Biometrika (2003), **90,** 3, *pp.* 669–678

Printed in Great Britain

Assessing landmark influence on shape variation

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Summary

Given two sets of landmark data which differ in shape, it is useful to determine the extent to which shape variation can be explained by the perturbations of individual landmarks. We propose a method for assessing this, based on analysing the relative reduction in distance between the shapes that can be achieved by varying the location of a single landmark. This method is applied to a set of landmark data from the cervical vertebrae of two subspecies of gorillas.

Some key words: Horizontal geodesic; Landmark; Procrustes mean; Shape; Shape difference; Shape distance; Weight function.

1. Introduction

Shapes of two-dimensional configurations are often described or analysed in terms of landmarks. Such a description may be a matter of convenience, or it may represent a recognition that the landmarks occupy positions of functional significance. The use of landmarks for the analysis of shape was proposed by Galton (1907), and the development of thin-plate splines by Bookstein (1991) for spatial interpolation allowed researchers the opportunity to couple Galton's landmark-based approach with D'Arcy Thompson's method of coordinates (Thompson, 1917). Kendall (1984) proposed that the shapes of k landmarks in two dimensions are representable on the complex projective space $\mathbb{CP}^{k-2}(4)$, which has $2k-4$ real dimensions and complex sectional curvature 4.

The problem that we shall address in this paper is how to assess the importance of individual landmarks in determining shape variation. For example, consider the two configurations of landmarks chosen from specimens of the fifth cervical vertebrae of two subspecies of *Gorilla gorilla*, as shown in Fig. 1. It is reasonable to suppose that the

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differences in shape between the two specimens are associated with the differing postural behaviours of the two subspecies. In particular, the differences in behaviour place different biomechanical demands on the vertebrae. Upright posture places extra stabilisation demands on the muscles, which are in turn anchored to the vertebrae. One possible adaptation to gain efficiency in head-neck stabilisation would be for the posterior tubercles, PT in Fig. 1(a), to extend and rotate anteriorly. This interpretation is supported by Figs 1(b), (c). The most prominent shape difference between the two specimens can be seen in the large triangle at the top of each configuration. The angle at the posterior spinous process, PSP, is smaller for the *Gorilla gorilla gorilla* specimen than for *Gorilla gorilla berengei*. This can be explained by the different location of PT relative to the other landmarks. On the other hand, if the landmark configurations are taken out of context, then the principal role of PT in the shape variation is not obvious. For example, a smaller angle at PSP could also be explained by lengthening the PSP–ASP segment. The question arises whether or not it is possible to identify which of the possible explanations is the most parsimonious without presuming any specific biomechanical explanation.

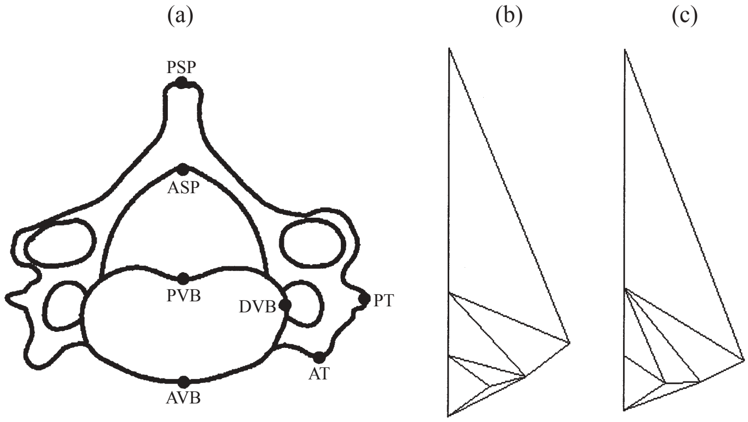

Fig. 1: Gorilla data. (a) shows 7 landmarks placed on the fifth cervical vertebra of a female gorilla; PSP/ASP, posterior/anterior surface of spinous process; PVB/AVB/DVB, posterior/anterior/dorsal surface of vertebral body; AT/PT, tip of the anterior/posterior tubercle. (b) and (c) show the corresponding landmark coordinates for two specimens of different subspecies of gorilla: (b) *Gorilla gorilla berengei*; (c) *Gorilla gorilla gorilla*. In (b) and (c) a Delaunay triangulation has been superimposed over the landmarks for convenience in comparing the shapes of the two configurations.

In simple terms, we seek to explain the variation in shapes between different configurations of landmarks by possible motions of the landmarks themselves. Obviously, the landmark perturbations that cause the observed variation in shape are not identifiable from the shape variation. Mathematically, this follows from the fact that the geodesic path between any two shapes in Kendall's shape space $\mathbb{CP}^{k-2}(4)$ can be 'lifted' in various ways to a geodesic path in an ambient space such as pre-shape space, form space or pre-form space; see Kendall et al. (1999, Ch. 6). The standard solution to this problem is to lift geodesics from Kendall's shape space to horizontal geodesics within the ambient space. For example, Fig. 2 shows two artificial configurations of landmarks, (a) and (b), which differ in shape. In Fig. 2(c), the vector displacements of the landmarks corresponding to a horizontal geodesic in pre-shape space are displayed. The vector displacements shown in Fig. 2(c) provide an adequate explanation for the observed shape differences. However,

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an alternative explanation for the observed differences between configurations (a) and (b) is that the observed variation in shape is caused by the displacement of a single landmark, namely the right-most landmark in each configuration. For biological models which seek to explain morphology through local transformations and changes to a few neighbouring landmarks, the latter interpretation is more useful. In the artificial example, all of the variations can be explained in terms of the influence of this one landmark.

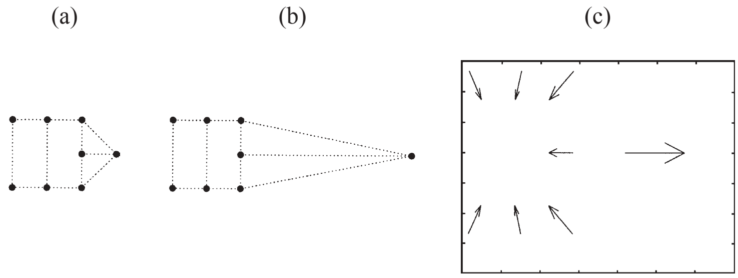

Fig. 2. (a) and (b) show two artificial configurations of eight landmarks each. (c) shows transforming landmarks along the geodesic from (a) to (b) in Kendall's shape space.

Two questions arise about the contributions of individual landmarks to shape variation. First, what landmarks are responsible for the observed shape changes? More precisely, what proportion of the observed shape changes are caused by local changes in a given landmark? Secondly, what landmarks can best explain the observed shape changes? More precisely, what proportion of the observed changes could possibly be caused by local changes in a given landmark?

The first question cannot be solved because a given shape change can be explained in different ways with different landmarks, so shape information itself cannot uniquely identify the local sources of variation in the landmarks which are responsible for the observed variation in shape.

We wish to answer the second question, which is relevant to the determination of landmark influence because, for reasons of parsimony, when everything else is equal, it makes more sense to explain variation by the perturbation of few landmarks than many landmarks. Thus, in a set of k landmarks, it would usually be better to explain the variation in shape by moving one landmark than by moving $k-1$ landmarks. This is not to say that shape variation will never be due to the movement of many landmarks. However, any analysis of the causes of shape variation often begins by studying the possible explanations due to local, i.e. single-landmark, variation.

We therefore seek a measure of landmark influence that is local in the sense that it measures the possible contribution of each landmark to shape variation. For each landmark, such a measure would determine the proportion of observed shape variation which can be explained by perturbations of that landmark alone. In this paper, we will propose and discuss a simple measure of this type. A secondary problem to be considered is how to test for significant differences of shape between two small sets of shape data.

The idea of assessing the influence of individual landmarks has been considered by Lele & Richtsmeier (1992) and by Cole & Richtsmeier (1998). Our analysis shares many of the goals of this previous research. However, it differs in one major respect, namely that it is tailored to accompany a Procrustes analysis of shape on Kendall shape space rather than an analysis through EDMA-I, Euclidean distance matrix analysis, and related tech-

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niques associated with the form difference matrix. Lele & Richtsmeier (1992) determined the influence of a landmark in form difference analysis EDMA-I by deleting the landmark to determine the effect on shape. A delete-one approach is not as directly applicable to Kendall's Procrustes analysis because landmark deletion also affects location, scale and orientation adjustments, which are used to define the Procrustes metric. Thus configurations with deleted landmarks must be similarity-adjusted. It follows that k landmarks are not commensurate with those for $k-1$ landmarks. The graphical tool proposed in Cole & Richtsmeier (1998) has similar goals to our method. However, it differs in being graphical rather than quantitative in nature. The properties of our weight function, as displayed in Theorem 4 below, provide much of the motivation for its use.

2. Preliminary definitions and constructions

Suppose that z and w are two configurations with k labelled vertices in the plane and write $[z]$ and $[w]$ for the shapes of z and w, respectively. As usual, we represent a configuration in $\mathbb{R}^2$ by a k-dimensional complex column vector $z=(z_1, \ldots, z_k)^{\mathrm{T}}$, where $z_1, \ldots, z_k$ are the k labelled vertices. Where needed, we shall represent the complex conjugate of a landmark coordinate z_j by z_j^*. We shall also let z^* represent the complex conjugate of the transpose of z, so that the usual Hermitian inner product between such vectors can be denoted by $w^*z=\sum_{j=1}^{k} z_j w_j^*$ and the norm of a vector z of landmark coordinates is determined by $\|z\|^2=z^*z$. Finally, let 1_k denote the vector $(1, \ldots, 1)^{\mathrm{T}} \in \mathbb{C}^k$ whose entries are all one.

To keep separate the contribution of the individual vertex of the configuration z in the properties that we are interested in, we standardise with respect to translation by moving configurations so that their centroids are at the origin. Then the resulting quotient space is

$$\mathbb{P}=\left\{z \in \mathbb{C}^k : \sum_{j=1}^{k} z_j=0\right\}.$$

Kendall's pre-shape sphere is isometric with the sphere in $\mathbb{P}$, and so the shape space with the quotient in this sphere by $SO(2)$. Thus, in particular, if $z=(z_1, \ldots, z_k)^{\mathrm{T}}$ and $w=(w_1, \ldots, w_k)^{\mathrm{T}}$ are two configurations with centroids at the origin, then the geodesic distance $\rho([z],[w]) \in [0, \pi/2]$ between two shapes $[z]$ and $[w]$ is determined by the equation

$$\cos \rho([z],[w])=\frac{|w^*z|}{\|z\|\,\|w\|}.$$

A 'horizontal' lift to the sphere in $\mathbb{P}$ of a geodesic from $[z]$ to $[w]$ is

$$\Gamma(s)=\frac{1}{\sin s_0}\left\{\frac{z}{\|z\|}\sin(s_0-s)+e^{-i\theta}\frac{w}{\|w\|}\sin s\right\} \quad (0 \leqslant s \leqslant s_0), \tag{1}$$

where $s_0=\rho([z],[w])$ and $\theta \in [0, 2\pi)$ is defined so as to satisfy $\Im\{e^{i\theta}(w^*z)\}=0$ and $\Re\{e^{i\theta}(w^*z)\} \geqslant 0$, in which $\Im(.)$ and $\Re(.)$ denote the imaginary and real parts of a complex number respectively. For the proof of this, see Small (1996) or Kendall et al. (1999, Ch. 6). Differentiating with respect to s, we see that the jth component v_j of the initial tangent vector $v=\Gamma'(0)$ to the curve Γ at $\Gamma(0)$ is

$$v_j=\frac{1}{\sin s_0}\left(e^{-i\theta}\frac{w_j}{\|w\|}-\frac{z_j}{\|z\|}\cos s_0\right). \tag{2}$$

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3. Methods and analysis

Suppose that z and w are two given configurations of k planar landmarks each. We standardise these two configurations so that $z^*1_k = w^*1_k = 0$ and $\|z\| = \|w\| = 1$. We wish to determine the importance or influence of a given landmark of z on the variation in shape between $[z]$ and $[w]$.

Let $e_j = (0, \ldots, 1, \ldots, 0)^{\mathrm{T}}$ be the vector with k entries, all zero except for the entry 1 in the jth position. Consider configurations $z' = z + \varepsilon e_j$, for $\varepsilon \in \mathbb{C}$, in a neighbourhood of z, which differ only in the position of the jth landmark. Such configurations no longer lie in the subspace $\mathbb{P}$, and so we translate z' so that the centroid becomes 0 to obtain $z^\varepsilon = z + \varepsilon e_j - (\varepsilon/k)1_k$. We are now in a position to define the weight function on each landmark.

Definition 1. *Let z and w be two configurations of k planar landmarks whose landmarks are labelled correspondingly. As a measure of the relative importance of the jth landmark in the shape transition from z to w, we define, for $j = 1, \ldots, k$, the weight function*

$$\mathscr{W}([z], [w], j) = \lim_{r \to 0^+} \max_{|\varepsilon| = r} \frac{\rho([z], [w]) - \rho([z^\varepsilon], [w])}{\rho([z], [z^\varepsilon])}. \tag{3}$$

Note that, if ρ is replaced by a monotone increasing function of ρ, such as one of the other commonly used Procrustes shape distances $\sin(\rho)$ and $2\sin(\rho/2)$, the effect on the landmark weights is to multiply each by a constant which depends only on the function and on the two shapes concerned, but is independent of the landmark label. This means that a change of function or metric does not change the ratio of any two landmark weights. In particular, ρ is the only metric which always assigns to a landmark the natural weight of one when the shape variation can be fully explained by perturbing that landmark alone.

To evaluate (3), we first note that $\|z^\varepsilon\|^2 = 1 + z_j\varepsilon^* + z_j^*\varepsilon + |\varepsilon|^2(1 - 1/k)$, so that

$$\frac{w^* z^\varepsilon}{\|z^\varepsilon\|} = w^*z + \delta_1 + O(r^2),$$

where $\delta_1 = \varepsilon w_j^* - (w^*z)\Re(z_j\varepsilon^*)$, which is linear in r. This gives

$$|w^*z + \delta_1 + O(r^2)| = |w^*z| + \delta_2 + O(r^2),$$

where $\delta_2 = \Re\{(w^*z)\delta_1^*\}/|w^*z|$. Therefore, since $\|z\| = \|w\| = 1$, we have

$$\begin{aligned}\rho([z^\varepsilon], [w]) - \rho([z], [w]) &= \cos^{-1}|w^*z + \delta_2 + O(r^2)| - \cos^{-1}|w^*z| \\ &= -\frac{\delta_2}{\surd(1 - |w^*z|^2)} + O(r^2). \end{aligned} \tag{4}$$

Similarly, since

$$\left|\frac{z^* z^\varepsilon}{\|z^\varepsilon\|}\right|^2 = 1 - (1 - 1/k - |z_j|^2)r^2 + O(r^3)$$

and since $\cos^{-1}\surd(1 - cx^2 + dx^3) = \surd cx + O(x^2)$, we have

$$\rho([z], [z^\varepsilon]) = r\surd(1 - 1/k - |z_j|^2) + O(r^2). \tag{5}$$

The ratio of numerator and denominator expansions in (4) and (5) gives

$$\mathscr{W}([z], [w], j) = \max_{|\varepsilon| = 1} \frac{\delta_2}{\surd\{(1 - |w^*z|^2)(1 - 1/k - |z_j|^2)\}}.$$

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The denominator of this expression does not depend on ε and so, to maximise the numerator, we must maximise $\Re\{(z^*w)\delta_1\}$ as a function of ε. However, the real part of $(z^*w)\delta_1$ is the same as the real part of $\varepsilon\{(z^*w)w_j^* - |w^*z|^2 z_j^*\}$. Since ε is a unit vector, the maximum of the real part is simply $|w^*z|\,|w_j-(z^*w)z_j|$, achieved when

$$\varepsilon = \frac{(w^*z)w_j - |w^*z|^2 z_j}{|w^*z|\,|w_j-(z^*w)z_j|}. \tag{6}$$

Therefore, we obtain the following result.

Theorem 2. *Let z and w be two configurations of k planar landmarks standardised so that $z^*1_k = w^*1_k = 0$ and $\|z\| = \|w\| = 1$. The weight function on the jth landmark is given by*

$$\mathscr{W}([z],[w],j) = \frac{|w_j - (z^*w)z_j|}{\surd\{(1-|w^*z|^2)(1-1/k-|z_j|^2)\}}. \tag{7}$$

Note that (6) gives the direction of movement of the jth landmark required to achieve this influence on the variation between $[z]$ and $[w]$.

We can also obtain a representation of the weight function $\mathscr{W}([z],[w],j)$ in terms of the horizontal lift Γ of the geodesic path from $[z]$ to $[w]$ as given in (1). We remind the reader that we shall continue to assume that $z^*1_k = w^*1_k = 0$ and $\|z\| = \|w\| = 1$.

Theorem 3. *The weight function can be expressed as*

$$\mathscr{W}([z],[w],j) = |v_j|\,\frac{1}{\surd(1-1/k-|z_j|^2)}, \tag{8}$$

where v_j is the jth component of $v = \Gamma'(0)$ given by (2).

To prove this, we compare (7) and (8). It suffices to prove that

$$|v_j| = \frac{|w_j-(z^*w)z_j|}{\surd(1-|w^*z|^2)},$$

which can be checked by plugging into equation (2).

Note that the factor $(1-1/k-|z_j|^2)^{-\frac{1}{2}}$ on the right-hand sides of (7) and (8) reflects the influence of the jth vertex of the 'standardised' configuration on the change of shape when only that vertex moves. It is this factor that makes $\sum_{j=1}^k \mathscr{W}([z],[w],j)^2 > 1$, since $\sum_{j=1}^k v_j^2 = 1$. We also note that the asymmetry is as one should expect: a given increment Δz_j makes a bigger contribution to the change in shape when $|z_j|$ is small than when $|z_j|$ is large. Hence, in the latter case, it requires a bigger weight to account for a given change in shape. Since the factor $|v_j|$ remains the same when the first two variables of $\mathscr{W}$ interchange, this is precisely the direction of asymmetry of $\mathscr{W}$.

Theorem 4. *The weight function has the following basic properties*:

(i) $0 \leqslant \mathscr{W}([z],[w],j) \leqslant 1$;

(ii) $\sum_{j=1}^k \mathscr{W}([z],[w],j)^2 \geqslant k/(k-1)$;

(iii) *if $k=3$, that is if z and w are both triangles on the plane, then*

$$\mathscr{W}([z],[w],j) \equiv 1;$$

(iv) *if two configurations of landmarks differ in shape by only one landmark, then the weight on that landmark is equal to one*;

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(v) $\mathscr{W}([z],[w],j)=\mathscr{W}([w],[z],j)$ *if and only if either* $\mathscr{W}([z],[w],j)=1$ *or* $|z_j|=|w_j|$.

Proof. (i) The lower bound is clear from either Theorem 2 or Theorem 3 and the upper bound follows from the triangle inequality $\rho([z],[w])\leqslant\rho([z],[z^\varepsilon])+\rho([z^\varepsilon],[w])$.

(ii) This follows from Theorem 3 and the fact that $\sum_{j=1}^{k}|v_j|^2=1$.

(iii) As the shape of any nondegenerate triangle can be obtained from any other non-degenerate triangle by moving a single vertex or landmark, it follows that, if we perturb the chosen jth landmark appropriately, we can always move $[z^\varepsilon]$ along the geodesic from $[w]$ to $[z]$. In doing so, we have $\rho([z],[w])=\rho([z],[z^\varepsilon])+\rho([z^\varepsilon],[w])$ and, by (i), this implies that $\mathscr{W}([z],[w],j)=1$.

(iv) Similarly to the proof of (iii), this is equivalent to showing that, in such a situation, the remaining $k-1$ landmarks do not change shape as one moves along the geodesic from one shape to the other. The latter is equivalent to showing that, in such a situation, the remaining $k-1$ landmarks do not change shape as one moves along a horizontal lift of the geodesic from one shape to the other. To see this, we may without loss of generality assume that $j=k$, that $w=z+ce_k$, where $c\in\mathbb{C}$, and that $z^*1_k=0$ and $\|z\|=1$. Translating w so that its centroid becomes zero maps w to $z+ce_k-(c/k)1_k$, which we still denote by w. Then, by (1), the configuration, formed by the first $k-1$ landmarks, at s on such a horizontal geodesic can be expressed as

$$\frac{1}{\sin s_0}\left[\left\{\sin(s_0-s)+\frac{e^{-i\theta}\sin s}{\|w\|}\right\}(z_1,\ldots,z_{k-1})^{\mathrm{T}}-\frac{e^{-i\theta}\sin s}{\|w\|}\frac{c}{k}(1,\ldots,1)^{\mathrm{T}}\right].$$

Clearly, the second term in the square brackets contributes only to the effect of translation and the coefficient of $(z_1,\ldots,z_{k-1})^{\mathrm{T}}$ contributes only to the size of the configuration. This implies that the shape of this configuration always remains the same as that of $(z_1,\ldots,z_{k-1})^{\mathrm{T}}$, as required.

(v) Suppose that $\mathscr{W}([z],[w],j)=\alpha$. Then the expression for $\mathscr{W}([z],[w],j)$ given by Theorem 2 implies that

$$-\{z_j^*w_j(w^*z)+z_jw_j^*(z^*w)\}=\alpha^2\left\{\left(1-\frac{1}{k}\right)(1-|w^*z|^2)-|z_j|^2\right\}$$
$$+(\alpha^2-1)|z_j|^2|w^*z|^2-|w_j|^2.$$

This, in turn, gives that

$$|z_j-(w^*z)w_j|^2=\alpha^2\left(1-\frac{1}{k}-|w_j|^2\right)(1-|w^*z|^2)+(1+\alpha^2)(1-|w^*z|^2)(|z_j|^2-|w_j|^2)$$

and then, again by Theorem 2,

$$\mathscr{W}([w],[z],j)^2=\frac{|z_j-(w^*z)w_j|^2}{(1-1/k-|w_j|^2)(1-|w^*z|^2)}=\alpha^2+\frac{(1-\alpha^2)(1-|w^*z|^2)(|z_j|^2-|w_j|^2)}{(1-1/k-|w_j|^2)(1-|w^*z|^2)}$$

so that the required result follows. □

Note that the converse of (iv) is not true, as is shown by the following counterexample. Take $k=4$ and let $z=(i/2,\frac{1}{2},-i/2,-\frac{1}{2})^{\mathrm{T}}$. Then $\sum z_j=0$, $\|z\|^2=\sum|z_j|^2=1$ and $|z_4|=\frac{1}{2}$. Consider the configuration

$$w=\frac{1}{2\sqrt{(26)}}(-i,1,5-4i,-6+5i)^{\mathrm{T}}.$$

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Then $\sum w_j = 0$ and $\|w\|^2 = \sum |w_j|^2 = 1$. Clearly, the shape of w cannot be obtained from that of z by changing just the fourth vertex of z. By Theorem 3, the weighting function associated with the shapes of z and w and with the fourth vertex of z is equal to

$$\frac{|v_4|}{\sqrt{(1 - 1/k - |z_4|^2)}},$$

where

$$v_4 = \frac{1}{\sin s_0}(e^{-i\theta} w_4 - z_4 \cos s_0),$$

in which s_0 is the Riemannian distance between the shapes of z and w and $\theta \in [0, 2\pi)$ is defined to satisfy $e^{i\theta} w^* z \geqslant 0$. Since $w^* z = 3/\sqrt{(26)}$, we have $\theta = 0$ and $\cos s_0 = 3/\sqrt{(26)}$. Hence, $\sin s_0 = \sqrt{(17/26)}$ and

$$|v_4|^2 = \frac{26}{17}|w_4 - z_4 \cos s_0|^2 = \frac{26}{17}\left| -\frac{3}{\sqrt{(26)}} + i\frac{5}{2\sqrt{(26)}} + \frac{3}{2\sqrt{(26)}} \right|^2 = \frac{1}{2}.$$

However, with $k = 4$, we have $1 - 1/k - |z_4|^2 = \frac{1}{2}$. Thus, the value of this weight function is equal to one.

4. Applications to the gorilla data

Our data concern the fifth cervical vertebrae of two groups of female gorillas, described in detail in an unpublished 1999 University of Pittsburgh Ph.D. thesis by S. R. Mercer. Seven vertebrae were obtained from *Gorilla gorilla berengei* and ten from *Gorilla gorilla gorilla*. From each vertebra, seven landmarks were selected as indicated above. The landmark coordinates for the data can be found at

`http://www.stats.uwaterloo.ca/~cgsmall/gorillas/landmarks.txt.`

Before undertaking an analysis of the influence of each landmark on the variation between the species, we first determine whether or not there is any statistically significant difference at all between the shapes corresponding to the two species. Let $\mathscr{A}$ represent the collection of seven landmark configurations for *Gorilla gorilla berengei*, and $\mathscr{B}$ the collection of ten configurations for *Gorilla gorilla gorilla*. By analogy with common two-sample tests, we shall find 'average' shapes $[\bar{z}]$ and $[\bar{w}]$ in $\mathscr{A}$ and $\mathscr{B}$ respectively and use the distance

$$T = \rho([\bar{z}], [\bar{w}]) \tag{9}$$

between the average shapes as a test statistic. It will be convenient to average samples of shapes using the full Procrustes mean as described in Dryden & Mardia (1998, § 3.3). Suppose $z_1, \ldots, z_n$ is a sample of n pre-shapes. Once again, each z_j is standardised to be a k-dimensional complex row vector with $z_j^* 1_k = 0$ and $\|z_j\| = 1$. The complex sums of squares and products matrix is $S = \sum_{j=1}^n z_j z_j^*$. The full Procrustes mean is an eigenvector corresponding to the largest eigenvalue of S.

If we choose to use the test statistic T in (9), then the next task is to calculate a null distribution for T under the assumption that $\mathscr{A}$ and $\mathscr{B}$ come from the same model. In the interests of model robustness, we ran a permutation test on the test statistic T. The entire sample $\mathscr{S} = \mathscr{A} \cup \mathscr{B}$ was partitioned randomly into two groups $\mathscr{A}'$ and $\mathscr{B}'$, where

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$\mathscr{A}'$ and $\mathscr{B}'$ were of the same cardinality as $\mathscr{A}$ and $\mathscr{B}$ respectively. For each such random partition we computed the full Procrustes averages $[\bar{z}']$ and $[\bar{w}']$ and the statistic $T' = \rho([\bar{z}'], [\bar{w}'])$. This computation was repeated over a large number of independently chosen random partitions. Finally, the rank of the actual intergroup distance T among those computed using random partitions was determined. Of interest is the p-value of the test statistic under this randomisation test, namely the proportion of times that the random statistic T' is greater than the value of T. In the case of the gorilla data, over 10 000 random partitions of the data, the actual intergroup distance T was greater than the random intergroup distance T' on 9993 of the trials.

Since we can conclude that the *Gorilla gorilla berengei* and *Gorilla gorilla gorilla* samples have significantly different shapes, the next task is to determine what contribution each landmark might provide to the observed differences in shape. Table 1 shows the landmark weights from formula (7) for the full Procrustes means of each group. It can be seen that the weights do not vary greatly with the direction in which they are computed. This is a consequence of the relatively small dispersion of the full dataset in the shape manifold $\mathbb{CP}^5(4)$. In order to assess the degree of uncertainty in the assignment of these weights, a nonparametric bootstrap analysis was performed. Seven configurations were chosen at random with replacement from the seven *Gorilla gorilla berengei* configurations to form a bootstrap sample, and ten were chosen with replacement from the *Gorilla gorilla gorilla* configurations to form another bootstrap sample. Under repeated bootstrap trials, the full Procrustes means of each of the bootstrap samples were computed, and the landmark weights in both directions were found. The results are given in Table 1.

Table 1. *Weights assigned to individual landmarks in the gorilla data in Fig.* 1(*a*) *using the full Procrustes means. First column indicates the direction of the comparison, with* $\mathscr{A}$ *representing the sample of landmarks for Gorilla gorilla berengei, and* $\mathscr{B}$ *that for Gorilla gorilla gorilla. Remaining columns are the weights assigned to each landmark using formula* (7). *The standard deviations of the bootstrap distributions of these weights are given in parentheses below each weight. The means of these bootstrap distributions are not given because they were not significantly different from the recorded sample values.*

	AVB	PVB	DVB	ASP	PSP	AT	PT
$\mathscr{A}\mathscr{B}$	0·5282	0·2171	0·2533	0·1896	0·8279	0·3583	0·7114
	(0·0398)	(0·0601)	(0·0451)	(0·0791)	(0·0703)	(0·1095)	(0·0874)
$\mathscr{B}\mathscr{A}$	0·5409	0·2220	0·2632	0·1981	0·7995	0·3647	0·7117
	(0·0342)	(0·0671)	(0·0487)	(0·0824)	(0·0641)	(0·1136)	(0·0956)

The motivation for studying this dataset was to consider whether or not there have been significant adaptations in the bony morphology of the upright spine to differing positional behaviours in non-human primates. Our conclusions about landmark influence can be interpreted in terms of the differing mechanical demands placed on the cervical spine by different behaviours. The principal feature in Table 1 is the relatively large weight attached to the landmarks PSP, PT and AVB. In *Gorilla gorilla gorilla* the relative length of the spinous process compared to the size of the vertebral body is greater than that in *Gorilla gorilla berengei*, and the posterior tubercle is, relatively, extended, and is rotated anteriorly. These observations are consonant with common-sense mechanical interpret-

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ations of the demands placed on the vertebrae through the differing positional behaviours of the two species.

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[*Received April* 2002. *Revised January* 2003]