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Near-isometric flattening of brain surfaces

Mukund Balasubramanian^{*,1}, Jonathan R. Polimeni², and Eric L. Schwartz^{1,3,4}

¹Department of Cognitive and Neural Systems, Boston University

²Department of Radiology, MGH, Athinoula A. Martinos Center for Biomedical Imaging, Harvard Medical School

³Department of Electrical and Computer Engineering, Boston University

⁴Department of Anatomy and Neurobiology, Boston University School of Medicine

Abstract

Flattened representations of brain surfaces are often used to visualize and analyze spatial patterns of structural organization and functional activity. Here, we present a set of rigorous criteria and accompanying test cases with which to evaluate flattening algorithms that attempt to preserve shortest-path distances on the original surface. We also introduce a novel flattening algorithm that is the first to satisfy all of these criteria and demonstrate its ability to produce accurate flat maps of human and macaque visual cortex. Using this algorithm, we have recently obtained results showing a remarkable, unexpected degree of consistency in the shape and topographic structure of visual cortical areas within humans and macaques, as well as between these two species.

1 Introduction

Brain-imaging modalities, such as MRI, PET and optical recording, have made it possible to directly observe and measure spatial patterns of functional activity that are naturally embedded in the folded cortical surface, e.g., topographic maps (Schwartz et al., 1984; Engel et al., 1994; Sereno et al., 1995; Lauter et al., 1985; Talavage et al., 2004; Meier et al., 2008), as well as spatial patterns of structural organization, e.g., cell density or myelination (Fatterpekar et al., 2002; Eickhoff et al., 2005; Duyn et al., 2007). These spatial patterns are often displayed on flattened representations of cortical surfaces, and several algorithms for constructing these flat maps have been introduced in the last few decades.

For the qualitative *observation* of surface patterns, many flattening algorithms are adequate, as long as they preserve the *topological* structure of the input surface (i.e., neighborhood relationships are maintained). For the quantitative *measurement* of surface patterns, it is important that the flattening also preserve the *geometric* structure of the input surface, to the extent possible. There is a lack of general agreement, however, as to which aspects of the geometric structure should be preserved, with some researchers emphasizing the preservation of distances (Merker and Schwartz, 1985; Schwartz et al., 1989; Fischl et al., 1999a; Wandell et al., 2000; Zigelman et al., 2002), some the preservation of angles (Angenent et al., 1999; Hurdal and Stephenson, 2004; Gu et al., 2004) or areas (Zhu et al., 2005; Chiu et al., 2008), and others attempting to preserve some combination of these

*corresponding author: 677 Beacon Street, Boston, MA 02215, 617-353-9481, 617-353-7755 (fax), mukundb@cns.bu.edu.

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geometric features (Carman et al., 1995; Drury et al., 1996; Goebel, 2000; Timsari and Leahy, 2000; Ju et al., 2005). Even when there is agreement, there is often a substantial difference in the way the relevant geometric quantities (e.g., distance) are computed, and in the accuracy of the computation, which is often left unspecified.

Consequently, flat maps can appear very different from one study to the next, even when the same cortical area is under investigation. This is illustrated in Figure 1, which shows flattened representations of human visual cortex from four recent neuroimaging studies—note in particular the high degree of variability in the shape and topographic structure of visual areas V1 and V2. Although each flat map shown in Figure 1 is from a different subject, it is unlikely that the differences seen in this figure reflect true differences between subjects: in recent work, it has been shown that even when the same cortical surface is given as the input to various commonly-used flattening methods, very different flat maps are returned as output (see Balasubramanian et al., 2006, and supplemental Figures S-5 to S-23). This variability due to flattening methodology compromises the comparison of results across different studies and is likely to obscure any regularity in the spatial patterns of structure and function within and across species.

In order to address this problem, we make the following contributions in this report: (i) we propose a set of basic criteria for accuracy and consistency that any distance-preserving flattening must satisfy, providing a standardized test bed with which any given flattening algorithm can be evaluated; (ii) we present the *DMflatten* algorithm, a novel flattening method that minimizes a measure of metric distortion based on exact, global shortest-path distances (Balasubramanian et al., 2009); and (iii) we demonstrate that the *DMflatten* algorithm satisfies the basic criteria for quantitative flattening and present accurate flat maps of human and macaque visual cortex.

Using the *DMflatten* algorithm, we have recently obtained results showing a remarkable, unexpected degree of consistency in the shape (Hinds et al., 2008) and visuotopic structure (Polimeni et al., 2005) of primary visual cortex within humans and macaques, as well as between these two species. A careful and rigorous approach to flattening may also reveal regularity in other brain areas which are currently thought to be highly variable, and will be important for studying the relationship between the geometric features of cortical areas and their underlying structural and functional organization.

Although the examples of brain surfaces shown in this report are taken from studies of visual cortex, the *DMflatten* algorithm and the ideas presented here are not limited to visual cortex and can be applied to a variety of cortical and subcortical surfaces, and even to non-neural and non-biological surfaces. Applications for accurately flattening such general surfaces include texture mapping in computer graphics (e.g., Zigelman et al., 2002) and dimensionality reduction in nonlinear data analysis (e.g., Tenenbaum et al., 2000).

2 Methods

2.1 Criteria for near-isometric flattening

An *isometric* mapping of a surface exactly preserves all aspects of its *intrinsic geometry*, including shortest-path distances on the surface, as well as angles and areas. Gauss's Theorem Egregium states that Gaussian curvature is also intrinsic (do Carmo, 1976)—consequently, it is impossible to isometrically map surfaces with non-zero Gaussian curvature to the Euclidean plane, which has zero Gaussian curvature.

We use the term *near-isometry* to mean a mapping that *maximally* preserves shortest-path distances (Bronstein et al., 2006). Unfortunately, neither theory nor intuition tells us what

near-isometric flat maps of complicated and convoluted surfaces (such as cerebral cortex) ought to look like, making it difficult to evaluate the quality of a given flat map (e.g., see Figure 1). There are, however, simpler surfaces for which the near-isometric flat map is known from theory and we can, at the very least, require that any near-isometric flattening algorithm correctly flatten these simple surfaces. Additional requirements of stability, reproducibility, continuity and invertibility lead us to a set of basic criteria that any near-isometric flattening algorithm must satisfy. These criteria are listed below, followed by a detailed description.

A near-isometric flattening algorithm must

- (C1) produce the identity mapping when the input is flat;
- (C2) be insensitive to small perturbations to the input;
- (C3) correctly flatten surfaces with zero Gaussian curvature;
- (C4) compute a homeomorphism;
- (C5) produce flat maps that are mesh-independent; and
- (C6) correctly flatten spherical caps.

Although it may seem trivial to require that a flattening algorithm produce the identity mapping (up to a rigid-body transformation) when the input surface is already flat (criterion C1), many of the algorithms currently in use fail to satisfy this requirement (see supplemental Figure S-6 and Balasubramanian et al., 2006). One reason for this is the widespread use of approximate (rather than exact) shortest-path distances—when the input surface is flat and convex, the discrepancy between these approximate distances and the true, Euclidean distances introduces errors into a distance-preserving flattening procedure. When the input surface is flat and *non-convex*, there is often an additional source of error due to the fact that exact shortest-path distances will not always be equal to Euclidean distances, as illustrated in Figure 2.

One might be tempted to modify an existing flattening algorithm to comply with criterion C1 simply by introducing the following rule: if the input surface is already flat, set the output equal to the input; otherwise, execute the original flattening algorithm. Since a tiny perturbation can convert a flat surface into one that is not flat, heuristics such as this will violate criterion C2, which requires that small perturbations to the input produce small changes to the output—a basic property of any stable algorithm.

Criterion C3 is based on the fact that surfaces that have zero Gaussian curvature everywhere (and are topological disks), such as hemicylinders and swiss rolls (Tenenbaum et al., 2000; Balasubramanian and Schwartz, 2002), can be mapped isometrically to the plane (do Carmo, 1976). Note that C1 is a special case of this criterion.

A *homeomorphism* is a mapping that is continuous and invertible (Frankel, 1999). A flattening algorithm that computes a homeomorphism (criterion C4) cannot produce a flat map that folds over on itself anywhere, since a point on such a flat map could correspond to multiple points on the input surface, resulting in a non-invertible mapping. When a polyhedral surface (i.e., a piecewise-flat approximation to a surface of interest) is the input to a flattening algorithm, folds in the flat map result in *edge-crossings*, as shown in Figure 3. Since polygons can easily be decomposed into triangles (Garey et al., 1978; Tarjan and Wyk, 1988), it shall henceforth be assumed that any polyhedral surface has been converted into a triangular mesh, without loss of generality.

A given surface can be approximated by many different triangular meshes. This can result from the application of different mesh-reconstruction techniques (e.g., Fuchs et al., 1977; Hinds et al., 2006; Lorensen and Cline, 1987; Fischl et al., 2001) to the same data, or from reconstructions based on scan-rescan data, or from refining (e.g., Shiue and Peters, 2005) or simplifying (e.g., Garland and Heckbert, 1997) an initial mesh. The result of a surface computation should not, however, be dependent on the particular mesh chosen for the computation. For example, surface-area calculations based on two different meshes should be in agreement, assuming that both meshes represent the underlying surface equally well. This requirement of *mesh independence* (criterion C5) means that flat maps of different meshes representing the same surface should be nearly identical—a requirement of reproducibility that most current flattening algorithms fail to meet (see Figure 4 and supplemental Figures S-13 to S-17).

A *spherical cap* (i.e., a subset of the sphere with a circular boundary) is one of the few surfaces with non-zero Gaussian curvature for which theoretical results on near-isometric flattening are available (Milnor, 1969; Pearson, 1982). Any near-isometric flattening algorithm must therefore produce flat maps that are consistent with these results (criterion C6). In particular, when shortest-path distances on spherical caps are to be preserved in a least-squares sense, the algorithm must produce flat maps that closely approximate Lambert's equal-area projection, which is near-optimal (Pearson, 1982).

The list of criteria presented here is by no means comprehensive. One could also require that a flattening algorithm be deterministic, producing exactly the same output when reapplied to the same input mesh, and that it have no free parameters that are manually adjusted depending on the input. Additionally, one could require that the algorithm report a quantitative measure of flattening error as a function of position, thus providing the user (or subsequent algorithms) with information about the regions of the flat map with the most distortion, where any results might need to be interpreted with greater caution.

In this report, however, we focus on the six criteria enumerated above, for the following reasons: (i) other than the DMflatten algorithm, which we present next, we are not aware of any flattening algorithms that satisfy even these basic requirements, as shown in supplemental Figures S-5 to S-20 and Balasubramanian et al. (2006), and (ii) each criterion can be associated with a simple test surface with which any given flattening method can be evaluated.

2.2 The DMflatten algorithm

The DMflatten algorithm is based on earlier work by Schwartz et al. (1989) on flattening surfaces represented by triangular meshes. Like the Schwartz89 algorithm, the DMflatten algorithm operates in two distinct stages: in the first stage, shortest-path distances along the surface are computed between every pair of mesh vertices; and in the second stage, the algorithm computes the planar configuration of the vertices that minimizes the discrepancy between shortest-path distances on the input surface and the corresponding Euclidean distances on the flat map (i.e., the flattening error). Many other flattening algorithms follow this basic two-stage strategy (e.g., Fischl et al., 1999a; Wandell et al., 2000; Zigelman et al., 2002), but differ in the method of computing distances and in the way flattening error is quantified. However, the Schwartz89 algorithm and its variants all fail to satisfy the basic criteria proposed in Section 2.1 (see supplemental Figures S-5 to S-20). In order to meet these requirements, several modifications are necessary—in this section, we present the details of the DMflatten algorithm, which incorporates these modifications, and in Section 3, we demonstrate that this algorithm does in fact satisfy the basic criteria for near-isometric flattening.

Before applying the DMflatten algorithm, we must verify that the input mesh has the appropriate topology for flattening: if the mesh is non-manifold (Edelsbrunner, 2001) or is closed (i.e., has no boundaries) or has one or more handles, it cannot be flattened without introducing folds, violating the homeomorphic criterion C4. Therefore, we only proceed to the first stage of the DMflatten algorithm if the input mesh is manifold, has at least one boundary, and has no handles (i.e., zero genus); otherwise, the procedure issues an error and terminates.

For the first stage of DMflatten, we use the *LOS-Floyd* algorithm—a recently developed algorithm for computing exact shortest-path distances on triangular meshes (Balasubramanian et al., 2009). The LOS-Floyd algorithm, which has cubic run-time performance, is practical for meshes containing tens of thousands of vertices and has been carefully validated on surfaces for which the correct solutions are known. To solve the problem illustrated in Figure 2, we discard distances corresponding to any shortest path whose interior intersects the surface boundaries (Balasubramanian et al., 2005; Bronstein et al., 2006), since it is the attempt to match these distances to planar Euclidean distances that distorts any (geodesically) non-convex input surface.

The second stage of the DMflatten algorithm involves formulating an error function that quantifies the amount of metric distortion associated with any given flat map, constructing an initial flat map, and then executing an optimization routine that adjusts the positions of the flattened vertices in order to minimize the error. The flattening error (as a percentage) is given by

$$E = 100 \sqrt{\frac{\sum_i \sum_j A_i A_j \left(\frac{d_{ij} - \delta_{ij}}{\delta_{ij}} \right)^2}{\sum_i \sum_j A_i A_j}},$$

where i and j are vertices connected by a shortest path on the input surface that does not intersect any boundary, δ_{ij} is the length of this shortest path, d_{ij} is the corresponding Euclidean distance in the flat map, and A_i and A_j are estimates of the Voronoi areas of vertices i and j , respectively, on the input surface. The Voronoi-area estimates are computed by the method of Meyer et al. (2003) and are introduced as weights in the error function in order to compensate for any non-uniformity in the spacing of vertices on the input surface, resulting in a flattening error (and therefore a flat map) that is mesh-independent, as demonstrated in Section 3. Note that a simple modification of the equation above yields the flattening error associated with vertex i , by only summing over j :

$$E_i = 100 \sqrt{\frac{\sum_j A_j \left(\frac{d_{ij} - \delta_{ij}}{\delta_{ij}} \right)^2}{\sum_j A_j}}.$$

To construct an initial flat map that serves as a starting point for the optimization, we use Tutte's algorithm for graph drawing (Tutte, 1963). Vertices on the largest boundary of the input mesh are spaced uniformly on a circle chosen to enclose an area that equals the surface area of the input mesh. Tutte's algorithm then calculates the positions of the remaining vertices such that each of these vertices lies inside the circle and at the centroid of its neighbors (see Figure 5(b)). The flat map generated by this procedure will be free of edge-crossings (Tutte, 1963; Floater, 1997; Gortler et al., 2006).

Given the error function E and the initial flat map provided by Tutte's algorithm, the final step is to adjust the positions of the flattened vertices in order to minimize E . Since E is differentiable with respect to the (Cartesian) coordinates of the flattened vertices, gradient-based optimization techniques (Press et al., 1988) can be used to compute the optimal flat map. We use gradient descent with momentum (Hertz et al., 1991), along with the following constraint: any vertex update that introduces an edge-crossing is discarded (Wandell et al., 2000). Since the initial flat map has no edge-crossings, this constraint guarantees that each iteration of the optimization will produce a flat map without edge-crossings. The optimization routine terminates when an iteration results in a decrease of E that falls below a small threshold, indicating that the routine has converged. The resulting flat map is the output of the DMflatten algorithm. (Further algorithmic details are given in supplemental Figures S-24 to S-26.)

The DMflatten algorithm has a total of three parameters: the gradient-descent step size β , the momentum weighting α , and the error-decrement threshold ΔE_{thresh} . We emphasize that these are not free parameters that need to be adjusted for each input surface—all of the results shown in this paper were obtained with fixed values of $\beta = 0.5$, $\alpha = 0.9$, and $\Delta E_{\text{thresh}} = 10^{-6}$. There is nothing special, however, about these particular parameter values: since these parameters only influence the number of iterations required to reach the minimum of the error function E , a slightly different choice of parameter values will not have a significant effect on the resulting flat map, but may alter the run time (which depends on the number of iterations), as shown in supplemental Tables S-1 to S-3. In other words, the output of the DMflatten algorithm is not sensitive to the choice of parameter values.

3 Results

In this section, we present a set of input surfaces (available as supplemental material) that were designed to test any near-isometric flattening algorithm against the criteria proposed in Section 2.1. We show the result of applying the DMflatten algorithm to these test surfaces, demonstrating that the algorithm does in fact satisfy the requisite criteria. We also show the result of applying the DMflatten algorithm to surface reconstructions of V1 in macaque and human, demonstrating that these surfaces can be flattened without introducing much distortion.

Figure 5(a) shows the test surface chosen to verify criterion C1, which requires that a flattening algorithm produce the identity mapping when the input is flat. Given this test surface as the input to the DMflatten algorithm, Figure 5(b) shows the initial flat map prior to the optimization step and Figure 5(c) shows an intermediate flat map produced by running the optimization routine for a few iterations. When the optimization routine terminates, the result is the output of the DMflatten algorithm, shown in Figure 5(d). The output is identical to the input, demonstrating that criterion C1 has been satisfied.

Figure 6(a) shows the test surface chosen to verify criterion C2, which requires that a flattening algorithm be insensitive to small perturbations to the input. Since this test surface differs only slightly from the surface shown in Figure 5(a), the corresponding flat maps should differ by only a small amount. By comparing Figure 6(b) to Figure 5(d), we see that this is in fact the case for the flat maps produced by the DMflatten algorithm, demonstrating that the algorithm has satisfied criterion C2 (see also supplemental Figure S-4, which shows the effect of adding various levels of random noise).

The hemicylinder (Figure 7(a)) was chosen as the test surface with which to verify criterion C3, which requires the correct, isometric flattening of surfaces with zero Gaussian curvature.

Figure 7(b) shows that, given the hemicylinder as the input, the DMflatten algorithm does indeed produce an isometric flattening.

Surfaces with a small boundary but large surface area pose a great challenge for near-isometric flattening methods, since the preservation of the length of the small boundary conflicts with the preservation of the large distances in the interior. This conflict often leads to the (inadvertent) introduction of folds, in the form of edge-crossings, into the flat map (e.g., see Figure 3). Thus, a surface with a large area relative to its boundary, such as that shown in Figure 8(a), is well-suited to serve as a test case for criterion C4, which requires a valid near-isometric flattening to be homeomorphic. Given this test surface as the input, the DMflatten algorithm produces a flat map with no edge-crossings (Figure 8(b)), demonstrating that criterion C4 has been satisfied.

The cube meshes from Figure 4 were chosen as the test cases for criterion C5, which requires that a near-isometric flattening algorithm produce mesh-independent results: in other words, the flat maps corresponding to different meshes representing the same underlying surface should be nearly identical. The DMflatten algorithm satisfies this criterion, as shown in Figure 9.

The hemisphere was chosen as the test surface with which to verify criterion C6, which requires the correct flattening of spherical caps. The DMflatten algorithm satisfies this criterion, as shown in Figure 10: the output of the algorithm closely matches Lambert's equal area projection, which has been shown to be near-optimal for spherical caps (Pearson, 1982).

The results above demonstrate that the DMflatten algorithm satisfies all of the criteria for near-isometric flattening described in Section 2.1. Criterion C4 is guaranteed to be met, since the initial flat map is free of edge-crossings and any subsequent vertex update that introduces an edge-crossing is discarded. For the remaining criteria, there is no such theoretical guarantee; however, these criteria are met in practice, as shown by the results above.

Figures 11 and 12 show the results of applying the DMflatten algorithm to macaque and human V1 surfaces, respectively, and supplemental Figures S-2 and S-3 demonstrate that these results are not sensitive to different initializations of the DMflatten optimization. Supplemental Figure S-1 shows several more examples of the DMflatten algorithm applied to human V1 surfaces. For both macaque and human V1, the flattening error is low ($E \approx 5\%$), indicating that the metric structure has been preserved well by the flattening, and the flat maps have an approximately elliptical shape with a very consistent aspect ratio, whereas the original, curved V1 surfaces appear very different. Further details on the similarity of the intrinsic shape of V1 in humans and macaques, revealed by use of the DMflatten algorithm, can be found in Hinds et al. (2008).

4 Discussion

4.1 Laminar structures and surface-based methods

A large number of brain areas have a layered, or laminar, anatomical structure, e.g., the hippocampus (archicortex), piriform cortex (paleocortex), and the huge expanse of neocortex with which the term “cortex” is frequently identified. Many of these laminar structures contain one or more topographic maps of a 2-dimensional sensory surface. Examples of such *receptotopic maps* are the projection of the retina to thalamus and visual cortical areas (retinotopic maps), the projection of the skin surface to thalamic and cortical

targets (somatotopic maps), and the projection of the surface of the basilar membrane to auditory cortex (tonotopic maps).

Laminar structures often exhibit *columnar organization*, i.e., a high degree of similarity of some functional property in the “radial” direction, perpendicular to the laminae (Mountcastle, 1997). Examples include ocular dominance columns, orientation columns, and cytochrome oxidase blobs/puffs in V1 (Hubel and Wiesel, 1968; LeVay et al., 1975; Hubel et al., 1977; Hubel and Wiesel, 1977; Horton and Hubel, 1981; Carroll and Wong-Riley, 1984; Horton, 1984); disparity columns in V2 (Clarke et al., 1976; Ts'o et al., 2001); direction columns in MT (Dubner and Zeki, 1971; Albright et al., 1984; Geesaman et al., 1997); modality-specific and place-defined columns in cat somatosensory cortex (Mountcastle, 1957; Favorov and Diamond, 1990); and whisker barrels in rodent somatosensory cortex (Woolsey and Van der Loos, 1970; Brumberg et al., 1988; Lübke and Feldmeyer, 2007). Even when this similarity does not exist or has not been identified, it is often useful to separate the tangential and perpendicular components of laminar data, e.g., when using cell density and myelination to define the architectonic boundaries of cortical areas (Schleicher et al., 1999; Annese et al., 2004; Malikovic et al., 2007). Thus, surface-based methods, which respect laminar structure, are a natural choice for these brain areas.

Brain imaging data, however, is typically represented with voxels, which do not explicitly encode laminar or surface structure. While it is possible to implicitly represent surfaces in a voxel-based analysis (Mémoli et al., 2004), it is more common to explicitly represent the relevant surfaces with triangular meshes (Teo et al., 1997; Dale et al., 1999; Van Essen et al., 2001; Han et al., 2004), which provide a piecewise-flat approximation to laminar or surface data.

4.2 Why flatten near-isometrically?

For certain computations, e.g., distance and surface-area measurements, it is practical to work directly with the surface of interest in its natural embedding in 3-dimensional Euclidean space (i.e., there is no need to flatten). However, many computations are facilitated by mapping the surface to a simpler 2-dimensional manifold, especially when the target manifold comes equipped with a natural and convenient coordinate system, such as 2-dimensional Cartesian coordinates when the target manifold is the plane. Although we have focused on mapping to the plane in this report, the ideas presented here generalize to mappings to other target manifolds—for example, mapping to the sphere, which provides a system of spherical coordinates (Fischl et al., 1999b; Van Essen et al., 2001; Tosun et al., 2004; Kwon et al., 2008). Working with such a system of global coordinates is a far more attractive option than the alternative of working with a collection of local coordinate patches, i.e., an “atlas of charts” (do Carmo, 1976).

Furthermore, target manifolds such as the plane or the sphere come equipped with a natural *metric* (the Euclidean metric or the spherical metric, respectively). Given a near-isometric mapping to the plane, this additional metric structure allows the well-understood mathematical techniques of planar Euclidean geometry and complex analysis to be used for the modeling and measurement of intrinsic spatial patterns of activity or structure within laminar surfaces. For example, the intrinsic shape and topographic structure of human V1 was measured by Hinds et al. (2008) and Polimeni et al. (2005), followed by a statistical analysis of these measurements which revealed a surprisingly low level of inter-subject variability. Although near-isometric flattening has proven to be useful in these studies of inter-subject variability (and, in the case of Hinds et al., 2008, inter-species variability), we emphasize that its applicability is not limited to investigations of variability: even if one only has access to a single data set, a measurement of shape or topographic structure for that individual still has relevance, and benefits from the use of an accurate near-isometric

flattening algorithm such as DMflatten (e.g., see Polimeni et al., 2006, for a measurement of the topographic structure of macaque V1 and V2 from a single atlas, or Storer et al., 2009, for a measurement of the topographic structure of the different layers of a single macaque lateral geniculate nucleus).

4.3 Comparison with other flattening methods

There has been little consensus to date as to which aspects of the geometry of the original surface should be preserved by a flattening method, with some researchers emphasizing the preservation of distances (Schwartz et al., 1989; Fischl et al., 1999a; Wandell et al., 2000; Zigelman et al., 2002; Sun and Hancock, 2008), some the preservation of angles (Angenent et al., 1999; Hurdal and Stephenson, 2004; Gu et al., 2004) or areas (Zhu et al., 2005; Chiu et al., 2008), and others attempting to preserve some combination of these geometric quantities (Carman et al., 1995; Drury et al., 1996; Goebel, 2000; Timsari and Leahy, 2000; Ju et al., 2005).

The approach we have adopted here is based on preserving shortest-path distances, which is also the approach taken by Schwartz et al. (1989); Fischl et al. (1999a); Wandell et al. (2000); Larsson (2001); Zigelman et al. (2002); Sun and Hancock (2008) and others. An important difference between these methods and the DMflatten algorithm described in this report is that our algorithm produces flat maps that are independent of the particular mesh used to represent the surface. Furthermore, our approach is guaranteed to produce flat maps that are free of edge-crossings, unlike the algorithms of Schwartz et al. (1989); Fischl et al. (1999a); Zigelman et al. (2002) and Sun and Hancock (2008), results in the correct flattening of geodesically non-convex surfaces, unlike Schwartz et al. (1989); Fischl et al. (1999a); Wandell et al. (2000) and Sun and Hancock (2008), and uses *exact* shortest-path distances, unlike the level-set approximations of Zigelman et al. (2002) or the approximations based on Dijkstra's algorithm (Dijkstra, 1959) used by Fischl et al. (1999a) and Wandell et al. (2000), which can introduce a substantial amount of error into the resulting flat maps. A comparison of the output of the DMflatten algorithm with the results produced by several commonly-used flattening methods is shown in Figures S-5 to S-23 of the supplement.

4.4 Flattening entire cortical surfaces

The computational demands of the DMflatten algorithm are dominated by its first stage, which uses the LOS-Floyd algorithm to compute and store the shortest-path distance along the surface for every pair of mesh vertices. Given a mesh with V vertices, the LOS-Floyd algorithm requires $\mathcal{O}(V^2)$ space (as would any other algorithm that computed the distance between every pair of vertices) and has $\mathcal{O}(V^3)$ run-time performance (Balasubramanian et al., 2009). While this poses no problem for cortical patches the size of a few Brodmann areas or smaller (e.g., see the results in Figures 11 and 12), the $\mathcal{O}(V^2)$ space requirement alone is prohibitive for applying the LOS-Floyd algorithm (and therefore the DMflatten algorithm) to the entire human cortical surface, which is typically represented with meshes that have approximately 10^5 vertices, on workstations that have only one or two gigabytes of memory.

Before considering modifications of the DMflatten algorithm (or its implementation) that enable the flattening of entire cortical surfaces, note that the flattening error E is likely to be high for such surfaces, since the boundary of the entire cortical surface is small compared to its surface area, with the preservation of the length of this small boundary conflicting with the preservation of the large distances in the interior, as in Figure 8. (We are referring here to the true, anatomical boundary of cortex, e.g., where the cingulate cortex terminates at the corpus callosum, and not to the artificial boundary that results from “relaxation cuts” that are

often made prior to applying current cortical flattening methods. These relaxation cuts, which are cuts *through* the cortical region of interest rather than *around* the region of interest, give a misleading impression of lowering the flattening error by ignoring a significant source of error: points that are near these cuts, but on opposite sides, will project to distant points on the flat map even though they are actually nearby in cortex—however, the error due to this distortion is typically not reported. Furthermore, these cuts can drastically change the shape of the resulting flat map, confounding the study of the intrinsic shape or the topographic structure of the region of interest. We emphasize that none of the DMflatten results shown in this paper made use of relaxation cuts.) Given a flat map with high flattening error (e.g., that of the entire cortical surface), it is not clear, at present, what the utility or the relevance of a geometric measurement on such a representation would be, since the high flattening error would propagate into such measurements. In contrast, when the flattening error is low (as in Figures 11 and 12), many useful measurements can be made on the flattened representation, as described in Section 4.2.

If, however, a valid reason for using the DMflatten algorithm to flatten the entire cortical surface does arise in the future, we make the following remarks: the memory required to store the full set of distances is approximately 20 gigabytes for an entire cortical surface (with $V \approx 10^5$). Although this is beyond the capacity of 32-bit workstations, it is completely feasible for 64-bit workstations, which are becoming increasingly available. With regard to the run time, note that the Floyd component of the LOS-Floyd algorithm can be replaced with Dijkstra's algorithm (forming the LOS-Dijkstra algorithm) without affecting the computed distances. Then, each vertex in turn can be taken as the source vertex for both the LOS component and for the Dijkstra component, resulting in a procedure that is fully parallelizable, since each parallel processor would only be responsible for computing the minimal geodesics and shortest paths originating from a subset of vertices. The resulting run time would therefore be limited primarily by the number of available parallel processors or cores. Thus, the space and run-time considerations involved with applying the DMflatten algorithm to a full cortical surface can be addressed with hardware that is available today and that will be increasingly commonplace in the future.

An alternate strategy for flattening large surfaces on 32-bit, single-processor workstations involves a small and simple modification of the DMflatten algorithm: instead of computing the distance between *every* pair of vertices, only distances out to some pre-specified radius could be computed and used in the DMflatten error function. This strategy, which can greatly reduce the run time and memory required (depending on the value chosen for the radius), was first proposed by Schwartz et al. (1989) and subsequently implemented by others (e.g., Fischl et al., 1999a). We have avoided the use of such a strategy in the work presented here because (i) it was not necessary for the surfaces we were interested in flattening, eliminating the need to introduce the radius as an additional parameter, and (ii) it is not clear how this radius should be chosen in a *principled* manner: what choice of radius ensures that the criteria described in Section 2.1 will be met? How should the radius be chosen for surfaces with different geometries (e.g., for human versus macaque cortex, or for cortical versus subcortical structures)? What is the relationship between the flattening error computed using only the distances below a given radius and the flattening error computed using the full set of distances? These are open questions for future research that are beyond the scope of the present report.

4.5 Summary

In this report, we have introduced a set of basic criteria that any reasonable near-isometric flattening algorithm must satisfy, along with a set of test surfaces that can be used to determine the extent to which these requirements are met. We have also introduced the DMflatten algorithm, a novel method for computing flat maps that is, to the best of our

knowledge, the only algorithm that satisfies *all* of the basic criteria for near-isometric flattening. A quantitative, rigorous approach to flattening has been, and will likely continue to be, an important factor in the minimization of extraneous sources of variability in studies of the structural and functional organization of laminar surfaces.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

Acknowledgments

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Figure 1.

Flat maps of human visual cortex from the studies of (a) Bles et al. (2006), (b) Slotnick and Yantis (2003), (c) Wandell (1999), and (d) Schira et al. (2007). The flattening procedure in BrainVoyager (Goebel, 2000) was used to produce (a) and (b), whereas (c) and (d) were produced by the flattening procedure in MrVista (Wandell et al., 2000). Although these figures suggest considerable inter-subject variability in the shape and topographic structure of V1 and V2, it is likely that much of this variability is due to the flattening procedures (see text). The stereotyped shape of human and macaque V1 is discussed in Hinds et al. (2008); see also Figure 11 and Figure 12.

Figure 2.

(a) The shortest path between two points on a flat, non-convex surface is shown in black. Any flattening algorithm that takes this surface as input and attempts to match the length of the shortest path shown in (a) to the length of the corresponding straight-line path on the “flattened” output (b) will inevitably distort the input surface, violating criterion C1. (The flat map shown in (b) was generated by the Schwartz89 algorithm described in Schwartz et al., 1989.)

Figure 3.

(a) A piecewise-flat surface with a pentagonal boundary and vertices uniformly spaced on the unit sphere. (b) The Schwartz89 algorithm produces a flat map of this surface with several edge-crossings (e.g., see arrow) due to folds, violating criterion C4.

Figure 4.

(a) A triangular mesh of a cube, minus the bottom (square) face. The front face is colored red for reference only. (b) A non-uniform refinement of (a), resulting in a different mesh representing the same surface. (c) The flat map of (a) produced by the Schwartz89 algorithm. Applying the same algorithm to (b) results in a very different flat map, shown in (d).

Figure 5.

(a) A flat, non-convex mesh was chosen as the test case for criterion C1. (b) The result of mapping (a) to a disk via Tutte's algorithm (Tutte, 1963). This provides an initial flat map (with error $E = 65.9\%$) that is used as the starting point for the optimization routine in the DMflatten algorithm. (c) After 10 iterations of the DMflatten optimization routine, E is reduced to 27.6% . (d) The algorithm terminates after 1291 iterations, taking less than a second on a workstation with a 3 GHz processor and 2 GB of memory. The final flat map, for which $E = 0.0\%$, is identical to the input mesh (a), demonstrating that the DMflatten algorithm satisfies criterion C1. (Red vertices are for reference only.)

Figure 6.

To construct a test case for criterion C2, the flat, U-shaped mesh shown in Figure 5(a) was gently deformed onto a large sphere, resulting in the mesh shown in (a). Given this surface as the input, the DMflatten algorithm produces the output shown in (b), with flattening error $E = 0.1\%$. By comparing this flat map to the one in Figure 5(d), we see that small deformations of the input to the DMflatten algorithm lead to small deformations of the output, satisfying criterion C2.

Figure 7.
(a) The hemicylinder is a surface with zero Gaussian curvature. (b) The DMflatten algorithm correctly produces an isometric flattening of this surface ($E = 0.0\%$), satisfying criterion C3.

Figure 8.

Given the surface with pentagonal boundary from Figure 3 as the input (a), the DMflatten algorithm produces a flat map (b) with no edge-crossings, satisfying criterion C4. Although this flat map is optimal, it is significantly distorted ($E = 33.0\%$), which is not surprising given the small boundary of the input surface, relative to its surface area.

Figure 9. Two different triangular meshes representing a cube (minus one face) are shown in (a) and (b). The corresponding flat maps, as computed by the DMflatten algorithm, are shown in (c) and (d), with flattening errors of 21.1% and 20.9%, respectively. Note that these two flat maps are nearly identical, demonstrating that the DMflatten algorithm produces mesh-independent flat maps (criterion C5).

Figure 10.

Given the hemisphere (a) as the input, the DMflatten algorithm produces the output shown in (b). This flat map ($E = 9.9\%$) is in close agreement with Lambert's equal area projection, which is shown in (c). In (d), Euclidean distances in the Lambert projection are plotted against the corresponding Euclidean distances in the DMflatten output, to further examine the level of agreement. These points lie almost exactly on the line $y = x$ ($R^2 > 0.999$). These results demonstrate that the DMflatten algorithm correctly flattens spherical caps, satisfying criterion C6.

Figure 11.

(a) Area V1 in macaque, reconstructed from serial tissue sections (Schwartz et al., 1988). (b) The result of applying the DMflatten algorithm to the surface shown in (a). The per-vertex error E_i is shown in color, both on the input surface and on the flat map, and the overall flattening error E is 4.2%. The time taken to flatten this mesh, which has 1237 vertices, is approximately 1 minute on a workstation with a 3 GHz processor and 2 GB of memory.

Figure 12.

(a) Human V1, reconstructed from manual tracings of the stria of Gennari in *ex vivo* 7T MRI scans (Hinds et al., 2008). (b) The result of applying the DMflatten algorithm to the surface shown in (a). The per-vertex error E_i is shown in color, both on the input surface and on the flat map, and the overall flattening error E is 5.7%. The time taken to flatten this mesh, which has 2585 vertices, is approximately 10 minutes on a workstation with a 3 GHz processor and 2 GB of memory.