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Sexually Dimorphic Ontogenetic Trajectories of Frontal Sinus Cross Sections

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A B S T R A C T

In this paper, we analyze a large published data set[1] of cross sections of frontal sinuses of 3 to 11-year-olds (105 males and 87 females) from Central Europe to investigate several issues relating to frontal sinus ontogeny. Despite a large variation in every one year age cohort, we detect no asymmetry of the left average versus the right average frontal sinus lobe cross-sectional areas in the population, neither for males nor for females. The growth rate is shown to be nonuniform and differs between males and females. We demonstrate the use of a sigmoid function interpolation to characterize one aspect of ontogeny, namely, the functional relation between the cross-sectional area of the frontal sinus and the age of the individual. Ontogenetic trajectories of these cross-sectional areas are remarkably well modeled by a sigmoid function (logistic curve) with suitably estimated parameters for development up to an age of 11 years (females) and 9 years (males). However, these developmental curves also reliably predict the average adult cross-sectional area at age 19 (99% for females, 95% for males). Apart from possible inadequacies of the data set, we also discuss the possibility of heterochrony in the ontogenetic trajectory before versus after puberty.

Introduction

The frontal sinuses of *Homo sapiens* begin to develop shortly after birth[2–4]. Up to now, models describing how these cavities develop must be considered inconclusive. The incomplete knowledge of their physiological role[5] is confounded by the observation that the frontal sinuses of adult *H. sapiens* vary enormously in size[1,6] (Figure 1).

It is difficult to find recent exposés dealing with the possible physiological functions of the frontal sinuses. Of the more than ten thousand (!) 'websites' mentioning frontal sinus(es) that any good

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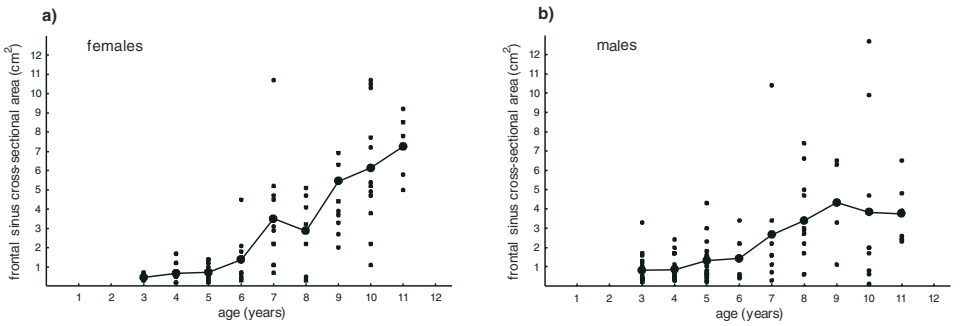

Fig. 1. The frontal sinus cross-sectional areas as a function of age of all 192 frontal sinuses analyzed in this paper; (**a**) *females, N = 87;* (**b**) *males, N = 105. The averages for each age cohort have been connected by straight line segments so as to demonstrate the non-linearity of the ontogenetic trajectory.*

search engine browsing the World Wide Web finds, practically all deal with their pathology or with remedial surgical techniques; the very few dealing with their anatomy are cursorily descriptive. Currently, there are two main views on the functional origin of the frontal sinuses: spatial models of supraorbital torus formation[7] and masticatory stress models[8] – and these two views are not necessarily incompatible with each other. Perhaps the paucity of explanations for the physiology and/or role of the frontal sinuses is due to their being evolutionary remnants[9] which have not been selected against.

Despite these inadequacies, the frontal sinuses remain a fascinating anatomical feature, not least because analyses of them may contribute to insights about the morphological evolution of the *Homo* cranium[8,10–13]. In this paper, we propose a further facet to the various approaches studying frontal sinuses: aspects of their ontogeny[1,13]. Specifically, here the facet is the developmental curve (ontogenetic trajectory) of the total cross-sectional areas as well as detectable asymmetry between left and right frontal sinus 'lobes' (i.e., the two parts separated by the main, central septum).

A comment about terminology: the cross-section of the frontal sinus (as of any anatomical feature) consists of (at least) two geometric properties: its outline morphology, which awaits analysis using Geometric Morphometrics[14] and its area, which will be analyzed here.

Data and Symmetry

From 1970 to 1978, Szilvássy took x-ray photographs of 257 adult male and 233 adult female frontal sinuses as well as those of 215 children (boys and girls aged 3–17 years) in an occipital-frontal orientation. (For details of the methodology, see Szilvássy, 1982[1]) All individuals in this sample population originated from eastern Austria (the provinces Vienna, Lower Austria and Burgenland). The x-ray images allow a reasonable determination (to 0.1 cm^2) of the transversal cross sectional area of the frontal sinuses. Any geometric distortions introduced by the imaging techniques are practically identical in all photographs, so the geometric aspect of the data can be considered consistent enough for the developmental curves presented and analyzed in this paper.

In 1981, the individual left and right cross sections of the infant and juvenile frontal sinus lobes were published[6]. From these data tables, we have extracted (and subsequently analyze herein) the left and right cross-sectional areas of 105 boys and 87 girls; aged three to eleven years (inclusive). The noteworthy advantage of this data set for our study is that all cross-sectional areas are given in one-year age cohorts (Figure 1). We therefore did not include the published data for the 12–17 year bracket, because these were lumped[6].

In a first analysis, we graphed the total cross-sectional areas for males and females, separately, by age, along with their averages (Figure 1); a pattern for the averages is clearly discernable, despite the large variation. We also graphed left lobe versus right lobe cross-sectional areas, by sex, in order to detect any possible asymmetry (Figure 2).

Second, we look at the overall population distribution of a possible asymmetry. We can find any left/right asymmetry by linearly interpolating A_{left} as a function of A_{right}, where A_{left}, A_{right} represents the cross-sectional area of the left, right lobe of the frontal sinus, respectively. If there is no asymmetry, then the linear interpolation function:

$$A_{\text{left}} = slope \quad A_{\text{right}} + A_0$$

should have unit slope (i.e., $slope = 1$) and zero intercept (i.e., $A_0 = 0$).

Conventionally, a linear interpolation algorithm assumes that the ordinate variable is the dependent variable and the abscissa variable is the independent variable. The independent variable is defined – in a statistical sense – as the variable with the smaller variance[15]. However, we must assume that neither the left nor the right cross sections are dependent variables, because the standard deviations are comparable (for females, Figure 2c; for males, Figure 2d). A linear interpolation in the case where there exists no dependent variable is found by minimizing the merit function[15]:

$$\chi^2_S \quad \sum_{i\ 1}^{N} \frac{A_{\text{left}\,i} \quad slope \quad A_{\text{right}\,i} \quad A_0}{1 \quad slope^2}^2$$

For this data set, we find the functions:

$$A_{\text{left}} = 0.999997 \quad A_{\text{right}} + 0.11\ \text{cm}^2 \ (P < 0.00001)$$

for the females (N = 87), and:

$$A_{\text{left}} = 1.000000 \quad A_{\text{right}} + 0.04\ \text{cm}^2 \ (P < 0.00001)$$

for the males (N = 105). Indeed, the data set we are investigating here suggests a spectacular symmetry of the frontal sinus cross-sectional area in the population when we use this appropriate interpolation regimen.

Mathematical Modeling of Cross-Section Ontogeny

We would like to know how the total cross-sectional areas of the frontal sinuses increase with age – i.e., the so-called ontogenetic trajectory. As a first step, we look at the averages of the one-year cohorts of males and females separately (Figure 1). Clearly, the age cohort averages are hardly collinear, so we should not attempt a linear interpolation. Furthermore, because the frontal sinuses cease to expand after a certain age, and a linear function is unbounded in its function values, even an approximation by a linear function is biologically questionable. Rather, we suggest to interpolate the averages by a biologically meaningful function, which allows us to assess some aspects of frontal sinus ontogeny.

We model (i.e., approximate) the development curve of a (scaled) total cross-sectional area A by a modified sigmoid function[13] of the form:

$$A \ t \quad \frac{1}{1 \quad \alpha \quad e^{-rt}}$$

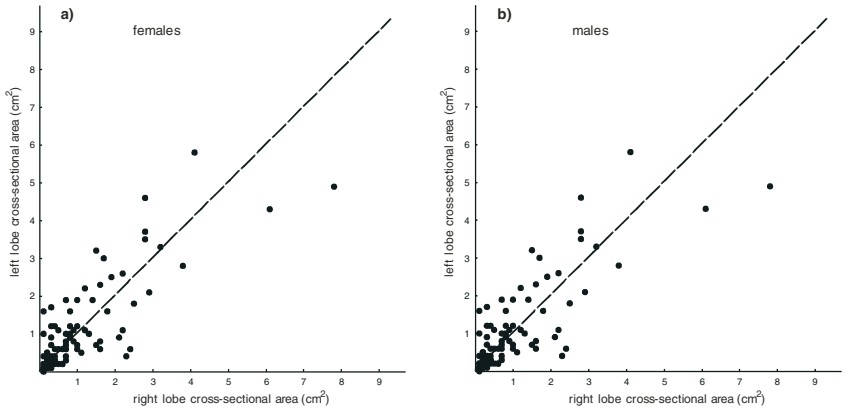

Fig. 2a, b. The results of linear interpolation of left lobe cross-sectional areas as a function of right lobe cross-sectional areas; (**a**) *females, N = 87;* (**b**) *males, N = 105. The (dashed) interpolation lines are very close to the first diagonal (see text), indicating a population symmetry for both sexes. The interpolation assumes that neither area can be considered a dependent variable*[15].

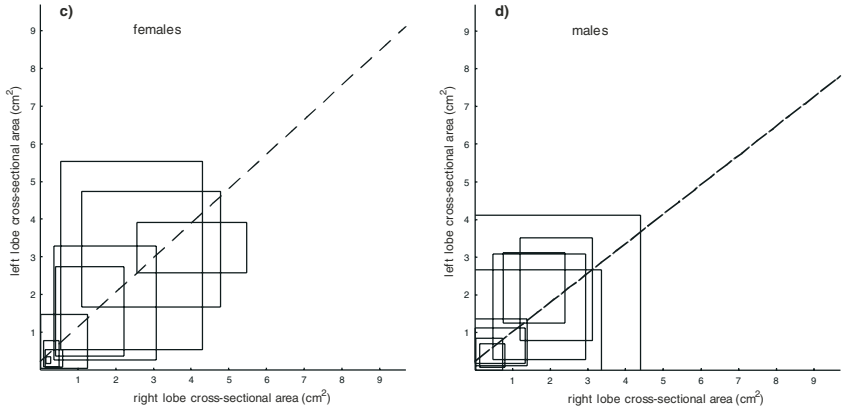

Fig. 2c, d. The standard deviation for each cohort is graphed as a rectangle about the arithmetic mean; i.e., the center of each rectangle is the average of that sex-specific age cohort. The resulting 18 rectangles (9 for the females, 9 for the males) are nearly squares, so one can conclude that the standard deviations of right and left lobes are comparable. (Two-tailed F-test for ratio of standard deviations, left vs. right: P = 1 for all age cohorts, both male and female.)

where t is the age of the individual. Because $A(t)$ 1 as t , we use the adult average of the same population as a scaling factor. We attempt to interpolate the average areas A_k (where the index k numbers the 9 age cohorts from 3 years to 11 years) by estimating values for and r so that the merit function:

$$\chi^2_{\mathrm{A}} \quad \sum_{k\ 1}^{9} \quad A_k \quad A\ t_k \quad ^2$$

is minimized. In this case, the age of each individual on the date when the x-ray photograph was taken is known rather precisely. The total cross sectional areas, on the other hand, vary considerably – in

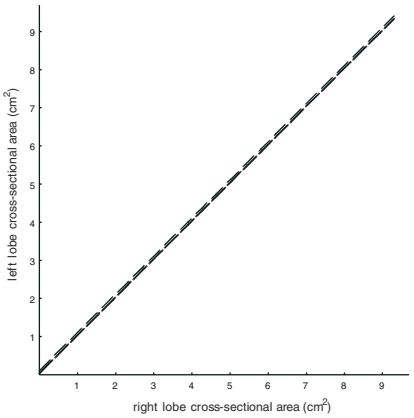

Fig. 2e. A superposition of the interpolation functions for the two sexes shows that the symmetry is sex independent; the two interpolation lines are almost indistinguishable when drawn on the same scale as used in Fig. 2a and in Fig. 2b.

every single age cohort (Figure 1). We may therefore take the age of the individual as the independent variable and the area as the dependent variable.

In order to make a statistical test for the reliability of the sigmoid function modeling the developmental curves, we linearize the function $A(t)$: we transform $A(t)$ into a function $L(A)$, such that $L_A(t)$ is a linear function[18]. The linear transform of the function $A(t)$ is:

$$L\ A \quad L_A\ t \quad \ln\frac{A}{1\ \ A} \quad \ln\frac{A\ t}{1\ \ A\ t}\ .$$

In the case of the sigmoid function $A(t)=(1+\alpha\ \ e^{-rt})^{-1}$, the linear transform is $L_A(t)=-1n\alpha+rt$.

An inspection of the graphs $L_A(t)$ for males and females shows that linearization is a promising approach (Figure 3). For the females, all linearly transformed averages lie very close to a straight line.

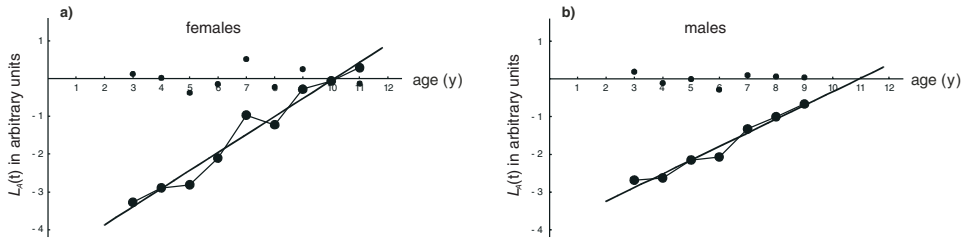

Fig. 3. The function values of the linearization function $L_A\ t \quad \ln\ A\ t\ /\ 1 \quad A\ t$ *for each cross-sectional area (ordinate) at the age cohorts* t_k *(abscissa);* (**a**) *females (k=1..9);* (**b**) *males (k=1..7). The small solid circles about the time axes are the residuals after linear interpolation. Note that for the males, only 7 age cohorts were used for the interpolation, while all 9 age cohorts were used for the females. For a justification, see text. The slopes r (not to be confused with the linear correlation coefficient) of the straight lines are* $r = 0.513\ year^{-1}$ *for the females and* $r = 0.362\ year^{-1}$ *for the males. The adjusted correlations* r^2 *are* $r^2 = 0.957$ *for the females and* $r^2 = 0.951$ *for the males.*

For the males, we observe such a striking collinearity only for the first 7 age cohorts (from 3 years to 9 years); we will comment on possible implications of this finding below.

For the females we obtain:

$$L_A(t) = -4.79912 + 0.51324t \quad (P < 1 \;\; 10^{-6},\; P < 3 \;\; 10^{-6})$$

and

$$A_{\text{female}}\; t \quad \frac{1}{1 \quad 121.404 \quad e^{\;0.51324t}},$$

while for the males we obtain:

$$L_A(t) = -3.96766 + 0.36261t \quad (P < 1 \;\; 10^{-5},\; P < 0.0001)$$

and

$$A_{\text{male}}\; t \quad \frac{1}{1 \quad 52.8609 \quad e^{\;0.36214t}}.$$

The ontogenetic curves $A_{\text{female}}(t)$ and $A_{\text{male}}(t)$ found by this interpolation method are shown in Figure 4.

Interpretations and Implications

We can rewrite the interpolation formula in a way that suggests a biological interpretation[13]. Let:

$$\alpha \quad e^{rt_o},$$

then we can rewrite the sigmoid function (logistic function) as

$$A\; t \quad \frac{1}{1 \quad e^{\;r\; t\; t_o}}$$

suggesting a characteristic time t_0 during development.

The time t_0 is indeed a characteristic of frontal sinus development. In order to see this, we first rewrite the functions $A(t)$. For females we obtain:

$$A_{\text{female}}\; t \quad \frac{1}{1 \quad e^{\;0.513\; t \;\; 9.35}}$$

and for the males we obtain:

$$A_{\text{male}}\; t \quad \frac{1}{1 \quad e^{\;0.363\; t \;\; 10.9}}.$$

The females thus have $t_0 = 9.35$ years, and for the males $t_0 = 10.9$ years.

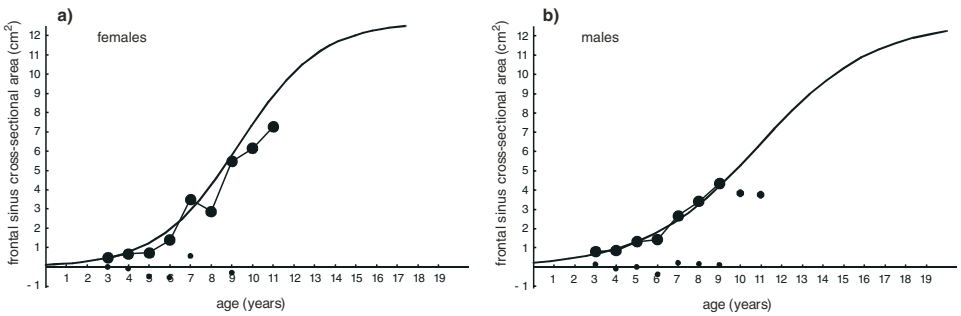

Fig. 4. The interpolated sigmoid functions $A\; t \quad 1 \quad \alpha \quad e^{\;rt \quad 1}$*, representing the ontogenetic trajectory of the frontal sinus cross-sectional area as a function of age of individual;* (**a**) *females;* (**b**) *males. The data values used for the interpolation are large solid circles; the small circles about the abscissa are the residuals. Note how small the residuals are; the sum of the absolute values of the 9 residuals is 3.2 cm² for the females and for the 7 male residuals the sum is 1.1 cm². Extending the interpolating sigmoid function to 19 years predicts that the females then have reached 99% of the average adult (i.e., final) cross-sectional area in this ontogenetic trajectory model, while at the same age, the males achieve only 95% of the average adult cross-sectional area. In the interpolation for the case of the males, the values at age cohort 10 and 11 years were not used; for implications and justifications, see text.*

To elucidate the (analytic and biological) meaning of the parameter t_0, we find the first and second derivative of the sigmoid function. The first derivative is:

$$\dot{A}\ t \quad \frac{dA}{dt} \quad \frac{re^{\ r\ t\ t_0}}{1 \quad e^{\ r\ t\ t_0\ \ 2}}$$

and the second derivative is:

$$\ddot{A}\ t \quad \frac{d^2A}{dt^2} \quad \frac{2r^2\ e^{\ 2r\ t\ t_0}}{1\ e^{\ r\ t\ t_0\ \ 3}} \quad \frac{r^2\ e^{\ r\ t\ t_0}}{1\ e^{\ r\ t\ t_0\ \ 2}}\ .$$

We are interested when the second derivative is zero, because the solution of $\ddot{A}\ T \quad 0$ indicates the moment T when there is a point of inflection on the developmental curve. This moment occurs exactly when $T{=}t_0$ (because $\ddot{A}\ t_0 \quad 0$). We conclude that the inflection occurs at 9.35 years for females, and 10.9 years for males – about 1½ years later.

Because t_0 occurs at the point of inflection, the 'growth' rate (the rate of increase in cross-sectional area is physiologically not a growth) is maximal. We find that at this maximum, the total cross-sectional area of the female frontal sinuses develops at a rate $\dot{A}(9.35) = 0.128$ cm^2/year and that of the males develops at a maximum rate of $\dot{A}(10.9) = 0.0906$ cm^2/year. The maximum developmental rate for females is thus about 141% higher – and considerably earlier. The developmental rate curves of both female and male frontal sinus cross-sectional areas are shown in Figure 5.

A further implication of modeling the development with a sigmoid function is a comparison of the asymptotic behavior. Models allow predictions; in this case, the model predicts the final total cross-sectional area of the frontal sinuses in the population from which the data have been drawn. For the females, the model predicts that the developmental rate drops down to 0.004 cm^2/year at age 19 years, or 3.1% of the maximum rate. For the males, the developmental rate drops to 0.018 cm^2/year (~4.5 times the female

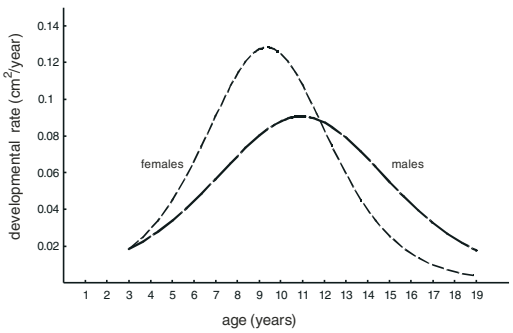

Fig. 5. The developmental rates $\dot{A}\ t \quad re^{\ r\ t\ t_0} \quad 1 \quad e^{\ r\ t\ t_0\ \ 2}$ *of the cross-sectional areas when the ontogenetic trajectory is modeled as a sigmoid function. Despite their appearance, these curves are not normal (Gaußian) distribution curves, but rather the derivatives of the estimated sigmoid functions. The female rate curve is the thinner short-dashed line, the male one is the thicker, long-dashed one. For the females: $r = 0.513$ year^{-1}, $t_0 = 9.35$ years; for the males: $r = 0.362$ year^{-1}, $t_0 = 10.9$ years. In this model, the maximum developmental rate for the females is 0.128 cm^2/year, for the males it is 0.0906 cm^2/year. At 19 years of age, the model predicts that the developmental rate of the males is roughly 4.5 times the rate for the females. Note that at 3 years, the model predicts that the developmental growth rate is essentially the same for both sexes (females and males: 0.018 cm^2/year; they differ – numerically – by 0.000003 cm^2/year).*

rate, incidentally), or still 20% of the maximum rate. According to the model, therefore, development is far from over at age 19 years for the males.

An intriguing prediction involves the asymptotic (final) total cross-sectional area – in other words, the average adult cross-sectional area. The small developmental rate for the females implies that the adult cross-sectional area must have been essentially arrived at by the age 19 years. The interpolated sigmoid function for the females predicts that the cross-sectional area would be 10.5 cm^2. For the population from which this sample of children was drawn, Szilvássy[1] finds the average cross section of the adult females to be 10.6 cm^2. Thus, according to the model, 99% of the average adult female cross-sectional area has been reached at 19 years of age.

The model prediction for the average adult male cross-sectional area shows that cross-sectional area increase is not completed by 19 years. At this age[1], the cross-sectional area is 12.05 cm^2, which is 95% of the observed adult average of 12.7 cm^2. Much later, at 23.6 years, 99% of the observed male adult average cross-sectional area is achieved.

Discussion

The variance of the cross section at each age cohort is very large. As shown in Figure 6a (females) and Figure 6b (males) the relative standard deviation (i.e., the standard deviation relative to the arithmetic mean) is never below 20% and it rarely achieves such a 'low' value. One should be surprised, therefore, at the success of this presented modeling despite such highly noisy data points. To some extent, it may be a statistical reliability inference due to large numbers. Our results show that noisy data can lead to meaningful insights, if analysis and modeling is prudent enough. However, the very low values of a large proportion of the male total cross-sectional areas in age cohort 10 years and 11 years warranted excluding them from the modeling.

The sigmoid function is numerically challenging, because its image domain is between 0 and 1 (and it reaches these values only asymptotically). We must, therefore, suitably scale the cross-sectional areas of the frontal sinuses in order to use this function. We have approached the problem of scaling by dividing the average area of each age cohort by the adult average area, females and males separately. The average adult cross section determined for both males and females separately are from the same population[1]. It may be that the sigmoid function is a successful model due to this fortuitous choice of a scaling factor (normalizing constant). This issue awaits further analysis. As can be seen from the sum of the absolute values of the residuals for the linearized function $L_A(t)$, the model is very successful, and the linearization process is not very sensitive to the chosen scaling factor. (Changing the scaling factor would primarily shift the interpolated line along the ordinate but hardly change the slope of $L_A(t)$.)

The correlation coefficients, which are a statistical measure of linearity, are very close to 1 – extremely close, in fact, when compared with many other biological data sets. In this paper, we have presented one method of assessing statistical significance of estimated parameters of the sigmoid function; the outcome of these tests can be considered encouraging, even in the presence of so much statistical noise in the raw data.

The data analyzed here is two-dimensional. We are inclined to speculate as to why modeling the developmental ontogeny for the males would be problematic if the 10 and 11 year-old age cohorts are included. We did not include these last two cohorts for statistical reasons, and we

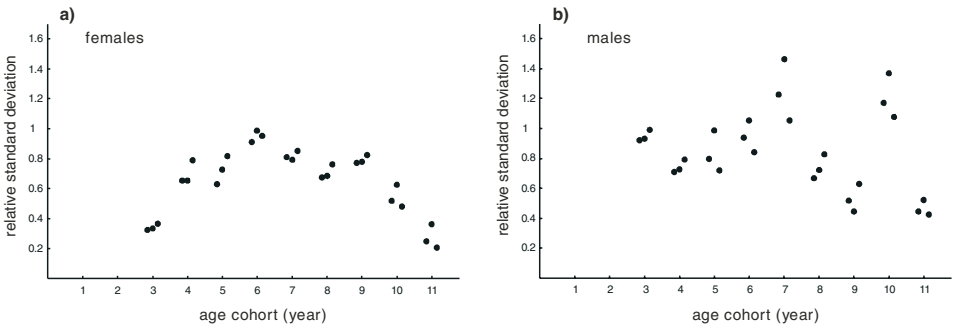

Fig. 6. The ratio of standard deviation to arithmetic mean for all frontal sinus cross-sectional areas (**a**) *females,* (**b**) *males. A triplet (three points) represents one age cohort; the first point of the triplet is the relative standard deviation for the total cross-sectional area, the second for the area of the right lobe, the third for the area of the left lobe; there are, therefore, 9 triplets. For the females, the smallest ratio is ~20%, for the males it is slightly less than 40%. This graph demonstrates how extraordinarily noisy this data set is.*

now seek a biological hint why the 10 and 11-year male age cohorts could exhibit this deviant behavior. Perhaps there is a growth spurt in the internal and external table of the frontal bone which results in a volume increase that is not reflected in the cross-sectional ontogeny during this age? Tanner[16] points out that growth rates in different parts of the skull are maximal at different times. Unfortunately, Tanner's published rates are not modeled numerically, so we cannot at present assess how these rates result in an overall change in morphology. A study of craniofacial growth using Geometric Morphometrics shows the complex outcome when differential growth rates combine[17], but ascribing specific geometric growth effects to a selected subset of these differential growth rates has not yet been achieved. A preliminary study using a small sample of 3D-data[13] shows that the maximum expansion rate for the frontal sinus volume occurs at 18–19 years. This age may have to be revised when we have access to more data, but the preliminary results do indicate that volume ontogeny seems to be heterochronous *sensu strictu*[18,19] with cross-sectional area ontogeny. Unquestionably, more data and further analysis, using the same methodology presented here, will help clarify whether these interpretations are meaningful. If we use heterochrony *sensu strictu*, then we are to expect that the ontogenetic trajectory in the third dimension will differ from the sigmoid functions presented here.

Conclusion

In this paper, we succeed in showing that a population has a symmetric frontal sinus cross-sectional area, despite the enormous individual variation in each age cohort. Perhaps this is an indicator that there are no functional asymmetries for the role of frontal sinuses – maybe because they are evolutionary remnants. If there is a functional role to be expected, then it is difficult to argue that it would be so symmetrically distributed throughout a population.

We note that the developmental curve has the same time derivative (i.e., rate of developmental increase) for all 3-year-old individuals, regardless of sex. The sexual

dimorphism expresses itself as a heterochrony *sensu lato* between the sexes only at a later age. The frontal sinus cross-section areas develop at a different rate during the maturation of the individual and this growth rate, as a function of time, differs between males and females. Other researchers are investigating such growth acceleration patterns[20], and the model presented here could contribute to such ongoing studies. We find that the females develop their frontal sinus cross -sectional areas much more rapidly than the males do, but complete their development much earlier. We find the ontogenetic trajectories to be sexually dimorph, both in rate and asymptotically.

We are aware that the data analyses presented in this paper are of a two-dimensional data set. As mentioned in the discussion, analysis of development in the third dimension is of paramount importance. Only preliminary studies of the ontogenetic trajectories of frontal sinus volume have been completed[13]. Because 3D-data is expensive to acquire, (and therefore two large data sets – one for each sex – will not be available in the immediate future) we have tested our ability to model ontogenetic heterochrony and sexual dimorphism in two dimensions first. Despite the data being statistically very noisy, we have found the presented models to be remarkably successful at interpreting frontal sinus cross-sectional area ontogeny. The insights presented here point out further venues of investigation.

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SPOLNO DIMORFIČNA ONTOGENIJA PRESJEKA FRONTALNIH SINUSA

S A Ž E T A K

U ovom radu, ponovno su analizirani već objavljeni podaci[1] presjeka frontalnih sinusa djece stare 3–11 godina (105 dječaka i 87 djevojčica) iz centralne Europe, kako bi se ispitalo nekoliko problema povezanih s ontogenijom frontalnih sinusa. Unatoč velikoj varijabilnosti unutar svake jednogodišnje dobne kohorte, niti u dječaka niti u djevojčica nije detektirana asimetrija prosječne površine lijevog režnja frontalnog sinusa u odnosu na desni. Međutim, stopa rasta pokazala se neuniformnom i razlikovala se među spolovima. Pokazalo se da interpolacija sigmoidne funkcije karakterizira jedan aspekt ontogenije, naime funkcionalni odnos između površine presjeka frontalnog sinusa i dobi pojedinca. Također je pokazano kako se ontogenijske putanje površina ovih presjeka mogu iznimno dobro modelirati pomoću sigmoidne funkcije (logistička krivulja) s prikladno procijenjenim parametrima za razvoj do dobi od 11 godina (djevojčice) i 9 godina (dječaci). No, ove razvojne krivulje također pouzdano prediciraju i prosječnu površinu presjeka i u odrasloj dobi (19 godina) i to na razini 99% za djevojčice i 95% za dječake. Neovisno o mogućoj neprikladnosti korištenih podataka, razmatrana je i mogućnost heterokronije u razvojnim putanjama prije puberteta u odnosu na one nakon puberteta.