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„Sibling-sibling dissimilarity of facial shape with an interpretation in terms of heritability“

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1 Summary

Introduction: For over a century craniofacial characters and their heritabilities have been extensively studied with the exception of profiles and shape using classical linear measurements. Here I present the statistical toolkit of Geometric Morphometrics as at least equally suited for measuring and comparing facial shape to quantify its dissimilarity in pairs of full siblings with an interpretation in terms of heritability. **Methods:** 46 landmarks and semilandmarks of 35 pairs (39 females, 31 males) of Caucasian full siblings from Upper Austria aged 17 to 29 years were digitized on frontal facial photos in standard position and orientation. Squared Procrustes distances between the configurations (and regional subsets) were averaged for pairs of siblings and compared to that between unrelated individuals under the expectation of a ratio of one half. Shape variables were also subjected to a relative warp analysis. **Results:** Ratios for siblings ranged from 0.56 to 0.65 in males, and 0.70 to 0.86 in females, but were regionally indifferent except for the nose-lips region in women. Siblings with different Pill regime exhibited greater variance there. The first two relative warps explained 52% - 68% of total shape variation, with siblings correlating. Global changes in both sex associated with the outline of the face, bigonial breadth, and mandibular shape; regionally with vertical lip measurements, intercanthal distance, and nasal height. **Conclusion:** Facial shape has a moderate heritability in pairs of siblings with little difference between the sexes, or facial regions, but estimates may vary for different configurations of landmarks. Although less dissimilarity was found among brothers, sex linked effects remain uncertain as hormonal contraceptives seem to affect female facial shape. Furthermore, the tools of Geometric morphometrics have proven to be a well suited alternative to traditional methods to estimate heritability among differently related individuals.

1.1 Zusammenfassung

Einleitung: Kraniofaciale Merkmale und deren Vererbung wurden mit Ausnahme von Profilen und Gestalt in den letzten hundert Jahren mittels klassischer, linearer Messmethoden erschöpfend untersucht. Aus diesem Grund widmet sich diese Arbeit der Messung und dem Vergleich von der Gestalt des Gesichtes zwischen Geschwistern unter den Gesichtspunkten der Erblichkeitsschätzung und stellt gleichzeitig die statistischen Methoden von Geometric Morphometrics als eine dafür geeignete und gleichwertige Alternative vor. **Methoden:** 46 Landmarks und Semilandmarks wurden in standardisierten Frontalaufnahmen von den Gesichtern von 35 kaukasischen, oberösterreichischen Geschwisterpaaren (39 Frauen, 31 Männer) im Alter von 17 bis 29 Jahren digitalisiert. Die durchschnittliche quadrierte Prokrustes Distanz zwischen den Landmark-Sets und den regionalen Teilsets von Geschwistern wurde mit denen aller Anderen verglichen unter der Erwartungshaltung eines Verhältnisses von einem halb. Anschließend erfolgte eine Relative Warp Analyse der Variablen. **Ergebnisse:** Die Verhältnisse für Geschwister bewegten sich bei Männern von 0,56 bis 0,65 und bei Frauen von 0,70 bis 0,86, wobei es keine regionalen Unterschiede außer für die weibliche Nasen-Lippen Region gab. Schwesternpaare mit unterschiedlichem Pille-Verhalten zeigten dort größere Unähnlichkeit. Die ersten beiden Relative Warps erklärten gemeinsam 52% - 68% der Gesamtvarianz während Geschwisterpaare darin eine Korrelation aufwiesen. Globale Veränderungen der Gestalt fanden bei beiden Geschlechtern im Umriss des Gesichts, der Untergesichtsbreite und der Gestalt der Mandibel statt, regional auch in den Höhen-Maßen der Lippen, der Interokularbreite und Nasenhöhe. **Schlussfolgerung:** Die Gestalt des Gesichtes weist eine mittlere Erblichkeit in Geschwisterpaaren auf mit nur geringfügigen Unterschieden in den Geschlechtern oder Regionen, allerdings könnten diese Ergebnisse in unterschiedlichen Konfigurationen von Landmarks variieren. Obwohl Brüderpaare geringere Unähnlichkeit aufwiesen bleibt eine X-chromosomale Vererbung ungewiss da hormonelle Verhütungsmittel einen Einfluss auf die Gestalt bei Frauen gezeigt haben. Die Methoden von Geometric morphometrics haben sich überdies als gut geeignete Alternative zu traditionelleren Methoden der Erblichkeitsschätzung zwischen unterschiedlich verwandten Individuen herausgestellt.

2 Introduction

Heredity, the passing of characters from one generation to the next, has been known to people through parent-child resemblance and artificial breeding long before its basic laws were derived by Gregor Mendel. Mendel's study of pedigree patterns in a population of common pea plants lead him to a theory of particulate inheritance in which characters were determined by discrete factors (genes), inherited intact without blending. But Mendel could only explain the passage of simple dichotomous characters, such as smooth and wrinkly pears, either present or absent. Continuous or quantitative traits exhibited far less tractable patterns by varying on a continuum rather than in kind. Instead one single gene of major effect, they are affected by a multitude, where each may contribute differently and act in concert with environmental conditions. One sound method to disentangle this complex interplay of underlying genes and environment to estimate each contribution was realized much later with the concept of heritability.

Heritability is formally an analysis of variances and was invented by R.A. Fisher in 1918 based on the Mendelian schemes of inheritance. Heritability estimates the effect of genetic differences upon quantitative characters within a certain population at a certain time. It describes the degree to which phenotypes are determined by their genotypes. More specific, the proportion of total variance that is attributable to genetic variance. Values range from 0.0 for no heritability at all, to 1.0 for a completely inherited character (Falconer, 1989) that could be reliably predicted from its genotype alone. But usually, estimates lie between these extremes as variation can arise for environmental reasons.

Two types of heritability are typically of interest. When considering 'the proportion of phenotypic differences due to all sources of genetic variance' (Plomin et al., 1990) it is referred to as heritability in its broad sense. This includes additive variation, dominant variation, and multi-genic interaction, as well as parental factors such as a mother's ability to sustain milk for her offspring, or prenatal development. Of the three genetic subdivisions the additive, where the effects of more genes simply add up for a greater expression of a character, is considered the major influence, and solely responsible for the resemblance among kin. When defined with only that in mind, it is called heritability in the narrow sense (Falconer & MacKay, 1996), or simply heritability (Plomin et al., 1990).

2.1 Estimating heritability

Heritability of a trait can be estimated in several ways. One way is to exploit the additive relationship between variances. Since the sum of genetic and environmental variance equals the phenotypic variance, which can be easily obtained through measuring, control of one allows for the estimation of the other. In the first of two complementary approaches individual organisms are raised with all environmental parameters carefully controlled. With little to none environmental variation left any persisting differences in phenotype may then be attributed to genetics. For obvious reasons, such intense control is only possible when studying plants or progenies of smaller animals, but impossible for higher organisms. The second approach, however, where individuals with similar or identical genotypes are placed in different environments, can be applied to humans. Ideally identical twins that have been reared apart since early life are used as they share the same genotype but almost none of their environment. Any phenotypic variation between them can then be ascribed to the environmental differences between their families.

While both methods have been popular, each entails issues of its own. The simple breakdown of total variance into genetic and environmental fractions completely ignores the fraction caused by errors in measurements, and gene-environment interactions. Although these contributions are considered to be relatively small in anthropometric characters, heritability tends to be overestimated that way. Twin adoption studies, on the other hand, completely rule out any correlations between the families' environments, and all shared input during prenatal development (Defrise et al., 2000).

A third, more practical way, is to compare the phenotypic correlation among close relatives to their genetic correlation as their resemblance is mostly driven by additive genetic variance. If a trait is heritable, biological relatives will resemble one another more than unrelated individuals do due to their genes in common. Family units studied with this method usually include parent-offspring couples, full siblings, half siblings, or monozygotic and dizygotic twins. Their degree of genetic correlation can be estimated through pedigree tables, which contain rough information about the expected fraction of identical alleles, shared by common ancestry. For monozygotic twins with all genes in common this degree equals one. For full siblings or dizygotic twins it is ½ on average as each child has an equal expectation of fifty percent to inherit the same or the different allele at a parent's gene-locus. With the same

reasoning applied for the other parent's half of genes the degree remains at ½. For half-siblings this applies only for their common parent, but not for the other. Respectively their proportion of genes in common averages at ¼.

Complications for this method mostly arise with familiality of traits. A trait is familial if it runs in a family for any reason, but is only heritable if the similarity is due to shared genes. If results are based on simple correlations among family members alone they can not distinguish those two and become genetically non-interpretable. It remains unknown whether a familial character is inherited unless the environmental correlations are broken. A second misassumption regularly made is a uniform environmental contribution among all studied individuals. Since close relatives in humans usually share a much more similar environment than nonrelatives do, most environmental correlations are positive and heritabilities will be overestimated. A third problem is pleiotropy, a one-to-many relation of genes to phenotype, where the effect of one gene does not simply add up on one trait but affects several at the same time.

2.2 Heritability in humans

Since its introduction more than a century ago heritability has played a pivotal role in the understanding of human variation. The genetic contribution to stature, weight, BMI, lengths and circumferences of extremities and trunk (Pearson, 1903; Martin, 1928; Clark, 1955; Visscher et al., 2006, to name only a few) became well understood, including the effects of age (Mueller, 1978), growth patterns (Mueller & Malina, 1980), and socio-economic factors (Arya et al., 2002) on these traits. Estimates on the composition and distribution of body mass (Bouchard et al, 1988) have shed much insight to the aetiology of diabetes, and cardiovascular diseases, but the concept of heritability has been extended to non-physical characters as well. And while the number of studies is constantly growing, estimates on craniofacial and cephalic traits have been proven invaluable to several fields of science for a long time.

2.3 Craniofacial and cephalic heritability

The first scientific paper on inheritance of physical characters in man was written by Pearson in 1903, where he compared the resemblance in stature by correlating lengths in about 1100 families, and for head measurements in about 3000 pairs of

siblings from school records. Pearson found a mean parental inheritance of .460 for both sexes and all characters in his family records, and an average degree of hereditary resemblance in siblings very close to one half. He concluded that the intensity of fraternal correlation in man is about .5 in the case of both measurable and immeasurable characters. Anthropometric facial and cephalic measurements became also widely applied during the advocacy of eugenics and the study of human races. Early studies were conducted on African-Caucasian offspring, the "Rehobother Bastarde" (Fischer, 1913), Australian Aborigines (Davenport, 1925), soon followed by those on Caucasian twins (Leicher, 1928; Abel, 1934; Scheidt, 1932; Quelprud, 1932). The soft-tissue measurements therein, lengths, breadths, and shapes of head, nose, lips, eyes and ears yielded medium to high heritabilities. Unfortunately many of these results became massively abused in scientific racism, which tried to justify racism by classifying individual inherited phenotypes into discrete races asserted to be superior or inferior, completely discrediting eugenics in the end. The concept of fixed biological races became largely abandoned as well, ironically through the same methods that tried to institute it in the first place. Still, some differences can be found between ethnics, mainly in the orbital region, lengths and widths of the nose (Farkas et al, 2005), and structure of the mandible (Scott, 1957).

In the mid-twentieth century inherited cephalic and facial characters were also the first and only way to determine paternity before tests on DNA became possible. The so called "Anthropologisch-erbbiologische Gutachten" (Schade, 1954) applied in courts in Austria and Germany compared eye-colour, shape of the head, ears, and iris of mother, child, and putative father for their concordance (Knussmann, 1988). The practice is now obsolete, apart from rare cases when individuals and genetic material are missing, but nonetheless in good agreement with later findings. The heritability of head size and shape (Susanne, 1975; Susanne & Sharma, 1978; Sharma & Sharma, 1984; Byard, 1985; Arya et al., 2002), interpupillary distance, dimensions of nose, lips (Susanne, 1975, Susanne & Sharma, 1978; Defrise, 1981), and ears (Byard, 1985; Sharma, 1986; Sengupta & Karmakar, 2007) has been repeatedly documented since among close relatives.

One frequent finding has been a higher heritability in vertical than in horizontal characters, or circumferences (Susanne, 1975; Manfredi et al., 1997; Sengupta & Karmakar, 2007), following the same pattern that had already been reported in

anatomical literature for the rest of the body since the early 20th century (Martin, 1928). Reason is that lengths are mostly influenced by growth of bones, whereas breadths and circumferences depend on soft-tissue, more susceptible to environmental strains like simple changes in weight. In fact, high plasticity of cephalic soft-tissue has been reported under the varying nutritional and socioeconomic conditions in different Indian casts (Arya et al., 2002). It also became evident, that heritability declines from dizygotic twins to siblings to parent-offspring couples, although their proportion of genes in common is basically the same (Susanne & Sharma, 1978; Sharma & Sharma, 1984). This may partly be ascribed to dominance variance of genes, which only adds up to covariance between siblings (Knussmann, 1988), but for the bigger part to different levels of environmental contribution. After all, dizygotic twins share the same pre-, peri-, and post-natal environment, siblings only the latter, and parent-offspring couples the least. The remaining portion may be due difference in age as some characters increase or diminish over time (Susanne, 1975), and due to individual growth patterns. As growth can occur at different times and rates in individuals (Hunter, 1970), correlations between siblings (Byard et al., 1984) and parent-offspring couples (Johannesdottir et al., 2005) are often lower in early childhood, but increase once they approach adulthood. Some argue that this applies only for vertical measurements, while horizontal ones decline (Peng et al., 2005).

2.4 Orthodontic and craniometric heritability

A more clinical application for craniofacial heritability lies within the diagnosis and treatment planning in orthodontics. A patient's growth may be predicted to some degree by using already existing data of a close relative. Natural morphology may also be more easily distinguished from that caused by injuries or by disease in reconstructive surgery. Orthodontic measurements are usually taken on lateral or postero-anterior cephalograms where soft- and hard-tissue can be evaluated independently at the same time.

Apart these methodical differences, orthodontic and anthropometric studies paint a similar picture of a polygenic craniofacial inheritance. Siblings, dizygotic and monozygotic twins show medium to high heritability for facial heights (Horowitz, 1960), height-indices, and widths (Manfredi et al., 1997; Baydas et al., 2005). Estimates for vertical characters are higher than for horizontal ones (Lundström &

McWilliam, 1987), sometimes ranking before anteroposterior dimensions (Hunter, 1965), sometimes not (Baydas et al., 2005). There are indications that single facial components are under stronger genetic control than the craniofacial complex as a whole (Lundström et al., 1954; Saunders et al., 1980), its proportions (Baydas et al, 2005), or their spatial relationship (Lobb, 1987). Size, and more so shape (Manfredi et al., 1997), and soft-tissue thickness (Baydas et al., 2005) of the mandible seems to be highly heritable, especially in father-offspring couples (Hunter, 1970) as indicated by linear measurements (Horowitz, 1960; Hunter, 1970) or superimposition (Lobb, 1987). Considering the lips, the lower one reveals less environmental plasticity than the upper, but still with only moderate levels of genetic influence (Baydas et al., 2005).

Historically, heritability of cranial characters has been of less interest in craniometry than the identification of race, ethnicity, and sex of unknown skeletal remains. However, in the last few decades craniometry has taken on a new relevance as phylogenetic tool to reveal the history and structure of human populations (Relethford & Lees, 1982). Given the heritability of a character one can test the likeliness of microevolutionary processes and scenarios against the remaining phenotypic plasticity. But craniometric estimates are scarce for one simple reason. They solely rely on genealogically well documented remains. Measurements on the living, with only a loose relationship between soft-tissue and underlying skull (Simpson & Henneberg, 2002), seem far too unreliable as a proxy for cranial dimensions (Formby et al., 1994). One of the few suited and repeatedly sampled remains left is the collection of ornamented skulls in Hallstatt (Austria).

Of the three studies conducted there, the first (Sjøvold, 1984) consisted mainly of radii, fractions, and sub-tenses, lacking most standard measurements present in the following two. Despite that, their main conclusion of a little to medium narrow sense heritability in general remained the same, while differing considerably in some of the rest. In the second study different portions of the skull were found highly variable, with facial measurements among the less heritable characters (Carson, 2006), whereas the face scored the highest number of significant characters along the highest mean heritability in the third (Martínez-Abadías et al., 2009). The common anthropometric and orthodontic view of lower heritabilities in breadths than lengths and heights became challenged to (Martínez-Abadías et al., 2009).

Measurements in functional regions such as the orbits, the nose and the masticatory apparatus proofed highly heritable (Martínez-Abadías et al., 2009) as predicted earlier (Sjøvold, 1984), regardless the many non-significant heritabilities in mid-face (Carson, 2006). Such rather diverse pattern of genetic variation within craniofacial characters (Martínez-Abadías et al., 2009) only proofs a polygenic inheritance with significant contribution by other than genetic factors.

2.6 Heritability and shapes

Although previously mentioned anthropometric, cephalic, orthodontic and craniometric studies have shown most facial characters to be at least partially heritable, few have actually dealt with profiles (Baydas et al. 2005), and virtually none with shape (Demayo et al., 2010). This may be due to several reasons, one of which is the limitations of multivariate morphometrics.

Multivariate morphometrics, now commonly called ‘traditional morphometrics’ (Bookstein, 1998), tried to quantify shape, the geometric information left when size, location, and rotation have been removed from an object, by applying multivariate statistics to sets of quantitative variables. These variables typically arrive as linear measurements such as lengths and breadths of structures, areas, volumes; sometimes angles and ratios are included. When used to describe regular objects their simplicity and low cost have rendered them an excellent choice especially under difficult conditions (Lestrel, 1989), but they are not particularly suitable for assessing complex profiles and shapes (Moyers & Bookstein, 1979).

First shortcomings arrive when complex structures such as outlines lack homologous anatomical loci, leaving morphological areas of interest uncovered, or simply when having to decide which variables to include in the analysis. Choosing freely among measurements may already impair scientific objectivity, and results might only reflect an investigator’s desire later.

Of far greater concern is variation of size within a sample, and deciding which way to deal with it. For an analysis of shape, each of the applied variables has to be independent of the scaling (Bookstein, 1998), but linear features are usually highly correlated with (Bookstein et al., 1985). Several methods have been introduced over time to extract size-free shape variables, all yielding slightly different results (Adams, Rohlf, Slice, 2004), which subsequently left comparisons between studies difficult.

Secondly, there is allometry, changes in shape as a function of size. With linear measurements only covering simple changes in distance between landmarks but not their directions (Cheverud et al., 1983), or their original position, distinguishing allometry from other morphological changes quickly turns into a rather complex matter (Hennessy & Moss, 2001). Angles, on the other hand, are completely unaffected by size and do share some actual relevance to shape. But angles contribute no information within the large areas they cover (Lestrel, 1989), and their usefulness strongly depends upon their distribution across the studied shape.

In the end, the final presentation of form and results typically arrives in diagrams of measured variables, their linear combinations, tables and scatterplots. Data depicted that way is hardly legible or interpretable without the proper knowledge of involved landmarks, and anatomy. Furthermore, the original shape is lost during this passage from form to numbers, and can not be restored from these variables alone, nor is it used in the analysis later (Rohlf & Marcus, 1993). Consequently heritability of facial shape has not received satisfactory quantification yet.

2.7 About this thesis

It is the emphasis of this study to quantify the dissimilarity in facial shape among differently related individuals with an interpretation of findings in terms of heritability. Assuming that facial shape is at least under some genetic control, biological relatives should on average resemble one another more than unrelated individuals do. To this end I will compare the average magnitude of shape differences between full siblings to that of unrelated individuals. If sibling-sibling correlation is 0.5, as assumed for many other characteristics and corresponding to their commonly expected genetic correlation, a half as big average variance can be expected as well. In case facial shape is negliably heritable or entirely determined by environmental factors, all variances should be approximately equal. Should unrelated individuals exhibit least variance, no plausible explanation other than nuisance variables, or methodological errors will be possible.

The comparison will be done regionally and also for each sex to control for any sexual dimorphism. There is the possibility that different proportions of the face may vary in degree of heritability the same way as on the human skull (Carson, 2006) or craniofacial characters (Martínez-Abadías et al., 2009). The question of whether

genetic control is higher in vertical characters than in horizontal ones (Carson, 2006; Lundström & McWilliam, 1987) will not be addressed by this study.

The second main challenge of this study lies within the implementation of Geometric Morphometrics (GM) as an at least equally suited alternative to traditional morphometrics. Based on coordinates of landmarks rather than on linear or angular measurements, GM conserves the whole spatial information of an object, along the possibility to calculate common variables as well. GM is capable of accessing all characters equally and at once, instead an arbitrarily extract of single characters albeit their possible interplay. It has been successfully introduced to questions concerning human facial- (Fink et al., 2005; Schäfer et al., 2005), cranial- (Badawi-Fayad & Cabanis, 2007), facial soft tissue (Fink et al. 2005; Schäfer et al. 2005), and more recently to the perception of facial shape (Schäfer et al. 2006), but barely in the context of heritability (Demayo et al., 2010). Its methods have already been described in detail elsewhere (Bookstein, 1991, 1997). A brief description can be found in the following ‘Material and Methods’ section.

3 Materials and methods

The computational design of this study is a comparison of dissimilarities in facial shape among siblings to those between unrelated individuals using Procrustes techniques. Sets of somatometric landmarks on facial photos in frontal view were Procrustes superimposed. Dissimilarity of facial shape was measured by squared Procrustes distance, square root of summed squared distances between corresponding landmarks. The ratio of the average squared Procrustes distance within siblings to that of all unrelated individuals was calculated and a relative warps analysis carried out. This was done four times for each sex: globally over the whole face, and separately for upper face, lower face, and the nose-lip region alone.

3.1 Participants

The sample comprised 35 pairs of full siblings: 22 brothers, 30 sisters, and nine mixed pairs. (Recruiting a sufficient number of twins was not possible, and establishing their zygosity would have required costly tests.) All subjects were Caucasians from Upper Austria, in meaning that siblings would not share a much more common environment than nonrelatives. Most participants were undergraduate students living in the Viennese dormitory (Haus Oberösterreich) where most of the recruitment took place. The others were directly recruited in their homes in Upper Austria.

The limited age range of 17 to 30 years ensured that participants had already finished their growth spurt. At age 17 the size and most soft tissue characteristics are already that of an adult (Bishara et al., 1985). A maximal age difference of seven years between siblings was imposed to control for changes related to aging as greater difference in age decreases phenotypic correlations (Mueller, 1978; Mueller & Malina, 1980). For obvious reasons, participants had to be physically normal without apparent defects in face or head. They were excluded if they had facial injuries or plastic surgery, suffered from diseases related to growth or metabolism, took any form of hormonal treatment (with the exception of contraceptives), were currently undergoing orthodontic treatment, suffered from birth complications, or were closely related to any other participant of the study except their sibling. These rules decreased the sample size from an original number of 86 to 70. The complete questionnaire, including additional demographic questions is in Appendix A.

After the questionnaire I informed all participants about the purpose of this study, and included data only from those who gave their written consent. Evidently such a sample cannot represent the Austrian or any other population.

3.2 Data recording

A set of 70 high resolution colour photos (3.6 Mega pixels, 1594 x 2294) of the participant's faces served as data in this study. All photos were taken in frontal view in front of a white background, using a digital single lens camera mounted on a tripod. At all time tripod and object position remained unaltered during data acquisition at a distance of approximately two meters. Ambient light conditions were held constant.

Prior to the procedure I instructed all subjects to remove any facial adornment and if necessary to pull back their cranial hair wearing a hair-band. They were asked to maintain a neutral expression with lips slightly closed, not applying any pressure. Instead of an osteological standardisation such as the "Frankfurt Horizontal", where *Porion* and *Orbitale* are in the same horizontal plane, they were told to "look directly into the camera". In frontal images, nodding (pitch) and head turning (yaw) create nuisance variance that cannot be distinguished from true differences in shape. So I controlled for both (figure 1) with the aid of the relative extent of helix exposure in the ears. Head tilting (roll) does not affect facial shape as it is removed later. Focus, orientation and expression were checked on the camera's LCD screen, eliminating any motion parallax errors. Other perspective distortions of photography are ignored in this study because all images would be affected by them in almost exactly the same way.

Every participant was photographed until at least three pictures met all criteria. Photo sessions of siblings occurred on different days. Images were saved in JPEG format under the highest available quality setting for the digitization to follow.

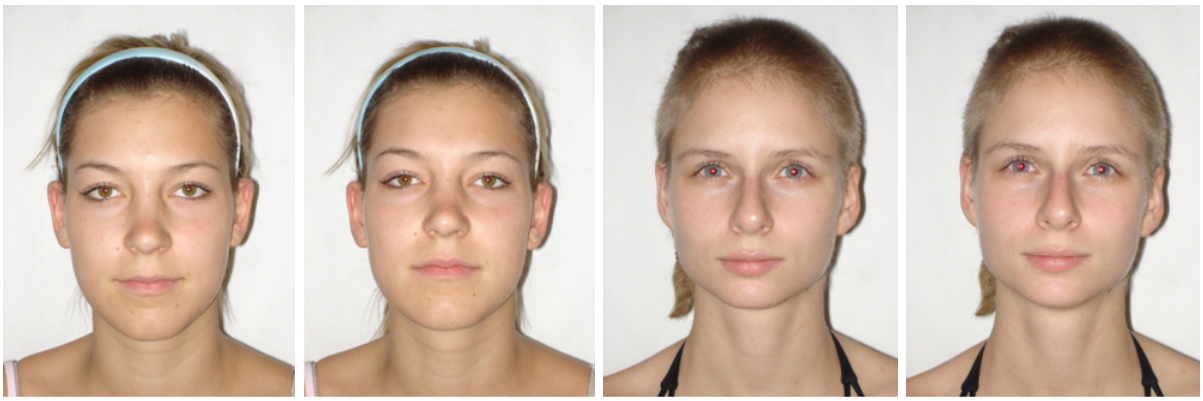


Figure 1. Four images of two female participants are shown at about 1% of their original resolution. Only the leftmost image was accepted for analysis. The others were rejected for nodding (pitch), head turning (yaw), and facial expression. The head tilting as present in the rightmost picture is removed during analysis and does not confound shape.

3.3 Acquisition of landmarks

The 2D landmark coordinate data was assessed by manually setting 46 predefined landmarks (Appendix B) on each image using tpsDig2 (Rohlf 2006, Version 2.10). Landmarks are discrete points lying on the forms or images they represent: biologically homologous loci defined by their surrounding anatomy only and corresponding across specimens. They should be recognizable on all specimens of a sample, and must provide an adequate summary of the shape studied (Bookstein, 1991; Dryden & Mardia, 1998; Moyers & Bookstein, 1979).

Despite the number of facial studies already in print there is no standard landmark configuration for faces in frontal view. Of all the available somatometric schemes we found Knussmann's (1988) the best suited for our experimental design. From the landmarks he mentioned, I included only those that could be found on every photo, and new ones that seemed to correspond just as well.

3.3.1 Sets of landmarks

Four different sets of 46 landmarks in total were used. All landmarks were included for the global analysis of the whole face. The other three subsets arose for the separate analysis of the upper face, lower face, and nose-lip region by removing landmarks from the global set in tpsUtil (Rohlf 2006, Version 1.38). Figure 2 illustrates the sets.

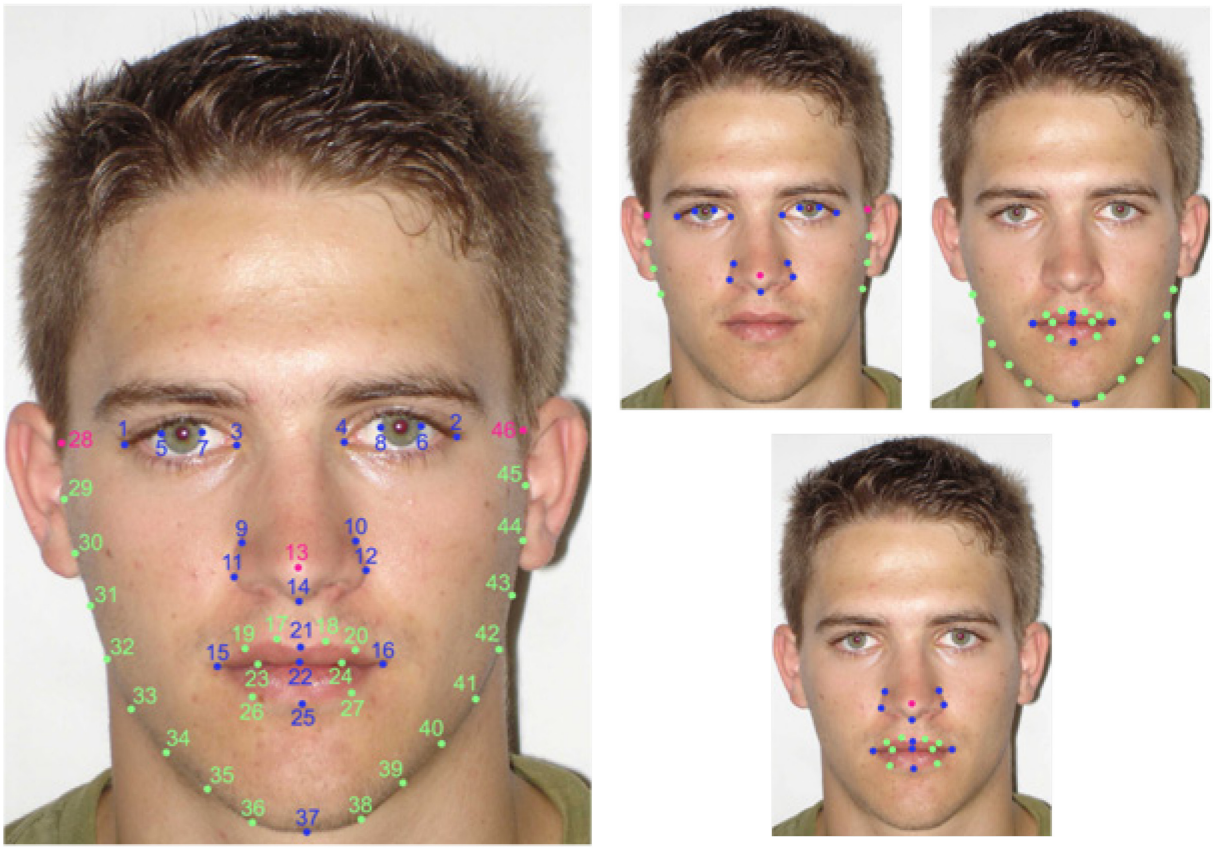


Figure 2. Left: the global set with all 46 landmarks. Right: subsets for the upper face, lower face and nose-lips region. Blue dots represent landmarks that can be identified unambiguously; semilandmarks are green. The endpoints of the facial outline (28, 46) were allowed to slide, resulting in an open curve. The tip of the nose (13) was slid by lighting, thus making it possible to be digitized in frontal view.

3.3.2 Landmarks

There are three categories of landmarks (Bookstein, 1991). Type I landmarks, the most meaningful for an analysis, are discrete juxtaposition of structures, intersections, or patches of unusual histology. Type II claims homology only by geometric evidence, for example points of maximal curvature. Extremal points and points constructed or identified by reference to other features or landmarks fall under Type III.

As most type I landmarks on soft tissue can be located only by touch, only the latter two types could be used in this study. Furthermore it can be difficult to adequately sample all morphological regions of the human face, for example the facial outline and the lips. These shapes lack anatomical loci that could be confidently identified in just one view. I described these by adding semilandmarks

(Bookstein, 1997). Semilandmarks are points on curves that serve only as local estimates of location along the normal to the curve. They are slid by an algorithm to minimize the most local shape change among all specimens. Though semilandmarks are points without names, they correspond across all specimens like homologous landmarks do and the same statistics can be applied (Fink et al, 2005).

18 of these semilandmarks were equidistantly distributed along the outline of the face (28-36, 38-46), and eight along the lips (17-20, 23, 24, 26, 27). *Gnathion* (37), a type III landmark on the outline, was not slid.

The endpoints of the facial outline (28, 46) were placed at the intersection of the facial border and the extension of a hypothetical line through the corresponding *Endocanthion* and *Exocanthion* of each side. As their vertical coordinate is only constructed, they were allowed to slide along an extended line through the last two semilandmarks, resulting in an open curve. *Pronasale (13*), the most anterior point of the nose, appeared as a bright spot in every image created by artificial lighting, and could thus be digitized even in frontal view.

3.3.3 Skipped landmarks

Landmarks from Knussmann's list that could not be accurately replicated or appeared to be perturbed by environmental factors and illnesses were not included. From all the vertical unpaired landmarks this applied to *Metopion*, *Ophryon*, *Glabella*, *Labiomentale*, and *Pogonion*, as they offered low reliability. *Nasion* and *Sellion* generally lack clear visibility on frontal images (Knussmann, 1988). *Vertex* and *Trichion*, used for measurements related to facial height, could not be included due to scalp hair or receding hairline.

From the paired landmarks around the facial border, the positional data of *Zygion* and *Gonion* were already covered by the facial curve and semilandmarks. Whiskers and facial fat deposits made them difficult to localize, and they were consequently not treated as landmarks.

Of the possible landmarks located at the eyes and orbits, the positions of *Palpebrale superius* and *inferius* depend strongly on the aperture angle of the eye, an angle sensitive to many environmental factors. *Superciliare*, *Superciliare laterale*, and *Orbitale superius* were omitted because some subjects tended to pick their eyebrows. The position of the center of the pupil is already implicit in the positions of landmarks 5-7 or 6-8 of each iris.

Although length measurements of the ears are reported highly heritable (Byard, 1985; Sengupta & Karmakar, 2007), *Superaurale*, *Subaurale*, *Porion*, *Otobasion superius* and *inferius* had to be removed from our scheme. All of them were often either hidden by facial hair or the face itself depending on the ears' protrusion.

3.3.4 Setting of landmarks

Landmarks were exclusively set by the author (C.H.) to eliminate interrater variation. Corresponding siblings were digitized on different days to avoid correlated errors. To assess digitizing replicability, images of three randomly chosen women and men were digitized four times on each of four days. Analysis showed a mean absolute error of ±2.7 pixels per landmark, which is negligible in comparison to actual sample variation. Of these pictures only the first digitisations were later used in the study.

3.4 Geometric morphometrics analysis

Instead of a traditional feature-by-feature approach, facial shape was assessed at once by the methods of GM. GM or statistical shape analysis consists of several tools well suited for multivariate statistical analysis and immediate visual presentation of variations in shape among individuals or between groups (Bookstein, 1991; Dryden & Mardia, 1998; Slice, 2005). When combined with photography it is a fast method to acquire data while keeping participant strain at low levels. Measurement errors related to soft tissue compression need not be considered, and one is allowed to go back at any time to retake measurements, or for modifications as suggested by new findings or insight from colleagues.

3.4.1 Procrustes fit and Procrustes distances

A Procrustes fit of raw landmark data marks the first step in a GM shape analysis. To this end, configurations of landmarks are translated with their centroid to origin (0,0), rescaled until centroid size - the square root of the sum of squared distances of each landmark to the centroid (Gower, 1971) – is exactly 1.0, and least square rotated to a consensus. To obtain a consensus a single configuration of the sample can be taken as trial reference at the beginning of an iterative fitting process (Rohlf & Slice, 1990). Each configuration is rotated to this trial reference until the sum of squared residuals

between corresponding landmarks is minimized. They are then averaged and rescaled again to obtain a new consensus, and the fitting process is repeated. Usually two or three iterations result in a consensus accurate enough.

There are several benefits to this procedure. The Procrustes fit removes the need for reference structures such as the sella-nasion plane for superimposition. While these planes are assumed biological stable, even the slightest variation will confound analysis, as apparent changes occur only in relation to them (Richtsmeier & Cheverud, 1986). A superimposition on the centroid instead of any arbitrarily chosen landmark also avoids the loss of possibly relevant data, and grants all landmarks equal weight in the superimposition as well.

After a Procrustes fit the resulting coordinates contain shape information only. Shape-to-shape variation can then be approximated by the Procrustes distance, the square root of the summed residuals between aligned configurations, quantifying shape dissimilarity to the consensus.

3.4.2 Relative warps analysis and the thin plate spline

The shape variables were then subjected to a relative warps analysis and the first two relative warps (RW) were plotted for each region and sex. A relative warps analysis is equivalent to a principal component analysis of shape (Bookstein, 1991; Rohlf, 1993). The variables of a dataset are rotated in such a way that the resulting new variables are ordered according to their magnitude of variance, and uncorrelated with each other. Customarily the variable accounting for most of the variance is called the first principal component, with subsequent variables named in the same way.

Principal component analyses are frequently used in explanatory data analysis to simplify the description and visualization of high dimensional data sets. Most of a sample's variance can be plotted with just the first few principal components. Spatial transformations along them can be intuitively visualized by the thin plate spline.

The thin plate spline is a mapping function expressing the spatial differences between two configurations of landmarks as a continuous deformation (Bookstein, 1991; Rohlf & Marcus, 1993). Displacements between homologous landmarks are modelled alike deformations at right angles to the plane of an idealized, infinitely large, and thin metal plate, hence the term thin plate spline. When the plate is bent at

a landmark the surrounding area is affected as well, which can be used to interpolate the deformations in areas without landmarks. The idealized energy required to lift or lower landmarks, the bending energy, is highest for most local deformations and minimizes towards more global ones. Bending energy is a physical metaphor derived from the theory of plates and shells, proportional to the integral of the summed squared second derivatives of these vertical displacements. The bending energy of a shape change is the sum of the bending energies of all non affine transformations. In affine transformations of translation, rotation, and scaling without bending it is zero. When combined with grid lines the thin plate spline can create transformation grids reminiscent to those of D'Arcy Thompson (1917), visually appealing and ideally suited to represent shapes.

3.4.3 Software and sliding of landmarks

I superimposed each of the four landmark sets, males and females separately, in tpsRelw (Version 1.45, Rohlf, 2007). The slider and links files were created in tpsUtil (Version 1.38, Rohlf, 2006) with semilandmarks slid to minimize bending energy between each specimen and the consensus (Bookstein, 1997). Sliding semilandmarks to minimize bending energy instead of Procrustes distances has several benefits. While both approaches optimize the spacing and remove any artefacts of their arbitrary placement establishing geometric correspondence between shapes, bending energy takes only local, non affine, deformations into account. Affine changes have no effect on the sliding. More importantly, bending energy is based on the whole configuration, so other semilandmarks and real anatomical landmarks have an influence in the sliding. It is also hardly possible for semilandmarks to slide beyond another semilandmark maintaining biological homology (Gunz & Mitteroecker, 2013). Procrustes distances were calculated in tpsSmall (Version 1.2, Rohlf, 2003) with the relative warp analysis conducted in tpsRelw (Version 1.45, Rohlf, 2007).

4. Results

4.1 Participants

The female participants of the sample were on average 22.0 years old (n=35, four missing values, range 16.4-26.8 yrs), and the males 23.8 years (n=31, range 16.7-30.3 yrs). For the distribution in age see figure 3. Sisters differed on average by 3.0 years in age (n=26, range 0.8-6.5 yrs) and brothers by 3.8 (n=22, range 2.1-5.7 yrs). While body height was evenly distributed in both sex (women: range 153-178 cm, mean 165.8 cm; men: range 165-194 cm, mean 179 cm), men varied more widely in weight than women (women: range 43-82 kg, mean 58.6 kg; men: range 52-114 kg, mean 74.3 kg). Since pairs of same-sex siblings and corresponding siblings of the mixed pairs displayed no significant differences in physical size (Mann-Whitney U-test, two-tailed, Alpha=0.05), they were pooled for additional Procrustes distances.

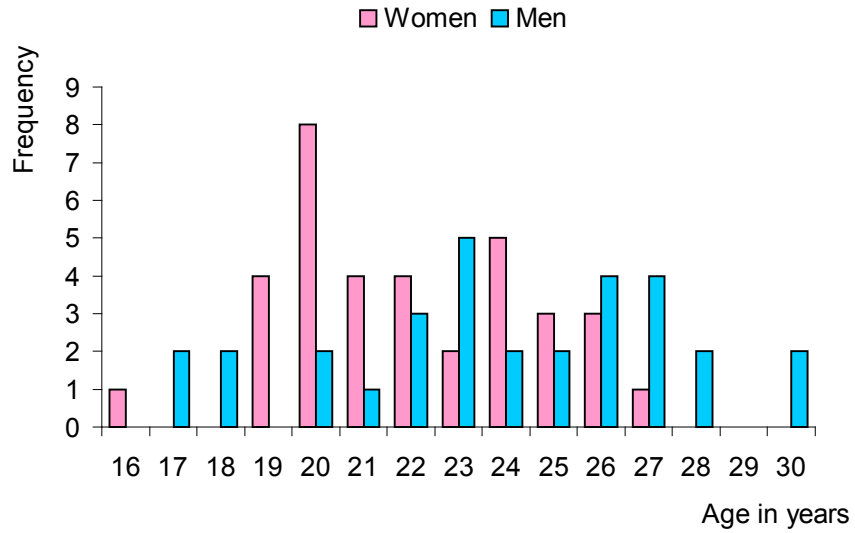


Figure 3. Age distribution of participants

4.2 Procrustes distances

Procrustes distances (table 1) within pairs of siblings (female: 15; male 11) were significantly smaller (Mann-Whitney U-test, 2-tailed, both sex, globally, $p<0.01$; regionally, $p<0.05$) than those between unrelated individuals (female: 726; male 454) except for the upper face and nose-lips region in males. As expected, the biggest Procrustes distances appeared between unrelated individuals, but surprisingly most minima also. The standard deviations within brothers were bigger than for men due to more outliers, while it was the opposite for women.

Procrustes Distances

	Females					***Males***				
	Mean	Min	Max	SD	Median	Mean	Min	Max	SD	Median
Globally										
Siblings	.0526	.0352	.0797	.0130	.0526	.0577	.0402	.1051	.0191	.0519
Unrelated	.0645	.0298	.1172	.0166	.0623	.0701	.0287	.1260	.0167	.0694
Upper Face										
Siblings	.0484	.0330	.0691	.0098	.0461	.0528	.0346	.0920	.0191	.0453
Unrelated	.0566	.0234	.1295	.0161	.0540	.0610	.0243	.1257	.0170	.0576
Lower Face										
Siblings	.0610	.0429	.0764	.0123	.0598	.0757	.0383	.1600	.0324	.0704
Unrelated	.0732	.0228	.1394	.0216	.0713	.0900	.0241	.1693	.0275	.0871
Nose-Lips										
Siblings	.0800	.0528	.1452	.0230	.0827	.0827	.0437	.1359	.0280	.0747
Unrelated	.0933	.0392	.1955	.0246	.0892	.0976	.0485	.1785	.0235	.0947

Table 1. Average Procrustes distances within siblings and between unrelated individuals.

The small sample size rendered the analysis quite sensitive to outliers, so we used squared medians instead means to calculate the sibling-stranger PD-ratios. The ratios for males were globally the lowest (0.56), followed by the upper face (0.62), the nose-lips (0.62), and the lower face region (0.65). Women ratios generally lay higher beginning with the lower face (0.70), second globally (0.71), then the upper face (0.73), and nose-lips region (0.86) last (figure 4).

With likewise ratios within each sex except for the nose-lips region in women, I checked for possible confounding factors there. Physical size and smoking habits yielded no significant effect, but the comparison of pairs with an equal pill regime

(eight) to those where only one took contraceptives (six). Equal pairs showed on average 35% less facial dissimilarity there than unequal pairs, and less in the other regions as well (table 2).

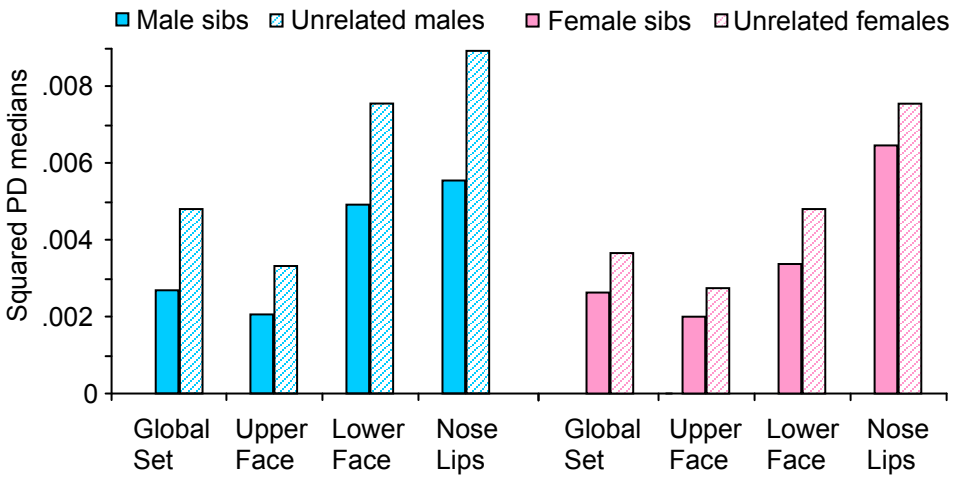


Figure 4. Squared Procrustes distance medians within siblings or unrelated individuals.

Procrustes Distances and oral hormonal contraceptives

	Mean	Min	Max	SD	Median
Globally					
Unequal pill regime	.0591	.0414	.0797	.0144	.0577
Equal pill regime	.0474	.0352	.0660	.0117	.0416
Upper Face					
Unequal pill regime	.0516	.0411	.0691	.0108	.0464
Equal pill regime	.0459	.0330	.0617	.0104	.0409
Lower Face					
Unequal pill regime	.0651	.0429	.0764	.0125	.0676
Equal pill regime	.0557	.0444	.0719	.0116	.0513
Nose-Lips					
Unequal pill regime	.0951	.0721	.1452	.0254	.0887
Equal pill regime	.0671	.0528	.0944	.0162	.0569

Table 2. Average Procrustes distances within sisters corresponding to pill regime

4.3 Relative warps analysis

I confined the relative warp analysis of the Procrustes shape coordinates to the first two warps only, which accounted for 52% to 68% of the total shape variation in the sample. Other subsequent warps were regarded as spherical noise and not further analysed. Shape changes along these RWs were assessed utilizing deformation grids. Large scale changes were covered in the global set of landmarks, whereas small scale changes were limited to the regional subsets for better visibility.

4.3.1 Global set

Figure 5 depicts the results of the global relative warp analysis, where each data point represents a participant. Both warps together explain approximately 54% of the total shape variation in men and women globally. The siblings of each pair are identically colour coded circles through all figures. Triangles symbolize PD outliers, while pluses are singletons from the split up mixed-sex pairs.

The difference in RW-scores averaged less within siblings than between unrelated individuals, showing greater correlation in the RWs on which individuals vary most. A closer look revealed that sisters differ more in the first warp than in the second, while brothers vary indifferent. The spatial changes along these warps are drawn as deformation grids in figure 6. Located in the middle is the average landmark configuration of each sex. Neighbouring panels illustrate the deformations from the consensus to the target faces two standard deviations away, but still inside the sample range.

The deformations in RW 1 affect bigonial breadth, the lower outline of the face, and the upper lip-mandible height index (subnasale-stomion:stomion-gnathion, Farkas & Munro, 1987) in women and men. At the lips, it is the upper vermillion height that changes in women, and the lower in men. These deformations look like changes in weight, and indeed showed a trend with BMI in females, and weight in males. Warp 2 mainly shifts the facial height-width ratio, with additional changes in the upper vermillion height and mandible height for women, and labial height (Labrale superius-Labrale inferius) for men.

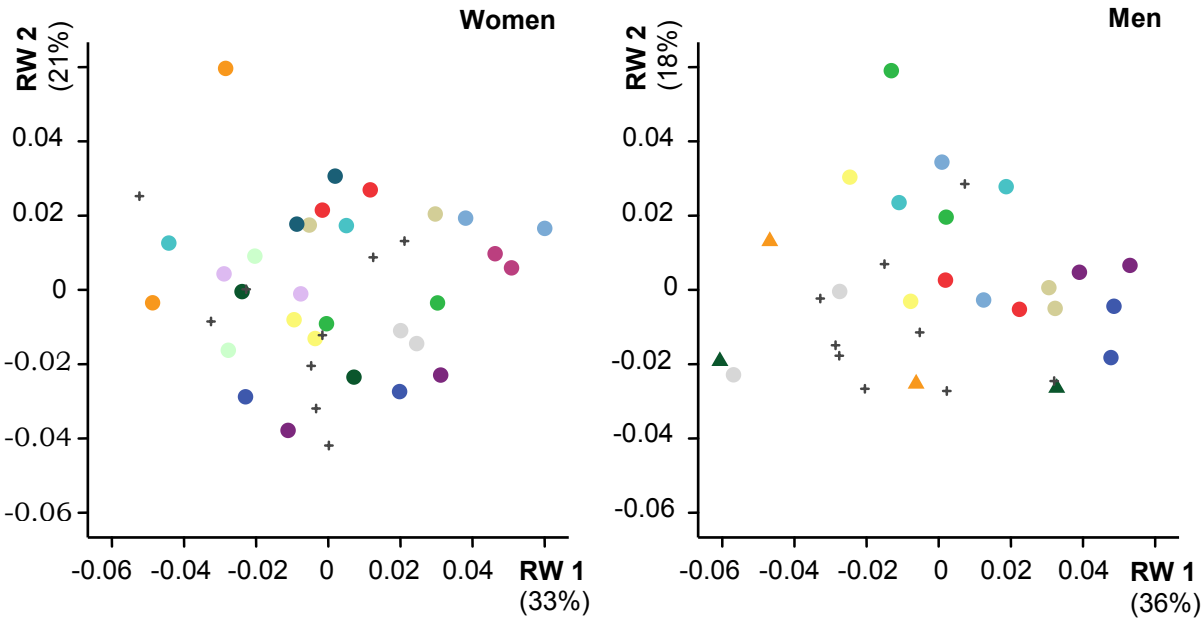


Figure 5. Relative warp one and two of the global landmark set.

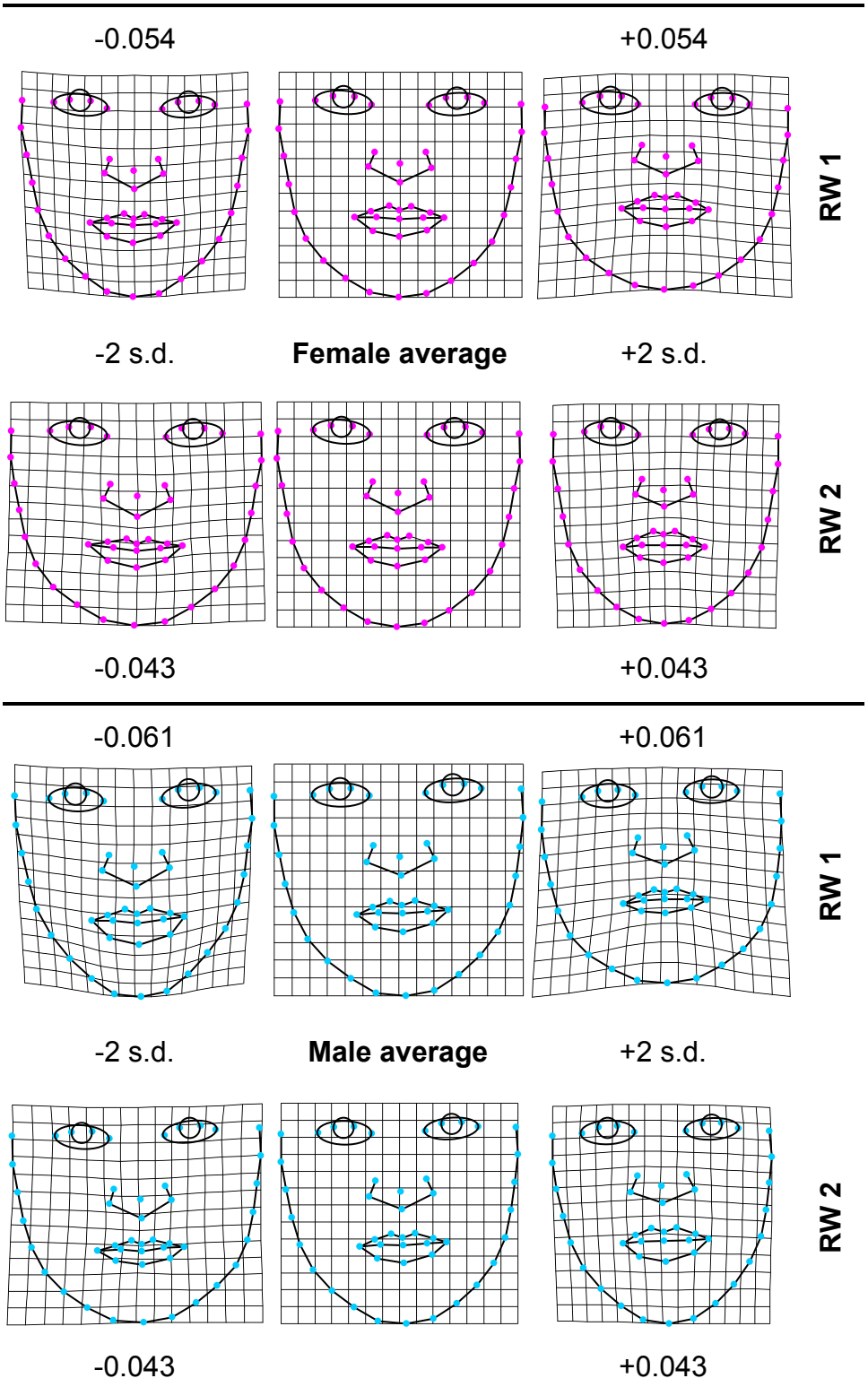


Figure 6. Shape changes along relative warp one and two applied to deformation grids. The average undeformed landmark configuration is located in the middle. Neighbouring grids visualize the deformations at the target faces two standard deviations away, but still inside the samples range.

4.3.2 Upper face

In the regional analysis I focused on the small scale changes of the upper face, lower face, and the nose-lip region due to their better visibility than in the global set.

Similar to the global approach, siblings continue to correlate pair-wise, differing less from their sibling than from the others in RW-scores. In the upper face the first two RWs explain approximately 52% of female and 60% of male total shape variation (figure 7). It can be seen in figure 8 that RW1 mainly affects the nasal height, and less the inclination of the eye fissures. Again there is little difference between the sexes. In RW2 the deformations are limited to the intercanthal distance (*Endocanthion-Endocanthion*) for both sexes, notably smaller in men, and an additional slight change in nasal breadth.

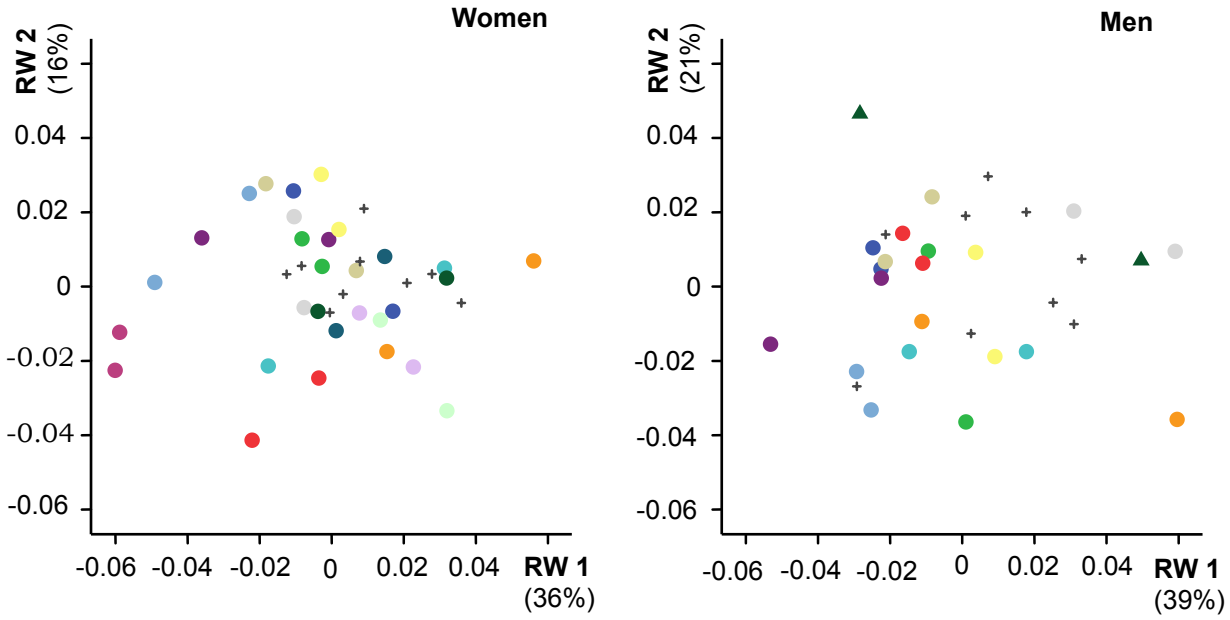


Figure 7. Relative warp one and two of the upper face.

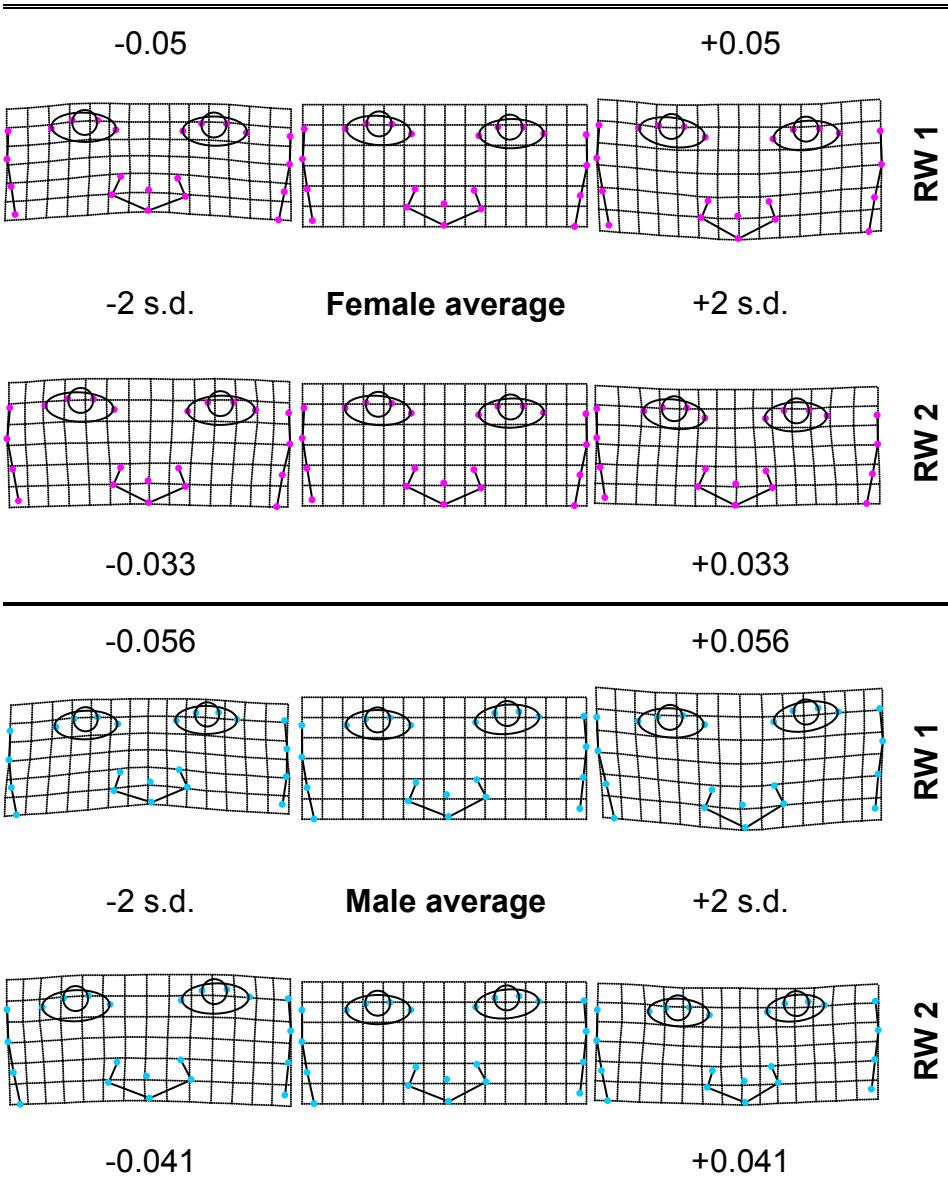


Figure 8. Shape changes along relative warp one and two of the upper face.

4.3.3 Lower face

The contribution of the first two RWs (figure 9) to total shape variation in all regions was largest in the lower face (women: 63%, men: 68%). Relative warp 1 for women mainly shifts vertical structures: the upper vermilion height, lower face height (*Gnathion-Subnasale*), and mandible height (figure 10), with a small change in mouth breadth, and scores correlate with BMI (r=0.42). Spatial changes in warp 2 are apparent in the mandibular index (*lower face height:bigonial breadth*; Farkas and Munro, 1987), and mouth breadth. Men exhibit spatial deformations in labial height, mandible height, and mouth breadth in warp 1. Warp 2 changes the mandibular index in the same pattern as for women.

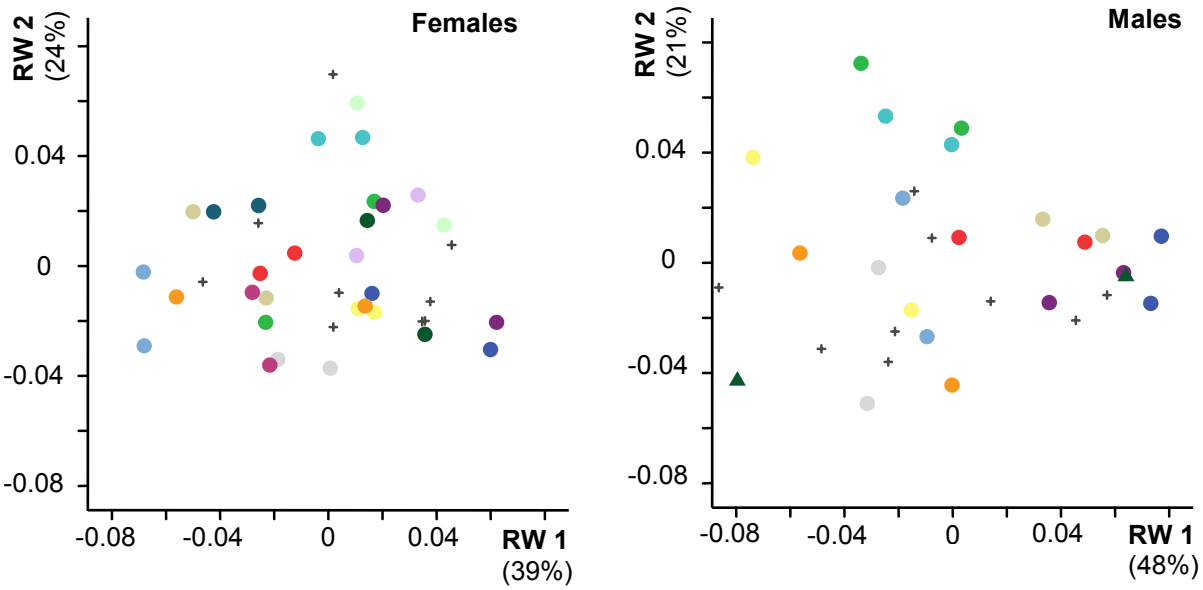


Figure 9. Relative warp one and two of the lower face.

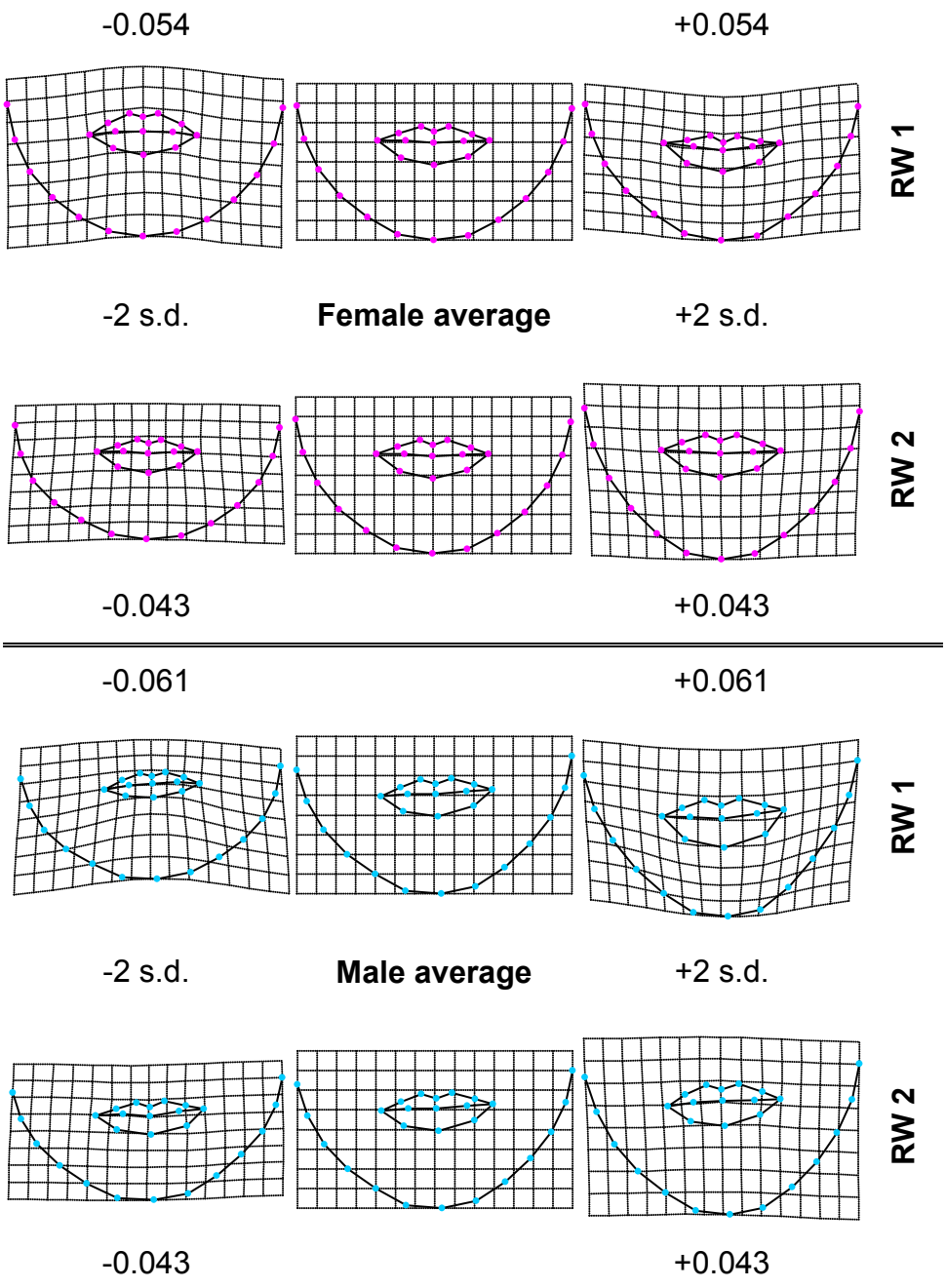


Figure 10. Shape changes along relative warp one and two of the lower face.

4.3.4 Nose-Lips

Figure 11 encompasses approximately 53% of the total shape variation in the nose-lip region for females, and 52% for males. Deformations (figure 12) in RW1 of women occur in the lip-index (labial height:mouth breadth), and the upper cutaneous height. Men show a shift in the lip-index. Warp 2 affects the upper vermilion height in females, and the upper cutaneous height in men along with relative size of the lips. None of these correlated significantly with size.

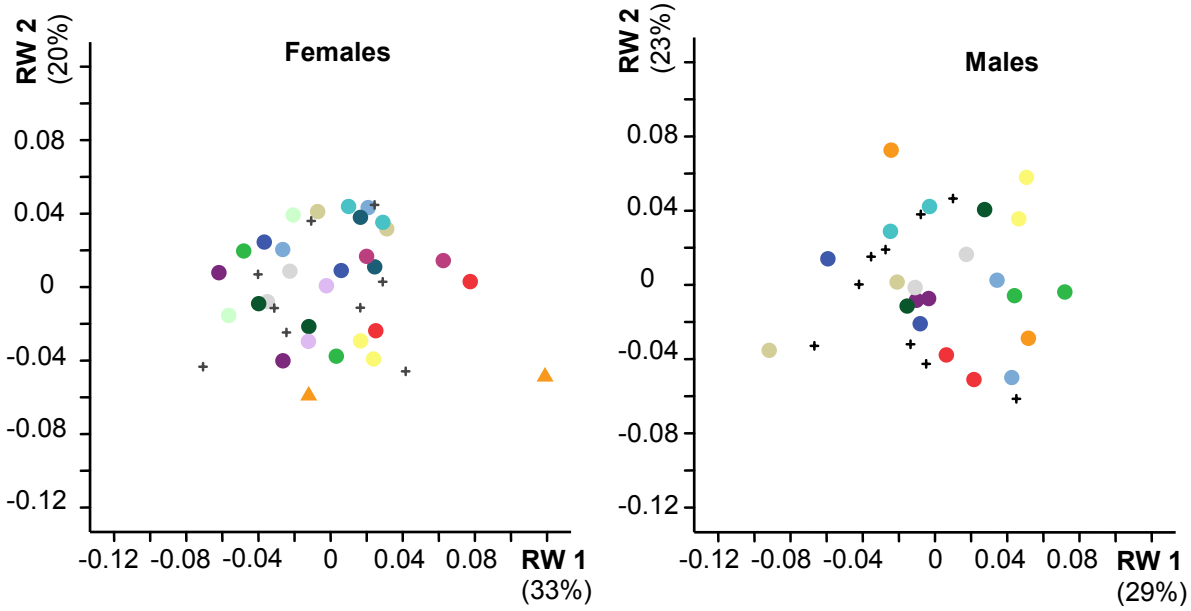
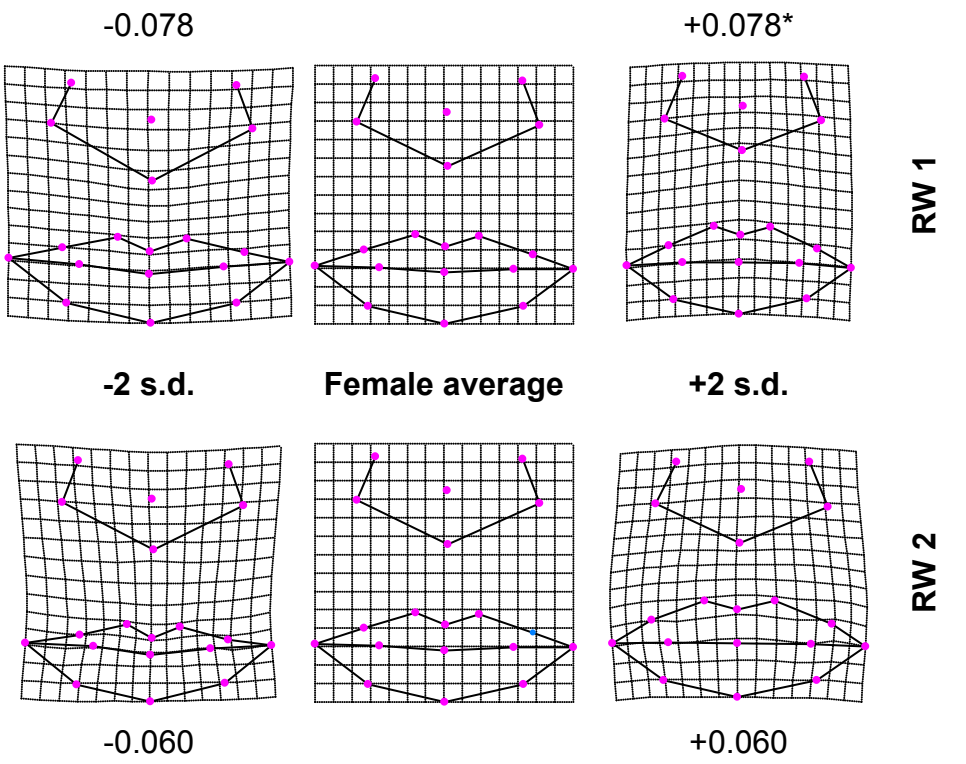


Figure 11. Relative warp one and two of the nose-lips region.



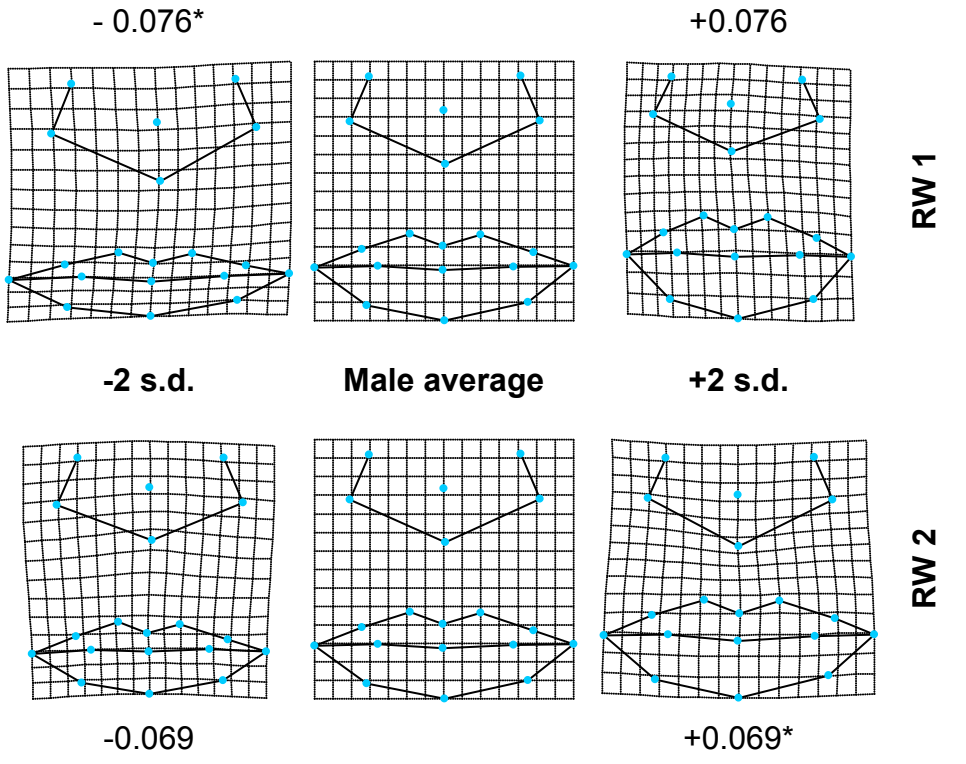


Figure 12. Shape changes along relative warp one and two of the nose-lips region.

5. Discussion

The main finding of my thesis corroborates the common notion of a moderate to high similarity for cephalic characters among close relatives by extending it to facial shape in full siblings. At the same time I introduced GM to move beyond the well established realm of traditional measurements and to evaluate its variability within siblings. For this reason, the interpretation and comparison of results need to be done with the methodical differences in mind.

As hypothesized the Procrustes Distances were significantly smaller within sibling-ships than between them (table 1). This clearly indicates a genetic contribution to facial shape-to-shape variation among siblings while following the pattern of a polygenic inheritance in close relatives. Susanne & Sharma (1978) have reported analogue findings for head measurements in Punjabi and Belgian families when they applied a related method of generalized distances to examine proportions as a whole. Their pair-wise distances increased from twins to siblings and further relatives inversely to genetic correlation, with slight nuances on those in intermediate positions. Though the same trend could be expected here for facial shape to, with only one grade of relatives studied results should not be used as normative data to predict others.

That shape-to-shape variation in the upper face and nose-lip region in males did not reach significance between groups, is likely the result of the many outliers among brothers, and should not be overrated for the following reasons. High standard deviations are not uncommon when studying quantitative characters, especially within exploratory samples sizes such as mine, and without a meaningful null hypothesis all tests of significance present in this thesis should be against a heritability of .5 instead of null. Unfortunately, the limited number of couples prevented such testing, but may be applied in future studies. The unexpected finding that some unrelated couples exhibited less dissimilarity than siblings in all but one region is simply a consequence of their far greater number of possible comparisons. Contrarily to siblings this number increases progressively with rising sample size.

5.1 Global and regional heritability

To facilitate a comparison with heritability estimates previously published, the following include only characters that could be derived from my landmarks as well. These estimates are furthermore averaged across traits to obtain a single mean heritability representative for each study. It is important to note that such mean can not substitute for shape and is only applied in default of similar shape studies.

The global interpretation of heritability through ratios (the complement in 1.0) yielded slightly different results in each sex at a moderate level of 0.44 in men, and 0.29 in women. These values are lower than most previously reported among twins, but twin studies have often been criticized to exaggerate heritabilities. Early estimates by Martin (1928) for like-sexed twins ranged from 0.54 to 0.76, averaging at 0.67. Similar were those published later for 11 facial measurements in a Belgian sample (Defrise, 1981), ranging from 0.37 to 0.80 and a mean of 0.64. Estimates based on familial correlations including siblings are more consistent with the values presented here. Arya and colleagues (2002), for example, examined the heritability patterns of 23 phenotypes including 6 craniofacial measurements in Indian casts. After accounting for non genetic effects their estimates averaged at 0.45. A recent Korean study (Kim et al., 2013) evaluated the familial correlations in facial morphology for a total of 14 measurements taken on digital photos. The genetic contribution to variance in those characters accounted for 37% on average. Compared to estimates for craniofacial dimensions as reported in the Hallstatt studies, values came up lower there at 0.27 (Carsen, 2006) and 0.26 (Martínez-Abadías et al., 2009). Considering the range in those values it becomes evident that heritability is an abstract concept working only on population levels, specific for one population at one time, and though one estimates a value it can never be a precise degree.

To answer the question whether different portions of the face vary in their genetic control in a similar way as the human skull (Carson, 2006) or craniofacial characters (Martínez-Abadías et al., 2009), I also estimated dissimilarity regionally. The likewise ratios found within each sex, except in the nose-lips region in sisters, suggest that this may not wholly apply, but can not answer for certain. It rather confirms the loose relationship between soft tissue and underlying skull earlier reported (Simpson & Henneberg, 2002) and that hard tissues are not the sole determinants of external

shape. Cranial estimates may simply be as unreliable as proxy for soft tissue as vice versa. However, results could vary greatly depending on the regional configuration of landmarks one chooses, or stay indifferent as many siblings show a strong family resemblance in some traits; the famous Habsburg family comes to mind, but clearly are different in others.

5.2 Shape variability

The relative warp analysis of the Procrustes shape coordinates revealed similar changes in shape in women and men in every region. Siblings showed a pair-wise correlation in the first two relative warps that explained 52% to 68% of total variation, indicating a hereditary influence where individuals varied the most. However, it should be kept in mind that relative warps are derived strictly statistically and may not necessarily relate to any traits, or bear a clear biological meaning.

Most of the large scale variation in the sample was covered in the first relative warp of the global set mainly involving mandibular height, bigonial breadth and the outline of the face. These results are in line with Demayo and colleagues (2010) who compared twins for concordance and found similar deformations in the first relative warp, and compliments the research of other ‘classical’ studies. Manfredi and colleagues (1997), for example, reported a strong genetic control in the lower third of the face and in the shape of the mandible. Horowitz and colleagues (1960) who studied fraternal and identical twins using linear measurements found a significant hereditary resemblance in the mandibular body length and lower face height. Moreover, a factor analysis by Kim and colleagues (2013) revealed that their first factor showing the highest heritabilities was mainly related to the lower portion of the face, and also found a significant correlation for bigonial breadth in siblings. Lobb (1987) further stated that the shape of the mandible in twins is similar in 100% of the cases when differences in angulation in the craniofacial complex are taken into consideration.

But deformations like these can also occur with changes in weight as fat deposits are known to result in greater measurements along the facial contour with larger mandibular and maxillary dimensions (Sadeghianrizi et al., 2005). The trends between warps scores and BMI in women and weight in men seem to further support this. So other than for genetic reasons the correlation in this warp may only reflect a

more common lifestyle between siblings including dietary habits. The nowadays not unusual desire in women to control ones weight would further explain why sisters varied more in the first relative warp than in the second. Unfortunately it is not clear from the questionnaire whether participants had experienced any significant changes in weight lately. The global deformations found in the second relative warp were mainly confined to facial proportions. Correlations for height and for width of the face (bizygomatic breadth) have been reported in Belgian siblings by Susanne (1975), to a higher degree in twins by Byard and colleagues (1985), and through estimates for heritability by many others (Susanne, 1977; Arya et al., 2002; Kim et al., 2013).

Other, more local shape variations too subtle for the global analysis happened to the height of the nose, to a lesser content in its breadth, and in the intercanthal distance in the upper face region. The heritabilities of nose dimensions have been confirmed in several studies with greatly varying results (Defrise, 1981; Martin 1928; Kim et al. 2013; Arya et al. 2002), whereas those for intercanthal distance are more stable at a moderate level (Raposo-do-Amaral et al., 1989; Im et al., 2010; Kim et al., 2013).

The mouth revealed to be an area of high variability, more affected in heights than in breadths throughout regions, and only appeared bigger or smaller in the global and lower face region as facial dimensions changed but the total size in configurations was held constant. The upper lip showed most variation in both gender, with additional changes in height for the upper vermillion in women but less in men. According to Baydas and colleagues (2007) study on facial proportions in lateral cephalograms the upper lip reflects both, environmental and genetic influences, and can be affected to a greater extend than the lower, which only showed moderate heritability. But interpretations should be exercised with caution as the lips and vermilions are susceptive to a number of factors including postural restraints, which may have been caused when all participants were photographed with them closed. In individuals with smaller lips, prognathism, and other malocclusions this may have imposed strain and deformed the natural outline.

5.3 The pill effect

Of all configurations, only the nose-lip region in sister deviated from the otherwise likewise pattern of ratios. As confounding variables are a worry, I found that sisters on an unequal Pill regime differed more than those sharing the same. With a higher

concentration of estrogen-receptors in the face than in the breasts or hips of women (Hasselquist et al., 1980), it seems feasible for hormonal contraceptives to affect facial shape. Unfortunately, no empirical evidence for this exists as previous Pill studies were mainly focused on possible health risks. Even in a broader sense there is only limited understanding of the effects of estrogens on the skin per se. Studies have reported increased thickness, improved hydration, and other cutaneous changes (Hall & Phillips, 2005; and references therein), but most of these results derive from hormone replacement therapy performed in postmenopausal women.

However, a link between morphological expression of certain facial features and hormone levels is much discussed in Evolutionary Psychology, where they could act as detectable cues (Gangestad & Simpson 2000; Scheyd et al. 2008). There, the size of lips is widely considered a 'hormone-marker' in women indexed by estrogen levels (Johnston & Franklin, 1993). The first lead to directly substantiate this assumption was recently published by Oberzaucher and colleagues (2011). They photographed women daily during their menstrual cycle, and compared their images with GM. During the peaks of estrogen in the ovulatory phase changes in shape were registered, including fuller lips.

Since the lips were present in all configurations where the equal Pill regime varied 24% to 30% less, a Pill induced variation could act as causal explanation why ratios were generally lower in women. But as much as notes of this sort might entertain ideas, without further evidence, and additional data on the participant's hormone levels and actual type of Pill, all these conclusions remain equivocal. Further studies may shed more insight on a possible link between facial shape and hormonal contraceptives.

5.4 Sex linked inheritance

As global and regional ratios were different between sexes, generally higher in men, sex-linked inheritance may be involved in the variation of facial shape. Sex linked inheritance describes the situation where the expression of a trait is affected by a gene located on the X-chromosome. Since males carry only one contrarily to women, their X-linked genes are always expressed regardless recessiveness, and the normally expected correlation between them changes. With 4% of the genome located there (Ross et al., 2005), it may be argued that this only surmounts to a

proportional, insignificant difference, but has been shown otherwise for several phenotypes (Pan et al., 2007).

While I cannot safely dismiss the possibility; a further decomposition of estimates would require a different statistical model and a sample in the hundreds, previous results by Susanne and colleagues (1975) have shown such bias unlikely for facial characters. An earlier study on the relation of family correlations by Mather and Jinks (1963) has further confirmed that if sex-linked inheritance is present, correlations would normally be bigger among sisters than among brothers, which is the inverse to the findings here.

5.5 Caveats and future improvements

Although sibling's ratios followed most of the expectations they were not exactly half as big as theoretically assumed. This may be partly explained by the reasons above, that it needs large sample sizes to offer expected results, or that my thesis is not without caveats.

The statistical model I used crucially depended on the expected level of genetic correlation among and between the groups compared. Since I based those levels upon pedigreed data alone, the possibility of confounding factors such as extra pair copulation can not be excluded. Extra pair copulation or paternity by someone other than the putative and domestic father has been reported to vary heavily between different populations from less than 1% in Switzerland (Sasse et al., 1994) to 30% in France, England and the US (Baker & Bellis, 1995) in Caucasians. With a best estimate at about 10% generally suggested (Baker & Bellis, 1995; Sasse et al., 1994), and the locally closest estimate from Munich at almost 10% (Ritz, 1985) a contamination of the sample with half-siblings is not unlikely. Half-siblings as well as any unknown cases of adoption would increase sibling variance, and effectively decrease the average correlations.

Genetic correlations may have been further affected by assortative mating, a non random strategy in mate choice that is often driven on phenotypical characteristics as major criterion (Buss, 1984; Thiessen & Gregg, 1980). Positive assortative mating, the coupling of like with like, has been reported for many phenotypes including the facial resemblance of couples (Hinsz 1989). By favouring a phenotype similar their own positive assortative mating raises correlations between

parents, subsequently between siblings, and heritability of characters will be inflated that way.

Caveats like these may be avoided by an assumption free indicator for genetic relatedness, which has already been done before. Visscher and colleagues (2006) have successfully quantified the actual genetic relatedness in full siblings via use of genetic markers to calculate the heritability of height. Though their results hardly differed from those in theory, the benefits are clear. Without the need for complex pedigree structures, bigger, more arbitrary samples independent of genetic correlations could be selected easily.

More technical points concern perspective distortions and the projection of shape in photos. Perfect photos are scare even when carefully taken as slight elements of rotation are usually present. A noteworthy study has pointed out, that up to 96% of the nuisance shape variability of distortions ends up in the first principle component (Slice, 2005). And while I controlled for rotation using the inner ears helix as reference structure, I may have only confounded analysis to individual positional bias there. But even when rotation is reduced to acceptable levels, other problems can not be avoided entirely. No matter how cunningly contrived a two-dimensional projection of a curved face is, it will only be most accurate when the landmarks are close to the plain of focus. More distant measurements will always suffer greater inaccuracies (Farkas, 1981). By choosing the frontal pictures over lateral I made a further trade-off as this view is known to show less individuality while loosing several landmarks at the same time, especially those located at the ears. On the other hand frontal pictures are known to be superior when it comes to precise measurements of orbits, lips and mouth (Farkas, 1981). The only solution to problems like these is to capture shape in 3D, which may also add new possibilities through the implication of additional landmarks.

5.6 Conclusion

If my thesis has demonstrated one thing, than that facial shape is conditioned by genetic factors like other cephalic traits, following the commonly expected correlation among close relatives due to their common ancestry. Siblings with a more similar genetic endowment have a greater average resemblance in facial shape than unrelated individuals do, without significant regional differences, or between the sexes. I have also demonstrated that GM is a well suited tool for capturing and

quantifying variation of facial shape among differently related individuals. I close with a plea for further corresponding studies to verify the statistical stability of my findings incorporating a greater sample while using some of the previous mentioned improvements.

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Geschwisterstudie

Bitte füllen Sie folgenden Fragebogen vollständig aus.
Ihre Daten werden anonym bearbeitet, es erfolgt keine Weitergabe an Dritte!
Bei Fragen hilft Ihnen Ihr Betreuer gerne weiter.

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Probandennr.: _____

1. Geburtsdatum: _____ Körperhöhe: _____ cm Körpergewicht: _____ kg

2. Wie viele Geschwister haben Sie? _____ Bruder/Brüder _____ Schwester/Schwestern _____ Halbgeschwister

3. Rauchen Sie: ☐ ja ☐ nein

Falls ja, Summe aller konsumierten Packyears bisher _____
(1 Packyear entspricht einer Packung Zigaretten täglich über ein ganzes Jahr,
2 Packungen täglich über 3.5 Jahre entspräche 7 Packyears)

4.Hatten Sie Operationen/Eingriffe im Kopf- oder Gesichtsbereich? ☐ ja ☐ nein
(Nasenkorrekturen, Polypen, Ohrkorrekturen, Zahnspangen oder ähnliches)

Wenn ja, welche? _____

5.Hatten Sie Verletzungen im Kopf- oder Gesichtsbereich? ☐ ja ☐ nein
(Brüche, Verbrennungen, Lähmungen oder ähnliches)

Wenn ja, welche? _____

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6. Verwenden Sie hormonelle Präparate oder Verhütungsmittel? ☐ ja ☐ nein
(Pille, Monatspflaster, Implantate oder ähnliches)

7. Sind/Waren Sie in längerer medizinischer/hormoneller Behandlung oder leiden Sie an chronischen Erkrankungen? ☐ ja ☐ nein
(Diabetes, Schilddrüsenerkrankungen, sonstige Stoffwechselerkrankungen oder ähnliches)

Wenn ja, welche? _____

8. Litten Sie in Ihrer Kindheit/Jugend an schweren Krankheiten? ☐ ja ☐ nein
(Essstörungen, Krebs oder ähnliches)

Wenn ja, welche? _____

9. Kam es zu besonderen Vorkommnissen während Ihrer Geburt? ☐ ja ☐ nein
(Komplikationen während Schwangerschaft, Frühgeburt, Saugglocken-, Zangengeburt oder ähnliches)

Wenn, ja welche? _____

Danke für Ihre Mitarbeit!

Probandennr.: _____

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Einverständniserklärung

Hiermit erkläre ich mich einverstanden, dass mein Foto unter Wahrung der Anonymität für wissenschaftliche Zwecke verwendet werden kann.

_____	_____	_____
Name des Probanden	**Datum**	**Unterschrift**

Weiters erkläre ich mich einverstanden, dass mein Foto gegebenenfalls in wissenschaftlichen Publikationen veröffentlicht werden kann.

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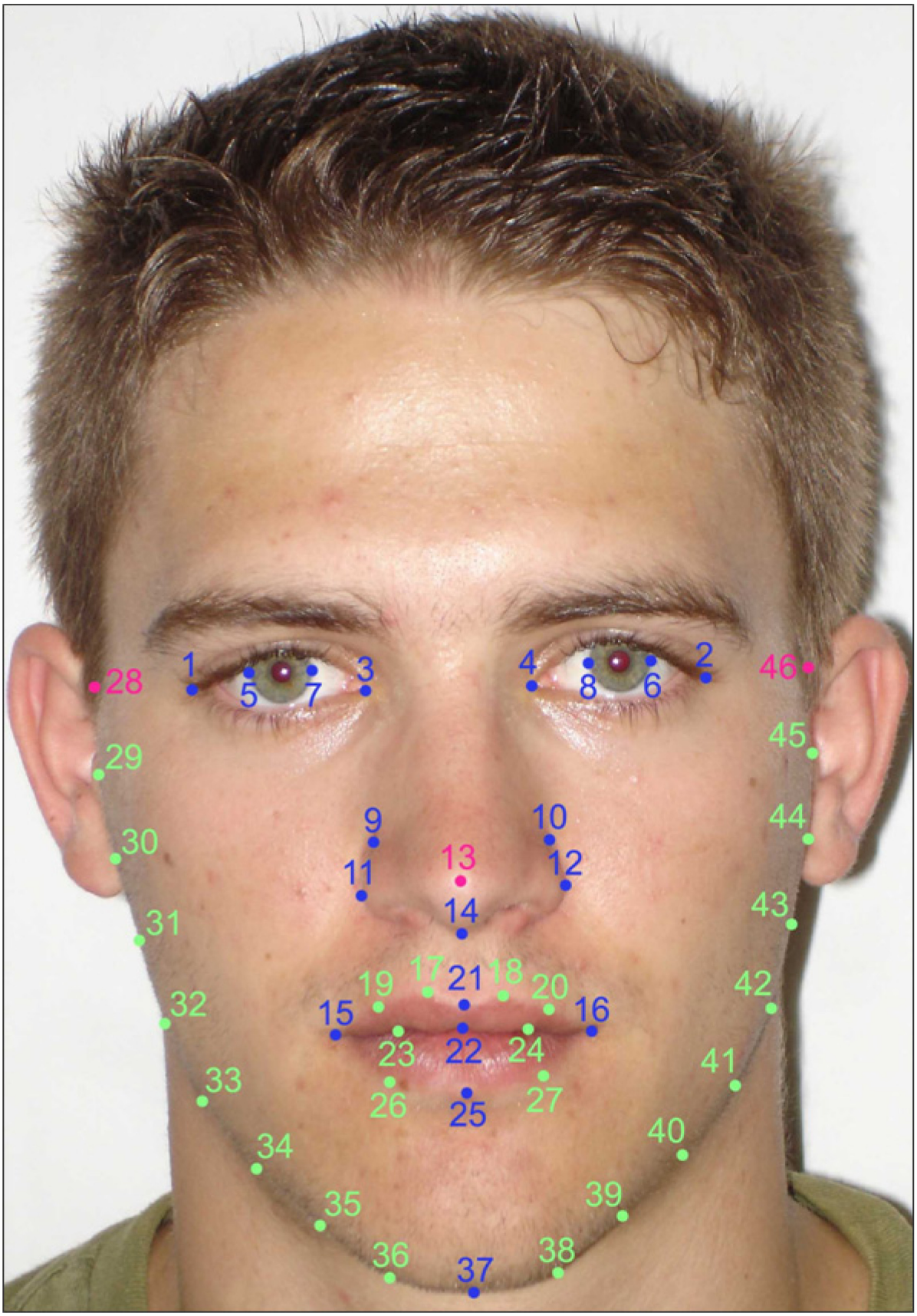
Name des Probanden	**Datum**	**Unterschrift**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B) List of used somatometric landmarks.

ID	Landmark	Type	Definition
1 2	Exocanthion (right) Exocanthion (left)	II	lateral corner of eye fissure where eyelids meet (Commissura palpebrarum lateralis)
3 4	Endocanthion (right) Endocanthion (left)	II	medial corner of eye fissure where eyelids meet (Commissura palpebrarum medialis)
5 6	Iris lateral (right) Iris lateral (left)	III	most lateral point of the iris
7 8	Iris medial (right) Iris medial (left)	III	most medial point of the iris
9 10	Alae origin (right) Alae origin (left)	II	origin of the alar wing of the nose
11 12	Alare (right) Alare (left)	III	most lateral point on each alar contour
13	Pronasale	SM	most anterior point of the nose
14	Subnasale	III	lowest point of the nose
15 16	Cheilion (right) Cheilion (left)	II	Point located at each labial commissure
17 18	Crista philter (right) Crista philter (left)	SM	most distal point on crest of Philtrum
19 20	Philtrum high (right) Philtrum high (left)	SM	middle point on Philtrum between Cheilion and Crista philtre
21	Labrale superius	II	midpoint of the upper vermillion line
22	Stomion	II	midpoint of labial fissure between closed lips
23 24	Labia middle (right) Labia middle (left)	SM	midpoint of the labial fissure between Stomion and Cheilion
25	Labrale inferius	II	midpoint of the lower vermillion line
26 27	Philtrum low (right) Philtrum low (left)	SM	midpoint on Philtrum between Cheilion and Labrale inferius
28	Cheekpoint (right)	SM	intersection of outline and line LM 1-3
29 to 36	Lower outer face (right)	SM	eight LMs roughly equidistantly distributed along the outline of the lower face between chin boss and the right cheekpoint
37	Gnathion	III	lowest midpoint of the chin
38 to 45	Lower outer face (left)	SM	eight LMs roughly equidistantly distributed along the outline of the lower face between chin boss and the left cheekpoint
46	Cheekpoint (left)	SM	intersection of facial outline and line LM 2-4

5. Literature

Abel, W. (1934). Die Vererbung von Antlitz und Kopfform des Menschen. Zeitschrift für Morphologie und Anthropologie Bd. 33, H. 2 (1934), pp. 261-345

Adams, D.C., Rohlf, F.J., Slice, D.E. (2004). Geometric morphometrics: Ten years of progress following the “revolution”. The Italian Journal of Zoology, 71(9), 5–16.

Arya, R., et al. (2002). Heritability of anthropometric phenotypes in caste populations of Visakhapatnam, India. Human Biology 74 (3), pp. 325-344.

Badawi-Fayad, J., Cabanis, E.A. (2007). Three Dimensional Procrustes Analysis of Modern Human Craniofacial Form. The Anatomical Record 290:268-276

Baker, R. R. and Bellis, M. A. (1995). Human Sperm Competition: Copulation, Masturbation, and Infidelity. London: Chapman and Hall.

Baydaş, B., Erdem, A., Yavuz, İ., Ceylan, İ. (2007). Heritability of facial proportions and soft-tissue profile characteristics in Turkish Anatolian siblings. American Journal of Orthodontics and Dentofacial Orthopedics Volume 131, Number 4, 504-509.

Bishara S.E., Hession T.J., Peterson L.C. (1985). Longitudinal soft-tissue profile changes: a study of three analysis. American Journal of Orthodontics and Dentofacial Orthopedics Volume 88, 209-226

Bookstein, F.L., Chernoff B., Elder R.L., Humphries J.M., Jr., Smith G.R., and Strauss R.E. (1985). Morphometrics in evolutionary biology. Special publication 15. Academy of Natural Sciences Press, Philadelphia.

Bookstein, F. (1991). Morphometric tools for landmark data: geometry and biology. New York: Cambridge University Press.

Bookstein, F.L. (1997). Landmark methods for forms without landmarks: morphometrics of group differences in outline shape. Medical Image Analysis, Volume 1, Number 3, 225-243.

Bookstein, F.L., (1998). A hundred years of morphometrics. Acta Zool. Acad. Sci. Hung., 44 7-59.

Bouchard, C., Perusse, L.: Leblanc, C., Tremblay, A. and Theriault, G.: Inheritance of the amount and distribution of human body fat. Int. J. Obes., 12: 205-15 (1988).

Buss, D.M. (1984). Marital assortment for personality dispositions: Assessment with three different data sources. Behavior Genetics, 14, 111-123.

Byard, P.J., Sharma, K., Russel, J.M., and Rao, D.C. (1984). A family study of anthropometric traits in a Punjabi community. II. An investigation in familial transmission. American Journal of Physical Anthropology, 64, 97-104.

Byard, P.J. (1985). Path analysis of familial resemblance for cranio-facial traits in Andhra Pradesh nuclear families and twins. Annals of Human Biology, 1985, Vol. 12, NO. 4, 305-314.

Carson, E.A. (2006). Maximum Likelihood Estimation of human Craniometric Heritabilities. American journal of Physical Anthropology 131:169-180 (2006).

Cheverud, J., Lewis, J.L., Bachrach, W., Lew, W.D. (1983). The measurement of form and variation in form: an application of three-dimensional quantitative morphology by finite-element methods. American Journal of Physical Anthropology 62, 151-165.

Clark, P.J. (1956). The heritability of certain anthropometric characters as ascertained from measurements of twins. Am J Hum Genet. 1956 Mar;8(1):49–54.

Davenport, C. (1925) Notes on Physical Anthropology of Australian Aborigines and Black-White Hybrids, Amer. Jour. Phys. Anthrop., 73-94.

DeFrise, E. (1981). Modèle polygénique pour les caractères mésurables. Bull. Soc. Roy. Belge Anthrop. Préhist., 92: 7-24.

DeFrise, J.C., McGuffin, P., McClearn, G.E., Plomin, R. (2000) Behavioral Genetics 4th Ed. W H Freeman & Co.

Demayo, C.G., Torres, M.A.J., Sinco, A.L., & Bonachita-Sanguila, M.L. (2010). Geometric morphometric analyses of facial shape in twins. The Internet Journal of Biological Anthropology, 4(1).

Dryden, I.L., Mardia, K.V. (1998) Statistical Shape Analysis. Chichester, UK: Wiley.

Falconer, D.S. (1989). Introduction to Quantitative Genetics. London, UK: Longman Scientific & Technical.

Falconer, D.S. and Mackay, T.F.C. (1996). Introduction to Quantitative Genetics, 4th edn. Longman, London.

Farkas, L.G. (1981). Anthropometry of the head and face in Medicine. Elsevier; New York: 1981, pp. 6-7, 47-51,75-77, 80.

Farkas, L,G., Munro, I.R., eds. (1987). Anthropometric facial proportions in medicine. Springfield, Charles C. Thomas.

Farkas, L.G., et. Al. (2005). International Anthropometric Study of Facial Morphology in Various Ethnic Groups/Races. Journal of Craniofacial Surgery 16 (4), pp. 615-646.

Fink, B., Grammer, K., Mitteroecker, P., Gunz, P., Schaefer, K., Bookstein, F.L., Manning, J.T. (2005). Second to fourth digit ratio and face shape. Proceedings of the Royal Society B Volume 272, 1995-2001

Fischer, E. (1913). Die Rehobother Bastards und das Bastardierungsproblem beim Menschen: anthropologische und ethnographische Studien am Rehobother

Bastardvolk in Deutsch-Südwest-Afrika, ausgeführt mit Unterstützung der Kgl. preuss, Akademie der Wissenschaften. Jena: G. Fischer.

Fisher, R.A., Arthur Thomson J. (1918). The correlation between relatives on the supposition of Mendelian inheritance. Transactions of the Royal Society of Edinburgh, 52: 399-433.

Formby, W.A., Nanda, R.S., Currier, G.F. (1994). Longitudinal changes in the adult facial profile. Am J Orthod Dentofacial Orthop 105:464-476.

Gangestad, S.W. (2000) Human sexual selection, good genes, and special design. Annals of the New York Academy of the Sciences 907: 50–61.

Gower, J.C. 1971. Statistical methods of comparing different multivariate analyses of the same data. Pp. 138-149 in F. R. Hodson, D. G. Kendall, and P. Tautu (eds.) Mathematics in the Archaeological and Historical Sciences. Edinburgh Univ. Press: Edinburgh

Gunz, P., Mitteroecker, P. (2013). Semilandmarks: a method for quantifying curves and surfaces. Hystrix, the Italian Journal of Mammalogy, 24(1), ---. doi:10.4404/hystrix-24.1-6292.

Hall G., Phillips T.J., (2005). Estrogen and skin: The effects of estrogen, menopause, and hormone replacement therapy on the skin. J. Am. Acad. Dermatol 2005; 53:555-68.

Hasselquist, M.B., Goldberg, N., Schroeter, A., Spelsberg, T.C. (1980). Isolation and characterization of estrogen receptor in human skin. J. Clin. Endocrinal Metab. 1980;50:76-82.

Hennessy, R.J., Moss, J.P. (2001). Facial growth: separating shape from size. European Journal of Orthodontics and Dentofacial Orthopedics Volume 23, 275-285.

Hinsz, V.B. (1989). Facial resemblance in engaged and married couples. Journal of Social and Personal Relationships, 6: 223-229.

Horowitz, S.L., Osborne, R.H. and DeGeorge, F.V. (1960) A cephalometric study of craniofacial variation in adult twins, Angle Orthodontist, 30, 1-5.

Hunter, W.S. (1965). A study of the inheritance of craniofacial characteristics as seen in lateral cephalograms of 73 like-sexed twins. Trans Eur Orthod Soc 1965;59:70.

Hunter, W.S., Balbach, D.R., Lamphiear, D.E. (1970). The heritability of attained growth in the human face. Am J Orthod 1970:58:128-34.

Johannesdottir, B., Thorarinsson, F., Thordarson, A., Magnusson, T.E. (2005) Heritability of craniofacial characteristics between parents and offspring estimated from lateral cephalograms. Am J Orthod Dent Orthoped 127, 200–207.

Johnston, V.S. and Franklin, M. (1993): Is beauty in the eye of the beholder? Ethol. Sociobiol. 14:183-199

Knussmann, R. (1988): Anthropologie, Handbuch der vergleichenden Biologie des Menschen. Bd. I, 1. Teil, Wissenschaftstheorie, Geschichte, morphologische Methoden; 4. Auflage; Gustav Fischer Verlag Stuttgart.
Leicher, H. (1928). Die Vererbung anatomischer Variationen der Nase, ihrer Nebenhöhlen und des Gehörorgans. - München.

Lestrel, P.E., (1989). Some approaches toward the mathematical modelling of the craniofacial complex Journal of Cranifacial Genet Dev Biol 1989: 9:77-91

Lobb, W.K. (1987). Craniofacial morphology and occlusal variation in monozygotic and dizygotic twins. Angle Orthod 1987;57:219-33.

Lundström, A. (1954). The importance of genetic and non-genetic factors in the facial skeleton studied in one hundred pairs of twins. Eur Orthod Soc Rep Cong 1954;30:92-107.

Lundström, A., McWilliam, J.J. (1987). A comparison of vertical and horizontal cephalometric variables with regard to heritability. European Journal of Orthodontics 1987;9:104-108.

Manfredi, C., Martina, R., Grossi, G.B., Guiliani, M. (1997). Heritability of 39 orthodontic cephalometric parameters on MZ, DZ twins and MN-paired singletons. Am J Orthod 1997;111:44-51.

Martínez-Abadías, N., Esparza, M., Sjøvold, T., González-José, R., Santos, M., Hernández, M. (2009). Heritability of human cranial dimensions: comparing the evolvability of different cranial regions. J Anat 2009;214:19-35.

Martin, R. (1928). Lehrbuch der Anthropologie, Vol. I. Jena: Verlag von Gustav Fischer.

Mueller, W.H. (1978). Transient environmental changes and age limited genes as causes of variation in sib-sib and parent offspring correlations. Ann Hum Biol 5:395-398

Mueller, W.H., Malina, R.M. (1980). Genetic and environmental influences on growth of Philadelphia black and white schoolchildren. Ann Hum Biol 7:441-448

Moyers, R.E., Bookstein, F.L. (1979). The inappropriateness of conventional cephalometrics. American Journal of Orthodontics and Dentofacial Orthopedics Volume 75, 599-617.

Pearson, K.; Lee, A. (1903). On the Laws of Inheritance in Man: I. Inheritance of Physical Characters. Biometrika, Vol. 2, No. 4 (Nov., 1903), pp. 357-462.

Peng, J., Deng, H., Cao, C., Ishikawa, M. (2005). Craniofacial morphology in Chinese female twins: a semi-longitudinal cephalometric study. Eur J Orthod. 2005 Dec;27(6):556-61.

Plomin, R., J.C. DeFries, *et al*. (1990). *Behavioral Genetics: A Primer*, New York: W.H.Freeman.

Quelprud, T. (1932). Untersuchung der Ohrmuschel von Zwillingen. Zeitschrift für Induktive Abstammungs- und Vererbungslehre 1932, Volume 62, Issue 1, pp 160-165

Relethford, J.H., Lees, F.C. (1982) The use of quantitative traits in the study of human population structure. Yearb Phys Anthropol 25, 113–132.

Richtsmeier, J.T., Cheverud, J.M. (1986). Finite element scaling analysis of human craniofacial growth. J Craniofac Genet Dev Biol. 1986;6(3):289-323.

Ritz E. (1985). The clinical spectrum of hereditary nephritis. Nephrol Forum Kidney Int 27:83.

Rohlf, F.J., Slice, D.E. (1990) Extensions of the Procrustes method for the optimal superimposition of landmarks. Systematic Zoology 39: 40–59.

Rohlf, F.J., Marcus, L.F. (1993) A revolution in morphometrics. Trends in Ecology and Evolution 8: 129–132.

Ross, M.T., Grafham, D.V., Coffey, A.J., Scherer, S., McLay, K. et al. (2005). The DNA sequence of the human X chromosome. Nature 434: 325-337

Sadeghianrizi, A., Forsberg, CM., Marcus, C., Dahllöf, G. (2005). Craniofacial development in obese adolescents. Eur J Orthod 27(6): 550-555.

Sasse, G., Mller, H., Chakraborty, R., Ott, J. (1994). Estimating the frequency of nonpaternity in Switzerland. Hum Hered 44:337–343.

Saunders, S.R., Popovich, F., Thompson, G.W. (1980). A study of craniofacial dimensions in the Burlington Growth Centre sample. American journal of orthodontics Volume 78:394-403.

Schade, H. (1954). Vaterschaftsbegutachtung, Schweizerbarth, Stuttgart

Schäfer, K., Fink, B., Mitteroecker, P., Neave, N., Bookstein, F.L. (2005). Visualizing Facial Shape Regression upon 2nd to 4th Digit Ratio and Testosterone. Coll. Antropol. Volume 29,2:415-419

Schäfer, K., Fink, B., Grammer, K., Mitteroecker, P., Gunz, P., Bookstein, F.L. (2006). Female appearance: Facial and bodily attractiveness as shape. *Psychological Science* 48: 187–204.

Scheidt, W. (1932). Untersuchung über die Erblichkeit der Gesichtszüge. Zeitschrift für Induktive Abstammungs- und Vererbungslehre 1932, Volume 60, Issue 1, pp 291-394

Scheyd, G.J., Garver-Apgar, C.E., Gangestad, S.W. (2008) Physical attractiveness: Signals of phenotypic quality and beyond. In: Foundations of Evolutionary Psychology (Crawford C, Krebs D, eds), 239–259. Hillsdale, NJ: Erlbaum.

Scott J.H. (1957). Muscle growth and function in relation to skeletal morphology, American Journal of Physical Anthropology 15 (1957) 197-234.

Sengupta, M., & Karmakar, B. (2007). Inheritance of six anthropometric traits in Vaidyas of West Bengal, India. Anals of Human Biology, January-February 2007; 34(1): 80-90

Sharma, K., & Sharma, J. C. (1984). Familial resemblance for head size in a Punjabi population of India. Annals of Human Biology, 1984, VOL. 11, NO. 6, 577-580.

Sharma, K. (1986). Heritability of morphological traits in a Punjabi population of India. Z Morph Anthropol 77:87–93.

Simpson, E., Henneberg, M. (2002). Variation in soft-tissue thickness on the human face and their relation to craniometric dimensions, American Journal of physical Anthropology 118:121–133 (2002)

Sjøvold, T. (1984). A report on the heritability of some cranial measurements and non-metric traits. In Multivariate Statistical Methods in Physical Anthropology (eds Van Vark GN, Howells WW), pp. 223–246. Dordrecht: Reidel Publishing Company.

Slice, D. E. (2005). Modern morphometrics in physical anthropology. Dodretch: Kluwer Academic.

Susanne, C. (1975). Genetic and environmental influences on morphological characteristics. Annals of Human Biology, 1975, VOL. 2, NO. 3, 279-287.

Susanne, C. (1977). Heritability of anthropological characters. Hum Biol 49:573-580.

Susanne, C., & Sharma, P. D. (1978). Multivariate analysis of head measurements in Punjabi families. Annals of Human Biology, 1978, VOL. 5, NO. 2, 179-183.

Thiessen, D.D., & Gregg, B. (1980). Human assortative mating and genetic equilibrium: An evolutionary perspective. Ethology and Sociobiology, 1, 111-140.

Thompson, D.W. (1917). On growth and form. Cambridge University Press, London

Visscher, P.M., Medland, S.E., Ferreira, M.A.R., Morley, K.I., Zhu, G. et al. (2006). Assumption-Free Estimation of Heritability from Genome-Wide Identity-by-Descent Sharing between Full Siblings. PLoS Genet 2(3): e41.

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