Examining the volume-efficiency of the cortical architecture in a multi-processor network model.

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Abstract

The convoluted form of the sheet-like mammalian cortex naturally raises the question whether there is a simple geometrical reason for the prevalence of cortical architecture in the brains of higher vertebrates. Addressing this question, we present a formal analysis of the volume occupied by a massively connected network of processors (neurons), and then consider the pertaining cortical data. Three gross macroscopic features of cortical organization are examined; the segregation of white and gray matter, the circumferential organization of the gray matter around the white matter, and the folded cortical structure. Our results testify to the efficiency of cortical architecture.

1 Introduction

A cortical neuron typically innervates one set of neighboring neurons via short-range connections, and another set of distant neurons via its long-range connections (Crick & Asanuma 1986, Abeles 1991, Braitenberg & Schuz 1991). A simple way to spatially organize a large number of neurons and their fibers would be to place them in a *homogeneously dispersed* manner in the spherical cranial cavity. However, the mammalian cortex typically has three prominent gross macroscopic characteristics, illustrated in figure 1: **A**. Neurons and their short range fibers compose the 'gray matter', while their long range fibers constitute the 'white matter', forming *segregated compartments.* **B**. The gray matter forms a thin surface on the envelope of the cranial sphere, *circumferentially surrounding* the white matter.
C. The gray matter sheet is markedly *folded.* Previous work has suggested the possibility that there has been considerable evolutionary pressure on the brain to organize itself so that its volume is minimized (Cowey 1979, Mitchison & Durbin 1986, Durbin & Mitchison 1990, Nelson & Bower 1990, Mitchison 1991). The goal of this paper is to show that the brain's macroscopic architectural characteristics are in accordance with this volume minimization principle.

To this end, various possible organizations, illustrated in figure 2, are considered. In section 2 we compare between a *homogeneously dispersed (HD)* organization, where the processors and all their connection fibers are intermingled, to a *segregated (SG)* organization, where the processors and their long-range connection fibers house two spatially distinct compartments. Section 3 compares between two segregated 'canonical' organizations. The first is the *inner core (IC)* organization, characterized by an inner core of gray matter surrounded by the white matter. The second is its 'mirror image' *external sheet (ES)* architecture, characterized by the gray matter forming the outer envelope of the sphere, as in the cortex. Finally, in section 4, the contribution of ES cortical folding and circumferential wiring are discussed.

As most of the brain's volume is occupied by nerve cells and fibers, we consider a schematic model composed of a network of massively connected processors housed in a spherical volume. The network is characterized by the number of processors (neurons) N, the processor's volume u, the average number of short range (n_s) and long range (n_l) *connection fibers* per processor (reflecting the cortical bimodal distribution of connections), and the fibers' average cross section area (f_s, f_l) and length (t_s, t_l). The results obtained in

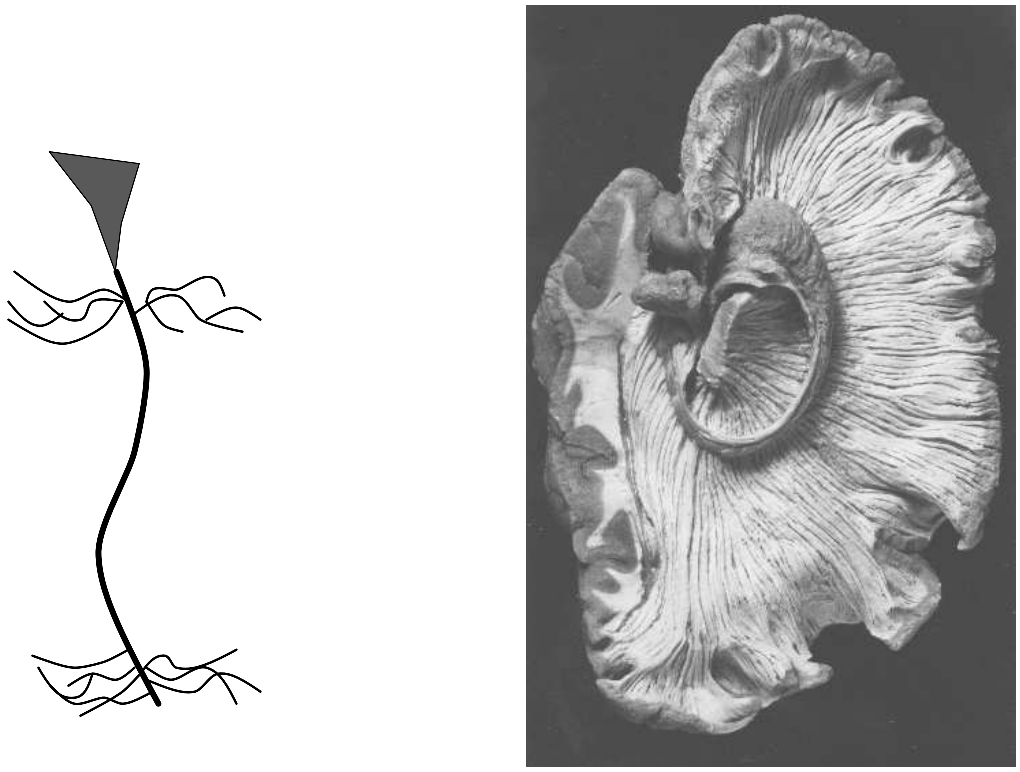

Figure 1: Right: The right cerebral hemisphere from the medial side. The segregated, circumferential, folded structure of the gray matter is evident (From “The Human Brain: a Photographic guide”, N. Gluhbegovic and T. H. Williams, with permission from the authors). Left: A schematic representation of a neuron with a single long range axonal fiber. The proximal and distal arborizations give rise to numerous short and long range connections.

the framework of this general ‘processor-wiring’ model are examined specifically in light of the relevant cortical data.

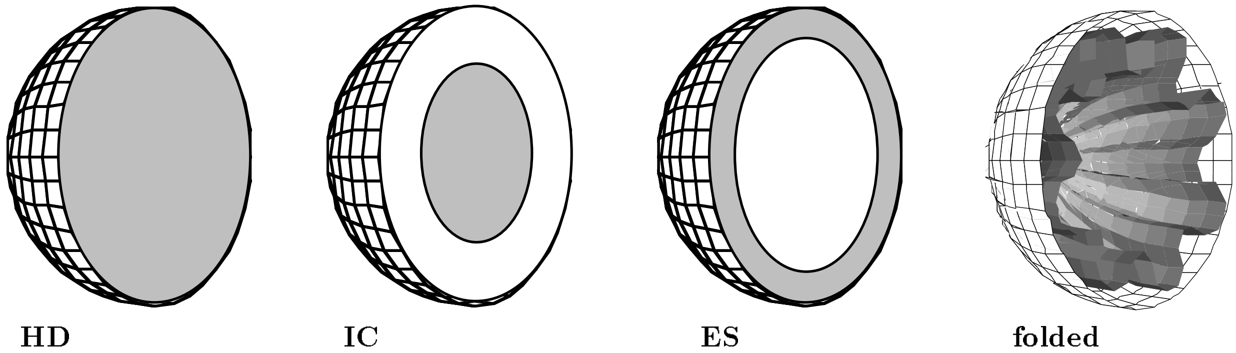

Figure 2: A schematic description of the various spatial organizations discussed. The logic of the paper is to show that, considering the cortical data, the ES organization is more economical than both the HD and IC ones. Folding the external sheet further decreases the brain’s volume.

2 Segregation versus homogeneous organization

We first compare the general class of segregated and homogeneously dispersed organizations. The volumes $V(SG), V(HD)$ of the two architectures are

$$V(HD) = N\left[u + n_s f_s t_s(HD) + n_l f_l t_l(HD)\right] \tag{1}$$

$$V(SG) = N\left[u + n_s f_s t_s(SG) + n_l f_l t_l(SG)\right]. \tag{2}$$

The average length of the short range connections is smaller when the processors are more densely packed. Therefore, by definition, $t_s(SG) < t_s(HD)$. Hence, by (1) and (2), if the ratio of short to long-range connections is such that

$$\frac{n_s}{n_l} > \frac{f_l\left(t_l(SG) - t_l(HD)\right)}{f_s\left(t_s(HD) - t_s(SG)\right)}, \tag{3}$$

then $V(SG) < V(HD)$.

To compare between specific organizations, their average fibers' lengths have been calculated, as shown in the Appendix. We shall first examine the dispersed HD organization versus the segregated IC one, both housed in a spherical volume $V = 4\pi R^3/3$. Their corresponding volumes are

$$V(IC) = N_1\left[u + \frac{3}{4}n_s f_s \sqrt[3]{\frac{n_s}{N_1}}r_1 + n_l f_l(\frac{7}{4}R + \frac{1}{4}r_1)\right] \tag{4}$$

and

$$V(HD) = N_2\left[u + \frac{3}{4}n_s f_s \sqrt[3]{\frac{n_s}{N_2}}R + \frac{36}{35}n_l f_l R\right], \tag{5}$$

where r_1 denotes the radius of the inner gray-matter core of the IC organization (as shown in figure 3). By expressions (4) and (5) we find that more processors can be housed in the IC organization than in the HD one (in the same volume) only if

$$\frac{V}{u + \frac{3}{4}n_s f_s \sqrt[3]{\frac{n_s}{N_2}}R + \frac{36}{35}n_l f_l R} = N_2 < N_1 < \frac{V}{u + \frac{7}{4}n_l f_l R} \tag{6}$$

I.e., the IC may be more efficient than the HD organization only if

$$\frac{n_s\sqrt[3]{n_s}}{n_l} > \sqrt[3]{N_2}\frac{f_l}{f_s}. \tag{7}$$

To examine our results in the realm of the brain, we consider the axons as the primary wiring material (as in (Mitchison 1991)). Each neuron (as illustrated in figure 1) has a main axonal branch that (in the majority of the cases (Abeles 1991)) projects into the white matter and comprises a single long-range connection fiber ($n_l = 1$), giving rise to numerous proximal and distal collaterals, both accounted for by taking $n_s = 10^4$ (Colonnier 1981, Cherniak 1990). In accordance with typical estimations (Cherniak 1990, Abeles 1991, Braitenberg & Schuz 1991), the number of cortical neurons is taken as $N = 10^{10}$, their average size as $u = 10^{-5} mm^3$, and the normal cranial volume averages 1400 cm^3. The long-range fibers have an average cross section area of $f_l = 10^{-6} mm^2$ (Blinkov & Glezer 1968, Valverde 1985), and shorter processes have an average cross section area of $f_s = 10^{-7} mm^2$ (Shkol'nik-Yarros 1971, Feldman 1984). This reflects the observation that the diameter of the axonal branches is much smaller than the main axonal fiber (Hillman 1979).

Before proceeding further, it should be noted that the calculation of the short-range connectivity length t_s performed for the case of a network of distributed processors, considerably overestimates the total length of the neuron's short-range connections. This measure is calculated assuming that each connection arises separately from the processor. However, in the case of neurons, most connections arise along the axonal tree and only few processes originate directly from the soma. Hence, the average short-range connectivity length of neurons is actually much smaller than that computed by the simple method we have used above in the general processor model. To account for this effect of neuronal arborization on connectivity length, we introduce an *arborization factor* α that reduces the length of the neuron's short-range connectivity. Throughout this paper we use $\alpha = 0.1$, i.e., assuming that when accounting for arborization the connectivity is 10 times shorter than the initial, arborization-free estimate. In the neural case, inequality (7) should hence be rewritten as

$$\frac{n_s \sqrt[3]{n_s}}{n_l} > \alpha \sqrt[3]{N} \frac{f_l}{f_s} \ . \tag{8}$$

As is evident, inequality (8) is barely satisfied by the cortical data. Substituting these values in (4) and (5), and introducing the arborization factor α, we find that both organizations house approximately 10^{10} neurons in the given cranial volume. (To calculate the number of neurons in the IC organization we use, in addition to (4), the expression of the IC gray matter volume $\frac{4\pi {r_1}^3}{3} = N_1 \left[u + r_1 \left(\frac{1}{2} + \frac{3}{4} n_s f_s \sqrt[3]{\frac{n_s}{N_1}}\right)\right]$). Segregation does not lead therefore to volume efficiency in the IC case. However, as we shall now proceed to show, the ES segregated organization is an order of magnitude more efficient than both the HD and IC organizations. It should be noted that this superiority of the ES organization is maintained along a very broad range of α values ($1 \geq \alpha \geq 0.001$), and is further enhanced as α gets smaller.

3 Circumferential organization

Next we compare the IC and ES organizations, both housing N processors in spheres of radius R. The ES volume is

$$V(ES) = N\left[u + \frac{3}{4}n_s f_s \sqrt[3]{\frac{n_s}{N}(R^3 - {r_2}^3)} + n_l f_l \frac{2}{\pi}(R + r_2)\right], \tag{9}$$

where r_2 is the radius of the inner ES white matter core, as shown in figure 3. As expressed

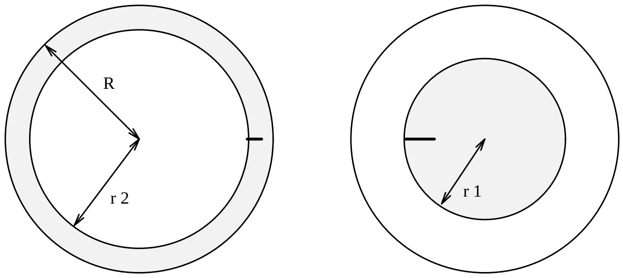

Figure 3: The ES (left) and IC (right) organizations. The horizontal line in both organizations' gray matter denotes the average traversal t_{l_g} of the long-range fibers in the gray-matter. We illustrate the case where the housing volumes required are large relatively to the gray matter volume, and therefore $t_{l_g}(ES) < t_{l_g}(IC)$.

in equations (4) and (9), the average length t_l of the long-range fibers is shorter in the ES than in the IC organization. The length t_s of the short-range fibers depends only on the volume V_g of the gray matter. V_g depends, in turn, on three factors; the processors' volume, the volume occupied by the short range fibers, and the volume of the long range fibers traversing the gray matter. Hence, it is t_{l_g}, the traversal length of the long range fibers in the gray matter, that actually determines the relation between the gray matter volume of two segregated organizations holding an identical number of neurons.

We shall show now that if $V > \frac{4}{3}V_g$, the ES organization is more efficient than the IC one. Using simple geometrical considerations, one may calculate that $t_{l_g}(IC) = \frac{1}{2}r_1$, and $t_{l_g}(ES) = 2\left[\sqrt[3]{\frac{R^3+{r_2}^3}{2}} - r_2\right]$. Examining the case where both organizations have equal gray matter volume V_g and traversal length t_{l_g}, we obtain the set of equations

$$2\left[\sqrt[3]{\frac{R^3 + {r_2}^3}{2}} - r_2\right] = \frac{1}{2}r_1 \tag{10}$$

and

$$\frac{4}{3}\pi {r_1}^3 = \frac{4}{3}\pi(R^3 - {r_2}^3) , \tag{11}$$

whose solution yields $V \cong \frac{4}{3}V_g$. Suppose then that N processors are placed in an IC organization filling a sphere of volume V, such that $V = \frac{4}{3}V_g$. By (10) and (11), an ES organization housing N processors in an identical sphere would have the same gray-matter volume. Since $t_l(ES) < t_l(IC)$, such an ES organization is possible. However, while the IC organization occupies the whole housing volume, the ES one occupies only part of it and additional processors and their connections may be added. When the ratio $\frac{V}{V_g} > \frac{4}{3}$, then $t_{l_g}(ES) < t_{l_g}(IC)$, and the relative efficiency of the ES versus IC organization further increases. As the cranial volume is one order of magnitude greater than the cortical gray matter volume, the ES organization is much more efficient than the IC one. Substituting the cortical data and the arborization factor α in (9), and considering the typical estimate of the average cortical width ($R - r_2 = 3mm$) (Crick & Asanuma 1986, Cherniak 1990), we find that the cranial volume can house $6 \cdot 10^{10}$ neurons. In the realm of the brain, the ES organization can therefore house six times more neurons than the HD and IC organizations.

4 Cortical folding and circumferential wiring

Given a fixed amount of processors stored in the ES organization, any reduction in the width of the external gray-matter sheet would result in a decreased cortical volume, due to a reduced t_{l_g}. Beyond some point, this can be achieved only by increasing the cortical surface area, implying that the cortex should be folded. As shown in figure 4, the level of possible folding is restricted by connectivity surface-area considerations: All the connection fibers traversing the inner face of the external cortical sheet must pass through an imaginary white-matter inner sphere, tangential to the folds. Cortical folding is feasible only as long as the surface area of the imaginary inner sphere is greater than the fraction of gray-matter sheet available for the long-range fibers' traversal. The total cut surface area of these long-range fibers ($Nf_l = 10^{10} \cdot 10^{-6}mm^2$) is equal to the surface area of the inner imaginary sphere, which is approximately the surface area of the cranial cavity (10^4mm^2). Hence, from a connectivity perspective, the cortex is folded to its maximal possible ratio. The notion that evolution tended to minimize cortical width is supported by the observation that, although the human brain is more than 3000 times larger than that of the mouse, its cortex is only 3 times thicker (Abeles 1991).

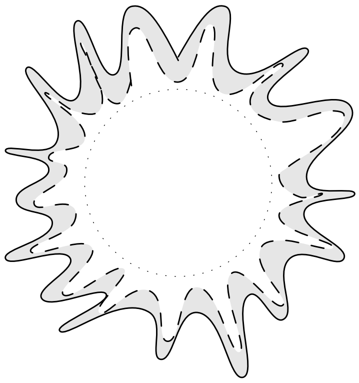

Figure 4: A schematic cross-section of a brain: Most fibers traversing the white matter pass through the marked imaginary dotted sphere. The inner face of the gray matter is marked by a dashed line, denoting that only part of it may be utilized for the fibers' traversal. The total surface area of the dashed part cannot surpass the surface area of the dotted inner sphere.

The traversal of the long-range fibers in the gray matter may be further reduced by letting the ES long-range connections project also externally, traversing the space peripheral to the gray matter. Since a direct path is shorter than a circumferential one, the most efficient organization would be to let fibers traveling to distant locations traverse directly through the inner white matter core, and fibers projecting to neighboring areas traverse via the circumference. Indeed, cortical layer I is comprised mainly of axonal fibers that (after giving away some proximal connections) travel via the cortical circumference for several millimeters (Braitenberg 1978, Eccles 1981).

5 Discussion

Previously, it has been shown that certain self-organizing models generate cortical maps that come close to minimizing the neuronal wiring required for local cortical operations (Kohonen 1984, Mitchison & Durbin 1986), and for simultaneously mapping retinotopic position and orientation (Durbin & Mitchison 1990). By comparing the wiring volumes resulting from various geometrical layouts of neurons, it has been shown that the volume minimization principle can account also for the formation of cortical stripe patterns seen within many cortical areas (Mitchison 1991). These studies show that keeping connections lengths to a minimum could be an important goal of cortical map development. Our work complements these studies, by examining whole brain organization, and showing that cortical ES organization does indeed contribute to the brain's total volume minimization. Accordingly, viewed on a coarse scale, the brain has developed its cortical organization as a result of an evolutionary effort to minimize brain volume. Concomittantly, on a finer scale, the wiring of the arising cortical sheet has formed, further enhancing volume minimization. Our results thus contribute to the plausibility of the assertion that brain volume minimization is an important principle in determining cortical architecture.

Adopting the view that mappings that minimize connections' volume are likely to be selectively favored, it has been shown (Nelson and Bower 1990) that principles for optimally mapping computations onto parallel computers may help illuminate the relationship between maps and computations in the brain. Our results may work in the opposite direction, as the efficiency of the brain's cortical organization testified to might be of relevance to the design of future massively connected computing devices.

Some brain structures, like the Basal Ganglia and the Thalamus are not 'cortical', but have a homogeneous, non-segregated, 'nuclear' shape. It is only the need to house a huge number of neurons having typical connectivity patterns that makes cortical architecture more efficient than the nuclear one. In fact, as we have shown, there exists a certain parameters' range where the nuclear IC organization is more efficient than the ES one.

However, as we consider the actual values of the relevant parameters in the brain, the present cortical ES organization turns out more efficient. It is interesting to note further in this regard that the only other brain structure holding an extremely large number of neurons, the cerebellum, has too a folded, ES organization.

To conclude, artificial and natural computing networks can be described by schematic connection diagrams. In reality, a given network can be implemented by numerous spatial architectures, satisfying different optimization criteria. We have shown that, in a system characterized by a high ratio of short to long range fibers and a large housing volume, the separation of the processors from the long range wires, and their circumferential folded organization, contributes to volume minimization. When the pertaining neuroanatomical data is considered, our analysis shows that the presently observed cortical ES organization is rather efficient.

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Appendix: Average connectivity lengths

Each processor has a bi-modal distribution of connections, such that every long-range fiber may reach any area of the sphere with equal probability, and each short-range connection fiber reaches any other processor within a given radius $d \ll R$, with equal probability. It is assumed that every long-range connection between any two processors traverses in its shortest possible path, i.e., on the plane defined by their locations and the center of the sphere.

A. HD organization

Observation 1. The average distance l from the center of a sphere of radius R to all the contained, homogeneously distributed, processors is $\frac{3}{4}R$.

Proof: Assuming an asymptotically large number of homogeneously distributed processors, l can be calculated as

$$l = \frac{1}{V}\int_0^R dr \int_0^\pi d\theta \int_0^{2\pi} d\varphi r^2 \sin\theta \cdot r = \frac{2\pi}{V}\int_0^R r^3 dr \int_0^\pi d\theta \sin\theta = \frac{4\pi}{V}\int_0^R r^3 dr = \frac{3}{4}R \ .$$

Observation 2. $t_s(HD) = \frac{3}{4}\sqrt[3]{\frac{n_s}{N}}R$.

Proof: Viewing each processor as a center of a sphere of volume $\frac{Vn_s}{N}$, The requested result follows from observation 1.

Observation 3. $t_l(HD) = \frac{36}{35}R$.

Proof: This result is known from Integral Geometry (Santalo 1976). The mean value of the distance in a n-dimensional ball of Radius R is given by

$$\mu(n) = \left(\frac{n}{n+1}\right)^2 \frac{\Gamma(n+2)\Gamma(n/2)}{\Gamma(n+\frac{3}{2})\Gamma(\frac{n+1}{2})}R \ ,$$

where Γ denotes here the gamma function, and $\mu(3) = \frac{36}{35}R$ in a sphere.

B. IC organization

Let r_1 denote the radius of the gray-matter inner core in the IC organization (see figure 3). Then

Observation 4. $t_s(IC) = \frac{3}{4}\sqrt[3]{\frac{n_s}{N}}r_1$.

Proof: similar to that of Observation 2.

Observation 5. $t_l(IC) \cong \frac{7}{4}R + \frac{1}{4}r_1$.

Proof: We are interested in calculating the average distance from all the processors in V_g to themselves, where the connections fibers are spread in the volume V. This amounts to calculating the average connection length when the connection fibers traverse the white matter at the circumference of $\frac{1}{2}(R+r_1)$. Instead of averaging upon the sums of the distances form all processors to themselves, we use observation 1. to approximate t_l by calculating the distance from a processor placed at distance $\frac{3}{4}r_1$ from the center of the gray-matter inner core, to another processor, placed at the same distance, but at an angle of $\frac{\pi}{2}$ radians. Hence

$$t_l(IC) = \frac{\pi}{2}\frac{1}{2}(R+r_1) + 2(\frac{1}{2}(R+r_1) - \frac{3}{2}r_1) \cong \frac{7}{4}R + \frac{1}{4}r_1 \ .$$

C. ES organization

Let r_2 denote the radius of the inner white matter core in an ES organization (see figure 3). Then,

Observation 6. $t_s(ES) = \frac{3}{4}\sqrt[3]{\frac{n_s}{N}(R^3 - {r_2}^3)}$.

Proof: similar to that of Observation 2.

Observation 7: $t_l(ES) \cong \frac{4R}{\pi}$.

Proof: $t_l(ES)$ can be estimated by calculating the average length over all chords adjacent to a point on the circumference of a sphere of radius R. Hence,

$$t_l(ES) = \frac{1}{\pi R}\int_0^\pi R\sqrt{(R\cos\theta + R)^2 + R^2\sin^2\theta}\; d\theta =$$

$$\frac{1}{\pi}\int_0^\pi \sqrt{2R^2(\cos\theta + 1)}\; d\theta = \frac{\sqrt{2}R}{\pi}\int_0^\pi \sqrt{\cos\theta + 1}\; d\theta$$

and after substituting $\cos\theta = u$ we get

$$t_l(ES) = \frac{\sqrt{2}R}{\pi}\int_1^{-1} -\frac{\sqrt{u+1}}{\sqrt{1-u^2}}du = -\frac{\sqrt{2}R}{\pi}\int_1^{-1}\frac{du}{\sqrt{1-u}} = -\frac{\sqrt{2}R}{\pi}| - 2\sqrt{1-u}|_1^{-1} = \frac{4R}{\pi}\ .$$