order to register both in the same shape space (Bookstein, 1991). Both configurations (original and RR) were centred to their Procrustes mean resulting in original and RR centred PSCs, respectively. FA expresses the extent to which the sample fluctuates around its own mean asymmetry (Mardia et al., 2000). Thus, the individual degree of FA was assessed as the total sum of squared distances (Procrustes shape distances) between centred PSCs of original and RR configurations (Bock & Bowman, 2006).

2.4.3. Shape regression

We determined the linear association between facial shape and three independent variables (attractiveness scores at youth, number of children, and number of pregnancies) for women who never used HCs only (not exactly frontally imaged facial portraits excluded, N=3). Based on a multivariate ordinary linear regression model (*shape regression*), we calculated a linear regression function for each shape coordinate separately. Estimated R^2 describes the quality of linear relationship between shape and independent variables [mean R^2=mean relation of all (semi)landmarks; min R^2=R^2 of single (semi)landmark with the weakest relation to the independent variable; max R^2=R^2 of single (semi)landmark with the strongest relation to the independent variable]. Results of shape regression were visualized via *thin-plate spline* (TPS) deformation grids (Bookstein, 1991). Estimated slopes correspond to the shape changes of a particular (semi)landmark (displacement of its positions) that occur in one unit change of the independent variable (Schaefer et al., 2006). In this study, TPS deformation grids illustrate the changes in shape from the Procrustes mean shape to the estimated shape corresponding to the most negative and the most positive change of the independent variables. To ease the visualization of a shape change, TPS grids were extrapolated 1.2 times in the negative and positive directions of the independent variable.

3. Results

3.1. Perceived facial attractiveness and reproductive success

Table 1 presents the association between perceived facial attractiveness (sexy and attractive) and reproductive success (number of children and pregnancies) of women who never used HC compared to women who used HC during their fertile years. Results are presented with and without adjustments for sociodemographic variables. We observed no relation between facial attractiveness and the use of HCs (N=88; attractive: p=.256; sexy: p=.278).

3.1.1. Women who never used HC (N=40)

Women who never used HC showed a positive association between facial attractiveness at youth and reproductive success. This association remained equally significant with adjustment for age, years of marriage, and income (Table 1). Education of subject (p=.945) and corresponding husband (p=.867), family contact of subject (p=.562), and religiosity of subject (p=.360) were not associated with the number of children. For descriptive statistics of the tested sociodemographic variables, see Tables 2 and 3.

As illustrated in Fig. 1, the lowest number and the highest number of children and pregnancies are represented by few data points. In order to test the stability of this finding, we performed the same analysis after excluding extreme values (women with zero, five, or six children/women with zero or

Table 1
Correlations of perceived facial attractiveness and reproductive success with and without adjustments for sociodemographic variables (SDVs)

	Adjustments for SDVs	No contraceptives (N=40)		Use of contraceptives (N=46)	
		No. of children	No. of pregnancies	No. of children	No. of pregnancies
Attractive	Not adjusted	r_s=0.374*	r_s=0.514**	r_s=−0.081 NS	r_s=−0.079 NS
	Age	r_s=0.364*	r_s=0.505***	r_s=−0.082 NS	r_s=−0.080 NS
	Years of marriage	r_s=0.372**	r_s=0.509***	r_s=−0.078 NS	r_s=−0.076 NS
	Income	r_s=0.374** (s)	r_s=0.516*** (s)	r_s=−0.058 NS (s)	r_s=−0.067 NS (s)
		r_s=0.379* (h)	r_s=0.517*** (h)	r_s=−0.043 NS (h)	r_s=−0.040 NS (h)
Sexy	Not adjusted	r_s=0.425**	r_s=0.568**	r_s=−0.102 NS	r_s=−0.076 NS
	Age	r_s=0.414**	r_s=0.553***	r_s=−0.103 NS	r_s=−0.079 NS
	Years of marriage	r_s=0.423**	r_s=0.563***	r_s=−0.092 NS	r_s=−0.068 NS
	Income	r_s=0.424** (s)	r_s=0.567*** (s)	r_s=−0.079 NS (s)	r_s=−0.065 NS (s)
		r_s=0.440** (h)	r_s=0.575*** (h)	r_s=−0.060 NS (h)	r_s=−0.031 NS (h)

NS: not significant; *.01 ≤ p<.05; **.001 ≤ p<.01; ***p<.001. Association of perceived facial attractiveness and reproductive success (test of zero correlation, 9999 permutations, Spearman correlation coefficient) in women who *did not use* contraceptives and women who *used* contraceptives. Values are presented with and without adjustments for age, years of marriage, and income (test of zero partial correlation, 9999 permutations, Spearman partial correlation coefficient). (s)=subject, (h)=husband.

six to eight pregnancies, N=5). The positive correlation with number of children remained but was no longer significant (Fig. 1, left panel, regression line adjusted), whereas the significant positive association with number of pregnancies persisted (Fig. 1, right panel, regression line adjusted).

3.1.2. Women who used HC (N=46)

In women who used contraceptives during their fertile years, we found no association between perceived facial attractiveness and reproductive success. This lack of an association remained after adjustment for age, years of marriage, and income (Table 1). Education of subject (p=.081) and corresponding husband (p=.517), family contact of subject (p=.058), and religiosity of subject (p=.359) were also not associated with the number of children born to women in this group.

3.2. FA and reproductive success

We found a negative correlation between the degree of postmenopausal FA and facial attractiveness at youth (attractive: r_s=−0.205, N=78, p=.034; sexy: r_s=−0.222, N=78, p=.03). The degree of facial FA was not related to subjects` present age [r_s=−0.108, N=78, not significant (NS)]. We observed no association between the degree of postmenopausal FA and reproductive success either in women who used HC (children: r_s=−0.10 NS; pregnancies: r_s=−0.02 NS) during their fertile years or in women who never used HC (children: r_s=0.15 NS; pregnancies: r_s=0.13 NS). The negative association between facial attractiveness and FA in the subsamples did not persist. In both groups, FA was independent of subject's age.

3.3. Shape regression

As women with extremely high and low reproductive success showed to have a strong effect on the association between attractiveness and reproductive success, we excluded women with no children/pregnancies and women with more than four children or more than five pregnancies (N=4, plus three not exactly frontally imaged facial portraits, see Section 2.4.3). This resulted in a sample size of 33 women.

The shape regression revealed covariations between the shape of postmenopausal faces and all three independent variables. The TPS deformations grids in Figure 2 illustrate facial shape associated with facial attractiveness at youth (upper row), number of children (middle row), and number of pregnancies (lower row). The middle column represents the consensus (Procrustes mean shape).

Faces corresponding to a decreasing level of attractiveness, number of children, and number of pregnancies (left column) have thinner lips, flatter noses, broader eyebrows, and more angular jaws than the consensus. Faces corresponding to an increasing level of attractiveness, number of children, and number of pregnancies (right column) have fuller lips, small and more tapered noses, higher arched eyebrows, and less angular jaws compared to the consensus.

Table 2
Descriptive statistics for sociodemographic variables (age, years of marriage, and income)

	Description	No contraceptives (N=40)	Use of contraceptives (N=46)
Age (in years)	Age at data collection (subject)	65.60 (9.15)	57.87 (6.04)
Years of marriage	Years between marriage and data collection	43.15 (9.09)	35.28 (6.51)
Income (after tax per month in Euro)	Subject	362.47 (600.34)	592.78 (672.68)
	Husband	1214.45 (491.73)	1788.98 (769.25)

Sociodemographic variables collected in continuous scale. Values are: means (S.D.).

Table 3
Descriptive statistics for categorical sociodemographic variables (family contact, education, and religiosity)

Variable	Contraceptives	Characteristics	Level 0	Level 1	Level 2	Level 3	Level 4	Level 5
[a]Family contact	No contraceptives	Frequencies	0	8	5	27	–	–
(subjects' contact	(*N*=40)	Percentages (S.D.)	0.00	20 (6.32)	12.5 (5.23)	67.5 (7.41)	–	–
to family members while	Use of contraceptives	Frequencies	1	12	3	30	–	–
raising children)	(*N*=46)	Percentages (S.D.)	2.17 (2.15)	26.09 (6.47)	6.52 (3.64)	65.22 (7.02)	–	–
[b]Education of subject	No contraceptives	Frequencies	0	2	12	22	1	3
(level of graduation,	(*N*=40)	Percentages (S.D.)	0.00	5.00 (3.45)	30.00 (7.25)	55.00 (7.87)	2.50 (2.47)	7.50 (4.16)
apprenticeship)	Use of contraceptives	Frequencies	0	2	5	31	5	3
	(*N*=46)	Percentages (S.D.)	0.00	4.35 (3.01)	10.87 (4.59)	67.39 (6.91)	10.87 (4.59)	6.52 (3.64)
[b]Education of husband	No contraceptives	Frequencies	0	1	5	31	2	1
(level of graduation,	(*N*=40)	Percentages (S.D.)	0.00	2.50 (2.47)	12.50 (5.23)	77.5 (6.60)	5.00 (3.45)	2.50 (2.47)
apprenticeship)	Use of contraceptives	Frequencies	1	0	0	38	3	4
	(*N*=46)	Percentages (S.D.)	2.17 (2.15)	0.00	0.00	82.61 (5.59)	6.52 (3.64)	8.7 (4.15)
[c]Religiosity of subject	No contraceptives	Frequencies	6	8	11	13	2	–
(church attendance)	(*N*=40)	Percentages (S.D.)	15.00 (5.65)	20.00 (6.32)	27.50 (7.06)	32.50 (7.41)	5.00 (2.47)	–
	use of contraceptives	Frequencies	3	20	18	5	0	–
	(*N*=46)	Percentages (S.D.)	6.52 (3.64)	43.48 (7.31)	39.13 (7.20)	10.87 (4.59)	0.00	–

Frequencies and percentages (with standard deviations) of sociodemographic variables collected in ordinal scale. [a]Family members (FM) including FM of subject and FM of corresponding husband (parents, grandparents, siblings, cousins, uncle, aunt). Levels: 0=no contact with FM, 1= contact with few FM, 2=contact with half of the FM, 3=contact with almost all FM. [b]Levels: 0=no education, 1=primary school, 2=low-level secondary school, 3=middle-level secondary school, 4=high-level secondary school, 5=university degree. [c]Religiosity (church attendance). Levels: 0=never, 1=on holy days, 2=once a month, 3=once a week, 4=several times a week.

4. Discussion

In the first part of our research, contemporary male students evaluated facial attractiveness of female participants based on pictures taken at the age of young adulthood. In order to determine the relation of facial attractiveness and reproductive success, we separated women who used HCs from women who did not. For the latter, facial attractiveness was positively related to the number of children and pregnancies (Table 1), supporting our hypothesis that physical attractiveness predicts female reproductive success. While this effect was strongly driven by women with very high or low reproductive success, it remained significant after exclusion of women with no or more than five pregnancies. For women who utilized birth control via HCs, the association was not present (Table 1), indicating that hormonal influence was decisive for our results. Hormone supplements are a common way to exert birth control in contemporary women and have to be considered in further research. During a fertility window of approximately 40 years, other contraceptive methods have been used (e.g., condoms, temperature measurements), and subjects might also have differed in terms of reproductive behaviour (e.g., copulation frequency). As these intervening factors were

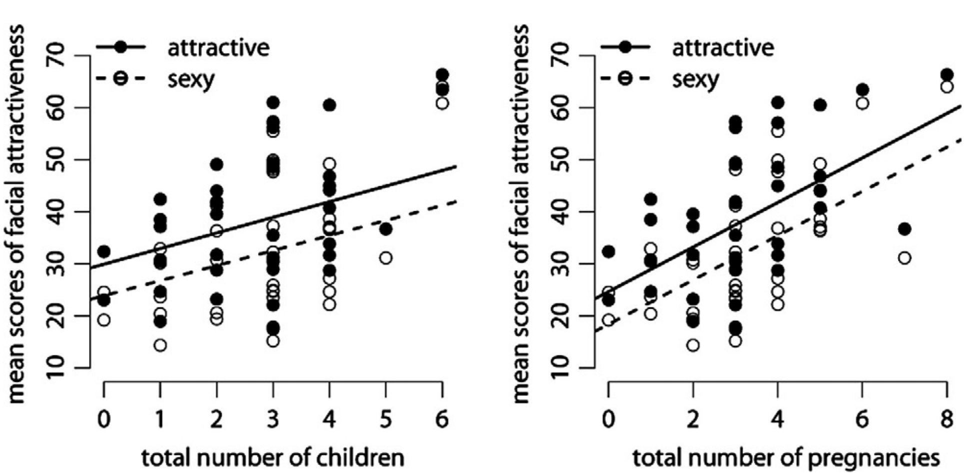

Fig. 1. Casual relation between reproductive success and perceived facial attractiveness in women *who never used HCs* (*N*=40). Left panel: correlation between number of children and facial attractiveness (sexy: r_s=.425, *p*=.001; attractive: r_s=.374, *p*=.01). Right panel: correlation between number of pregnancies and facial attractiveness (sexy: r_s=.568, *p*<.001; attractive: r_s=.514, *p*<.001). Regression lines (*N*=35) are calculated after excluding extreme values, resulting in women with: one to four children in the left panel (sexy: r_s=.265, *p*=.061; attractive: r_s=.240, *p*=.071) and women with one to five pregnancies in the right panel (sexy: r_s=.468, *p*=.002; attractive: r_s=.432, *p*=.005).

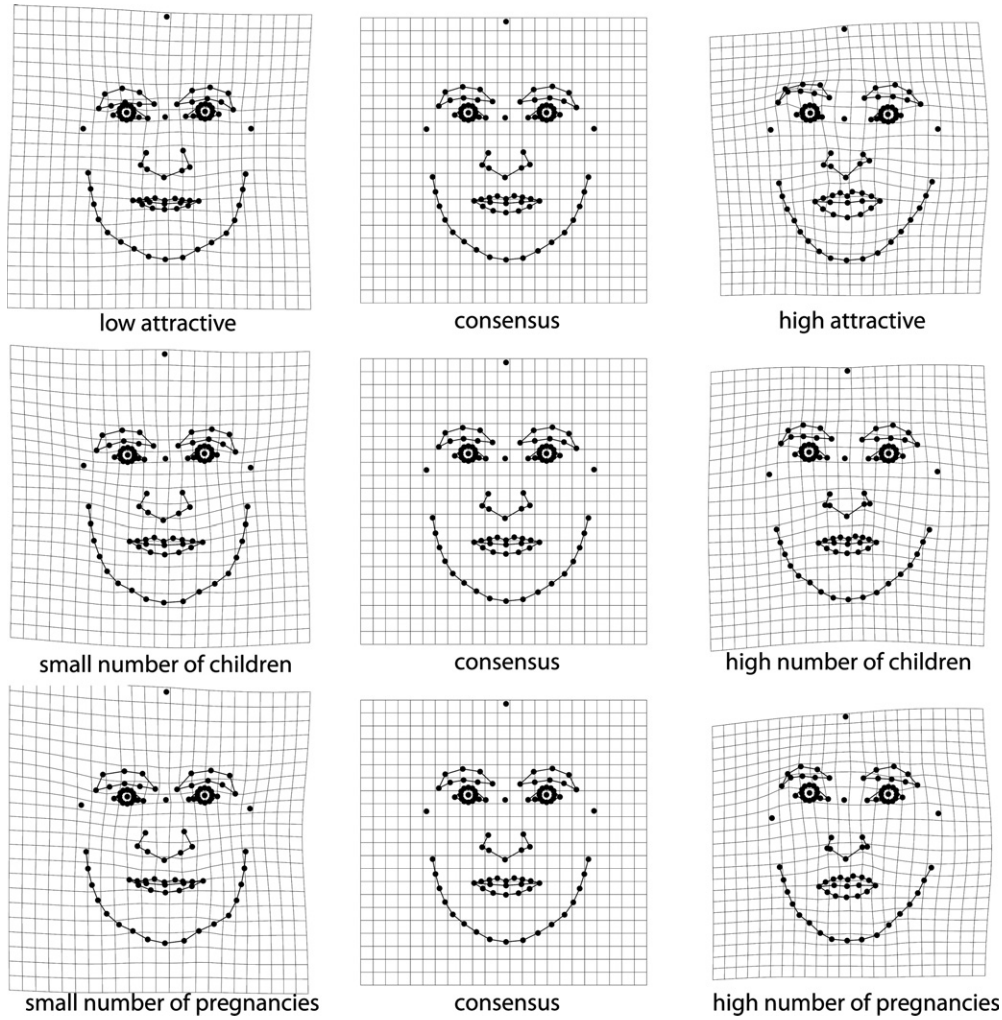

Fig. 2. Shape regression of women *who never used HCs* visualized by TPS deformation grids (N=33). Top: facial shape and (perceived) attractiveness at youth (mean R^2=.178, min R^2=.011, max R^2=.456). Middle: facial shape and number of children (mean R^2=.236, min R^2=.029, max R^2=.463). Bottom: facial shape and number of pregnancies (mean R^2=.242, min R^2=.035, max R^2=.459). Middle panels of each row correspond to the Procrustes mean shape (no deformation of the grid). Panels on the left correspond to a low (minimal) value of independent variable. Panels on the right correspond to a high (maximal) value of the independent variable. To ease the visualization, TPS grids were extrapolated 1.2 times in negative and positive direction of each independent variable.

impossible to retrace, a future longitudinal study is needed in which those parameters are constantly recorded throughout the fertile period.

Almost all of our participants were mountain farmers and were therefore supposed to be quite homogenous in terms of socioeconomic factors. Nevertheless, we have an age range of approximately 30 years in our sample. Also, subjects' own income in both subsamples and religiosity of women who never used contraceptives were highly variable (Tables 2 and 3). We controlled for the effect of all sociodemographic variables even though none of these variables were related to the number of children or influenced our findings in either of our subsamples.

In line with previous research (e.g., Grammer & Thornhill, 1994; Mealey et al., 1999), we identified a negative correlation between FA and facial attractiveness in our pooled sample of N=78 women. While previous studies used the same images for attractiveness ratings and determination of FA, our ratings were based on pictures taken at youth, while the facial shape was measured from photos taken approximately 40 years later. This indicates that the link between FA and attractiveness does not dissociate in life history. In our subsamples of women who used HC and women who did not, FA was neither related to attractiveness nor to reproductive success. The former can be explained by an insufficient subsample size compared to the pooled sample of 78 women. Nonfindings for the latter are less surprising because for women who reported a use of HC results are biased by hormone intake. In our sample of women who did not take contraceptives, we additionally regressed facial shape on evaluated attractiveness and lifetime reproduction. Visualizations of shape regression via TPS deformation grids revealed distinctive facial proportions in postmenopausal faces corresponding to a highly attractive appearance at youth: full and large lips, a small and tapered nose, high eyebrows, big pupils, and a less angular jaw. Those sexually dimorphic or neotenous features were not found in faces corresponding to a low level of perceived attractiveness. Interestingly, postmenopausal faces corresponding to a high reproductive success (high number of children and pregnancies) displayed the same 'typically female' features. As mentioned above, sexually dimorphic proportions or so-called hormone markers (Fink et al., 2005) are known to affect judgments of facial attractiveness in mate choice (Cunningham, 1986; Jones et al., 1995; Grammer et al., 2003) and are supposed be honest cues to fertility and health (Grammer, Fink, Moller, & Manning, 2005). All three independent variables used for shape regression were found to be independent of current age and explained approximately the same amount of shape changes (attractiveness at youth: 18%; number of children/pregnancies: 24%). In conclusion, our findings underline our assumption that facial attractiveness at the age of mate choice (young adulthood) is related to female reproductive success unless HCs were used. Our findings also indicate that postmenopausal faces still possess anthropometric indicators, which have driven the perception of attractiveness at young age. In this manner, we assume that a low degree of FA does not explain female attractiveness and reproductive success as a *single* feature, as it seems to be interconnected with other 'honest' cues to fertility.

Supplementary Materials

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.evolhumbehav.2012.05.005.

Acknowledgments

We thank all our participants for their willingness to take part in our research. Special thanks goes to M. and E. Oberzaucher for their generous help and hospitality during data collection. We also thank our colleagues S.F. Schmehl, K. Meindl, M. Coquerelle, and S. Senck for their support.

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