

# Common Scaling Laws for City Highway Systems and the Mammalian Neocortex

A variety of scaling laws are known for the mammalian neocortex relating gray matter volume, total number of synapses [1, 2], white matter volume [3–9], number of neurons [6, 10–12], surface area [4, 5, 13–16], axon caliber [1, 17], and number of cortical areas or compartments [18]. These neocortical scaling laws appear to be a consequence of selection pressure for a sheet-like structure (namely, gray matter) to economically maintain a high level of interconnectedness [1, 2, 19, 20]. We might therefore expect to find similar scaling laws for any sheet-like structure under similar selection pressures, in which case the neocortex would be just an instance of a more general kind of structure.

Here, we investigate city highway systems as a potential kind of network which may be driven by similar principles as the neocortex. In contrast to neurons, which are conduits for information-related signals on which brain computations rely, highways are conduits for physical materials and people. But from the perspective of the city as a whole, the materials and people that highways transport are crucial to the large-scale function carried out by the city, and are, in a sense, signals—that one signal is electric and the other physical may not matter in regards to the fundamental principles governing them. In addition to the *prima facie* analogy between city highway networks and the brain's neural connections, there are several other reasons we chose to examine city highway networks. First, the organization of city highway networks tends to be driven by political and economic forces over decades, rather than being planned in advanced following known principles of highway engineering [21]—i.e., city highway systems are a result of an evolution-like mechanism. Second, cities are under selection pressure to efficiently interconnect via highways and roads. Third, because cities lie on the land they are approximately a surface, or a sheet. Fourth, highway network data are readily available (and our data set consists of 60 U.S. cities varying in population from  $10^4$  to nearly  $10^7$ , see Table 2 for raw data). Finally, the organization of city highway systems is interesting in and of itself: nearly half of Earth's 6.6 billion people now live in cities, and cities are becoming ever larger and densely populated. The proper functioning of a city requires that people and materials be quickly moved throughout it. This is a very difficult design problem, one that is magnified by the fact that city population tends to grow much faster than city surface area, and cities tend to increase in population over time, so that the efficient highway network must constantly evolve from the pre-existing one. Identification of scaling laws governing how highway organization scales with city size could potentially lead to better highway systems, and more efficiently running cities.

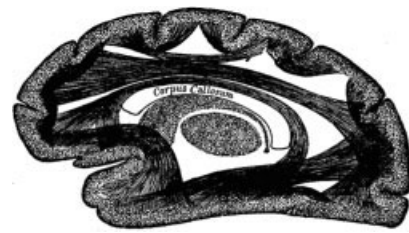
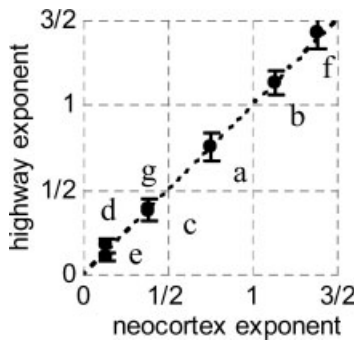
**MARK A. CHANGIZI AND  
MARC DESTEFANO**

*Mark A. Changizi and Marc Destefano are affiliated with the Department of Cognitive Science, Rensselaer Polytechnic Institute, Troy, New York 12180. (e-mail: changizi@rpi.edu)*

**TABLE 1**

Comparison of City Highway System and Neocortex Exponents for Quantities as a Function of Surface Area

Generic Name	Variable for City Highways	City Highway System Exponent	Variable for Neocortex	Neocortex Exponent
Surface area	Land area	1	Total convoluted surface area	1
(a) No. of conduits	No. of highways	0.759 ( $\pm 0.083$ )	No. of pyramidal neurons	$3/4 = 0.75$
(b) Total no. of leaves	Total no. exits	1.138 ( $\pm 0.072$ )	Total no. of synapses	$9/8 = 1.125$
(c) No. of leaves per conduit	No. of exits per highway	0.379 ( $\pm 0.064$ )	No. of synapses per neuron	$3/8 = 0.375$
(d) Diameter of conduit	No. of highway lanes	0.174 ( $\pm 0.038$ )	Diameter of white matter axon	$1/8 = 0.125$
(e) Propagation velocity	Velocity of cross-city travel	0.108 ( $\pm 0.021$ )	Propagation velocity of white matter axon	$1/8 = 0.125$
(f) Total surface area of conduits	Total surface of highways	1.433 ( $\pm 0.096$ )	Total surface area of white matter axons	$11/8 = 1.375$
	Population	1.462 ( $\pm 0.141$ )	Total volume of white matter axons	$3/2 = 1.5$
(g) No. of compartments	No. of concentric ring regions	0.390 ( $\pm 0.055$ )	No. of cortical areas	$3/8 = 0.375$



**RESULTS**

**Number of Highways and Number of White-Matter-Projecting Pyramidal Neurons**

The number of highways in a city is prima facie analogous to the number of white-matter-projecting, pyramidal neurons in neocortex. Because cities have a tendency to be organized radially around an urban city center, we measured the number of highways as the number of radially directed “spoke” highways plus the number of concentric “ring” highways. Combinations of highway segments were categorized as

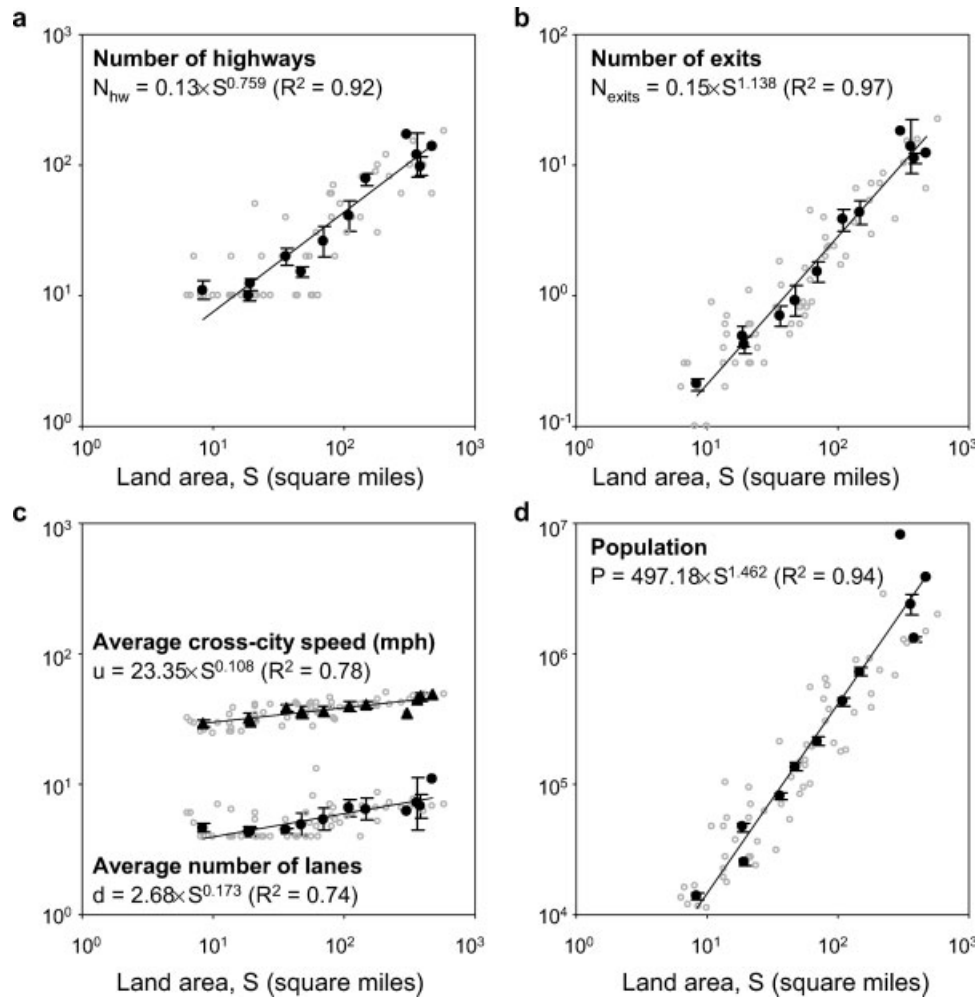
a “ring” if they tended to allow circumferential travel around the city center, and as a “spoke” if they tended to move radially away from the city center. One can easily see this spokes-and-rings organization in most of the larger cities (e.g., the map of Houston is shown above the city columns in Table 1). The number of highways increases in larger cities as approximately the 0.759 (95% confidence interval:  $\pm 0.083$ ) power of land area [Figure 1(a)], similar to the exponent of  $3/4$  found for the number of neurons as a function of total convoluted surface area in neocortex (Table 1a;

exponents range from about 0.7 to 0.81) [10–13]. (We have chosen not to study surface-streets because it is the highways that determine the global-interconnectivity of cities—highways are the “short-cuts” in cities that break out of the local grid and make cities well-connected, analogous to white-matter-projecting neurons.)

**Number of Highway Exits and Number of Neuronal Synapses**

Analogous to synapses in neocortex are highway exits in city highway systems (measured as the number of exits for a unidirectional traversal of all

**FIGURE 1**



(a) Number of highways, (b) number of highway exits, (c) average number of lanes and cross-city (design) speed, and (d) population as a function of land area. Data are from 60 U.S. cities with highways, ranging in population from  $10^4$  to  $10^7$ . Best fit power-law for the binned data shown (raw data shown in light gray, and see Table 2 for raw data values).

highway stretches), and Figure 1(b) shows that the number of highway exits increases as about the 1.138 ( $\pm 0.072$ ) power of land area, or approximately as the 9/8 power. The number of exits therefore increases more quickly than land area, with surface density of exits increasing as the 0.138 power, or approximately the 1/8 power, of land area. In our data gathering, we also measured the number of zip codes

(using [www.city-data.com](http://www.city-data.com)) and the number of public high schools (using [www.greatschools.net](http://www.greatschools.net)), and found that each scales similarly to the number of exits ( $N_{zip} = 0.103S^{1.084 \pm 0.076}$ ,  $R^2 = 0.97$ , and  $N_{pubhigh} = 0.106S^{1.120 \pm 0.097}$ ,  $R^2 = 0.95$ , where  $S$  is land area), so that they, too, have similarly increasing surface density as cities enlarge. Some of the increasing surface density of these infrastructure-like variables may be

accommodated by the “thickness” of cities increasing, because larger cities tend to have taller buildings (for post offices and high schools, for example), and greater numbers of raised highways. We do not currently possess “city thickness” data (e.g., average building height) on which to test whether city thickness rises slowly as approximately the 1/8 power of land area. For neocortex, it is known that the total number of

synapses—which scales proportionally to gray matter volume [1, 22]—scales approximately as the  $9/8 = 1.125$  power of total convoluted surface area (Table 1b; exponents range from about 1.085 to 1.124; Refs. 4, 5, and 13–16). This is very close to the exponent of 1.138 for the total number of highway exits (Table 1b), suggesting perhaps that  $9/8$  may be the theoretical exponent for exits (as well as for number of zip codes and number of public high schools). As was the case for city highway networks, the surface density of synapses rises approximately as the  $1/8$  power of neocortex surface area, and this is entirely accommodated by the thickness of gray matter increasing as the  $1/8$  power [4, 5, 13–16], amounting to a slow increase from about half a millimeter in the smallest mammals to a couple millimeters in man. Gray matter thickness may, then, be akin to the surface density of a city (some of this surface density increase in cities which may literally be due to increasing “thickness,” i.e., to cities growing in the third dimension). An immediate consequence of how the number of leaves (i.e., exits and synapses) and conduits (i.e., highways and white-matter axons) scale is that for both city highway systems and neocortex, the number of leaves per conduit (i.e., no. of exits per highway and no. of synapses per neuron) scales approximately as the  $3/8$  power of surface area (Table 1c). (It also follows that the number of leaves per conduit scales approximately as the square root of the number of conduits.)

### Number of Highway Lanes and Diameter of White-Matter Axons

The number of highway lanes (measured by sampling from each highway using maps.google.com) is *prima facie* analogous to the caliber of an axon, and rises as approximately the  $0.174 (\pm 0.038)$  power of surface area [Figure 1(c), bottom; Table 1d], close to an exponent of  $3/16 = 0.1875$ . In neocortex, the diameters of white-matter

axons scale more slowly than this, namely approximately as the  $1/8 = 0.125$  power of the total convoluted neocortex surface area (Table 1d) [1, 2, 19, 20]. Evidence for this comes both from derivations from other scaling exponents [1, 2], as well as from more direct measurements across myelinated and unmyelinated neurons in corpus colosum leading to exponents of 0.118 [17] and 0.146 [23, extracted from their Figure 1(e)]. [Although these data are across both myelinated and unmyelinated white matter axons, most of the diameter increase in larger brains occurs among the myelinated axons [23]; so the scaling exponent of about  $1/8$  for axon caliber is representative of how myelinated axons scale, not unmyelinated axons.] Highway “caliber” thus appears to scale more quickly than white matter axon caliber (Table 1d). Highways are inherently two-dimensional (or one-dimensional cross section), however, whereas axons are three-dimensional (or two-dimensional cross section), and so some differences in how conduit diameter increases as a function of the number of leaves per conduit may be expected. For neocortex, the number of synapses per neuron,  $\delta_{\text{syn}}$ , appears to relate to axon diameter,  $d_{\text{axon}}$ , as  $\delta_{\text{syn}} \sim d_{\text{axon}}^3$  consistent with Murray’s Law [2, 24–26]. For city highway systems, however, the number of exits per highway,  $\delta_{\text{ex}}$ , appears to relate to highway diameter,  $d_{\text{highway}}$ , as  $\delta_{\text{ex}} \sim d_{\text{highway}}^{0.379/0.174} = d_{\text{highway}}^{2.18}$ . That is, rather than Murray’s  $d^3$ -law holding, it appears closer to a  $d^2$ -law for highways.

### Cross-City Travel Speed and White Matter Axon Conduction Velocity

We measured cross-city travel speed (measured as the road distance traveled across the city divided by the travel duration, using design speeds—i.e., no traffic models were used—, averaged for two trips, one across the “long” axis of the city and the other along the “short” axis, and using a combination of Mapquest and Google

Earth) as the analog of white matter propagation velocity, and found that cross-city travel speed increases as the  $0.108 (\pm 0.021)$  power of land area [Figure 1(c), top; Table 1e]. For neocortex, myelinated axon conduction velocity is directly proportional to axon diameter [27–29], and so white matter axon conduction velocity scales as approximately the  $1/8 = 0.125$  power of total convoluted surface area (Table 1e), which is close to the exponent for cross-city travel speed. Unlike the direct proportionality between speed and conduit diameter for neocortex conduits, cross-city travel speed scales much more slowly than highway diameter [Figure 1(c), and Table 1]—namely speed,  $u \sim d_{\text{highway}}^{0.108/0.174} = d_{\text{highway}}^{0.62}$  (although the slope confidence intervals are sufficiently high that neither a direct proportionality nor a square root law can be rejected).

### Total Highway System Surface Area and Total Surface Area of White Matter Axons

Neocortex white matter volume scales as approximately the  $3/2$  power of total convoluted surface area (with exponents ranging from about 1.4 to 1.52, Table 1) [3–9]. The most straightforward analog of white matter volume for city highway networks would be the entire volume utilized by highways, but we do not currently possess data for highway “depth,” and cannot calculate volume (we do not know, for example, if highway depth scales in the same manner as width). However, highway volume may not be an interesting measure because highway traffic would appear to depend on the width of the highway (or number of lanes), not on the depth. Thus, the total surface area of highways would appear to be of interest, and the neocortical analog of this is the cumulative surface area of white matter axons. Total white matter surface area is the product of the number of neurons, the length of white matter axons, and the axon di-

ameter. Assuming axon length scales as the cube root of white matter volume, one may derive (using exponents in Table 1) that the total surface area of white matter axons scales as the  $11/8 = 1.375$  power of total convoluted surface area. The total highway surface area may similarly be estimated, and assuming highway length scales as the square root of city land area, one may derive (using exponents in Table 1) that total highway surface area scales as the  $1.433 (\pm 0.096)$  power of city land area, close to the  $11/8$  exponent for the analogous quantity in neocortex (Table 1f).

### Population

Population of a city scales approximately as the  $1.462 (\pm 0.141)$  power of city land area [Figure 1(d), Table 1], meaning population density increases nearly as the square root of land area. How do larger cities accommodate such relatively fast increases in population density? Based on the similarity of this exponent to that for total highway surface area, one might speculate that highway surface area per population may be an invariant (although see Ref. [30] where population scales as the 1.205 power of road (not highway) surface area for a set of 29 German cities). That is, it suggests that rather than population being driven by city surface area, population may be being driven by the total surface area of highways, as if each person requires some fixed allotment of highway surface area (e.g., the area required by a car for safe travel). An alternative hypothesis is that perhaps population actually scales as the  $3/2$  power of surface area (also within the 95% confidence interval), and this could be explained by modeling the population as flowing on a surface with a central source or sink (such as the city center), where it has been shown [31] that the mass of the flowing material scales as the  $3/2$  power of the surface area (and,

more generally, as  $(D + 1)/D$  where  $D$  is the dimension of the system).

### City "Ring Region" Compartments and Cortical Areas

An explanation for neocortical scaling concerns the economical manner in which neocortex compartmentalizes as the brain enlarges, and has been successful in predicting the number of cortical areas, interarea connectivity, and intra-area connectivity scale with brain size [1, 2, 18–20]. Cities compartmentalize as well. For example, there tends to be a downtown business district, rather than finding these businesses uniformly distributed throughout the city. Such compartmentalization may tend to minimize costs for the infrastructure needed near businesses, as well as minimizing travel costs for business-business and business-infrastructure interactions, keeping travels short and on surface streets within each functionally specialized area. Too few compartments in a city will tend to be uneconomical because within-compartment travel will become too costly, and too many compartments will tend to be uneconomical because (given that each compartment will tend to require a highway route to all the other areas) of unnecessarily high highway costs. For neocortex, this tradeoff leads to the compartments increasing approximately as the  $3/8$  power of total convoluted surface area [1, 18]. For cities it is not yet clear to us how to measure compartmentalization. Because cities tend to change their make-up as a function of radial distance from city center, one hypothesis for what city compartments might be are the concentric ring regions around the city, starting with city center. For example, the city map shown in Table 1 possesses four concentric ring regions. Interestingly, this notion of city compartments does scale approximately as the  $3/8$  power of land area (no. of ring regions  $\sim 0.335^{0.390 \pm 0.055}$ ,  $R^2 = 0.88$ , Table 1g), although whether this is an

appropriate measure of the number of city compartments we do not yet know.

### DISCUSSION

Cities are not brains, of course, and the metaphor can only be pushed so far. For example, whereas a single white matter axon tends to connect just two regions of neocortex, and makes no direct axon-axon connections, a single highway makes *en passant* exits all along its length, and connects directly to other highways via interchanges (no. of interchanges  $\sim 0.0515^{0.993 \pm 0.127}$ ,  $R^2 = 0.92$ , or approximately directly proportional to land area). And it is not clear what the brain analogy for population might be. Nevertheless, Table 1 and its plot on the upper left show that there are wide similarities for these two radically different kinds of network, suggesting that they are instances of a more general class of network. City highway networks may actually provide a model for better understanding fundamental properties of neocortical scaling, having the benefit of comparably infinite amounts of easily-accessible, free data.

### METHODS

Data were selected so as to have approximately six cities for each 0.25 interval in the logarithmic population range from 4 (i.e., small populations of around 15 k) through 7 (i.e., large populations of nearly 10 million); this could not be kept up among the largest cities because of their rarity, and fewer were accordingly used for several of the upper logarithmic bins. To fill these logarithmic population bins, cities were sampled randomly from <http://www.city-data.com>; a city was rejected if it possessed no highway within its city boundary, or if it was a suburb of a larger city (and thus not the center of its highway network). The data are shown in Table 2. City boundaries were used to determine the extent of the city. The number of high-

**TABLE 2**

Raw Data from 60 Cities Used in the Analysis

Ranges for Binning Logarithm of Population	City	Population	Surf. Area (sq miles)	No. of Highways (Spokes and Rings)	No. of Highway Exits	No. of Public High Schools	No. of Zip Codes	No. of Interchanges	No. of Ring Regions	Average Speed (mph)	Average No. of Lanes
4-4.25	Los Lunas, NM	11,338	10	1	1	2	1		1	24	4
	Williamsburg, VA	11,751	8.5	1	2	3	3		1	26	4
	Amherst, OH	11,872	7.2	2	3	1	1		1	29	5
	Berkeley Heights, NJ	13,407	6.3	1	2	1	1		1	32	6
	Wilsonville, OR	16,075	6.7	1	3	1	1		1	30	6
	Greenfield, IN	16,654	8	1	1	1	1		1	25	4
	Canton, GA	17,685	14.3	1	5	3	2		1	39	4
	Gallup, NM	19,378	13.4	1	4	2	2		1	34	4
	Gillette, WY	22,685	13.4	1	4	4	3		1	30	4
	Elizabethtown, KY	23,450	24.1	2	5	2	1		1	27	4
4.25-4.5	Helena, MT	27,383	14	1	2	2	2		1	27	4
	Douglasville, GA	27,568	21.4	1	3	6	2		1	34	6
	Cookeville, TN	27,743	21.9	1	6	2	1		1	31	4
	Bangor, ME	31,074	34.4	2	8	1	1	1	1	28	5
	Cape Girardeau, MO	36,204	24.3	1	4	2	2		1	35	4
	Wausau, WI	37,292	16.5	1	3	3	2		1	25	4
	Bellevue, NE	47,334	13.3	1	3	2	3		1	25	4
	Tigard, OR	47,968	10.9	1	9	1	1	1	1	30	7
	Battle Creek, MI	53,202	42.8	1	5	8	4	1	1	42	4
	Springfield, OR	55,641	14.4	1	7	5	2	1	1	42	4
4.5-4.75	Cheyenne, WY	55,731	21.1	1	6	4	3	1	1	39	4
	Janesville, WI	61,962	27.5	1	3	2	2		1	41	4
	Medford, OR	70,147	21.7	1	3	3	2		1	41	4
	Santa Fe, NM	70,631	37.3	2	12	6	2	2	1	32	4
	Las Cruces, NM	82,671	52.1	2	6	3	6	2	1	35	4
	Albany, NY	93,523	21.4	5	11	2	10	6	3	41	5
	Macon, GA	94,316	55.8	2	9	9	8	1	1	41	5
	Davenport, IA	98,845	62.8	3	13	6	6	3	1	42	5
	Lowell, MA	103,111	13.8	2	6	1	4	3	1	25	6
	Peoria, IL	112,685	44.4	1	6	12	8	2	1	40	4
5-5.25	Stoux Falls, SD	139,517	56.3	1	16	16	7	3	2	38	4
	Hampton, VA	145,579	51.8	2	8	6	6	1	1	34	6
	Rockford, IL	152,916	56	1	7	10	9	1	1	42	4
	Jackson, MS	177,977	104.9	3	17	10	13	1	1	38	6

**TABLE 2**

(Continued)

Ranges for Binning Logarithm of Population	City	Population	Surf. Area (sq miles)	No. of Highways (Spokes and Rings)	No. of Highway Exits	No. of Public High Schools	No. of Zip Codes	No. of Interchanges	No. of Ring Regions	Average Speed (mph)	Average No. of Lanes
5.25–5.5	Little Rock, AR	184,564	116.2	4	20	11	12	4	3	40	6
	Boise, ID	193,161	63.8	1	9	10	11	1	1	35	4
	Spokane, WA	196,818	57.8	1	8	27	14		1	27	8
	Durham, NC	204,845	94.6	5	24	9	8	5	2	39	5
	Rochester, NY	211,091	35.8	4	18	24	23	5	2	39	5
5.5–5.75	Toledo, OH	301,285	80.6	4	20	24	17	4	2	39	5
	Wichita, KS	354,865	135.8	4	36	14	23	5	2	41	4
	Honolulu, HI	377,379	85.7	2	24	11	11	1	1	31	5
	Tulsa, OK	382,457	182.6	10	71	11	28	15	2	45	5
	Cleveland, OH	452,208	77.6	6	39	25	28	9	2	45	7
5.75–6	Albuquerque, NM	494,236	180.6	3	29	18	18	1	1	39	9
	Washington, DC	550,521	61.4	3	44	41	26	5	2	36	13
	Seattle, WA	573,911	83.9	7	23	34	36	3	2	32	7
	Baltimore, MD	635,815	80.8	6	28	62	20	5	2	42	6
	Memphis, TN	672,277	279.3	6	38	42	28	5	3	43	7
6–6.25	Columbus, OH	730,657	210.3	12	72	32	30	15	3	50	7
	Detroit, MI	886,671	138.8	8	66	38	26	10	4	39	7
	San Jose, CA	912,332	174.9	9	54	44	28	10	3	40	7
	Dallas, TX	1,213,825	342.5	15	153	38	48	29	3	47	8
	San Diego, CA	1,255,540	324.3	10	103	45	30	23	4	45	7
6.25–6.5	San Antonio, TX	1,256,509	407.6	10	158	62	60	17	3	48	6
	Phoenix, AZ	1,461,575	474.9	6	65	42	39	8	3	47	7
	Houston, TX	2,016,582	579.4	18	223	97	96	32	4	49	7
	Chicago, IL	2,842,518	227.1	8	87	116	55	5	4	41	7
	Los Angeles, CA	3,844,829	469.1	14	125	81	61	20	3	49	11
6.75–7	New York, NY	8,143,197	303.3	17	181	110	65	35	4	35	6

The first column indicates the logarithmic range for the populations of cities.

ways was operationalized as the number of radially directed “spoke” highways plus the number of concentric “ring” highways (motivated by the fact that cities have a tendency to be organized radially around an urban city center); combinations of highway segments were categorized as a “ring” if they tended to allow circumferential travel around the city center, and as a “spoke” if they tended to move radially away from the city center; in nearly all

cases counting the number of “spokes” and “rings” suffered little or no ambiguity. The total number of highway exits in a city was measured as the number of exits for a unidirectional traversal of all highway stretches; these data were accessed utilizing Google Maps. The number of zip codes within a city boundary was acquired from [www.city-data.com](http://www.city-data.com). The number of public high schools within a city was acquired from [www.greatschools.net](http://www.greatschools.net).

The average number of highway lanes was determined via Google Maps, sampling the number of lanes for each highway. Cross-city travel speed was measured as the road distance traveled across the city divided by the travel duration, using design speeds—both Mapquest and Google Earth were used to get these estimates—two estimates were made for each city, for trips along the “long” axis and along the “short” axis of a city.

## REFERENCES

1. Changizi, M.A. Principles underlying mammalian neocortical scaling. *Biol Cybern* 2001, 84, 207–215.
2. Changizi, M.A. *The Brain from 25,000 Feet: High Level Explorations of Brain Complexity, Perception, Induction and Vagueness*; Kluwer Academic: Dordrecht, 2003.
3. Frahm, H.D.; Stephan, H.; Stephan, M. Comparison of brain structure volumes in insectivora and primates. I. Neocortex. *J Hirnforsch* 1982, 23, 375–389.
4. Hofman, M.A. On the evolution and geometry of the brain in mammals. *Prog Neurobiol* 1989, 32, 137–158.
5. Hofman, M.A. The fractal geometry of convoluted brains. *J Hirnforsch* 1991, 32, 103–111.
6. Prothero, J. Scaling of cortical neuron density and white matter volume in mammals. *J Brain Res* 1997, 38, 513–524.
7. Allman, J.M. *Evolving Brains*; Scientific American Library: New York, 1999.
8. Zhang, K.; Sejnowski, T.J. A universal scaling law between gray matter and white matter of cerebral cortex. *Proc Natl Acad Sci* 2000, 97, 5621–5626.
9. Bush, E.C.; Allman, J.M. The scaling of white matter to gray matter in cerebellum and neocortex. *Brain Behav Evol* 2003, 61, 1–5.
10. Tower, D.B. Structural and functional organization of mammalian cerebral cortex: The correlation of neurone density with brain size. *J Comp Neurol* 1954, 101, 9–52.
11. Jerison, H.J. *Evolution of the Brain and Intelligence*; Academic: New York, 1973.
12. Passingham, R.E. Anatomical differences between the neocortex of man and other primates. *Brain Behav Evol* 1973, 7, 337–359.
13. Jerison, H.J. Allometry, brain size, cortical surface, and convolutedness. In: *Primate Brain Evolution*; Armstrong, E.; Folk, O., Eds.; Plenum: New York, 1982; pp 77–84.
14. Prothero, J.W.; Sundsten, J.W. Folding of the cerebral cortex in mammals. *Brain Behav Evol* 1984, 24, 152–167.
15. Hofman, M.A. Size and shape of the cerebral cortex in mammals. I. The cortical surface. *Brain Behav Evol* 1985, 27, 28–40.
16. Prothero, J. Cortical scaling in mammals: A repeating units model. *J Brain Res* 1997, 38, 195–207.
17. Shultz, J.R.; Wang, S.S.-H. How the neocortex got its folds: Ultrastructural parameters underlying macroscopic features. *Soc Neurosci Abstr* 2001.
18. Changizi, M.A.; Shimojo, S. Parcellation and area-area connectivity as a function of neocortex size. *Brain Behav Evol* 2005, 66, 88–98.
19. Changizi, M.A. Brain scaling laws. In: *New Encyclopedia of Neuroscience*; Squire, L.R., Ed.; Elsevier: London, 2007.
20. Changizi, M.A. Scaling the brain and its connections. In: *Evolution of Nervous Systems*; Kaas, J.H., Ed.; Elsevier: London, 2007.
21. Mannering, F.L.; Kilareski, W.P. *Principles of Highway Engineering and Traffic Analysis*, 3rd ed.; Wiley: New York, 2004.
22. Abeles, M. *Corticonics: Neural Circuits of the Cerebral Cortex*; Cambridge University Press: Cambridge, 1991.
23. Wang, S.S.-H.; Shultz, J.R.; Burish, M.J.; Harrison, K.H.; Hof, P.R.; Towns, L.C.; Wagers, M.W.; Wyatt, K.D. Functional trade-offs in white matter axonal scaling. *J Neurosci* 2008, 28, 4047–4056.
24. Murray, C.D. The physiological principle of minimum work. I. The vascular system and the cost of blood volume. *Proc Natl Acad Sci USA* 1926, 12, 207–214.
25. Cherniak, C.; Changizi, M.A.; Kang, D. Large-scale optimization of neuron arbors. *Phys Rev E* 1999, 59, 6001–6009.
26. Chklovskii, D.B.; Stepanyants, A. Power-law for axon diameters at a branch point. *BMC Neurosci* 2003, 4, 18.
27. Hursh, J.B. Conduction velocity and diameter of nerve fibers. *Am J Physiol* 1939, 127, 131–139.
28. Rushton, W.A.H. A theory of the effects of fibre size in medullated nerve. *J Physiol* 1951, 115, 101–122.
29. Bullock, T.H.; Horridge, G.A. *Structure and Function in the Nervous Systems of Invertebrates*; W. H. Freeman: San Francisco, 1965.
30. Bettencourt, L.M.A.; Lobo, J.; Helbing, D.; Kühnert, C.; West, G.B. Growth, innovation, scaling, and the pace of life in cities. *Proc Natl Acad Sci USA* 2007, 104, 7301–7306.
31. Dreyer, O. Allometric scaling and central source systems. *Phys Rev Lett* 2001, 82, 038101.