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The left human speech-processing cortex is thinner but longer than the right

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We present histological data from 21 post-mortem, adult human cases that indicate the neocortex on the left planum temporale (secondary auditory cortex) is thinner but longer than that on the right side. The volumes of the left and right regions are approximately equal. Thus, the left planum temporale cortex is long and thin and the right short and thick. The present data fit excellently with previous studies of the volume, surface area, cytoarchitectonics, and neuronal structures of these areas. From these studies we suggest that the hemispheric differences arise from a so-called “balloon model” of cortical development. In this the cortex is extended and stretched by white matter growth. The stretching is greater on the left side, leaving greater distances between neuronal columns and more tangentially (to the pial surface) oriented dendrites on that side. This difference in fine structure can result in more independent activity of individual columns on the left, and could be an anatomical factor in the usual dominance of the left hemisphere for speech perception (Seldon, 1982, 1985).

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It is known that the dominant (usually left) auditory cortex, including the planum temporale and the superior temporal gyrus, can “process” speech signals, which the non-dominant side cannot do to the same extent. Psychophysical and physiological evidence is accumulating that this capability is due to the ability of one side to process and identify shorter temporal transitions in a speech signal, e.g., the transitions in some consonants (Schwartz & Tallal, 1980; Shtyrov, Kujala, Palva, Ilmoniemi, & Näätänen, 2000; Studdert-Kennedy & Shankweiler, 1970; Tallal, Miller, & Fitch, 1993). Steinschneider, Arezzo, and Vaughan (1982) showed that cortical neurons (in monkeys) tend to sum input for the duration of a syllable, implying that detection of a short transition would be a prerequisite to summing signals for a syllable containing it. When whole word processing is studied with psychophysics, the left hemisphere is associated with activation of narrow semantic fields and the right hemisphere with wide semantic fields (Nakagawa, 1991; Rodel, Cook, Regard, & Landis, 1992). On the other hand, the right hemisphere superior temporal cortex appears to have speech/language functions related to identifying context and is activated during processing of paragraphs, metaphors, and linguistic context, as shown by fMRI (Kircher, Brammer, Andreu, Williams, & MacGuire, 2001).

The question for neuroanatomists is whether these differing capabilities are reflected in the anatomy of the regions. That is, is there something in the structure of the dominant side that allows it to perform actions which differ from the other side?

Since the discovery of lateralisation of brain functions, numerous studies have compared the cytoarchitecture of the left and right temporal lobe cortices (Galaburda, Corsiglia, Rosen, & Sherman, 1987; Galaburda, Sanides, & Geschwind, 1978; Galuske, Schlote, Bratzke, & Singer, 2000; Jacobs, Batal, Lynch, Ojemann, Ojemann, & Scheibel, 1993; Jacobs, Schall, & Scheibel, 1993; Jacobs & Scheibel, 1993; Rosen, Sherman, & Galaburda, 1993; Seldon, 1981a, 1981b, 1982, 1985; von Economo & Horn, 1930; von Economo & Koskinas, 1925; Witelson, Glezer, & Kigar, 1995; Witelson & Kigar, 1988, 1992; Witelson & Paillie, 1973).

Differences in surface area of the superior temporal lobe cortices have been reported by Geschwind and Levitsky (1968), Steinmetz, Rademacher, Jäncke, Huang, Thron, and Zilles (1990), Steinmetz, Volkman, Jäncke, and Freund (1991), Jäncke & Steinmetz (1993), Kulynych, Vladar, Jones, and Weinberger (1994), Foundas, Leonard, and Heilman (1995), Penhune, Zatorre, MacDonald, and Evans (1996), Steinmetz (1996), Harasty, Double, Halliday, Kril, and McRitchie (1997), Moffat, Hampson, and Lee (1998) and Honeycutt, Musick, Barta, and Pearson (2000). However, volume measurements show no difference between the two sides (Harasty et al., 1997; Penhune et al., 1996). Thus, we must examine the cortex more closely, to seek whether differences in micro-structure resolve the length/volume puzzle.

The present study looks at one more parameter related to the volume and surface area of the auditory cortices, specifically the thickness of the planum temporale cortex. This, combined with previous findings on cortical volumes, surface areas and cytoarchitectonics, tells us more about the differences between the dominant and non-dominant sides.

THE STUDY

Materials and methods

The brains of 21 individuals free of known neurological and neuropathological abnormalities were studied; the details of these individuals have been published previously (Harasty et al., 1997; Harasty, Halliday, Kril, & Code, 1999). Ages ranged from 20 to 92 years. None of the cases had a history of cerebrovascular disease, trauma, heavy alcohol consumption, or dementia. There was no record of handedness. The post-mortem interval was 5–36 hours (median 20 hours). The study was approved by the Human Ethics Committees of the Universities of New South Wales and Sydney under the Human Tissue Transplantation and Anatomy Act of New South Wales, 1983.

The methods have been described previously with details and volume analyses of the male cases (Harasty et al., 1997; Harasty, Halliday, & Kril, 1996; Harasty et al., 1999).

Standardised brain preparation. Following fixation in 15% buffered formalin, the anteroposterior lengths and the volumes of the cerebral hemispheres were determined. As has been reported (Harasty et al., 1997), all brains were embedded in agar and cut with a rotary slicer into 3 mm coronal slices. The mean slice thickness for each individual was determined by dividing the hemisphere length by the number of slices. Each of the 3 mm slices was photographed, together with a scale bar; 5" × 7" black and white prints were developed to the same magnification and numbered sequentially. From the scale bars on the photos a scale factor representing real length over "photo length" was calculated.

There were no significant brain volume changes between fresh and fixed brain measurements. Formalin-induced changes were assessed. Brain volumes were measured using water displacement at post-mortem and again following the 2 weeks in 15% formalin. The calculated differences between these volumes was minimal (mean change of $0.7 \pm 0.7\%$ volume). Although fixation in formalin may affect brain volume overall, only a hemispherically asymmetric fixation, which has never been described, would affect the intra-individual comparisons made in this study.

Boundary definition. The anterior border of the planum temporale was set at the most anterior part of Heschl's sulcus (Leonard et al., 1993; Steinmetz et al., 1991; Witelson & Kigar, 1992), while the posterior border was defined as the

posterior end of the Sylvian fissure, not including the ascending parietal wall (Leonard et al., 1993). The lateral border was the outer surface of the gyri (outside surface of the cortex) that enclose the planum temporale. The superior temporal gyri were divided into three sections: the anterior superior temporal gyri, Heschl's gyri, and the planum temporale. Delineation of the borders was reached via consensus among three researchers (JH, GH, & PC). The anterior and posterior extent of these areas was determined with over 90% agreement. When disagreement occurred, a consensus of two of the three examiners was utilised.

Volume and length analysis. The grey and white matter volumes in the planum temporale regions were estimated with a point-counting method as previously published (Gundersen & Jensen, 1987; Harasty et al., 1997). Repeated measures of a single slice by two raters gave < 5% variation between raters. Hemisphere and planum temporale lengths were measured using calipers on the whole brains. The Figure 1 schematic represents the areas identified at horizontal section and coronal slice. Linear measurements (anteroposterior lengths) of the posterior external surface of the planum temporale were also performed. The A-P lengths were determined using large vernier calipers on the whole brain specimens, i.e., before slicing. This gave the most accurate measure as they were from the external surfaces of the appropriate landmarks. The caliper lengths were then measured on a ruler to determine the A-P lengths. The consistent positional identification of brain landmarks and thereby the A-P measurements were established using point to point agreement (McReynolds & Kearns, 1983; Ott, 1988). Point to point agreement was chosen as it provides a measure of the direct correspondence between different measures, which is required for reproducibility. Point to point agreement was 90% for the A-P measurements used.

Cortical thickness analysis. Depth of the cortex was measured as the perpendicular distance between the outer surface of the grey matter and its inner edge (boundary with the white matter). This was measured at seven to ten random positions in each hemisphere of each planum temporale slide (if the planum was present on that slide), and the results (in mm) were averaged and multiplied by the scale factor of the photo. This yielded 3–12 samples of the depth for each planum temporale, each sample representing 7–10 measurements.

One source of variation in depth measurements is the variability of the cortical depth from the cap of a gyrus to the bottom of a sulcus. The use of multiple, randomly selected positions on each image is intended to yield a more reliable average. Visual inspection of the photos showed that in no case did either the top of a gyrus or the bottom of a sulcus comprise a major part of the planum temporale cross-section.

Another source of variation is the orientation of the sections. Insofar as the planum temporale is not necessarily perpendicular to the plane of section at

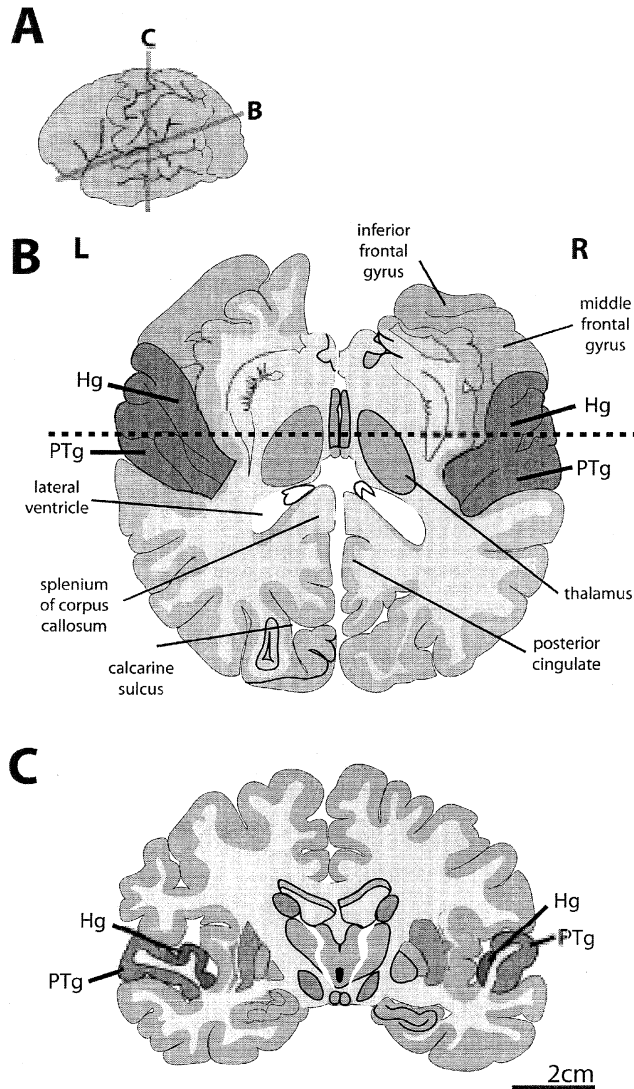


Figure 1. Auditory and speech-processing cortex of the temporal lobes. **A:** A schematic diagram of the lateral surface of the brain showing the approximate positions of the horizontal cut (B) and the coronal cut (C). **B:** A schematic drawing of a brain taken at a 30-degree horizontal section cut at the Sylvian fissure to show the horizontal surfaces of the temporal lobe. This shows the external features of this region, including Heschl's gyrus and the planum temporale. The external length of this posterior section was determined. The obvious leftward asymmetry in length is denoted. **C:** A schematic drawing of a coronal slice showing the posterior superior temporal cortex at the level of Heschl's sulcus showing the cortical area point-counted and then determined three dimensionally for volume using Cavalieri's principle. Hg = Heschl's gyrus, Hs = Heschl's sulcus, PTg = Planum temporale gyrus.

all points, the depths measured may be larger than the true ones. This is best described by the equation: $\text{depth}_{\text{real}} = \text{depth}_{\text{measured}} * \sin \phi$, where ϕ is the acute angle between the planum temporale surface and the plane of section. As the planum temporale is not flat, ϕ varies within and among sections. The influence of the section angle could be very apparent at the posterior end of the planum temporale. The slicing method (perpendicular to the longitudinal axis of the brain) meant that sections were approximately perpendicular to the planum temporale surface, but considerable local variations could not be excluded. When $\phi = 90^\circ$, the measured cortical thickness will be equal to the real thickness. At other angles the measured thickness will be greater than the real one, i.e., will be a larger number. Therefore, we surmise that the smallest depth measured will approximate the real depth, while others may be falsely increased by an oblique section orientation. Thus, we evaluated the sections showing the smallest average depth. Conversely, because greater apparent depths may be influenced by (random) section angles as well as actual cortical depth, we hypothesise that a comparison of them may not show significant differences.

The overall angle of the planum temporale to the plane of the slices could influence these results, especially if it were different in the two hemispheres. However, as mentioned above, the posterior boundary of the measurement area was set at the inflection point between the horizontal Sylvian fissure and the posterior ascending (or descending) ramus. We have found no reports of hemispherically different angles of inclination of the horizontal fissure. Witelson and Kigar (1988) did report that the posterior ascending ramus is more vertical on the right than on the left. Finally, the planum temporale is not a completely flat surface. In some slices it will certainly not be perpendicular to the plane of section, whereas in others it may well be perpendicular; the latter ones would show the "true" thickness of the cortex.

Statistical analysis. Results were tabulated in a spreadsheet (Microsoft Excel 97). We used the *t*-test for sample means and the Wilcoxon test to compare left and right sides for:

- (1) the smallest measured depth,
- (2) the second-smallest measured depth,
- (3) the average of the two,
- (4) the median depths,
- (5) the mean depths, and
- (6) the maximum depths.

Results for the median depths are not reported here, as they were very similar to those for mean depths. Separate comparisons were made for male and female subjects for the first three tests. Cortical volumes and anterior-posterior lengths of the PT were also compared. Only a summary of the latter is presented.

Results

A summary of the results for cortical thicknesses is given in Table 1. The Table also contains the measured cortical volumes for comparison.

The comparison of minimum measured depths (Min in Table 1, putatively the depths perpendicular to the pial surface) of all cases ($N = 21$) shows the left side to be significantly thinner than the right at the 5% level (two-tailed p value, $p = .013$). This is still true for the average of the two smallest depth samples (Ave1–2, which represent 14–20 measurements over two sections, $p = .023$). Comparing only the second-smallest samples (Min2) does not show a significant difference. As we expected a priori, because the maximal measured depths do not relate to the depth perpendicular to the pial surface and thus do not show the actual cortical depth, the comparison of maximum (Max) depths also shows no significant hemispheric differences. For the same reasons, neither the medians nor the means (Mean) are even near significant differences. (Medians are not shown in the Table, as the results for them are similar to those for means.)

The t -test calculates the mean of each sample, and Table 1 shows that in all cases except the maximum depths, the mean of the left-hemisphere samples is less than that of the right-hemisphere ones, even for cases where the difference is not significant. For example, the mean of the left-hemisphere means is less than the right-hemisphere one.

Due to the small number of cases, selecting sub-samples would decrease the chance of finding significant differences. However, we find that for the males ($N = 10$) the left-hemisphere minimum depths are still significantly smaller than the right-hemisphere ones—for the minimum, second smallest, and average of the two ($p < .05$). For females ($N = 11$) the “left less than right” tendency still prevails, but none of the differences is significant. This is due to a much greater variance among the measurements for females compared to males.

The Wilcoxon signed rank test gave similar results (Table 1, bottom row). For the total cohort the left–right differences were significant for the minimum depth measurements (Min1, $p < .02$) and for the average of the two smallest measurements (Ave1–2, $p < .01$). None of the other measurements showed significant hemispheric differences, including the volumes (p not significant).

The results of the linear measurements of the posterior external surface of the planum temporale were as expected and have been reported previously (Harasty et al., 1997). Of the 21 brains, 15 (71%) had a longer left PT, 4 (19%) had a longer right PT, one had equal left and right lengths, and for one brain PT lengths were not available. Our sample portions reflect the more prevalent pattern of left-sided asymmetry found in the general population (Galaburda et al., 1978) and confirm the findings of Geschwind and Levitsky (1968) and others. The hemispheric differences were significant, as were the gender differences. The mean of the left side was 39.5 ± 8 mm for males and 30 ± 8 mm for

TABLE 1
Summary of measures of thickness of the planum temporale (mm)

Subject	Sex	Left Min1	Right Min1	Left Ave1-2	Right Ave1-2	Left Min2	Right Min2	Left mean	Right mean	Left Max	Right Max	Left Volume	Right Volume
16	F	2.56	3.11	2.67	3.30	2.76	3.50	3.34	3.97	4.51	5.97	3.28	3.48
13	F	2.05	2.89	2.51	2.91	2.98	2.93	3.02	3.21	3.44	3.68	3.18	5.66
14	F	3.18	2.92	3.21	3.09	3.24	3.27	3.72	3.91	4.39	5.70	2.66	3.86
20	F	2.90	3.70	3.03	3.90	3.17	4.09	3.45	4.26	4.10	4.98	3.48	2.66
21	F	3.47	2.37	3.50	2.53	3.54	2.70	4.30	3.40	4.16	3.85	6.47	5.16
(5)	F	2.68	2.90	2.92	2.91	3.16	2.91	3.12	3.13	3.39	3.83	3.96	4.05
6	F	2.25	3.13	2.72	3.17	3.18	3.20	3.73	3.33	6.85	4.67	4.11	3.60
1	F	3.30	4.25	3.63	4.34	3.97	4.43	4.75	4.48	3.63	3.47	3.51	0.00
7	F	2.53	3.07	2.60	3.07	2.68	3.07	2.96	3.42	5.96	5.11	3.43	4.13
19	F	3.12	2.94	3.65	3.18	4.18	3.42	4.64	3.87	3.68	3.95	4.20	5.21
2	F	2.99	3.58	3.05	3.63	3.11	3.69	3.52	3.90	4.46	3.90	4.07	3.53
(8)	M	3.28	3.84	3.31	3.85	3.33	3.87	3.70	4.26	7.84	5.03	2.47	2.20
11	M	2.97	3.10	3.18	3.24	3.39	3.38	3.49	3.43	3.38	3.48	2.47	2.18
3	M	3.08	3.32	3.23	3.33	3.38	3.33	3.37	3.38	4.71	5.00	1.78	2.18
9	M	2.81	3.48	2.89	3.58	2.97	3.69	3.86	4.03	5.23	3.61	3.32	3.48
10	M	2.84	3.12	2.85	3.34	2.85	3.55	3.70	3.90	7.30	4.75	3.71	2.38
18	M	2.66	3.06	2.79	3.15	2.92	3.25	3.25	3.45	4.22	4.97	4.64	2.78
12	M	2.71	2.78	2.85	2.82	2.99	2.87	3.43	3.23	3.58	5.99	2.62	1.56
15	M	3.28	3.28	3.29	3.28	3.30	3.28	3.95	4.12	5.77	4.61	6.09	7.17
17	M	2.82	3.17	2.92	3.27	3.03	3.36	3.17	4.02	3.95	4.43	4.33	8.14
4	M	3.38	3.01	3.39	3.27	3.41	3.53	3.60	3.70	4.46	4.51	1.39	3.91

<i>t-test, total</i>												
Mean	2.90	3.19	3.06	3.29	3.22	3.40	3.62	3.73	4.71	4.55	3.64	3.95
Variance	0.14	0.16	0.11	0.16	0.13	0.17	0.23	0.16	1.72	0.62	1.60	2.89
Observations	21	21	21	21	21	21	21	21	21	21	19	19
Pearson Corr	0.20	0.29	0.29	0.29	0.29	0.29	0.48	0.29	0.28	0.28	0.54	0.54
<i>t</i> Stat	-2.73	-2.47	-2.47	-1.78	-1.78	-1.78	-1.16	-1.16	0.58	0.58	-0.93	-0.93
<i>p</i> (<i>T</i> < <i>t</i>) 2-tail	0.013	0.023	0.023	0.091	0.091	0.091	0.278	0.278	0.570	0.570	0.363	0.363
<i>Female</i>												
Mean	2.82	3.17	3.05	3.28	3.27	3.38						
Variance	0.20	0.25	0.17	0.26	0.21	0.28						
Observations	11	11	11	11	11	11						
Pearson Corr	0.12	0.26	0.26	0.32	0.32	0.32						
<i>t</i> Stat	-1.83	-1.36	-1.36	-0.65	-0.65	-0.65						
<i>p</i> (<i>T</i> < <i>t</i>) 2-tail	0.097	0.205	0.205	0.530	0.530	0.530						
<i>Male</i>												
Mean	2.98	3.21	3.07	3.31	3.16	3.41						
Variance	0.07	0.08	0.05	0.07	0.05	0.08						
Observations	10	10	10	10	10	10						
Pearson Corr	0.41	0.37	0.37	0.20	0.20	0.20						
<i>t</i> Stat	-2.47	-2.74	-2.74	-2.54	-2.54	-2.54						
<i>p</i> (<i>T</i> < <i>t</i>) 2-tail	0.036	0.023	0.023	0.032	0.032	0.032						
Wilcoxon test	<i>z</i> = -2.51	<i>p</i> < .02	<i>z</i> = -2.96	<i>p</i> < .01	<i>z</i> = -1.57	<i>ns</i>	<i>z</i> = -1.26	<i>ns</i>	<i>z</i> = 0.22	<i>ns</i>	<i>z</i> = -0.36	<i>ns</i>

The measurement values are shown in the top part of the table as pairs of left-versus-right results in millimetres. The *t*-tests below were generated with Microsoft Excel 97. Only the probability for the two-tailed test is shown (*p* 2-tail). Separate tests were run on the female and male cohorts; the results of these for means, medians, etc., were not significant and are not shown. The bottom row shows the results of the non-parametric Wilcoxon tests on each left-right pair of columns; the results are similar to those of the *t*-tests.

females while the right side was 31 ± 5 mm and 27 ± 7 mm, respectively (sex $F_{1,38} = 10.5$, $p = .003$; side $F_{1,38} = 6.6$, $p = .01$; sex by side $F = 1.5$, $p = .23$).

Despite these expected leftward asymmetries in our sample, the left and right planum temporale volumes showed no significant hemispheric differences in the same sample, as previously reported (Harasty et al., 1997). The current data about cortical thickness may help to explain this anomaly.

We are aware that in a sample this size we should expect an average of two left-handed subjects (assuming a population prevalence of 10% for left-handedness), and that their data might skew the results. However, the personal details for these cases did not indicate handedness; thus, we cannot exclude any cases.

Discussion

As mentioned in the introduction, surface areas and volumes of the planum temporale have often been discussed. However, combining this cortical depth analysis with the volume and length measurements sheds new light on the problem of hemispheric dominance or functional lateralisation.

We can summarise our model of the planum temporale (and other, similar cortical regions). Homologous cortical regions actually have the same volume in both hemispheres, which could include having similar numbers and/or densities of neurons. During or after development, some cortical regions have more or bigger afferent processes than their homologues (in the other hemisphere). In order to physically accommodate the greater volume of afferents and connections, the cortex expands tangentially, i.e., dilates like a balloon, becoming larger in area but thinner. Alternatively, we can think of the non-dominant side losing afferent inputs, with the accompanying shrinkage of the processes and contraction of the cortical layer to become smaller in area but thicker. The larger planum temporale surface area on the dominant side has been shown in numerous previous studies. In turn, this stretching means that the structural units (neuronal columns) spread apart as the surface area increases. This is consistent with findings of Seldon (1981a), Galuske et al. (2000) and Buxhoeveden and Casanova (2000). Also, Penhune et al. (1996) found similar volumes of grey matter in left and right auditory cortices, but a greater volume of white matter on the left. A side effect of this expansion could be that the dendritic trees on the expanded side become flatter (more tangential) and more disentangled (less overlapping) than on the other side (Seldon, 1982). A consequence of the more tangential dendrites could be the capability of a neuron to interact with more afferents. A consequence of the lesser overlap is that this cortex becomes capable of more individual responses to a particular input signal; the neuron columns become more disjointed and more individual or independent in function, as proposed by Seldon (1982, 1985). This is shown diagrammatically in Figure 2. This in turn means that this cortical region has more differentiated analytical or serial abilities

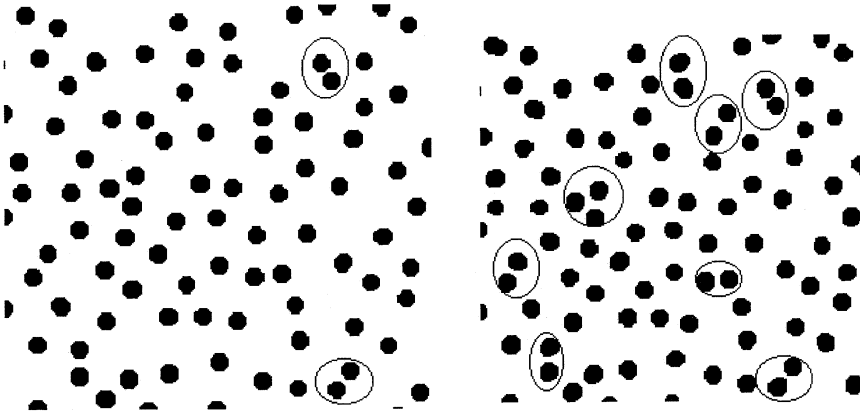


Figure 2. Diagram of the implications of the balloon model of cortical expansion. The pictures show tangential views (from the pial surface) of the left and right auditory cortices respectively. Each spot represents a neuronal column. Circles around spots indicate those columns that tend to function as a single unit due to their proximity. On the left side most columns act independently. On the right side, due to the lesser tangential expansion and greater proximity of neighbouring columns, more columns act together in sets. Thus, with the same number of columns (and neurons), the left side has more independent units and can better differentiate incoming signals.

for the particular input. For the planum temporale and associated auditory cortex, the parameter that could be differentiated might be the temporal duration of a signal. The dominant hemisphere would have more differentiated responses to short speech signals. In contrast the right hemisphere shows greater overlap among columns, which might correlate with less differentiated or more “holistic” responses. We hypothesise that this might be involved when processing context, humour, or wider semantic fields. A study by Yvert, Crouzeix, Bertrand, Seither-Preisler, and Pantev (2001) on the electrophysiological response to a very short (20 ms) 1 kHz tone shows that individual activity peaks in the left hemisphere are spatially more restricted and spatially further apart than the responses in the right hemisphere. This fits very well with our anatomical model.

That the cerebral cortex expands tangentially during development has been known for a long time. The balloon model provides an explanation of:

- how tangential expansion can lead to asymmetries in cortical fine structure;
- how such anatomical asymmetries can lead to functional asymmetries, in this case specific to speech perception;
- how the seemingly irreconcilable observations of differential length but similar volumes of the planum temporale can be accounted for.

A potential test of this model could be measurements of other cortical areas with notable serial capabilities. One example might be the extended parietal

lobes of Albert Einstein, as reported by Witelson, Kigar, and Harvey (1999). It would be interesting to see if the neuronal column intervals were greater and the cortical thickness less than in “average” parietal regions. In contrast, numerous authors have reported reduced size (surface area) of the left planum temporale in various pathologies, especially schizophrenia. It would be interesting to know if the lesser surface area in such cases is accompanied by a greater thickness—if so, that might imply less differentiated responses to speech signals, similar to the non-dominant right hemisphere.

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