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Growing old – do women and men age differently?

Author list: Olivia A. M. **Smith**¹, Christian **Duncan**², Nick **Pears**³, Antonio **Profico**⁴,
Paul **O'Higgins**^{1,4}

1. Hull York Medical School, University of York, York, UK, YO10 5DD

2. Dept. of Plastic Surgery, Alder-Hey Hospital, Liverpool, UK, L12 2AP

3. Department of Computer Science, University of York, York, UK YO10 5GH

4. PalaeoHub, Dept. of Archaeology, University of York, York, UK YO10 5DD

Corresponding author:

Paul O'Higgins, BSc, MBBS, PhD, DSc
PalaeoHub,
Dept. of Archaeology and Hull York Medical School,
University of York,
York,
UK
YO10 5DD
paul.ohiggins@hyms.ac.uk

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Abstract

Background

Aging of the head and especially the face have been studied intensively, yet questions remain about the timing and rates of aging throughout adulthood and about the extent to which aging differs between men and women. Here we address these issues by developing statistical models of craniofacial aging to describe and compare aging through the life course in both sexes.

Methods

We selected cranial surface meshes from 254 females and 252 males, aged from 20 to 90 years from the *Headspace* project, Liverpool, UK. 16 anatomical landmarks and 59 semilandmarks on curves and surfaces were used to parameterise these. Modes and degrees of aging throughout adulthood were assessed and compared among sexes using Procrustes based geometric morphometric methods.

Results

Regression analyses of form through the whole age range indicate that age accounts for a small proportion of total variance in both sexes, but form is significantly related to age and males and females age in significantly different ways. Further analyses indicate that aging differs in character, timing and rates in both sexes between early and later phases of adulthood. Sexual differences in aging are evident in early and later phases of adulthood.

Conclusions

The study adds to knowledge of the aging of adult craniofacial form and sexual dimorphism. It is based on a local population and so the findings are directly applicable to that population. Further studies are needed to assess generalisability and to provide better data on population differences to facilitate clinical assessment and treatment planning.

Key words: Facial aging; sexual differences; surface scanning; morphometrics

56

57 **Introduction**

58 With aging, the form of the head and especially the face transforms in well studied
59 and recognized ways (Albert et al., 2007; Coleman and Grover, 2006; Farkas et al.,
60 2013; Pitanguy et al., 2008). Decreased soft tissue elasticity, creasing,
61 subcutaneous fat redistribution, and skeletal remodelling all contribute to changes in
62 the three dimensional topography. Coleman et al. (Coleman and Grover, 2006)
63 describe changes to the upper forehead and periorbital region, that result in ‘fixed
64 glabellar frown lines, fixed transverse forehead furrows, temporal hollowing, a
65 skeletonized supraorbital rim, and a relative excess of upper eyelid skin’. In the
66 midface they note that subcutaneous fullness is lost, giving rise to a deeper and
67 wider orbit, relative prominence of infraorbital fat pads, development of nasolabial
68 folds, cheek concavity, chin pad ptosis and depleted malar fullness. Farkas et al.
69 (Farkas et al., 2013) identify a rotation of the midface relative to the cranial base that
70 reduces the angle of the pyriform and maxilla. Likewise it has been noted (Matros et
71 al., 2009) that the malar eminence, infraorbital rim, and piriform aperture become
72 more retroclined with age. ‘The illusion’ of increased nasal length with age has been
73 attributed (Coleman and Grover, 2006) to flattening of the medial forehead, this is
74 accompanied by nasal ptosis and changes in the alar region with narrowing of the
75 nasolabial angle. The lower face develops a relative excess of loose skin which
76 blunts the jawline and with redistributed fat deposits, contributes to the development
77 of jowls (Özdemir et al., 2002). Accompanying this, it has been noted (Coleman and
78 Grover, 2006) that the chin develops a relative protrusion, attributable to loss of
79 tissue volume lateral and inferior to the central portion. However, in a geometric
80 morphometric study of longitudinal radiographs it was found (Pessa et al., 2008) that

the mandible continues to grow and develop and so contributes this aspect of aging of the lower face.

Despite an extensive literature, questions remain about the time course of aging and the extent to which its features are shared among the sexes (Lambros, 2020). Thus, in an extensive review of facial aging (Albert et al., 2007) it was noted that sexual differences in patterns of aging have been found by various authors, with the consensus being that females tend to age faster or earlier than males. Additionally they point out that features of head and facial aging vary throughout the decades in both sexes. A geometric morphometric study (Windhager et al., 2019) found that, in their sample, females and males follow a common pattern of aging until menopause (albeit slightly faster in females), at which point there is a disruption of this pattern in females accompanied by an increase in rate of aging. These findings suggest that aging of the face is a non-linear process, varying in pattern and rate over time and between the sexes.

In this paper we measure the external form of the head and apply state of the art imaging and statistical methods for the analysis of 3D variation to build statistical models of whole head surface variation of individuals of both sexes in the UK whose ages range between 20 years and >80 years, to characterise and compare the modes and tempos of aging, a term used in this paper to refer specifically to change in form with time, in both sexes.

In particular, we test the hypotheses that: i) males and females each age in a consistent manner (within sex co-variation with age) and ii) males and females age in the same ways (between sex co-variation with age). To test hypothesis i), multivariate regressions of form on age are undertaken, either for the whole sample

or for subsamples of age groups, testing the significance of any apparent divergence of regression vectors between ages. The analyses also provide the opportunity to identify the detail of any identified differences between the sexes. To test hypothesis ii), a series of multivariate regressions of form on age are carried out within age groups, and the significance of any apparent divergence of regression vectors between sexes is tested. Where significant, the differences are visualized to allow detailed comparison.

Methods

Ethics approval

Alder-Hey Hospital and The Hull York Medical School granted ethics approval. All volunteers, or their legal guardian if <18years, gave written informed consent for 3D photography of their heads and subsequent analyses of variation. We confirm adherence to the tenets of the Declaration of Helsinki.

Sample

Surface meshes (typically 180K vertices and approx. 360K triangles) stored as Wavefront™ .obj files were collected from 254 females and 252 males ranging in age from 20 to 90 years (females) and 20-86 years (males). These came from the sample of .obj files obtained by the *Headspace* project in Liverpool, UK, from September 2013 – January 2014 (Dai et al., 2017) using a 3dMD five-camera system. We excluded individuals who had previous craniofacial surgery, declared mixed or unknown ethnicity, bulky hair or were missing surface data from the .obj file to, as far as possible, limit sources of variation to individual differences and age within the indigenous local population. All participants wore tight fitting, smooth latex

caps to flatten the hair against the scalp. Individuals varied in hair mass and so, the extent to which the cap flattened the hair also inevitably varied.

Sampling is uneven in terms of the age distributions of volunteers. Thus, the 20-29 year olds are best sampled with 96 males and 114 females; There are 73 males and 46 females aged 30-39 years, 28 males and 33 females between 40-49 years, 24 males and 25 females between 50 and 59 years, and 31 males and 36 females over 60. The majority of individuals over 60 are younger than 70 years with only 6 older individuals of either sex.

Digitisation

Anatomically homologous landmarks and curves were manually digitized by the same person (OAMS) using the Evan Toolbox for geometric morphometrics (Weber and Bookstein, 2011). This provides tools to trace curves manually, to semi-automatically locate fixed landmarks for subsequent manual refinement and to automatically distribute semilandmarks on curves and surfaces. We utilized a symmetric (Mardia et al., 2000) template comprising 16 landmarks (Table 1) and an exemplar head surface mesh with traced curves marked up by 59 semilandmarks, chosen because it represents a young individual with relatively gracile features (Fig. 1).

Semi-landmark configurations were used to describe the curves of the right and left jawlines, the right and left eyebrows and the midline curves, as well as the cranial surface. No landmarks or semilandmarks are placed on the ears, neck or clothing and so their apparent deformations in visualisations should be ignored. Using thin plate splines (Bookstein, 1989), semilandmarks were warped and projected from the template onto the mesh of each individual. They were then slid along curves and

over the surface to minimise bending energy of the thin plate splines with respect to the fixed landmarks (Bookstein, 1989; Gunz and Mitteroecker, 2013).

Statistical analyses

The analyses examined changes in size and shape with age in each sex. Centroid sizes and shape variables for subsequent analyses were derived from the landmark and semilandmark coordinates by generalized Procrustes analysis. Analyses of form (shape and size; Mitteroecker et al., 2013) use the shape coordinates together with the natural logarithm (ln) of centroid size.

Form variation was assessed in preliminary analyses through principal components analysis (PCA) and modelled in detail using multivariate regressions. These analyses were carried out using the EVAN Toolbox. Regression vectors were compared between age groups and sexes using a permutation test on the angles between them (R Core Team, 2020). Results were visualized in the EVAN Toolbox by warping the template surface mesh (using thin plate splines) between pairs of landmark and semilandmark configurations representing forms of interest (e.g. mean young and old configurations). To facilitate interpretation of these, the target surface mesh was colour mapped to represent the changes in area of each triangle with respect to the reference, using the *localmeshdiff* function in the R package, Arothron (Piras et al., 2020; Profico et al., 2020). The resulting maps represent a key aspect of form variation; the extent of expansion or contraction of surface regions. The relative directions of expansion can be visually gauged by comparing warped surfaces.

The visualisation of local surface area change is drawn by warping a surface mesh to fit the mean coordinates and then by warping the coordinates according to the coefficients of the regression of interest. The surface is warped with the landmarks, using thin plate splines. Here we use the surface mesh from a young gracile male to minimise the effect of initial surface choice on the appearance of gender (Fig.1). Inevitably features such as the form of nose tip, with few landmarks and skin folds are to some extent retained throughout the warpings so, the original surface is recognisable, but the interpretation of these diagrams should focus on changes, and so on the colours displayed in these visualisations rather than on the form of the face itself. This visualisation is not affected by registration, but it is potentially affected by where and how the surface mesh cuts through (sections) the deformation field. To minimise the effects of this, we consistently visualise deformations using the mean landmark configuration, warped to represent particular ages. From exploratory experiments, testing the effects of using different configurations (representing the limits of the ranges of variation on PCs 1 and 2 in Figure 2a) on the visualisation, it is very stable and fairly represents the average local changes in surface area during aging.

Results

There is no significant correlation between centroid size and age, over the entire age range of the sample, in either sex (males $r=-0.046$, $p=0.1226$; females $r=0.098$, $p=0.123$). However males are significantly larger ($p<0.001$) than females, with mean centroid size for males of 876mm and for females, 832mm.

Figure 2. shows the first three principal components (PCs; 59.6% of total variance) from a principal components analysis of form (the shape coordinates plus the ln of centroid size). There is some separation between males and females on PC1 (Fig. 2a) and on the combination of PC2 and PC3 (Fig. 2b) the older individuals tend to group towards the lower right quadrant of the plot and younger, towards the upper left.

Patterns of covariation with age in each sex are explored further, while taking account of the whole statistical space (total variance) by multivariate regression of form and shape on age for the whole sample of each sex (Table 2). In both sexes the regressions are significant and explain a similar small proportion of the total variance (3.3-4.5%). The angles between sex specific regression vectors are significant (form: 49° , $p=0.045$; shape: 44° , $p<0.001$; permutation tests with 1000 permutations of sex). Thus, while age accounts for a small proportion of total variance in both sexes, form and shape are significantly related to age and males and females age in significantly different ways.

Figure 3 presents the regression prediction of form in each sex at 20, 80 and 200 years. The last was drawn to exaggerate differences in the warpings to make them more visible. The static faces making up the sequence are warpings of a single surface and therefore share similarities of texture and features such as the nose tip, which has few landmarks. The reader should focus on the differences between these rather than the similarities, since it is the differences (changes with age) that concern us. To make this focus on difference explicit we also show colour maps, indicating localized changes in surface area between warpings. The distribution of colours indicating regions of surface expansion and contraction is invariant to registration and almost invariant (very stable in terms of how colours map to equivalent regions

224 and features) to the form used to visualise them. Because these changes are more
225 readily seen in the colour map, we visualise them between the more reasonable age
226 limits, 20 to 80 years.

227 Most aspects of aging appear very similar between sexes. From the warpings
228 between 20 and 200 years in Figure 3, both sexes show a degree of broadening of
229 the cheeks, formation of jowls, increase in the size of the nose and lengthening of
230 the philtrum and upper lip, with the chin and nose coming to lie relatively more
231 anterior to the lips. The colour maps show that these changes result in the largest
232 expansion of surface area over the philtrum and nose, and a reduction over the jowls
233 and supraorbital regions. In detail, semilandmarks on the mid cheek and those on
234 the jawline come to lie closer together and so reduce the area of the mesh in the
235 vicinity of the jowls. There are subtle changes over the cranial vault in both sexes
236 with reduction in surface area locally over the frontal region, particularly in males and
237 some increase in area locally over the lateral aspects of the vault, especially in
238 females. These changes may well relate to variations in hair mass with age, as such
239 we note them but, given the uncertainty over the effects of the hair cap on apparent
240 vault form, we interpret them no further.

241 Consistent with the significant angle between sex specific regression vectors males
242 and females show some differences in aging (Figure 3, compare 200 year male and
243 female trajectory warpings) appear to differ in the greater degree of broadening of
244 the face in males. Figure 4 visualises the subtle differences in aging using a colour
245 map of the differences in predicted 80 year old forms. Between 20 and 80 years,
246 males show greater expansion of the malar region and tip of the nose and chin, with
247 less expansion of the nasal bridge, anterior chin and central lower lip. Males also

show a relatively greater reduction in the area of the periorbital and frontal regions than females.

These comparisons are calculated over the whole age range, so do not account for possible temporal variation in aging trajectories or rates within in each sex. To explore these further, mean head form was calculated for each decade and for the over 60s combined (small sample) and a PCA of form was carried out using these means. Neither sex specific aging trajectory is linear on the combination of the first three PCs (Fig. 5). In both, on the combination of PCs1 to 3 there is an approximately consistent mode of aging (direction of vector between ages) between 20 and 40 years, followed by deviation of the trajectory into the 50s and 60s. This suggests differences between early (20-40+ years) and late (50+) modes of aging. The distances between means are variable and these suggest differences in rates of aging. Note that sample sizes are small, especially in older age groups and variances are large (see Figure 2). As such, we do not formally test for changes in aging among these age groups, but instead carry out tests comparing aging between broader age groups, 'younger' vs 'older' using multivariate regression, as described below.

To investigate rates of aging, these were computed as the Procrustes distances between the mean shapes from successive years. To account for sampling error and other sources of variation that affect between year shape differences, the mean shape in each year was computed as the moving average over 5 years centred on the year of interest. In Figure 6 the resulting rates of aging are presented for males and females. The curves overlap between the sexes, however, in both there appear to be varying rates of aging. In males aging is slow but accelerates slightly between 20 and 40 years, then it shows a dramatic acceleration between 40 and 50 years,

before slowing between the mid-fifties and sixties and then accelerating again into old age. In females the trend is different, with slow aging in the twenties, accelerating through the mid-thirties, before slowing again until 50 years when aging accelerates until 60 years before slowing a little between 60 and 70 years and finally accelerating again into old age.

The possibility that modes of aging differ between younger and older age groups, as indicated by the PCA of Fig 5 was explored through, a series of multivariate regressions of form on age. Each sex was split into younger and older groups and the vectors of aging were compared between age groups and sexes. Because it is not clear (if and) when a change in aging occurs, we explored differences between 20-39 years and 40-90 years and between 20-49 years and 50-90 years, in and between each sex. Table 3 presents the results of the multivariate regressions of form on age in each of these age groups for each sex. All are significant, as assessed by a permutation test (1000 permutations of age) on explained variance, except in females aged over 50, however the proportion of total variance explained by these regressions is generally small, indicating that other sources of variation (error and individual differences) predominate.

To assess the extent to which aging differs between younger and older age groups within and among sexes, vector comparisons were carried out (Table 4). Within each sex, divergences of aging trajectories between younger and older age groups are highly significant ($p < 0.001$), 20-39 year old males and females also diverge significantly ($P = 0.008$), while the divergence between 40-90 year old males and females is on the borderline of significance ($p = 0.052$). Between 20 and 40 years (Fig. 7), in both sexes there is expansion of midline facial structures, from nasal bridge to chin, but the nasal bridge and lateral nose expands to a greater extent in

females and the philtrum and chin in males. In males, and more so in females, the eyebrows medially approximate and lower slightly while the region around the lateral brow reduces in area. The middle and lateral malar regions expand in males. Between 40 and 80 years changes appear more marked, but this visualisation spans twice the age range of that between 20-40 years. In both males and females changes are more asymmetric than in the younger age group. The jawline and lower cheek show localized regions of shrinkage due to the formation of jowls and skin folds, and the upper chin and lower lip reduce in area while the philtrum expands. In females the whole nose enlarges markedly while in males this is less marked and more focussed on the nasal tip. In males there are dramatic localized and somewhat irregular changes in area around the eyes and over the central forehead reflecting local wrinkling.

Finally, to directly compare rates and patterns of aging between age groups and between the regression analyses of age groups and those of the whole sample, age changes per 20 years were visualized. The rates of relative expansion and contraction of facial regions show minor differences between sexes when aging is modelled by regression of form on age over the whole age range of 20-80 years (Fig. 8, top row), but when the form of age groups 20-40 and 40-80 is separately regressed on age, localized differences in aging between sexes and age groups become evident (Fig. 8, bottom row).

Discussion

In this study we tested two hypotheses. The first is that males and females each age in a consistent manner between 20 years and old age and the second is that males and females age in the same ways. Our analyses indicate that shape rather than

size variation characterises aging, and that changes due to age are small relative to interindividual differences due to other sources, such as sex (Fig. 2). There is clear evidence that males and females age differently when the sample age range is considered in its entirety (Table. 2, Fig. 3 and 4). More detailed analysis of changes in the tempo and mode of aging throughout adulthood (Figure 5) show that mean head form varies in a somewhat non-linear manner and variable rate with age. Particularly younger adults of each sex appear to age in ways that are different to older adults. A major change occurs approximately between 40 and 59 years in each sex, with some evidence of a slightly earlier change in females. Males and females age at similar rates when considered over the whole time course, but each sex appears to show accelerations and relative decelerations of aging throughout adulthood (Figure 6). Sample sizes are not as large in older age groups as in younger and variances are large (Figure 2). As such, we must treat this finding with some caution. However, one other study has similarly examined rates of aging (Windhager et al., 2019) and in this they noted a peak in female aging rate between 50 and 60 years, which they attributed to menopause. Our estimates of aging rates follow a very similar pattern but differ in one key respect, we find a very similar average rate of aging in both sexes, between 40 and 70, whereas the study of Windhager et al. (Windhager et al., 2019) suggests males age more slowly. This could be a population difference (UK vs Croatia), and merits further investigation.

The visualisations (Fig. 7- 8) of the multivariate regressions of form on age (Table 3) show that aging differs between younger and older adults and between sexes but there are commonalities, consistent with the findings of previous workers (Coleman and Grover, 2006; Lambros, 2020; Özdemir et al., 2002; Pessa et al., 2008; Pitanguy et al., 2008), in that the eyebrows medially approximate and lower somewhat, the

lateral brows droop, the lower lip thins, the chin becomes more prominent and jowls develop. Expansion (increase in local surface area) but not the rotation evident in the skeleton of midline facial structures (Farkas et al., 2013; Matros et al., 2009; Pessa, 2000) is common to both sexes but the extent of this varies markedly, with the philtrum and chin expanding more in males and the nasal bridge and lateral nose expanding more in females, rather than giving the ‘illusion’ of doing so (Coleman and Grover, 2006). Indeed, in contrast to a previous study (Otto et al., 2012), in both sexes age related changes in the form of the nose are among the most prominent features of aging. Ramaut et al., (2019) compared MR scans of 100 men and women at two ages, 20-30 and 65-80 demonstrated that the upper lip lengthens in both sexes as we find here (Figure 7). Lambros, (2020) compared almost 600 3d images of males and females using a best fit facial averaging method and noted a number of changes that have been identified in this study, including flattening of the forehead, orbital enlargement that was more noticeable in men than women, lengthening of the upper lip, splaying of the alar base and lengthening of the nose due to loss of support. The overall conclusion however was that men and women aged in the same way.

It is worth considering some limitations of this study. They primarily reflect sampling and underline the need for very large databases of human facial scans with full life and medical histories such as has recently been made available for whole body CT scans (Edgar et al., 2020). Our data were from the headspace dataset (see Software, tools and data availability) which has ethnicity, age, eye and hair colour information. This, together with limited sampling of ethnicities other than Caucasians limited our analyses to assessment of aging without being able to take account of relevant medical and orthodontic history. A further issue arises since many more

372 young than old people volunteered their images. This has limited the reliability of
373 results especially with respect to the over 60s, where three decades are represented
374 by successively fewer individuals. Despite these limitations the data were sufficient
375 to undertake statistical testing in the analyses presented here, but it has limited our
376 ability to explore details of age related form changes in the head and covariances
377 between form, age, medical history and lifestyle factors.

378 The findings of this study falsify both hypotheses in indicating that males and
379 females vary in rates of age related changes in form throughout adulthood, in
380 complex ways that differ between the sexes. They provide detailed information on
381 aging in a specific population and the methods and technologies used in this study
382 can readily be applied to other populations. Such knowledge can inform patient
383 expectations of aging and of how surgical intervention might reverse its effects. It will
384 be of interest in future studies to relate the identified features of aging to the timing
385 and nature of surgical interventions commonly carried out in each sex.

386

387 **Software, tools and data availability**

388 The Headspace data are available via the project website, [https://www-](https://www-users.cs.york.ac.uk/~nep/research/Headspace/)
389 [users.cs.york.ac.uk/~nep/research/Headspace/](https://www-users.cs.york.ac.uk/~nep/research/Headspace/). Our VPN for the EVAN toolbox
390 analyses are distributed via <https://www.evan-society.org/>. The template can be
391 downloaded from <https://doi.org/10.5281/zenodo.4266290>, together with the data
392 used in this study. The R tool for the visualisation of differences in meshes are
393 available on CRAN at <https://CRAN.R-project.org/package=Arothron>, the function is
394 *localmeshdiff*.

395

396

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Legends for figures

Figure 1. a. The male surface used in all subsequent analyses with landmarks shown in red and digitized curves in white, curve semilandmarks and surface semilandmarks shown in white. Frontal, b, and lateral, c, screengrabs in the EVAN Toolbox of the landmark and semilandmark configuration (green).

Figure 2: a) PC1 (45.32% total variance) vs PC2 (7.22%) and b) PC3 (7.07%) vs PC2 of form, from a PCA of all individuals aged 20-90 years. Rectangle = male, circle = female, small symbol = young, large = old

Figure 3: Predicted form at the ages of 20, 80 and 200 years from the regressions of form on age of the whole adult samples of each sex. Landmarks and semilandmarks (see Fig. 1) indicated by red markers. Top row, females, bottom row, males. The last column shows colour maps that describe the ratios of areas of surface regions between 20 and 80 years in each sex (indicated by the scale).

Figure 4: Visualisations of regression predictions of age related form changes in each sex (left column males, right column, females). The centre column shows the differences in aging between males and females exaggerated 20 times to facilitate interpretation. Age related changes are shown as colour maps that indicate the ratios of areas of craniofacial regions between these ages (left and right columns, colour map keys below each frontal view) and between the regression prediction of the 80 year old female and 80 year old male means (centre column). The difference is magnified 20 times in the centre column, relative to the left and right columns.

Figure 5. Top: PC1 (47.8%) vs PC2 (10.5%). Bottom: PC1 vs PC3 (9.3%) from PCA of mean head form for decade and over sixty age groups. Rectangle = male, circle = female, small symbol = young, large = old

Figure 6. Average rates of aging (shape change as measured by Procrustes distance per year) in each sex from 23 to 74 years.

Figure 7: Visualisations of regression predictions of age related form changes in each sex (females columns 1 and 3; males, 2 and 4) between 20 and 40 years (left two columns) and between 40 and 80 years (right two columns). Age related changes are shown as colour maps of the ratios of areas of equivalent craniofacial regions between these ages as indicated by the key.

Figure 8: Visualisations of regression predictions of age related form changes in each sex (females left; males right). Top row: visualisations of regressions between 20-80 years. Bottom: between 20 and 40 years and between 40 and 80 years. Age related changes are shown as colour maps of the ratios of areas of equivalent craniofacial regions scaled to represent change per 20 years.

499 **Legends for Tables**

500 **Table 1:** Definitions of fixed facial landmarks.

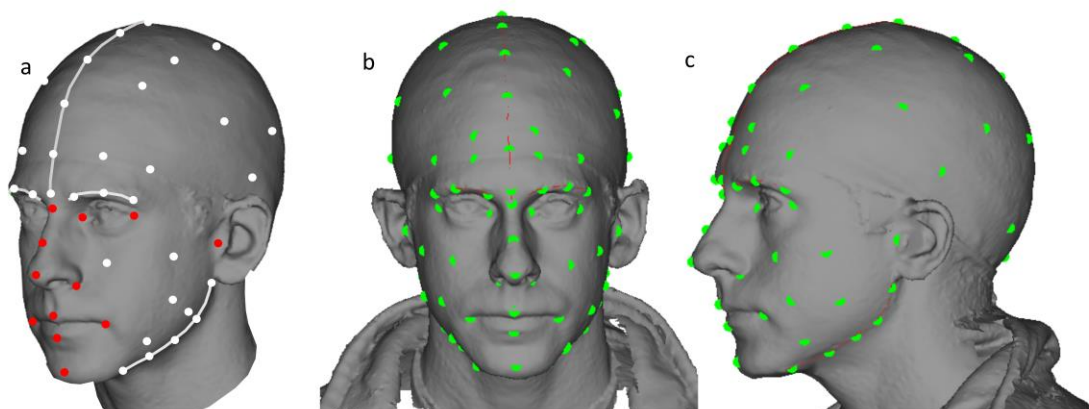
501 **Table 2:** Multivariate regressions of form and shape on age in each sex for the full
502 sample

503 **Table 3:** Multivariate regressions of form on age in each sex for subsamples of
504 younger and older individuals in each sex

505

506 **Table 4:** Vector comparisons between multivariate regressions of form on age between age
507 subgroups and sexes

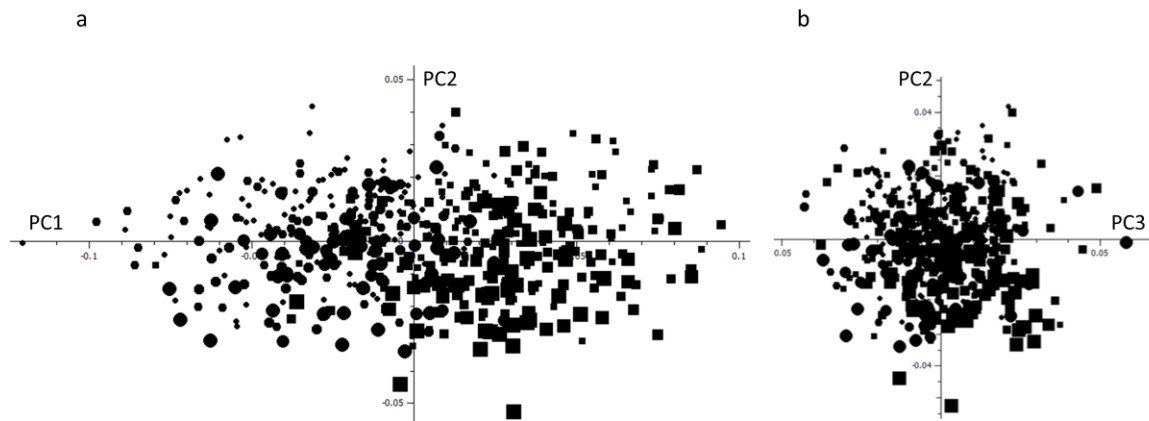
508



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515

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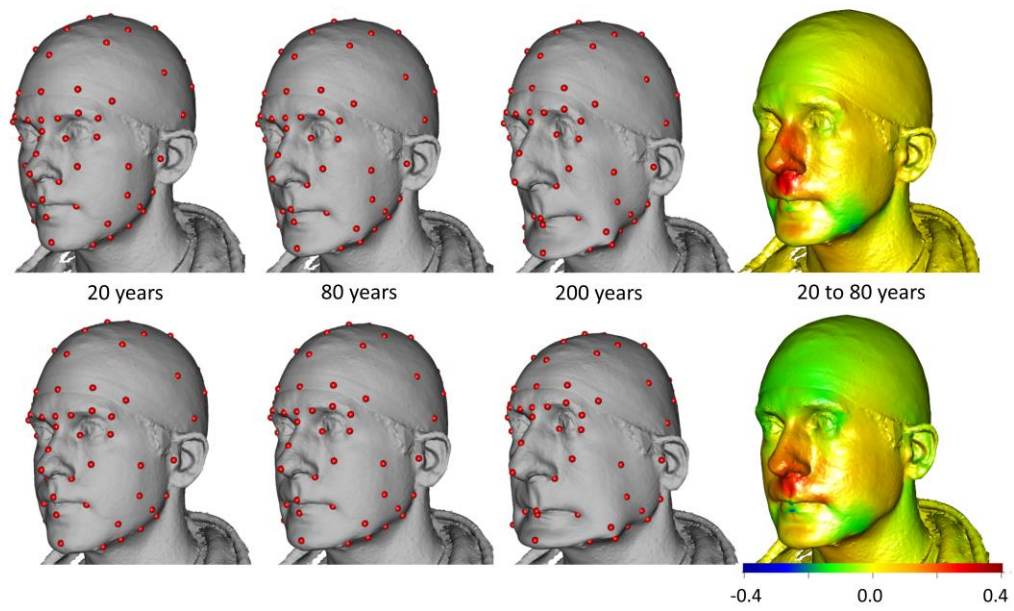


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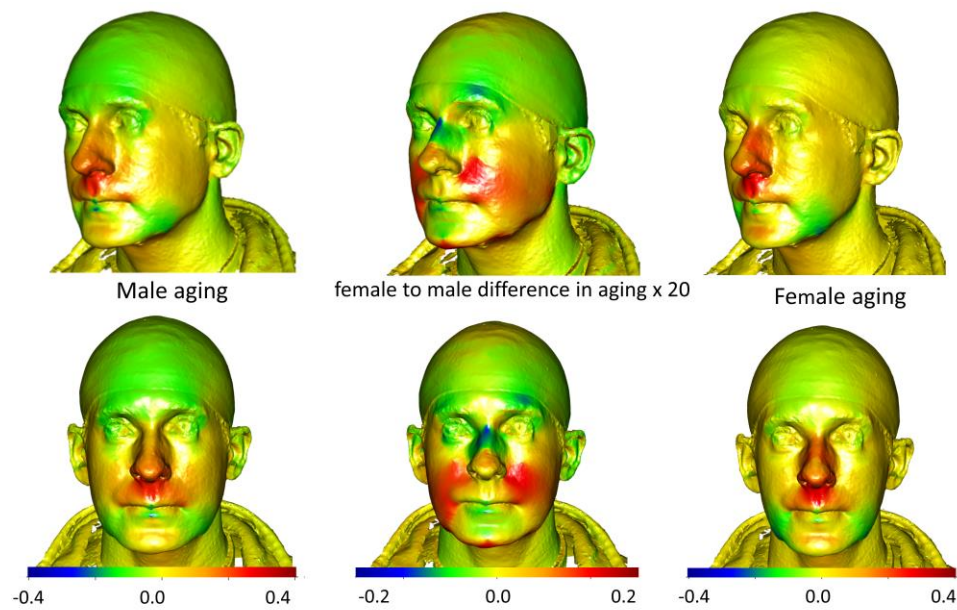


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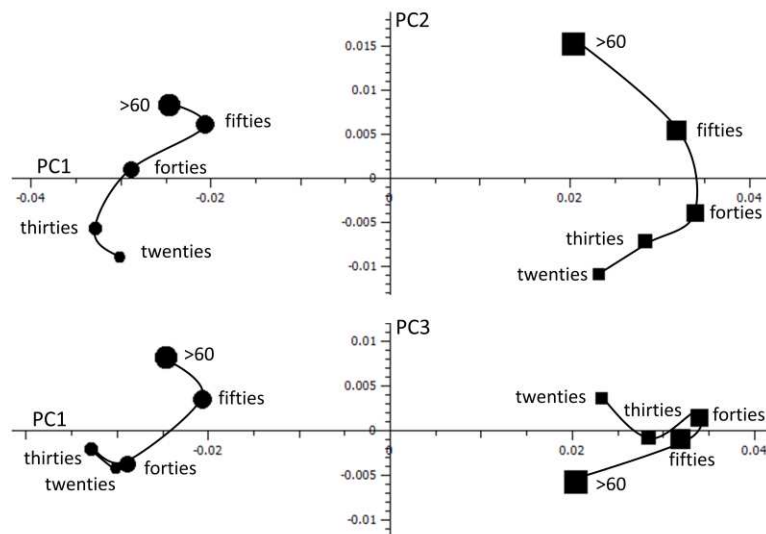
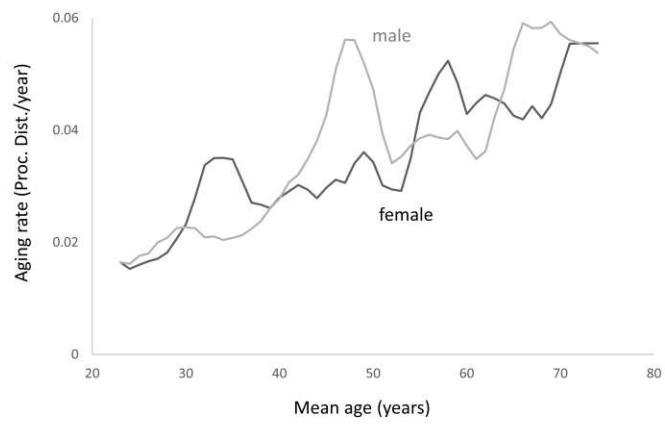


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542

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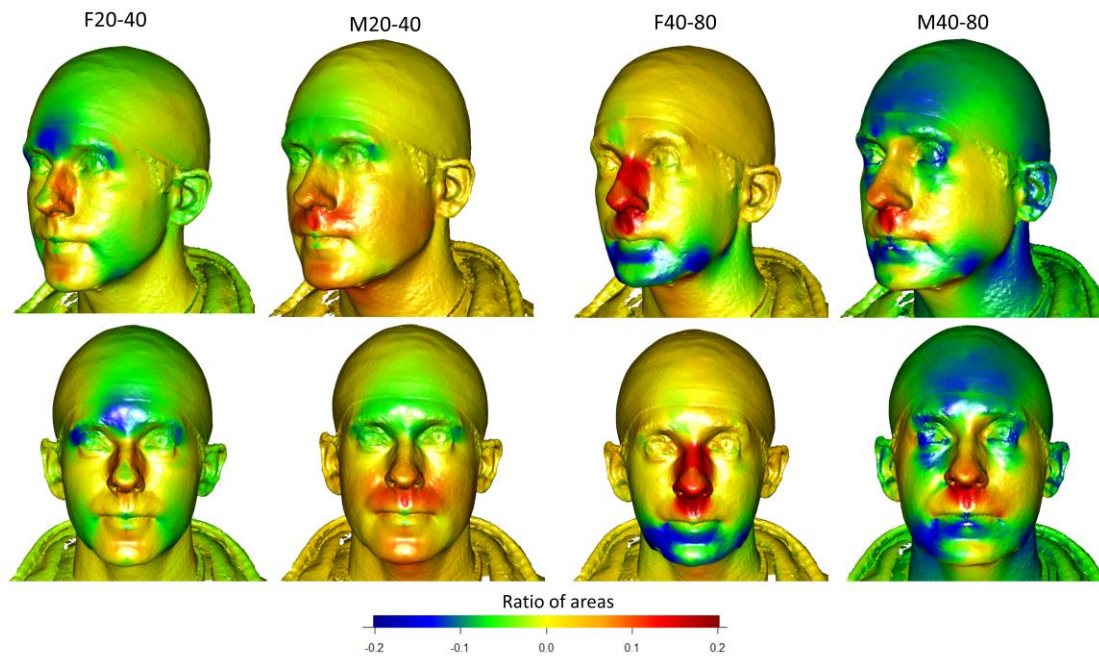


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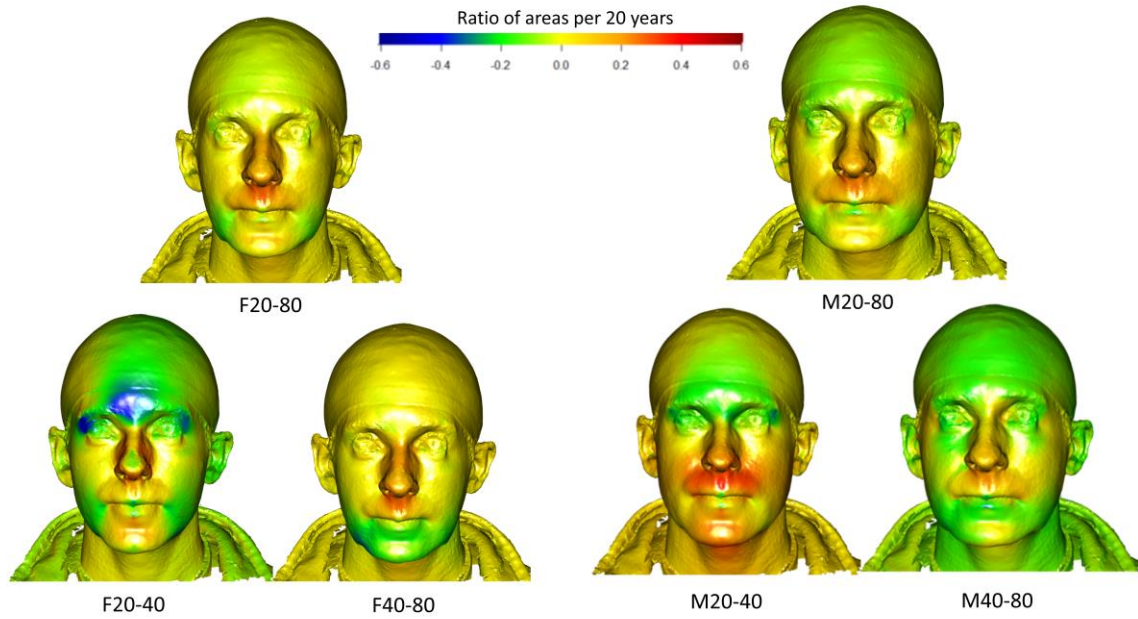


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No.	Landmark description
1 & 3	Medial canthus
2 & 4	Lateral canthus
5	Nasal bridge
6	Middle of nose
7	Tip of nose
8 & 9	Corner of mouth
10	Middle of cupid's bow upper lip
11	Middle of bottom lip
12	Tip of chin
13 & 14	Tragus
15 & 16	Lateral nasal alar rim

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572 **Table 1:** Definitions of fixed facial landmarks.

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Regressions on age	% explained variance (R^2)	p (1000 permutations)
Form males	3.3%	<0.001
Form females	3.3%	<0.001
Shape males	4.5%	<0.001
Shape females	4.2%	<0.001

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576

577 **Table 2:** Multivariate regressions of form and shape on age in each sex for the full
578 sample

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Regression of form on age	R^2	p (1000 permutations)
Males 20-39	0.01607	0.011
Males 20-49	0.01868	0.005
Males 40-90	0.04242	0.002
Males 50-90	0.03619	0.023
Females 20-39	0.0122	0.047
Females 20-49	0.01595	0.007
Females 40-90	0.02322	0.022
Females 50-90	0.01067	0.814

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582 **Table 3:** Multivariate regressions of form on age in each sex for subsamples of
583 younger and older individuals in each sex

584

Form vector comparisons	Angle degrees	p (1000 permutations)
males 20-39 vs males 40-90	94.3	<0.001
males 20-49 vs males 50-90	104.7	<0.001
females 20-39 vs females 40-90	80	<0.001
females 20-49 vs females 50-90	89.5	<0.001
females 20-39 vs males 20-39	81.3	0.008
females 20-49 vs males 20-49	65	0.085
females 40-90 vs males 40-90	85.6	0.052
females 50-90 vs males 50-90	69.2	0.609

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588 **Table 4:** Vector comparisons between multivariate regressions of form on age between age
589 subgroups and sexes

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