A parallel growth model for shape

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Abstract. We present a model for analysing the change in shape of two-dimensional biological objects growing with time. Procrustes coordinates are used to represent the shape of each object, and a set of parallel polynomial curves (one per individual) is fitted to the data using multivariate regression. Statistical tests for the parallel hypothesis are presented. The model is shown to be approximately independent of the choice of coordinate system used to represent the shape.

1 Introduction

The simplest way to describe the growth of a set of biological organisms is to assume that they all grow in the same fashion. Such a pattern of growth can be represented by a set of parallel trajectories in an appropriate space. Here we will discuss a modelling framework where the objects are represented by a set of landmarks, the shapes of the objects are represented by Procrustes tangent coordinates and the individuals are assumed to grow along parallel trajectories in Procrustes tangent space. Specifically we use the parallel growth model for shape which has the form $\gamma(t) + \mathbf{u}_i$ where t is time, $\gamma(t)$ is a common curve, and the $\mathbf{u}_i$ represent individual displacements. In our previous work [1, 2] the curve γ was taken to be a simple straight line. Here we use a richer description where γ is taken from a larger function space, e.g. either low degree polynomials or cubic splines. Our work relies heavily on the theories of growth curves [3] and shape analysis [4].

We will use Procrustes tangent coordinates to represent the *shape* of an object. These coordinates are independent of the location and orientation in space of the object. They are also independent of the size of the object. We have chosen to remove size as it is often the dominant factor in growth and can mask the effects of changes in shape. The Bookstein registration scheme [5], obtained by fixing the position of two landmarks, provides an alternative coordinate system for shape. We shall see below that the choice of coordinate system does not have an important effect on the description of growth.

2 The data

The data used here has been taken from a study of 21 rats skulls, where the positions of eight biological landmarks lying in the two dimensional midsagittal plane were measured at eight successive ages. We will study a subset of 18 rats for which there is a complete set of data. Moss [6] has studied the data from a finite element perspective. Bookstein [5] has examined the data in terms of inter-landmark distances where some non-linear effects were noticed. He has also examined several ways to visualise the data and interpret the dominant changes in shape of the rat skulls. These descriptions do not explicitly have time as a factor.

Let T be the number of time-points, N be the number of individuals and K be the number of landmarks. Here $T = 8$, $N = 18$, $K = 8$. Let $x_{itk} \in \mathbf{C}^2$ be the complex representation of the position of the k-th landmark for the i-th individual at the t-th time point. Let $\mathbf{x}_{it} = (x_{it1}, \ldots, x_{itK}) \in \mathbf{C}^K$ be the configuration of the K landmarks for the i-th individual at time t. Let $\mathbf{y}_{it} = (y_{it1}, \ldots, y_{it(2K-4)}) \in \mathbf{R}^{2K-4}$, be the real valued Procrustes tangent coordinates for the shape of $\mathbf{x}_{it}$. Procrustes coordinates are obtained in a number of steps: 1) each object is centred and rescaled to have unit centroid size; 2) a mean shape is found [7]; 3) each object is rotated to match the mean shape as closely as possible, the coordinates of these shapes are the Procrustes coordinates; 4) the Procrustes coordinates are projected onto a $2K - 4$ dimensional linear subspace to give the Procrustes tangent coordinates. Full details of this process can be found in [4].

3 The parallel growth model

3.1 Model fitting

Let $\mathcal{P}$ be the function space spanned by a basis $\{P_m(t) : m = 1, \ldots, M\}$ of M real-valued functions of time t. The data are modelled by a set of parallel curves, $\gamma(t) + \mathbf{u}_i \in \mathbf{R}^{2K-4}$, with one curve per individual. The vectors

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$\mathbf{u}_i \in \mathbf{R}^{2K-4}$ give a constant displacement term for each individual. The l-th component of $\gamma(t)$ is a function, $\gamma_l(t) \in \mathcal{P}$, with $\gamma_l(t) = v_{l1} f_1(t) + v_{l2} f_2(t) + \cdots + v_{lM} f_M(t)$. Explicitly the model is

$$\mathbf{y}_{it} = \mathbf{u}_i + P_1(t)\mathbf{v}_1 + P_2(t)\mathbf{v}_2 + \cdots + P_M(t)\mathbf{v}_M + \mathbf{e}_{it}, \tag{1}$$

where $\mathbf{v}_m = (v_{1m}, v_{2m}, \ldots, v_{(2K-4)m})$ is a vector of coefficients and $\mathbf{e}_{it} \in \mathbf{R}^{2K-4}$ is a vector of error terms, initially taken to be iid. This is a multidimensional growth curve model [3] and the coefficients, $\mathbf{u}_i \in \mathbf{R}^{2K-4}$, $i = 1, \ldots, N$, $\mathbf{v}_m \in \mathbf{R}^{2K-4}$, $m = 1, \ldots, M$, can be estimated using linear regression.

In this work the function $P_m(t)$ is taken to be a polynomials of degree m with $m = 1, \ldots, M$. We actually use orthogonal polynomials as they are easy to work with numerically and allow the effect of each term to be visualised separately. It would also be possible to investigate a similar model with a basis of spline functions.

A MANOVA analysis assuming iid errors for the rat data is described in Table 1. The sum of squares effect indicates the relative contribution of each factor to the model, high values indicating a strong effect. The p-values indicate the statistical significance of each factor. The individual, linear, quadratic and cubic effects are all extremely significant with p-values close to zero. The linear effect is seen to dominate the other terms. The quartic effect has a considerably higher p-value though it is still statistically significant at the 5% level. However the effect of the quartic term is much smaller and can be dropped from the model in an initial investigation.

	Individual	Linear	Quadratic	Cubic	Quartic	Residuals
Degrees of Freedom	216	12	12	12	12	1464
Sum of Squares Effect	0.03407	0.59263	0.03962	0.01443	0.00127	0.06417
p-values	≈ 0	≈ 0	≈ 0	≈ 0	0.004121	

Table 1. The effect of each factor in the model (1).

The very large number of residual degrees of freedom contributes to the exceptionally low p-values. The error model does not take the autocorrelations of errors or the correlation between Procrustes coordinates into account. This may lead to over-confidence and to extremely small p-values. However preliminary analysis with a more sophisticated error model in this dataset indicates that the estimates of p-values are fairly reliable.

3.2 Interpretation

The top row in Figure 1 shows the Procrustes registered shapes for the fitted model at times 1, 3, 4.5, 6, 8. The principal change is an elongation of the shape: it becomes relatively longer and narrower. The other major feature is that the rightmost line segment develops a flatter slope.

The use of orthogonal polynomials allows the linear, quadratic and cubic effect to be separated out, which are also shown in Figure 1. The second row shows the linear effect, the third row shows the quadratic effect magnified by a factor of ten and the bottom row shows the cubic effect magnified by a factor of ten. The shapes are shown for $t = 1, 3, 4.5, 6, 8$. The mean shape is in the centre of the second row. Note that the quadratic effect is symmetrical about $t = 4.5$ and exhibits an out and back pattern of change. The cubic effect is anti-symmetrical with an out, back and out again pattern with the same shapes for times $t = 1, 6$ and $t = 3, 8$. More work is needed on the interpretation of these results.

3.3 Tests of the parallel hypothesis

Central to the parallel growth model is the assumption that the growth happens along parallel curves. This can be tested by considering a model which has a global linear time effects, $P_1(t)\mathbf{v}_1$, and additional linear time effects, $P_1(t)\mathbf{w}_i$, $i = 1, \ldots, N$, for each individual. Specifically

$$\mathbf{y}_{it} = \mathbf{u}_i + P_1(t)\mathbf{v}_1 + P_2(t)\mathbf{v}_2 + \cdots + P_6(t)\mathbf{v}_6 + P_1(t)\mathbf{w}_i + \mathbf{e}_{it}.$$

If the individuals followed strictly parallel trajectories then the individual-linear time factors would not be significant in the MANOVA tests. In fact the individual-linear effect is significant with a p-value effectively zero. However, the sum-of-squares effects is small, 0.018, about half the size of the of the individual-constant effect. This leads us to conclude that there is a small lack of parallelism in the data. The parallel growth model does, however, provide a first approximation to the behaviour of the data. More sophisticated models could include polynomial time effects for each individual.

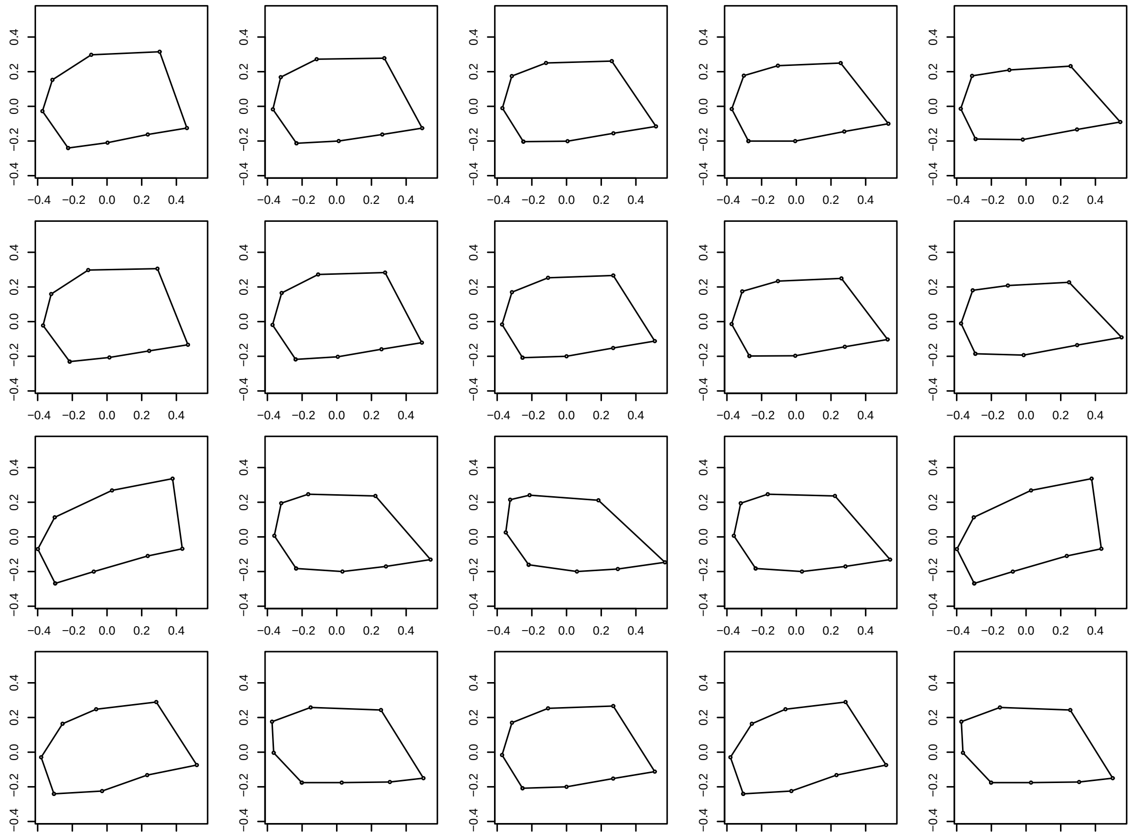

Figure 1. The fitted model and the variation due to linear, quadratic and cubic factors at times 1,3,4.5,6,8 (left to right). Top row: Fitted Model; second row: linear effect; third row: quadratic effect magnified ten times; bottom row: cubic effect magnified ten times. The mean shape is shown in the middle of the second row.

4 The effects of changing coordinate system

Changing the coordinate system used to represent shape will have a slight effect on the resulting fitted model. In this section we will work with one triple of landmarks and compare fitting the parallel growth model in Procrustes tangent coordinates with fitting the model in Bookstein coordinates [5]. The map $\Phi : \mathbf{R}^2 \rightarrow \mathbf{R}^2$, induced by re-registering from Procrustes tangent coordinates to Bookstein coordinates, sends straight lines to circles but for highly concentrated data the map is approximately linear [7]. To illustrate the extent of any possible nonlinearity, a rectangular grid, whose extent matches the range of the data, was constructed in Procrustes coordinates and the image of this grid under the map Φ for one particular baseline was plotted in Figure 2. The baseline was chosen to emphasize the nonlinearity.

Even though the map Φ is nonlinear, fitting a model in both Procrustes coordinates and Bookstein coordinates results in very similar descriptions of growth provided nonlinear time factors are included in the model. This property is illustrated in Figure 3 where parallel growth models with linear, quadratic and cubic effects are fitted to the data in Procrustes tangent coordinates and in Bookstein coordinates. The fits in Bookstein coordinates have been re-registered back into Procrustes tangent coordinates. Note how each curve describes approximately the same pattern of growth.

5 Conclusion and future directions

We have shown how the parallel growth model can provide a good model to describe a set of shapes varying with time. We have also seen how this description does not depend significantly upon the method for representing the shape. The model could easily be extended to work with three-dimensional data.

There is some evidence that the parallel hypothesis does not fully describe the data. However, these effects are small compared to the parallel component. Further investigation is needed on this effect.

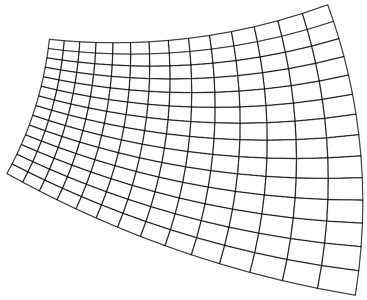

Figure 2. The image of a rectangular grid in Procrustes coordinates re-registered into Bookstein coordinates.

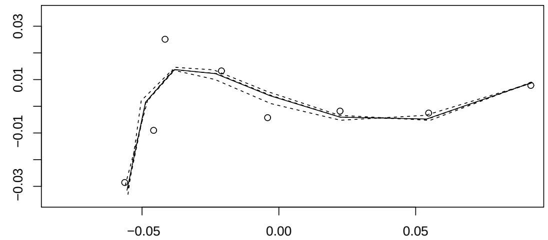

Figure 3. Cubic fits in Procrustes tangent coordinates (solid) and Bookstein coordinates re-registered into Procrustes tangent coordinates (dashed).

One unsatisfactory feature of the model is that cubic polynomials do not provide good biological intuition about the change in shape. This may be especially important at the end points where cubic polynomials can be badly behaved. A more natural description may be obtained by using cubic splines.

More work is needed on the interpretation of the resulting changes in shape. One possibility is to look at the changes in individual triangles of landmarks. Bookstein [5] has presented several possible visualisation techniques. However most of these do not specifically have time as a factor. It should be noted that choice of coordinate systems is important when visualising the data.

There is a close link with principal component analysis and active shape models [8]. Constructing an active shape model is essentially the same as performing principal component analysis on the Procrustes tangent coordinates. Under suitable assumptions it can be shown theoretically that the first principal component will be approximately $\mathbf{v}_1$, which is confirmed for this data set. Furthermore, the space spanned by the first three PCs and the space spanned by $\mathbf{v}_1$, $\mathbf{v}_2$ and $\mathbf{v}_3$ can be theoretically shown to be similar which again is confirmed for this data set.

Our description of the pattern of growth has not taken size into account. Size information could be included by adding a component of log size to the Procrustes Tangent Coordinates [1].

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