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Original Article

The sound of female shape: a redundant signal of vocal and facial attractiveness

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ABSTRACT

There is more to female attractiveness than a pretty face. Human mate choice decisions are guided by different cues, which in combination may give a better estimate of a general condition. We hypothesized that such signal redundancy might be true for vocal and visual cues of human female attractiveness. To test this we used photographs of women's faces, recorded their voices and asked men to rate both types of stimuli on attractiveness. We found a significant relationship between males' ratings of female faces and voices. Moreover, low levels of fluctuating asymmetry of women's bodies and faces were associated with high ratings on facial and vocal attractiveness. Applying the Geometric Morphometric Methodology we performed a multivariate regression analysis of attractiveness ratings with landmark data obtained from women's faces. We found similar facial shape changes for ratings of facial and vocal attractiveness that are both negatively related to facial and body FA. Findings suggest that females with an attractive face also tend to have an attractive voice and that this redundant information is reflected in female facial shape.

1. Introduction

Animals show a great variety in how they advertise their mate value. In some species courtship behaviors are highly complex and often involve multiple cues from different modalities. For instance, several bird and fish species present bright colors in concert with elaborate songs or other intricate courtship behaviors.

While in animal species multiple cues are most prominent in males, findings in human research suggest that multiple cues are important when males assess female mate quality.

The female face alone – the most reliable predictor for overall physical attractiveness (Currie & Little, 2009) – bears multiple features that play a crucial role in the perception of attractiveness. Such features are skin texture, skin coloration (*e.g.*, Fink, Grammer, & Thornhill, 2001; Matts, Fink, Grammer, & Burquest, 2007; Stephen, Law Smith, Stirrat, & Perrett, 2009), non-average sexually dimorphic features so called 'hormone markers' (*e.g*, Johnston, 2006) and facial symmetry (*e.g.*, Grammer & Thornhill, 1994; Perrett et al., 1999).

Although the significance of different cues in the perception of female attractiveness is undisputed, questions remain on the role of multiple cues in human mate choice. For instance, if a single feature already indicates mate quality, what is the benefit of having additional cues communicating the same mate value? Moreover, the development of anatomical structures or complex behaviors entails energetic costs. For this reason there must be a trade-off between the costs and benefits of using multiple cues in human mate choice.

To explain the adaptive function of multiple cues in animal mate choice several theoretical models have been devised that might be also applied to human mate choice decisions. For instance, the 'multiple-message' hypothesis (Johnstone, 1996; Møller & Pomiankowski, 1993) claims that different cues convey different aspects of mate quality. More precisely, preferences for different features evolved because each of these features communicates a specific quality or fitness aspect. Cues may either inform about an overall condition over long time scales or about a current physical state. The former may be good indicators of gene quality or immunocompentence (Kanda, Tsuchida, & Tamaki, 1996; Verthelyi, 2006) whereas the latter refer to rather flexible cues such as peculiarities of the skin texture and skin coloration (Fink et al., 2001; Matts et al., 2007; Stephen, Law Smith, Stirrat, & Perrett, 2009) that indicate the current female reproductive state. Although different features convey different qualities, they may add up to enable an connective evaluation of a potential mate's overall quality (Candolin, 2003).

In contrast to the 'multiple-message', the 'redundant signaling' hypothesis (or 'back-up signal' hypothesis) claims that multiple cues convey similar information on different communication channels, thereby lowering the probability of making inaccurate assessments of mate quality. In other words, multiple cues serve as a back-up signal that ensures a low rate of mate choice errors because a potential partner is assessed by two or even more features. Consequently, the 'redundant signaling' or 'back-up' hypothesis requires multiple cues as reliable indicators of a common mate value. These 'redundant' indicators are more

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likely to inform about an overall condition over long time scales rather than being context dependent such as indicators of a current physical state. Moreover, assessments of an overall condition for long-term decisions may be more reliable when they are based on multiple features with a stable appearance. Morphological features have such a stable appearance and are largely context independent because they are manifested during the course of gestation. Therefore they represent good candidates to empirically test the back-up hypothesis with regard to human mate choice decisions. Particularly correlations between morphological traits such as facial symmetry and sexual dimorphism (*i.e.*, 'hormone markers') are considered as evidence that these traits signal a common underlying mate value (Gangestad & Thornhill, 2003; Koehler, Simmons, Rhodes, & Peters, 2004; Little et al., 2008).

Symmetry of bilateral structures is estimated as a low level of asymmetry, which is the formal sum of directional asymmetry (DA) and fluctuating asymmetry (FA). In contrast to DA, which measures whether one side is consistently different from the other, FA describes small random deviations from perfect bilateral symmetry (Valen, 1962). These small deviations arise during embryogenesis and reflect the ability of a developing organism to cope with environmental stressors (Waddington, 1957). Hence, a low level of FA of fully developed anatomical structures is assumed to be a non-falsifiable signal of individual's immune competence and developmental stability (Gangestad, Thornhill, & Yeo, 1994; Thornhill & Gangestad, 1993). The significance of FA on mate choice decisions has been demonstrated for several species (Møller & Thornhill, 1998). Low levels of FA in both faces and body structures positively influence ratings of human attractiveness and health (Gangestad, Simpson, Cousins, Garver-Apgar, & Christensen, 2004; Grammer & Thornhill, 1994; Perrett et al., 1999). Previous research showed that attractiveness ratings of the female face and body are significantly associated with both the amount of fluctuating asymmetry and specific localized shape differences in regions of known estrogen sensitivity (Schaefer et al., 2006). These findings support the assumption that symmetry might serve as a back-up signal in human mate choice decision (Currie & Little, 2009).

It is a plausible conclusion that the signal of FA may be present in all anatomical structures because they are subjected to the same developmental conditions during ontogeny. Hence, FA also occurs in non-visible inner anatomical structures such as the voice apparatus (Hirano, Kurita, Yukizane, & Hibi, 1989) and might therefore be perceptible in acoustic cues produced by this voice apparatus. Since vocal communication plays a predominant role in human social interactions, acoustic cues should transport important information about potential mates particularly when visual cues are ambiguous or not available. Also, a relationship between body symmetry and vocal attractiveness in both sexes has been illustrated (Hughes, Harrison, & Gallup, 2002) but the link between acoustic cues in relation to female facial and body FA has not been investigated yet. Previous studies have already found an influence of acoustic characteristics (*e.g.*, voice pitch) on perceptions of female attractiveness (Collins & Missing, 2003; Feinberg, DeBruine, Jones, & Perrett, 2008). For example, Feinberg et al. (2005) found that men preferred face images of women with higher pitched voices over women with lower pitched voices. Moreover, in their female samples, the author showed that voice pitch is moderately correlated with facial femininity, which has been assessed via a composite index of some facial distance ratios as defined by Penton-Voak et al. (2001). However, such a composite index omits any information about facial shape. For example, this composite index includes the ratio between the cheekbone distance D3 (distance between the leftmost and rightmost pixels of the face on a horizontal line beneath the eyes) and the jaw width D6 corresponding to the face width at the *y* coordinates of the mouth corners. This ratio, like any ratio, lacks information about the relative positions of all the endpoints of the measurements (Slice, 2005). Thus, it is unlikely that such a composite index conveys sufficient information about facial cues relevant for the perception of attractiveness or femininity. This may be the reason why the ratio used to compute the composite index or the composite index itself is not significantly correlated or shows significant but low correlation with visual judgments of facial attractiveness (Penton-Voak et al., 2001). Therefore, facial shape analysis should include morphometric tools that preserve the relative position of the above mentioned endpoints to quantify and visualize facial cues related to perceived attractiveness.

It was the aim of the current study to show that multiple cues that share a common mate value serve as back up signals in human mate choice decisions. To identify such a redundancy we investigated both visual and acoustic cues and their association with measures of shape.

For the purpose of our study, we collected photographs of female faces and recordings of female voices and we measured females' body and facial FA. Subsequently we asked two different pools of male raters to evaluate either the attractiveness of the female faces or the attractiveness of the corresponding voice recordings. A third pool of males was recruited for ratings of an independent sample of female faces. To go beyond previous research we applied a landmark-based Geometric Morphometric Methodology (GMM)—a multivariate statistical tool which was developed to capture, statistically analyze and visualize shape information of anatomical structures (Bookstein, 1991). On the basis of single landmark configurations we related visual and vocal attractiveness ratings to the underlying facial shape. Compared to other statistical procedures, GMM provides a more comprehensive picture of how single features of facial shape change in concert with ratings on attractiveness. We hypothesized that auditory and visual cues convey a redundant signal of female attractiveness. Therefore we expected that both ratings of facial but also vocal attractiveness are reflected in low levels of body FA and facial FA. Using GMM we projected ratings of visual and acoustic attractiveness onto facial shape. This enabled us to provide visual representations of the interrelations between the two modalities. The shape regressions were also performed using an independent sample of female faces to test whether this resulted in similar changes of facial shape as expected for the initial samples.

In summary, our study intended to uncover commonalities between the perception of vocal and visual attractiveness and whether these cues communicate redundant information. We also aimed to contribute to the discussion on the use of multiple cues in human mate choice decisions by showing that the 'redundant signaling' hypothesis might be valid for morphological features that signal female mate quality.

2. Materials and methods

2.1. Participants

2.1.1. Initial samples

We measured the body asymmetry, recorded the voices and photographed the faces of 42 female students of the University of Vienna (mean age = 24.2, SD = 5.5, range = 19–42). Bone injuries were enquired in a questionnaire. 103 heterosexual males (mean age = 26.0, SD = 7.1, range = 19–67) rated the female voices on attractiveness. Two thirds of the participants were students from the University of Vienna. One third of the participants were recruited in a public place.

Sixty-two heterosexual male students (mean age = 25.2, SD = 4.1, range = 18–44) rated the photographed female faces on attractiveness. All participants were native German speakers, who had no speech or hearing pathology.

2.1.2. Independent sample

Facial photographs from 34 female students of the University of Vienna were taken. None of these facial stimuli were involved in the initial sample. A group of 42 heterosexual males (mean age 31.7, SD = 7.1, range = 20–44) recruited via an online interface rated the female faces on attractiveness. None of these males participated in the rating studies mentioned above.

All participants that were involved in our study did not receive any financial compensation and were kept blind to the study's aims.

2.2. Stimulus preparation

To collect a sample of different sound expressions female participants were asked to count from 1 to 10 (Hughes et al., 2002), to read a selection of nonsense syllables (*e.g.*, 'hehehee'), nouns (*e.g.*, 'Otto') and a question ('Würdest du bitte das Fenster öffnen?' English: 'Would you open the window, please?'). These sound expressions were chosen, because they contain a high number of vowels. Utterances were recorded in mono with a resolution of 16 bit/48 kHz in a shielded room. We used a Sony CR-72 super cardioid capacitor microphone with an M-Audio Mobile-Pre USB audio interface. All recordings were done on a Macintosh computer using Peak (Berkley Integrated Audio Software, 2005).

Participants were instructed to speak at talk volume (~70 dB) and to avoid an emotionally colored pronunciation. To standardize speech volume the sound files were normalized to 99% of the maximum level. Sound file editing was done in WaveLab (Steinberg Media Technologies GmbH, 2004).

Female facial portraits were taken with a Canon EOS 300D under constant light conditions. To prevent optical distortion the camera was positioned at a distance of 3.5 meters between the camera and the face. To standardize the photographs, female participants were asked to remove any facial decoration, to show neutral facial expressions and to look straight into the camera. Further they were instructed to avoid head tilts, and to meet the conditions of the Frankfurt plane (Farkas, 1994). Photographs ($N = 16$), on which the participants smiled or had their head rotated horizontally or laterally, were excluded from the study. Digital pictures were cropped to an oval shape in Photoshop CS3 (Adobe, USA). This preserved information about hairline, chin and ears but removed information about hairstyle and accessories.

2.3. Rating procedure of voices and faces

Vocal stimuli were presented via an interactive web script on two Apple MacBooks equipped with AKG K271 closed headphones. Male participants listened to the voice recordings and assessed vocal attractiveness by moving a bipolar slider with the computer mouse. Slider values ranged from 1 (unattractive) to 100 (attractive). To avoid contrast effects (Kenrick & Gutierres, 1980) samples were randomly selected from all stimuli available (*i.e.*, counting, nonsense syllables, nouns, question). Each rating session consisted of 10 voice samples. In total, each vocal stimulus was rated at least 20 times.

Ratings of facial attractiveness were performed on four transportable Apple MacMini computers. Ratings of the independent sample were performed online using an interactive web script (www.stimulus-evaluation.net). In both conditions the graphical interface of the rating program was the same that we used for the vocal stimuli. Again, males rated a random selection of 10 stimuli by moving a bipolar slider with the computer mouse. Slider values ranged from 1 (unattractive) to 100 (attractive). Both ratings on facial attractiveness resulted in at least 12 ratings per stimulus. In order to obtain a single numeric variable for vocal and facial attractiveness we aggregated the participants' ratings for each stimulus by calculating the mean.

2.4. Fluctuating asymmetry of the body

To determine body asymmetry, we measured foot width, ankle breadth, knee breadth, elbow breadth, ear length, ear breadth, wrist breadth and hand breadth of the subjects (according to Livshits & Kobyliansky, 1989) with a digital calliper to 0.01 mm accuracy. All measurements were done twice to minimize measurement error. Data from participants who had reported bone injuries were excluded from further analyses.

To discriminate FA from measurement error we used a two-way mixed model ANOVA with repeated measurements. The between-subject effects for each measured trait were *Individuals*, *Sides*, *Individual* × *Sides* and *Measurement Error* (Palmer & Strobeck, 1986, 2003). The *Individual* component quantified variations among individuals after deduction for asymmetry. The *Sides* component quantified the directional asymmetry (DA) between the left and the right side of the measured traits. Variance explained by FA was determined as interactions between *Individuals* and *Sides* after correction for *Measurement Error* (Leamy, 1984; Palmer & Strobeck, 1986). The term *Measurement Error* was obtained from differences between two replicated measurements. All measured traits showed significant fluctuating asymmetry ($p = 0.001$). FA mean square were distinctively higher than the mean square of measurement error for each measured trait ($F_{41,84}$ ranges from 15.39 to 98.10; see Supplementary Table S1 and Table S2, available on the journal's Web site at www.ehbonline.org). Hand breadth showed a significant DA ($F_{1,41} = 5.73$, $p = 0.021$) and was excluded from subsequent analysis.

For further calculations we used the mean of the two measurements. For every measured trait we calculated the FA index (Palmer & Strobeck, 1986, 2003), which is $(|L - R|)/0.5 \times (L + R)$. Finally, we estimated the mean of these indices to create an overall composite FA index for each participant (Livshits & Kobyliansky, 1989). The composite FA index (body FA) entered the subsequent statistical analyses.

2.5. Facial shape analysis

2.5.1. Landmark set-up and Procrustes Superimposition

To capture the geometry of the face a set of 38 homologous facial landmarks (LM) were digitized as two dimensional coordinates using the software tpsDig2 (Rohlf, 2008). In order to improve the shape description on curved facial features, 34 evenly spaced semi-landmarks were digitized along the eyebrow, lip and chin outlines according to Windhager, Schaefer, and Fink (2011; for an extensive LM definition see Supplementary Materials, available on the journal's Web site at www.ehbonline.org). The semi-landmarks were allowed to slide along curves to minimize the bending energy of the thin-plate spline (TPS) interpolation function computed between each specimen and the pooled sample Procrustes average (Bookstein, 1997; Gunz, Mitteroecker, & Bookstein, 2005). After sliding, landmarks and semilandmarks were treated as homologous points and converted to Procrustes shape coordinates (PSC) by a Generalized Procrustes Analysis [GPA; (Bookstein, 1996; Mitteroecker & Gunz, 2009; Rohlf & Slice, 1990)] using the software tpsRelw (Rohlf, 2010). This involves rescaling the landmark coordinates so that each configuration has a unit Centroid Size (CS: square root of the summed squared Euclidean distances from all (semi)landmarks to their centroid; Slice, Bookstein, Marcus, & Rohlf, 1996). Then all configurations are translated and rotated to minimize the overall sum of the squared distances between corresponding (semi)landmarks.

The resulting centered Procrustes shape coordinates (PSCs) capture shape information only insofar as they are invariant to change in location, rotation, and scale (Slice et al., 1996). PSCs (*i.e.*, shape variables) were used for subsequent multivariate statistical analysis.

2.5.2. Fluctuating asymmetry of the face

In order to determine and decompose facial FA from facial DA we applied Klingenberg's object symmetry method (2002). This method presumes variations across LM's to be equal and isotropic. Based on a Procrustes adapted two-way mixed model ANOVA (Klingenberg, Barluenga, & Meyer, 2002; Klingenberg & McIntyre, 1998) the method calculates the asymmetry by the Procrustes distance between one side of each face and its median reflected and appropriately relabelled form. This approach is similar to the model described in 2.4, but uses Procrustes distances instead of conventional measures of length (Palmer & Strobeck, 1986, 2003). The measurement error was estimated by repeatedly digitizing facial LM as described in Section 2.5.1. To test FA for significance we performed a permutation with 5000 passes ($p = 0.001$; see Supplementary Table S2 and Table S3, available on the journal's Web site at www.ehbonline.org). The FA mean square was higher than the mean square of measurement error [$F_{2870,5880} = 30.35$; see Supplementary Table S2 and Table S3, available on the journal's Web site at www.ehbonline.org (Palmer & Strobeck, 1986, 2003)]. All calculations were done in SAGE (Márquez, 2008). To assess individual levels of facial FA we calculated the sum of squares of the Procrustes distances between the original and the corresponding relabelled reflected configurations (Mardia, Bookstein, & Moreton, 2000).

2.5.3. Shape regression and visualization

We carried out a Principal Component Analysis (PCA) of the matrix of Procrustes shape coordinates in order to assess facial shape variation in the pooled sample. We also calculated a Multivariate Linear Regressions (MLR) of the Procrustes shape coordinates onto the variables facial FA, body FA, facial attractiveness, facial attractiveness of the independent sample and vocal attractiveness. A shape regression was performed using these variables as single predictors. The significance of the MLR was estimated by permutation tests (Good, 2000) using 5000 random permutations and the explained variance as the test statistic. The regression estimates were subsequently projected in the shape space PCA of the pooled sample so that one can evaluate the relative orientation of all investigated variables (see above) related shape trajectories within the variability of the samples. Finally, Thin-Plate Spline (TPS) deformation grids (Bookstein, 1991) were used to visualize the association between facial shape and these five variables. The data analysis and visualization of the warps were carried out in the software R (R Development Core Team, 2011). The software tpsSUPER (Rohlf, 2013) was used to visualize the shape variations based on real faces.

3. Results

3.1. Attractiveness ratings and fluctuating asymmetry

As expected, ratings of the initial sample on female facial attractiveness and female vocal attractiveness were positively correlated ($r = 0.592$, $N = 42$, $p = 0.001$). We also found a clear negative correlation between facial FA and judgements of facial attractiveness ($r = -0.497$, $N = 42$, $p = 0.001$) as well as a negative relation between body FA and judgments of facial attractiveness ($r = -0.467$, $N = 42$, $p = 0.002$). This and the relation between ratings of both conditions was further supported by a negative correlation between vocal attractiveness and both FA measures (body FA: $r = -0.444$, $N = 42$, $p = 0.003$; facial FA: $r = -0.445$, $N = 42$, $p = 0.003$). In addition, analyses yielded a positive correlation between facial FA and body FA ($r = 0.327$, $N = 42$, $p = 0.035$).

3.2. Shape analysis and visualizations

Fig. 1 shows a scatterplot of the first two principal components (PC1 and PC2) of the pooled sample shape coordinates, accounting for 41%

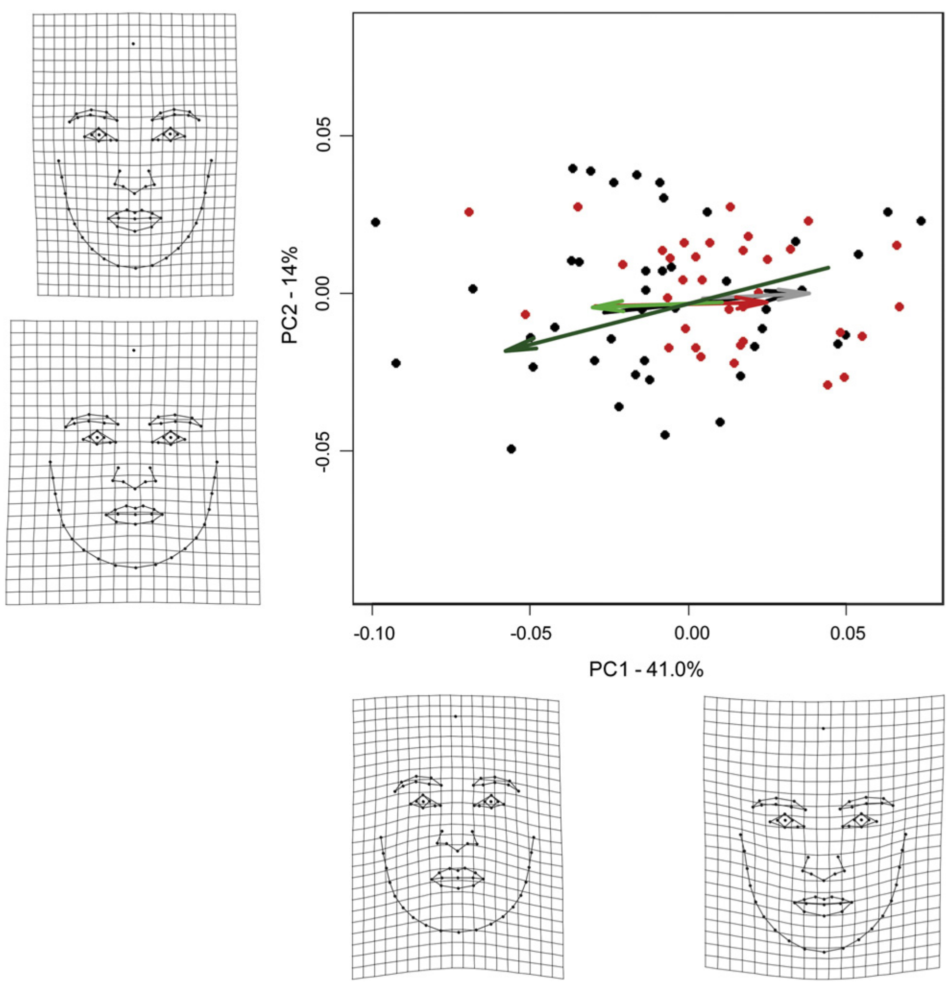

Fig. 1. Scatterplot of the first two principal components (PC1 and PC2) of facial form. The arrows represent the coefficient vectors for the regression of shape on facial attractiveness of the initial sample (facial attractiveness, black arrow, $N = 42$) and the independent sample (facial attractiveness of the independent sample, red arrow, $N = 34$) as well the coefficient vectors for the regression of shape on facial FA (light green arrow, $N = 42$), body FA (dark green, $N = 42$) and vocal attractiveness (gray arrow, $N = 42$). The facial reconstructions visualize the form differences associated with the first two PCs. The shape deviation of these grids correspond to the lowest (−0.10) and highest (0.05) values of the PC1 scores and to the lowest (−0.05) and highest (0.05) values of the PC2 scores.

and 14% respectively. The facial reconstructions visualize the form differences associated with the first two PCs. For a direct comparison of the shape regressions, the depicted coefficient vectors were standardized to unit length and subjected to a PCA (Mitteroecker, Gunz, Windhager, & Schaefer, 2013). The arrows represent the coefficient vector for the regression of shape on facial attractiveness of each sample (facial attractiveness of the initial and the independent sample) and on facial FA, body FA, and vocal attractiveness of the initial sample. These arrows are aligned along PC1, with the facial attractiveness, facial attractiveness of the independent sample, and vocal attractiveness arrows pointing in a similar direction, towards positive PC1 scores, whereas the arrows of facial FA and body FA point in the opposite direction, toward the negative PC1 scores.

Fig. 2 visualizes the grid deformations based on the regression of the shape coordinates on vocal attractiveness and facial attractiveness of the initial and the independent sample. The shape changes are presented as deviations from the sample average (middle column). The grid deformation that corresponds to low vocal attractiveness (vocal attractiveness, Fig. 2*a*) resulted in a longer face, a more prominent chin, a smaller interocular and eyebrow distance, a bigger nose and smaller lips compared to the sample average. Deformation of the grid that corresponds to low facial attractiveness of both samples (facial attractiveness of the initial sample, Fig. 2*d*; facial attractiveness of the independent sample, Fig. 2*g*) shows a similar pattern. Highly attractive voices (vocal attractiveness, Fig. 2*c*) and highly attractive faces of both samples (facial attractiveness of the initial sample, Fig. 2*f*; facial attractiveness of the independent sample, Fig.2*i*) also provided similar grid deformations. Here, deviations from the sample average resulted in a smaller face, a broader interocular and eyebrow distance, lifted jawbones, a smaller nose and chin, and larger lips compared to the sample average. In order to provide a more realistic illustration of the mentioned deviations, variations in shape were also visualized on the basis

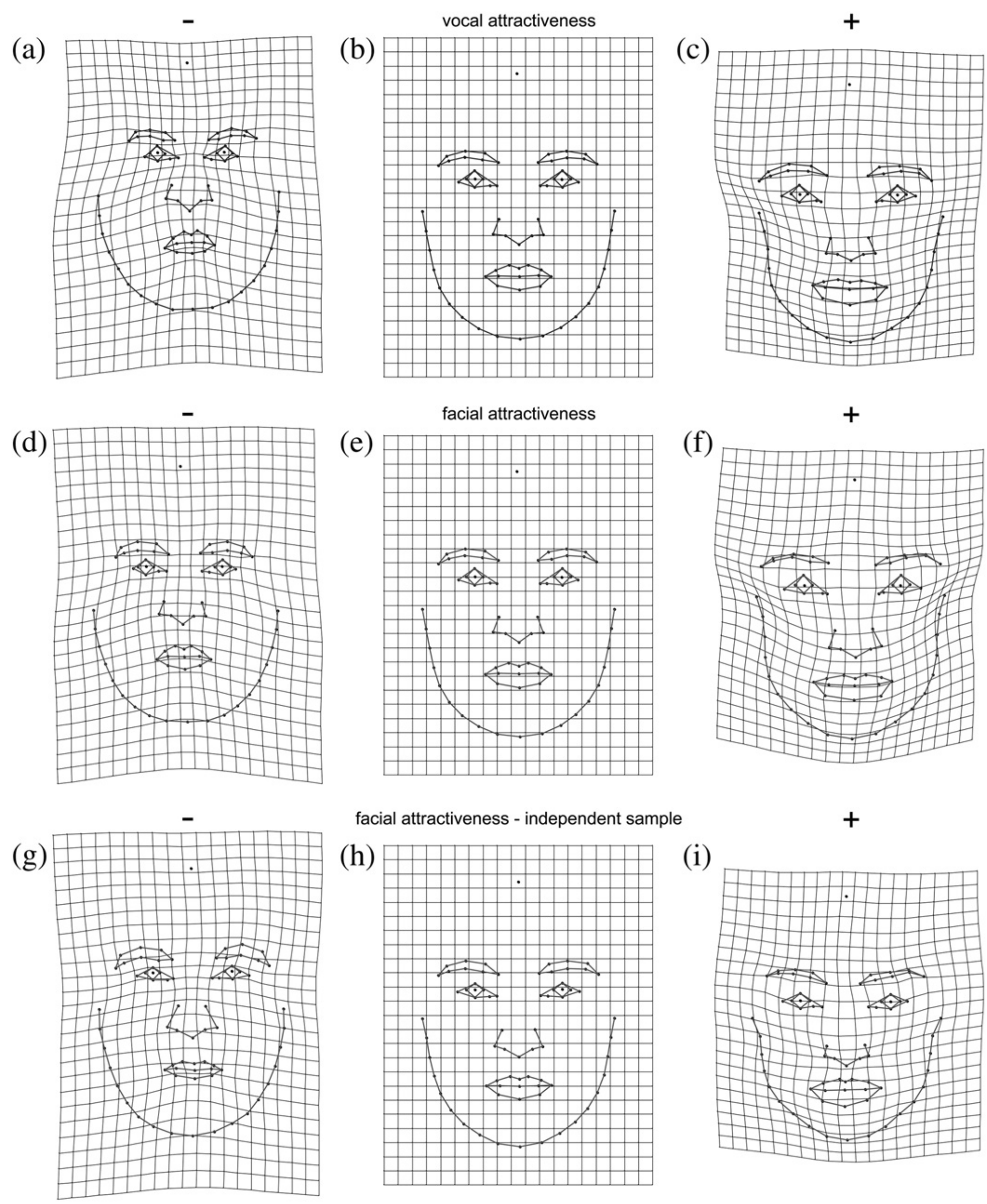

Fig. 2. Visualization of shape regressions on female vocal attractiveness ($R^2 = 0.052$, $N = 42$, $p = 0.055$ with 5000 permutations), female facial attractiveness ($R^2 = 0.081$, $N = 42$, $p = 0.008$ with 5000 permutations) and female facial attractiveness in an independent sample ($R^2 = 0.070$, $N = 42$, $p = 0.033$ with 5000 permutations) based on TPS deformation grids. To ease interpretation, specific landmark shifts were extrapolated by factor 3 in both directions of independent variables. (*a*) Low level of vocal attractiveness. (*b*, *e*, *h*) Sample average of facial shape. (*c*) High level of vocal attractiveness. (*d*, *g*) Low level of facial attractiveness. (*f*, *i*) High level of facial attractiveness.

of real faces (see Supplementary Fig. S1, available on the journal's Web site at www.ehbonline.org).

The shape regressions on both FA scores yielded similar grid deformations as the regressions on facial attractiveness of both (initial and independent) samples and vocal attractiveness but with low and high levels reversed (see Supplementary Fig. S2, available on the journal's Web site at www.ehbonline.org).

Explained variances (R^2) and *p*-values of the shape regressions on each independent variable are presented in Table 1.

4. Discussion

What is it that makes an attractive woman attractive? Do female vocal and visual cues of attractiveness communicate redundant information? To give answers to these questions we recorded the voices of females, photographed their faces, and then asked independent pools of males to rate these stimuli on attractiveness. Subsequently, we examined whether vocal and visual cues convey a redundant signal of female attractiveness and whether they are related to female FA and facial shape.

In line with previous research in this field we found a distinct positive correlation between males' assessment of female vocal and facial attractiveness (Collins & Missing, 2003). As expected our findings also support a negative correlation between males' assessments of both features of attractiveness and facial FA and body FA. The latter goes beyond the study of Hughes et al. (2002) who only showed that body FA is negatively correlated with vocal attractiveness in both male and female subjects. Although for the initial rating experiments female photographs and voice recording were collected from the same set of stimuli, they were assessed by independent pools of males. This underlines that the obtained results are largely unaffected by individual preferences of the male judges and that female attractiveness is indeed perceptible in both visual and acoustic cues.

However, simple correlations between attractiveness ratings and pre-defined features of shape lack detailed information about on which cues males base their assessments of attractiveness. For example, Feinberg, Jones, DeBruine, et al. (2005) found that vocal and facial attractiveness and facial femininity were positively correlated, indicating that they constitute one ornament that signals female mate quality. However, as already mentioned before, the authors made use of a composite index of distance ratios to measure facial shape femininity that do not convey any shape information (Slice, 2005). Such an approach bears the risk to miss specific features of facial shape relevant for the perception of facial as well as vocal attractiveness. Our study aimed to overcome this limitation by using geometric morphometric methods that allow gathering shape information that preserves the geometry of the face.

Our analyses was divided into two stages and performed on the basis of the Geometric Morphometric Methodology (GMM). In the first stage shape variables (*i.e.*, based on landmark information) were reduced to two principal components (PCs) that explain most of the shape variance within the sample pool. The different attractiveness ratings and measures of FA were then projected into the shape space of these two PCs. This corroborated the results obtained by our correlational analyses. We found a similar vector alignment for all of the attractiveness ratings but in accordance with the negative correlation between attractiveness ratings and FA, the FA vectors and the vectors of attractiveness point in opposite directions.

In the second stage we regressed the facial shape coordinates on ratings of attractiveness as well as FA and visualized female facial shape on the basis of deformation grids. In contrast to research focusing on single features of attractiveness, this provided a more comprehensive illustration of how such features merge into a single ornament and jointly influence the perception of attractiveness.

The visualizations of shape regressions on facial attractiveness provided similar grid deformations for both experimental conditions. In addition, similar deformations were also found for shape regressions on vocal attractiveness. This supports the results of our correlational analyses and that shape vectors on the basis of attractiveness ratings point in the same direction. Interpretation of the deformation grids suggests that high levels of perceived vocal and facial attractiveness result in lifted jawbones, less robust jaws and fuller lips compared to the consensus. These specific features have been previously described as honest cues of female mate value (Cunningham, 1986; Johnston & Franklin, 1993, Pflüger et al., 2012).

Of all variables that have been fed into a shape regression body FA explained the largest portion of variance. Hence, there was a pronounced relationship between body FA and the shape variables. This supports the assumption that a low FA is associated with those features that have been already described as honest cues of female mate value (Schaefer et al., 2006). This indicates that body FA is indeed reflected in female faces and involved in the perception of facial but also vocal attractiveness. Depending on whether males seek a long-or short term relationship, body and faces seem to be weighted differently in mate choice decisions (Currie & Little, 2009; Jonason, Raulston, & Rotolo, 2012). Nevertheless, due to its developmental origin, we can assume that FA is ubiquitous in all anatomical structures and therefore serves as a reliable indicator for mate choice decisions in both the body and the face. However, compared to body FA, the explained variance for facial FA with the shape variables was far lower indicating a weaker relationship. This might be due to differences in measuring facial and body FA. First, body FA was based on a composite measure and therefore consisted of more measures than facial FA. Second, measurements of facial FA may contain a greater portion of error variance because they were performed on a two-dimensional abstraction of a three dimensional structure. In order to overcome such limitations we recommend the use of three dimensional facial scans for the assessment of facial FA in future research.

Given the strong correlation between body and facial FA, it seems obvious that fluctuating asymmetry does not only occur in outward symmetric structures but also occurs in all other bilateral structures of the body.

The basic configuration of human morphological features is bilaterally symmetric. However, environmental stressors act on the development of morphological traits during ontogeny resulting in fluctuating asymmetry. This also encompasses inner structures such as the vocal apparatus, including the vocal folds, larynx (Hirano et al., 1989), pharynx, and nasal cavities. Thus, FA-sensitive bilateral structures may not only be visible to the eye but also perceptible in voices. Our findings support this assumption revealing a strong association between female vocal cues of attractiveness and both measures of FA.

We hypothesized that shape-related cues in general can serve as more stable indicators of an overall condition than cues which are more strongly subjected to temporary physical states. The deciphered relationship between vocal and facial attractiveness cues and the proposed morphological link between them might be interpreted in the light of the redundant signalling hypothesis. More precisely, vocal and facial cues may convey redundant information about female attractiveness that enables males to make less error prone assessments of female mate quality.

Table 1

Explained variances and corresponding *p*-values of the shape regressions on vocal attractiveness, facial attractiveness, facial FA and body FA.

Variable	R^2	*p*-Value
Vocal attractiveness	5.2	0.055
Facial attractiveness	8.1	0.010
Facial attractiveness – independent sample	7.0	0.033
Facial FA	4.1	0.090
Body FA	14.9	0.001

R^2 = explained variance. Resulting *p*-values after 5000 random permutations.

However, at this stage of our research we are only able to establish a relationship of vocal and facial attractiveness with body FA, facial FA and facial shape. It is not possible to provide clear evidence for the existence of a redundant signal transmitted by both vocal and facial cues. We cannot exclude that cues of the different experimental conditions also convey different information and multiple messages.

However, it is conceivable that shape related cues such as symmetry being present in the body and the face serve as back-up signals while other cues may convey different messages (Currie & Little, 2009). Therefore, future studies should disentangle effects more clearly and estimate how much variance one modality explains and if attractiveness ratings are influenced by additive effects or not. We are aware that males' assessments of female attractiveness are not only affected by facial shape. Hence, follow up work should extend the focus and integrate other features of female attractiveness that rather rely on females' current physical state (Candolin, 2003) such as skin coloration or skin texture (Fink et al., 2001; Jones et al., 2004; Matts et al., 2007, Stephen, Coetzee, Smith, & Perrett, 2009).

In the current study we mainly examined attractiveness features of facial shape, but there is a need to analyze its relation to vocal cues in more details. Research has already filtered some acoustical parameters that affect the perception of vocal attractiveness. Findings suggest that females perceive males with a low voice pitch as attractive (Apicella & Feinberg, 2009; Collins, 2000; Feinberg, Jones, Little, & Perrett, 2005; Pisanski & Rendall, 2011), while vocal attractiveness of females is associated with higher voice pitch (Collins & Missing, 2003; Feinberg et al., 2008; Pisanski & Rendall, 2011). Other studies found that variations of the fundamental frequency (Hodges-Simeon, Gaulin, & Puts, 2011; Puts, Hodges, Cárdenas, & Gaulin, 2007), formant position (Bruckert et al., 2010; Puts, Apicella, & Cárdenas, 2012) and formant dispersion (Xu, Lee, Wu, Liu, & Birkholz, 2013) have an impact on perceptions of vocal attractiveness. Consequently, follow up work that combines such acoustical parameters with GMM would give more detailed insights into the relationship between vocal and facial cues. The investigation of single acoustical parameters in relation to FA will provide further insights in a common biological basis of vocal and facial cues that convey redundant information.

In conclusion, we found that attractive faces also tend to have attractive voices. Using landmark information and GMM we were also able to demonstrate that perceptions of facial attractiveness and vocal attractiveness are related to similar changes in facial shape. These changes resembled facial features that have already been associated with female facial attractiveness and mate quality in previous studies. The shape analyses also yielded a strong association between female vocal cues of attractiveness and both facial and body FA. These findings, obtained from different experimental conditions, demonstrate that vocal and facial cues convey redundant information about a female's mate value and thus may serve as a back-up signal for human mate choice decisions.

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