UMIACS-TR-2018-01 **June 2018**

Cell Maps on the Human Genome

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[Keywords: genome, somatotopic map, homunculus, “cellunculus”, organelle-specific gene, connection optimization]

Abstract
Sub-cellular organization is significantly mapped onto the human genome: Evidence is reported for a “cellunculus” -- on the model of a homunculus, on the *H. sapiens* genome. We have previously described a statistically significant, global, supra-chromosomal representation of the human body that appears to extend over the entire genome. Here, we extend the genome mapping model, zooming down to the typical individual animal cell. Basic cell structure turns out to map onto the total genome, mirrored via genes that express in particular cell organelles (e.g., “nuclear membrane”); evidence also suggests similar cell maps appear on individual chromosomes that map the dorsoventral body axis.

1. Introduction

This report proceeds from body maps to cell maps. We converge from macro-scale down to micro-scale. We test a genome mapping model for the individual eukaryotic animal cell. Results are described for significant reflection of cell organization in gene patterns on the human genome.

In plots of mean positions on the genome’s central–peripheral axis of genes expressing in each of 10 major cell organelles (from "nucleus" to "plasma membrane") vs corresponding positions of the organelles themselves within the typical animal cell, the cell-genome correlation is statistically significant (as strong as $p < 0.004$).

As for the body maps reported earlier [1], each of the individual organelle-gene distribution trends by itself is nonsignificant; but the "trend of trends" progression of the set of these slopes together is significant.

We also report evidence suggesting cell maps on individual dorsoventral [DV] chromosomes (i.e., chromosomes that map the dorsoventral axis of the body). This DV cell map is significantly stronger than cell maps on anteroposterior [AP] chromosomes.

Previously, for body maps on individual chromosomes, we had found a “division of labor” for individual chromosomes: Half of the chromosomes appear to represent the DV body axis, the other half the AP body axis. (See Table 2, in [2].) Here, we also find cell mappings are more significant on DV chromosomes than on AP ones. In addition, when our earlier division of labor findings for the body map DV axis on DV chromosomes are combined with similar results for cell maps on DV chromosomes, a functional rationale emerges for observed clustering of DV chromosomes in the core of the spermcell nucleus.

The underlying framework of the research program here is “genome as palimpsest” -- that is, a maps within maps model. The human genome appears to have overlapping layers of various somatic mappings intercalated at different scales. This report focusses on maps of cell microstructure, along with maps of the human body outlined earlier elsewhere [1].

As discussed previously, a functional explanation for these maps would be that they help minimize message-passing costs within the genome. (See [3] for a similar account of connection-optimization in the brain.)

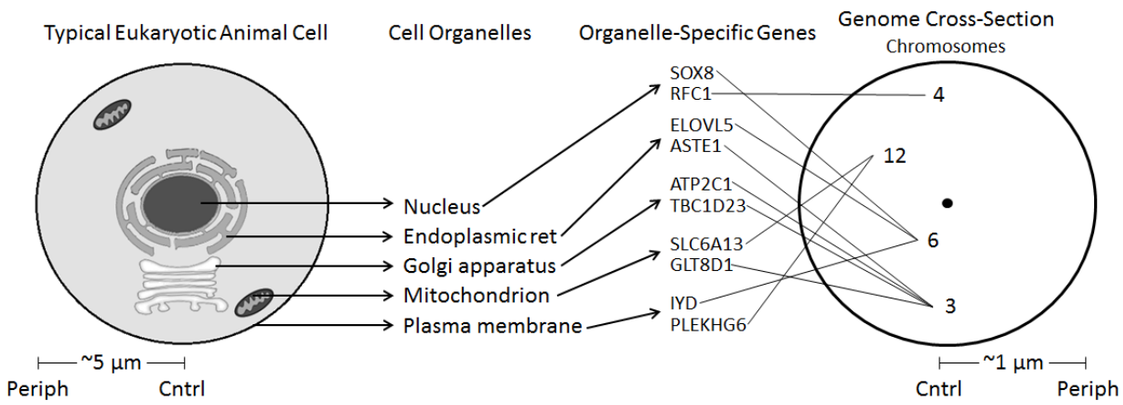

Figure 1. A first approximation: Mapping the typical eukaryotic animal cell onto the human genome, on the central-peripheral axis. Five cell organelles of the ten examined are illustrated. For each organelle, two of the genes that express uniquely in that organelle are shown (derived from [4]). Each gene is then traced to its chromosome. Approximate chromosome sites in the sperm cell nucleus are indicated (based on Table S2, in [1]). So, organelle → genes → chromosomes → nucleus locations.

2. Methods

Fig. 1 diagrams the scheme here for evaluating a cell-genome mapping hypothesis. We start with a cell anatomy model based on the familiar observation of approximate radial organization of the typical eukaryotic animal cell plan.

For instance, on Google, under, e.g., "cell diagram", etc., are hundreds of images (some copying from others), with comparatively few disagreements on the basic radial map of cell organelle positions, from center (nucleus) to periphery (plasma membrane). A familiar illustration of this groundplan is [5].

Because of its extensive, consistent, and recent curation, the Human Protein Atlas [4,6] is used here. The cell schematic then is [7]. (For explanation of cell-anatomical positions of each organelle, see [8].) (See also "Locate" subcellular localization database [9].)

Cell organelles were excluded from this analysis that were not topologically compact on their radial axis (e.g., plasma membrane is included, but not centrosome). Ten organelles then remain. In center-to-periphery order: Nucleus, Nuclear Fibrillar Center, Nucleolus, Nuclear Speckle, Nuclear Body, Nuclear Membrane; Endoplasmic Reticulum, Golgi Apparatus, Mitochondrion, Plasma Membrane.

Appended is supplementary Table S1, a datafile containing our full Protein Atlas genecount datatable. A mean total of 37 distinct genes are expressed in each organelle included. The human Y chromosome has the smallest total gene count, and so does not appear in the present analyses.

It should be observed that, unlike the TiSGeD tissue gene database [10] used for our earlier study of body maps on chromosomes, the Protein Atlas database here does not include information on how strongly a gene expresses in a given target (here, a cell organelle). Therefore, as a first approximation, we next include only genes that each express uniquely in a single type of organelle.

One question is whether this select geneset would suffice to map cell component genes onto the whole genome, as in our report [1] on tissue gene body maps. Another issue is whether the genecounts of the Protein Atlas database would suffice to filter for the most selectively-expressed genes. -- For instance, for genes that each uniquely express in only one cell component. Or, would such a restriction reduce genesets so much that too many empty cells arise in the resulting main table (S2)?

To attempt in this way to boost resolution and sharpen focus of a cell map on the genome, genes maximally specific for *H. sapiens* cell organelles were identified that are listed as expressing for only *one* organelle (e.g., "nucleolus"). For each such cell component, there are a mean 10 such uniquely expressing genes per chromosome. None of the organelles here in fact occur with empty (0) selective gene counts for 1/3 or more of the 23 chromosomes.

Also appended below is supplementary Table S2, with this select Protein Atlas genecount dataset. The original full Protein Atlas datatable S1 includes 8558 distinct genes. The maximally select datatable S2 consists of 2325 genes that each express uniquely in only a single organelle, i.e., 27% of the original full total geneset.

For locating organelle genes in the total genome, chromosome positions can be identified in the genome via Table S2 in [1]. (See Fig. 2 gene distribution example below.)

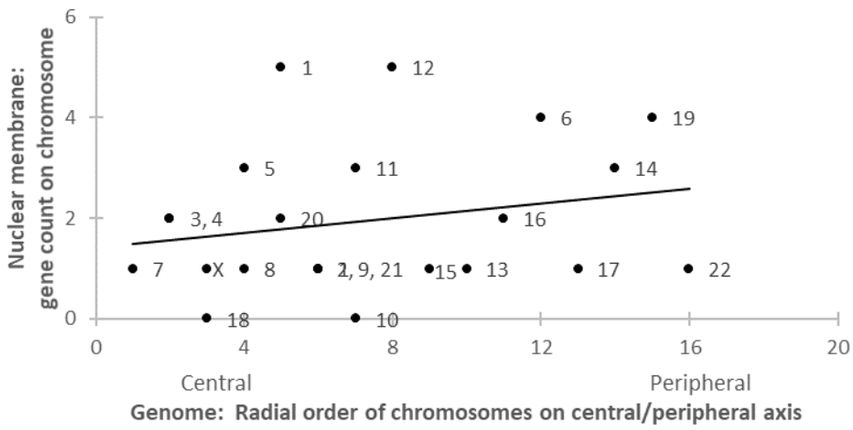

Figure 2. Typical example of distribution of organelle-specific genes on 23 chromosomes in the human genome: here, genes each uniquely expressed in "nuclear membrane" of cell. The positive distribution trend is not strong (r^2 = 0.05); however, when all 10 such sets of organelle-specific genes are fitted together, a statistically strong trend emerges (cf. Fig. 3 below). Each datapoint is labelled with its chromosome number. (Chromosomes 2, 9, and 21 share same genome site on central-peripheral axis, and same organelle-specific gene counts; similarly for chromosomes 3 and 4.)

3. Results

a. Genome Cell Maps

Three successively stronger replications of the cell - genome mapping result are reported here: A simple linear model for the trendlines appears to suffice.

(a) For the original full Human Protein Atlas (Table S1), as opposed to the select Human Protein Atlas, including all genes expressing in the 10 organelles, the cell map on the genome already shows a significant pattern (r^2 = 0.494, p < 0.024, 2 tail).

(b) For the select Human Protein Atlas (Table S2), in the Fig. 3 plot of the 10 organelles, a similar cell-genome correlation is significant and stronger (r^2 = 0.540, p < 0.015, 2 tail).

(c) With datapoints each weighted by their own magnitude of effect r^2 (as in [1]): In a plot of the 10 organelles, the cell-genome correlation further increases in significance (to: r^2 = 0.677, p < 0.004, 2 tail).

Table 4. Cell organelles: Their Central-Peripheral [CP] positions in cell, and the gradient of their genes' distribution in the genome. (Abbreviations of organelle names in Fig. 3 are listed in boldface.) Each gene expresses only uniquely in one organelle-type.

Central		CellAnat **Cell CP Order**	(Slope) **GeneCt Gradient**	r^2	Select GeneCt
Nucleus	**Nucleus**	1	0.1397	0.0027	463
Nuclear Fibrillar Ctr	**NucFibCtr**	2	0.1112	0.095	41
Nucleolus	**Nucleolus**	3	-0.0184	0.0003	178
Nuclear Speckle	**NucSpec**	4	-0.0253	0.0003	221
Nuclear Body	**NucBod**	5	-0.1395	0.0792	83
Nuclear Membrane	**NucMem**	6	0.0730	0.0488	45
Endoplasmic Ret	**EndoRet**	7	-0.1155	0.0105	223
Golgi Apparatus	**GolgiAp**	8	-0.0280	0.0003	253
Mitochondrion	**Mitoch**	9	-0.0520	0.0005	574
Plasma Membrane	**PlasMem**	10	-0.2816	0.0449	244
Peripheral		means	-0.0336	0.0283	232.5
		total			2325

(For explanation of cell-anatomical positions of organelles, see [7,8].)

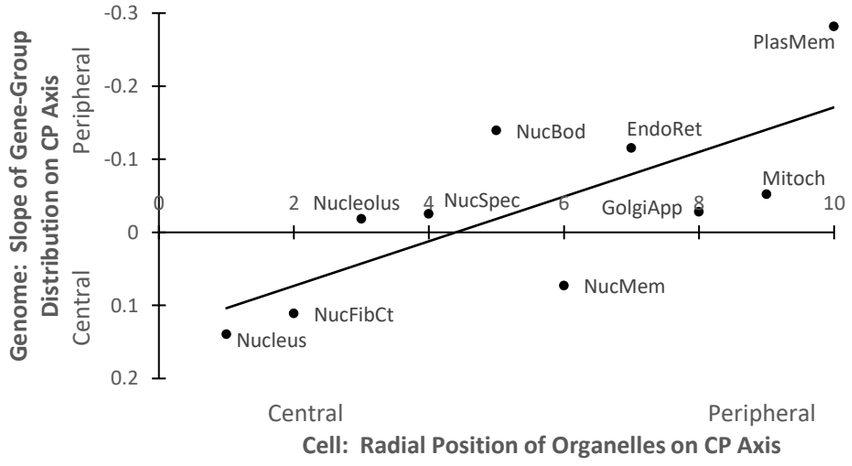

Figure 3. Isomorphism of cell microanatomy and largescale human genome structure: Components positioned more centrally in a cell tend to have their genes correspondingly concentrated on chromosomes sited more toward the center of genome. -- For the maximally selective subset of the Human Protein Atlas (Table S2), where each gene expresses uniquely in only one organelle. Each datapoint is labelled with its organelle-name (see Table 4).

Earlier, we have reported comparable correlation patterns for mapping the human body onto the human genome (cf. Figs. four, five, six in [1]). Again, each individual organelle trend by itself is nonsignificant; but the "trend of trends" progression of the set of these slopes pooled together is significant.

The correlation patterns hold for organelle and gene positions on the Central / Peripheral axis of the genome; in contrast, for the orthogonal Head / Tail genome axis, the pattern is not significant (r^2 = 0.163, p < 0.248, 2 tail).

b. Chromosome Cell Maps

Progressing down to a finer-scale level, we examine cell maps on individual chromosomes: For the plots of the 23 chromosome cell maps, the correlation of cell maps for individual chromosomes is weak, with mean r^2 = 0.022 . (E.g., compared with mean r^2 value for the 10 organelle gene sets in Table 4: 0.028 .) Chr 19 has the strongest r^2 value, r^2 = 0. 0.268 , p < 0.09 . (See attached supplementary summary Table S3.) Once more, each of the individual trends by itself is nonsignificant; but a "trend of trends" cumulative progression of the set of these slopes together approaches significance. Aggregating the 23 correlations yields significant results:

As mentioned earlier, the gene expression databases here for cell organelles do not include a measure of strength of gene expression in a given organelle, while gene expression databases for the earlier body map analyses did include strength of expression. – A project remains open.

Still, as we saw above for cell maps on the complete genome, the chromosome correlations are much stronger for the DV than the AP axis of the genome. Next, comparing magnitudes of cell maps on DV vs AP chromosomes: See earlier chromosome "division of labor," Table 2, in [2]. In this way, cell maps on individual DV chromosomes also seem stronger than those on AP chromosomes. This constitutes further independent converging support of the earlier DV vs AP chromosome distinction for body maps in [2]. (Of the 11 AP chromosomes, 21 & 11 had the two weakest body map r^2 values; hence in this respect, they are the most marginal members of the AP group.)

For mean slope values of cell maps on DV vs AP chromosomes: The DV chromosome set has a mean 25% greater (steeper) slope than the AP chromosome set (p < 0.087, 2 tail). In addition, for mean r^2 values of body maps vs cell maps on DV chromosomes: On DV chromosomes, cell maps have a mean 9% stronger r^2 value than corresponding body maps (p < 0.056, 2 tail). See also Fig. 4 below.

Further localization of cell maps: In the spermcell nucleus, the DV chromosome cluster is positioned significantly rearward of the AP cluster (p < 0.011, 2 tail); so, on the head-tail axis, the cell map chromosomes group in the posterior of the nucleus. In these ways, cell maps appear stronger than body maps.

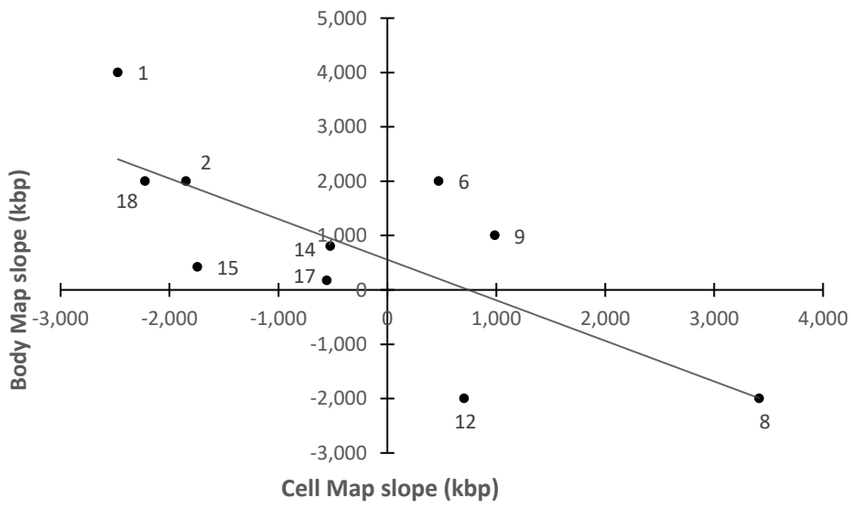

Figure 4. Body map - cell map relationship on DV chromosomes. For each DV chromosome, its body map slope and cell map slope tend to be inversely related ($r^2 = 0.543$, $p < 0.015$). That is, the more positive the body map gradient, the more negative the cell map gradient, and vice versa. (Each datapoint is labelled with its DV chromosome number.) In contrast, AP chromosomes show no significant body map - cell map relationship. Nor do r^2 values of body maps and cell maps show a significant relationship.

4. Conclusion: Global genome structure and function

In the human spermcell nucleus, the concentration of cell maps on DV, not AP chromosomes, suggests an explanation for the significant central cluster of DV chromosomes in the genome. (See Fig. 4, in [2].)

A functional rationale for grouping cell map chromosomes in a compact core, surrounded by a shell of AP chromosomes (as opposed to vice versa (instead positioning DV chromosomes in the shell), or mixing DV and AP sites) can be discerned: Such separation would tend to minimize distances between cell organelle genes, thereby reducing message-traffic costs among cell genes. A typical cell has message-propagation distances that are orders of magnitude smaller than such distances in the entire body of an organism.

Another rationale along similar lines: As a germ cell, the sperm cell has a haploid nucleus. Adult somatic cells are diploid, and do not show the DV-core / AP-shell configuration. (E.g., cf [11].) One interpretation for this difference would be that intracellular message-passing peaks early in the developmental trajectory.

In this way, these cell map findings also provide independent convergent support, and a functional explanation, for earlier body map results regarding the global "core / shell" layout of DV vs AP chromosomes. (See Fig. 5 below.)

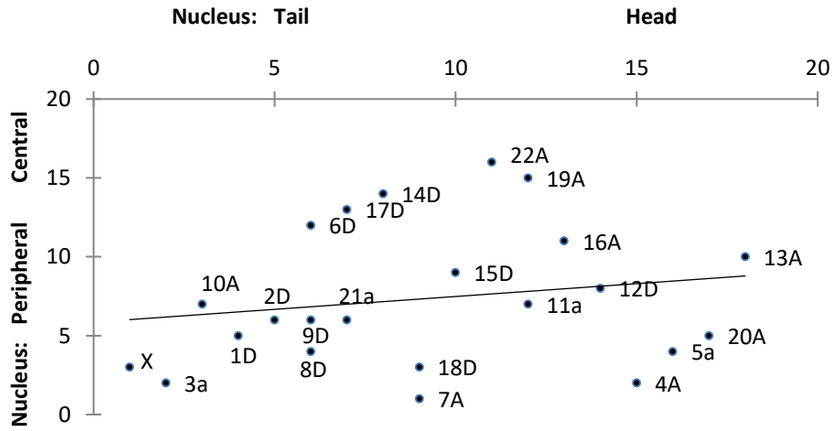

Figure 5. Partial map of centroids of chromosome sites in *H. sapiens* spermcell nucleus (updated). **A**, chromosomes with AP body map; **D**, chromosomes with DV body map (Chrs 3 and 5 are marginally AP). Each chromosome group appears to have a topologically distinct meta-territory in the nucleus: Anteroposterior chromosomes tend to occupy an anterior outer border region (with exception of Chrs 11 and 21), which surrounds an inner core that dorsoventral chromosomes occupy. (Of the 11 AP chromosomes, 11a and 21a have the two lowest AP r^2 values; in this way, they are the weakest (most marginal) members of the AP group.) Each axis gives position-order of chromosomes. (Nucleus map is constructed from Tables S1 and S2, in [1]; based on Figures two and four of [12].) Best fit line for all 23 chromosome positions is included.

* * *

How, if at all, do these cartographic phenomena relate to the rest of genetic physiology? Is so extensive a structure as a genomic map merely functionless ornament upon the genome's terra incognita? As mentioned earlier, a design rationale for this mapping is that such maps may help economize costs of interconnections in the genetic system.

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Supporting Material: Tables S1, S2, & S3.

References

1. Cherniak C, Rodriguez-Esteban R, 2013. Body maps on the human genome. Mol. Cytogenet. 6: 61. doi: 10.1186/1755-8166-6-61

2. Cherniak C, Rodriguez-Esteban R. 2015. Body maps on human chromosomes. College Park, MD: University of Maryland Institute for Advanced Computer Studies Tech Report, UMIACS-TR-2015-04. http://drum.lib.umd.edu/handle/1903/17177 doi: 10.13016/M2MM73

3. Cherniak C, Mokhtarzada Z, Rodriguez-Esteban R, Changizi K. 2004. Global optimization of cerebral cortex layout. Proc Natl Acad Sci USA. 101: 1081-1086. doi: 10.1073/pnas.0305212101

4. Thul P, et al, 2017. A subcellular map of the human proteome. Science. 356(6340).

5. https://commons.wikimedia.org/wiki/File:Animal_Cell.svg

6. http://www.proteinatlas.org/ENSG00000135218-CD36/cell https://www.proteinatlas.org/search

7. http://www.proteinatlas.org/humancell

8. http://www.proteinatlas.org/learn/dictionary/cell

9. Sprenger J et al. 2007. D230-3. LOCATE: a mammalian protein subcellular localization database. Nucleic Acids Res (Database issue) D230-3. doi: 10.1093/nar/gkm950 http://locate.imb.uq.edu.au/

10. Xiao S, Zhang C, Zou Q, Ji Z. 2010. TiSGeD: a database for tissue-specific genes. Bioinformatics 26: 1273-1275. doi: 10.1093/bioinformatics/btq109

11. Bolzer A, et al. 2005. Three-dimensional maps of all chromosomes in human male fibroblast nuclei and prometaphase rosettes. PLoS Biol 3: e157. doi: 10.1371/journal.pbio.0030157

12. Manvelyan M, Hunstig F, Bhatt S, Mrasek K, Pellestor F, Weise A, et al. 2008. Chromosome distribution in human sperm -- a 3 D multicolor banding-study. Mol. Cytogenet. 1: 25. doi: 10.1186/1755-8166-1-25

Table S1. GeneCts per chromosome and cellular location. (Gene entries include **all** subcellular targets.) Website: Human Protein Atlas available on www.proteinatlas.org
Compiled from: **full** Human Protein Atlas v16.1 [Thul P, et al, 2017. A subcellular map of the human proteome. Science 356(6340)].

Cell anatomy	Chromosome	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**X**	**MeanCts**	**Totals**
	Cell Organelle																									
Center	**Nucleus**	173	137	103	73	84	98	87	62	93	85	121	101	28	73	56	81	95	28	160	43	19	43	78	83.52	1921
	Nucleolus fib ctr	20	21	11	11	13	10	9	8	7	15	18	7	5	8	7	13	13	5	22	11	3	5	10	10.96	252
	Nucleolus	127	104	59	51	61	53	49	51	52	58	73	57	22	46	36	53	69	15	86	37	16	26	65	55.04	1266
Ordered by position	**Nuclear speckles**	58	23	25	11	20	31	21	14	13	13	24	20	4	14	12	25	27	8	33	14	3	12	19	19.3	444
on radial axis	**Nuclear bodies**	43	35	30	20	22	22	15	20	18	24	25	22	10	16	17	20	32	5	37	12	5	17	15	20.96	482
	Nuclear membrane	23	27	7	15	11	13	15	8	8	9	19	14	5	11	7	10	17	5	24	8	5	5	6	11.83	272
	Endoplasmic ret	36	31	26	16	24	20	18	21	13	22	28	20	8	14	13	21	21	7	26	17	1	9	18	18.7	430
	Golgi apparatus	103	50	55	37	46	43	46	33	39	42	65	49	15	27	34	39	55	19	69	25	6	17	45	41.7	959
	Mitochondrion	106	75	70	45	48	47	50	32	42	57	73	55	14	41	27	42	56	18	65	17	10	38	38	46.35	1066
Periphery	**Plasma membrane**	148	94	84	52	82	72	71	46	53	59	87	88	30	45	45	60	77	27	92	38	15	33	68	63.74	1466
	[10 of 27 organelles total]																									
	Mean Gene Counts	83.7	59.7	47	33.1	41.1	40.9	38.1	29.5	33.8	38.4	53.3	43.3	14.1	29.5	25.4	36.4	46.2	13.7	61.4	22.2	8.3	20.5	36.2	**37.21**	
	Totals	837	597	470	331	411	409	381	295	338	384	533	433	141	295	254	364	462	137	614	222	83	205	362		**8558**

Range of gene counts for an organelle: 1 - 173 genes (i.e., for each gene expressed in one or more organelles).
Mean count of **all** genes for each organelle: 37.2 genes per chromosome. (Vs total all genes for each chromosome: 372.1)

Table S2. GeneCts per chromosome and cellular location. (Only for genes each with a **single** subcellular target.) Website: Human Protein Atlas available on www.proteinatlas.org
For genome cell map: Compiled from Human Protein Atlas v 16.1 [Thul P, et al, 2017. A subcellular map of the human proteome. Science. 356(6340)].

Cell anatomy		Chromosome	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**X**	**Mean Cts**	**Totals**
		Cell Organelle																									
Center	1	**Nucleus**	52	30	25	12	18	29	31	15	25	16	23	22	6	15	10	18	26	6	45	13	5	7	14	20.13	463
	2	**Nucleolus fib ctr**	5	2	2	2	1	2	1	1	1	0	0	0	2	1	0	5	2	1	6	2	2	2	1	1.783	41
	3	**Nucleolus**	18	13	8	10	8	4	11	9	7	6	7	8	3	3	1	10	15	3	18	4	4	3	5	7.739	178
Radial axis	4	**Nuclear speckles**	32	12	15	7	14	15	6	7	6	3	13	14	3	5	4	11	12	3	17	8	3	3	8	9.601	221
	5	**Nuclear bodies**	5	3	3	5	9	3	6	4	6	5	3	2	3	3	3	5	1	0	6	4	0	0	4	3.609	83
	6	**Nuclear membrane**	5	1	2	2	3	4	1	1	1	0	3	5	1	3	1	2	1	0	4	2	1	1	1	1.957	45
	7	**Endoplasmic ret**	25	16	14	8	10	11	12	8	7	11	12	10	5	8	4	12	11	3	10	12	0	7	7	9.696	223
	8	**Golgi apparatus**	29	14	17	8	12	10	14	3	14	10	18	11	2	7	8	8	14	6	25	8	1	5	9	11	253
	9	**Mitochondrion**	57	41	28	30	28	21	33	15	25	37	40	21	6	25	13	23	32	10	36	9	6	15	23	24.957	574
Periphery	10	**Plasma membrane**	25	17	18	7	14	8	11	11	12	7	19	17	3	5	6	10	12	5	15	7	2	4	9	10.609	244
		Mean Gene Counts	25.3	14.9	13.2	9.1	11.7	10.7	12.6	7.4	10.4	9.5	13.8	11	3.4	7.5	5	10.4	12.6	3.7	18.2	6.9	2.4	4.7	8.1	**10.11**	
		Totals	253	149	132	91	117	107	126	74	104	95	138	110	34	75	50	104	126	37	182	69	24	47	81	**101**	**2325**

[10 of 27 organelles total. Filtered by: compact distribution in cell. And less than 1/3 of chromosomes have 0 genes uniquely expressing in each organelle.]

Range of gene counts for an organelle: 1 - 57 maximally selective genes (i.e., each gene expressed in only one organelle).
Mean maximally selective gene count for each organelle: 10.1 genes per chromosome. (Vs **all** genes for each organelle included: 37.2)

Table S3. Mean position of each cell organelle-specific gene set on its chromosome (in base units, from p-arm origin).
For chromosome cell maps: Compiled from Human Protein Atlas v 16.1 [Thul P, et al, 2017. A subcellular map of the human proteome. Science. 356(6340)].
Each gene position on a chromosome is derived from the Human Protein Atlas entry itself (mean of start and end sites of each gene). Website: Human Protein Atlas available at www.proteinatlas.org

	Chromosome		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	X	
	Cell	Organelle																								
Center	1	**Nucleus**	1.08E+08	9.70E+07	1.08E+08	6.68E+07	1.09E+08	6.87E+07	9.31E+07	1.00E+08	9.35E+07	8.51E+07	8.30E+07	6.95E+07	5.55E+07	5.81E+07	6.87E+07	4.28E+07	4.44E+07	3.59E+07	3.69E+07	4.06E+07	4.28E+07	3.33E+07	7.81E+07	**Nucleus**
	2	**NucFibCtr**	8.04E+07	1.50E+08	1.05E+08	7.76E+07	5.28E+07	3.70E+07	1.06E+08	1.44E+08	3.78E+07				6.95E+07	5.78E+07		6.40E+07	2.58E+07	3.55E+07	4.00E+07	1.05E+07	3.29E+07	3.72E+07	1.04E+08	**NucFibCtr**
	3	**Nucleolus**	9.34E+07	1.18E+08	8.17E+07	9.32E+07	1.08E+08	3.07E+07	9.01E+07	8.05E+07	7.27E+07	7.85E+07	5.79E+07	5.95E+07	5.95E+07	6.32E+07	4.18E+07	4.40E+07	4.93E+07	2.88E+07	3.59E+07	2.70E+07	3.83E+07	3.25E+07	8.13E+07	**Nucleolus**
	4	**NucSpec**	1.07E+08	1.73E+08	9.78E+07	9.94E+07	1.17E+08	5.47E+07	1.05E+08	8.23E+07	1.02E+08	6.03E+07	6.65E+07	6.74E+07	4.83E+07	6.61E+07	6.36E+07	3.23E+07	4.52E+07	2.31E+07	3.97E+07	3.93E+07	3.80E+07	3.95E+07	7.02E+07	**NucSpec**
	5	**NucBod**	1.14E+08	9.87E+07	2.72E+07	6.25E+07	1.03E+08	7.98E+07	6.18E+07	4.90E+07	1.15E+08	7.08E+07	4.95E+07	2.93E+07	6.81E+07	6.22E+07	5.78E+07	5.76E+07	4.01E+07		3.34E+07	2.26E+07			6.79E+07	**NucBod**
	6	**NucMem**	2.14E+08	2.19E+08	5.14E+07	1.25E+08	6.52E+07	3.29E+07	8.57E+05	1.33E+08	9.66E+07		5.92E+07	6.58E+07	2.62E+07	8.76E+07	7.56E+07	8.11E+07	4.02E+07		2.26E+07	1.68E+07	4.44E+07	3.88E+07	3.46E+07	**NucMem**
	7	**EndoRet**	1.23E+08	1.33E+08	9.86E+07	6.91E+07	1.04E+08	6.72E+07	9.14E+07	5.49E+07	9.49E+07	5.57E+07	6.08E+07	5.37E+07	5.34E+07	5.49E+07	7.40E+07	4.39E+07	4.58E+07	4.32E+07	2.05E+07	4.25E+07		3.41E+07	8.99E+07	**EndoRet**
	8	**GolgiApp**	1.13E+08	1.36E+08	1.03E+08	9.78E+07	1.24E+08	5.49E+07	8.80E+07	7.92E+07	8.57E+07	5.47E+07	5.91E+07	5.65E+07	4.91E+07	5.58E+07	6.21E+07	5.47E+07	4.74E+07	5.46E+07	2.53E+07	4.13E+07	4.55E+07	3.60E+07	7.64E+07	**GolgiApp**
	9	**Mitoch**	1.10E+08	1.22E+08	1.13E+08	8.01E+07	1.00E+08	8.19E+07	8.39E+07	9.33E+07	8.31E+07	8.03E+07	7.44E+07	7.75E+07	3.78E+07	6.82E+07	6.37E+07	3.53E+07	4.58E+07	3.89E+07	2.39E+07	2.40E+07	3.64E+07	3.40E+07	6.83E+07	**Mitoch**
Periphery	10	**PlasMem**	1.33E+08	1.44E+08	1.03E+08	7.49E+07	9.56E+07	5.97E+07	6.67E+07	1.04E+08	8.01E+07	9.99E+07	6.58E+07	3.08E+07	7.54E+07	6.96E+07	5.77E+07	3.01E+07	3.28E+07	4.42E+07	3.72E+07	3.61E+07	3.96E+07	4.28E+07	9.30E+07	**PlasMem**

[10 of 27 organelles total. Filtered by: compact distribution in cell. And less than 1/3 of chromos have 0 genes uniquely expressing in each organelle.]

Range of gene counts for an organelle: 1 - **57** maximally selective genes (that is, for each gene expressed in only **one** organelle).
Mean maximally selective gene count for each organelle: 10.1 genes per chromosome. (Vs all genes for each organelle included: 37.2)

(In order to compact the original ChromoCellMap table S3 so that it can be easily printed out, the cellformat of the numerical values has been converted to exponential representation. (E.g., in the above rendering of the table, the mean position-value on Ch 1 of the "nucleus"-specific genes is 1.08E+08 bp ; however, in the original Excel file, the explicit format of this value is still retained as 108166622.3 bp .)