The Bounded Brain:
Toward Quantitative Neuroanatomy

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Abstract

■ An idea that human cognitive resources are virtually without limit turns up at all levels of mind/brain science. This tacit unbounded-resource assumption has paradoxical consequences in neuroscience, particularly involving the quantitative incoherence of some key anatomical studies of cortical connectivity resources: cortical sheet area, synaptic density there, and giant axonic arborizations in visual cortex. This inattention to quantitative consistency checking in neuroanatomy appears to stem from, as a notable instance, something of the nonspatial character of the Cartesian concept of mind being extended to the brain as physical structure. ■

INTRODUCTION

A picture of human cognitive resources as effectively unbounded pervades mind/brain science to a significant extent, in particular at its most concrete level, neuroanatomy. Predominant models of brain structure appear to be profoundly nonquantitative—in some respects, not quantitatively coherent. We will focus on evaluating recent estimates of area of the human cortical sheet, estimates of synaptic densities there, and studies of giant axonic arborizations in the visual cortex. This examination yields some information on actual available cortical connectivity resources that is presently of interest as a basic constraint on models of computation in the brain. Finally, some of the conceptual etiology of the nonquantitative character of brain anatomy will be explored. Although the discussion may somewhat improve estimates of cortical resources, emphasis will be at the level of philosophy and methodology of neuroanatomy, and on how they can productively shift perspectives that guide scientific practice.

"IMPOSSIBILITY ENGINES"

Of several distinct philosophical origins of current tacit ideas of an unbounded mind/brain, perhaps the most important is the Cartesian concept of mind as a nonspatial substance. Descartes (1960) gave his key argument in 1641: "I have a clear and distinct idea of myself in so far as I am only a thinking and not an extended being." Since "by 'body' I understand all that . . . can be located in some place and occupy space," Descartes drew the dualist conclusion that his mind is not a body, or physical object located in space. Over the next three hundred years, Descartes and many others struggled with familiar puzzles of how mind and brain are supposed to be related. But besides this "myth of the ghost in the machine," there is the prior Cartesian claim that the essential feature of mind is its *nonspatial* character. A second "myth" or tacit picture seems to continue to operate in even the most concrete reaches of mind/brain science, even among antidualists: something of the nonspatial character of the Cartesian mind is unthinkingly extended to the brain. (Such a tendency is, perhaps, only natural, once one opts for mind–brain identity.) The mind, and therefore the brain, cannot be numbered. To the extent that the brain is being tacitly conceived of not as a physical object located in three-dimensional space, its structures will tend not to be thought of as having spatial dimensions. Trends toward an unscaled, nonquantitative "Cartesian anatomy" are then all too understandable.

The pervasiveness of the idea that our cognitive resources have no bounds—in some cases, are actually infinite—is worth emphasizing. At least since the emergence of the formal theory of computation in the 1930s, three levels of abstraction in describing and explaining computational entities have been distinguished: (1) the highest level of the pure function or logical operation, (2) the level of the algorithm or software for executing a given operation, and (3) the most concrete level of the hardware for physically realizing a given algorithm. Interestingly, "impossibility engines" requiring quite unrealistic resources seem to occur in the models at all levels. Much of the basic philosophical conception of a cognitive system consisting of belief and goal structures is drawn from the idea of man as a perfectly rational

animal with unlimited ability to process information. One of the most striking features of this rationality idealization, which has been tacitly incorporated into many of the models in philosophy, is that it entails the triviality of much of the deductive sciences. It was uncovering such logical impossibility engines in philosophical models of mind (Cherniak 1986) that prompted the present author to wonder whether similarly extreme unrecognized idealizations might lurk at more concrete levels in cognitive science.

The next explanatory level of mind/brain science is that of specific algorithms for accomplishing a given operation. Cognitive psychology and artificial intelligence are concerned with identifying such procedures, whether actually employed by human beings or to be executed by machine. Yet the decrease in abstractness here does not seem to yield that much gain in real-world feasibility of the models. One can argue (Cherniak 1988) that the fundamental framework of computational psychology, the very idea that much of human mentality can actually be represented by some huge superprogram, takes no account of the size of this "big text," nor, consequently, of the issue of the profound unmanageability of such an enormous artifact for the cognitive scientist himself. Similar questions can be raised about tendencies in recent connectionist work on massively parallel and massively interconnected "neural" networks; some of the networks, if they were actually realized in nerve cells, would each require a brain the size of a bathtub (Cherniak 1990).

The bottom level of concreteness concerns hardware specification; in the case of human cognition, of course, this is the physiology and anatomy of our brain. But, perhaps most surprisingly, when we turn to this most down-to-earth level, a parallel tacit picture of resource unboundedness seems to persist. This blind spot contrasts strongly with the insightful meticulousness that characterizes other aspects of neuroanatomy. The models rather frequently turn out still to be quite unrealistic quantitatively regarding available spatial and temporal resources—for instance, regarding volume budgets of the structures described. Shepherd (1979, p. 8) notes that Cajal's epochal work (1911) did not include a single scale marker for any diagram; Carpenter and Sutin (1983), a current standard medical textbook of neuroanatomy is still sparse, giving only some magnifications for photomicrographs. The one-of-a-kind extended effort toward a quantitative atlas of the brain was Blinkov and Glezer's (1968) compilation, now out of print in English for over a decade. This discussion will draw heavily on its hundreds of tables. A little more attention to scale seems worthwhile, just in terms of some neuronal bean-counting to check the basic bookkeeping.

To sharpen the thesis, it should be noted that a strong tradition certainly exists in neuroanatomy of collecting quantitative measurements; the crucial oversight focused on below is, rather, at the higher level of simple consis-

tency checking of these lower level descriptive results for quantitative coherence. A further point in defining the present enterprise: Exhaustive historical review, analysis, and evaluation of the large primary literature of the last century of neuroanatomy on the three specific topics below would be an unwieldy task. Instead of focusing on practical problems of technique, we pursue a division of labor: our primary objective concerns a methodological metaissue—the pervasiveness of inattention to basic analytical questions of quantitative coherence in these key neuroanatomical studies. As will be seen in the next section, there is profound disagreement on even the most basic numerical estimates; hence any specific quantitative conclusions based upon them here can be regarded only as provisional starting points.

AREA OF THE CORTICAL SHEET

The human cerebral cortex is a complex, convoluted structure, but still, of course, a physical entity entirely located in three-dimensional space—not some hyperdimensional Klein's Bottle. Since it is conventionally viewed as the seat of most higher cognitive processes, "cortical imperialism"—a tendency for research attention to focus on it—is only natural. One of the most basic questions about the cortical sheet concerns its total flat surface area. Table 1 lists several influential estimates of this figure, all except those of Blinkov and Glezer's published within the last decade or so, many by major anatomists and physiologists.[1] The striking feature of the set of estimates, of course, is that they range over more than *an order of magnitude*. (If the estimate of 4 m^2, given to the author in a recent personal communication by a cerebellar anatomist at a major United States medical school, were added to this table, the estimates would range over closer to a factor of 100; 9 m^2 is the highest estimate offered by any of the neuroscientists so far queried.) A 1 m^2 or greater estimate is not idiosyncratic; Hubel and Wiesel (1979, p. 150) had to correct them-

Table 1. The Human Cerebral Cortex Sheet: Surface Area Estimates[1]

Cortex area (mm^2)	Source
80,000	Rakic (1981, p. 3)
~120,000	Shepherd (1979, p. 221)
139,000	Hubel (1979, p. 150)
160,000	Blinkov and Glezer (1968, p. 172)
200,000	Colonnier (1981, p. 126)
200,000	Carpenter and Sutin (1983, p. 644)
307,500	Hofman (1983, p. 111)
400,000	Mountcastle (1978, p. 37)
1,000,000	Anderson and Hinton (1981, p. 32)

selves, "In a 1963 article . . . one of us gave the area [of the cerebral cortex] as 20 square feet and was quickly corrected by a neuroanatomist friend in Toronto, who said he thought it was 1.5 square feet—'at least that is what Canadians have.'"

It is as if higher quality published estimates of the height of a normal human adult varied from 1 to 12 feet. A more apposite comparison might be early maps of the New World dating from the voyages of discovery; yet in fact calculations from Mercator's 1587 map of the world yield an area estimate for the North American land mass, despite some *terra incognita*, that appears to differ from current figures by less than a factor of two (Paullin 1932, p. 14B). No doubt there are many explanations of such remarkable divergence in ideas about the size of the cortical sheet. Some of the techniques employed differ considerably. But it is also worth noting that both simpler estimations of normal cranial volume and more abstract norms for IQ do not show such extreme variability. Determining the area of a complex structure is a nontrivial task, but still seems feasible in an era, as the platitude goes, when science can land men on the moon. The role of the present discussion cannot be second-guessing in a highly technical field; however, a basic metaneuroanatomical point still emerges, that there seems to have been little, if any, recognition or discussion in print of these striking disparities. As a bit of informal sociology of the field, a few dozen anatomists have been Socratically queried about these estimates; all expressed surprise about their wide range. Hence, the possibility emerges of considering and explaining this nonrecognition in terms of some deep, tacit tendencies toward a way of viewing the brain.

For, the higher estimates of cortex area are quantitatively incoherent in a very concrete sense: As noted, there is no disagreement about normal cranial volume averaging a little below 1.4 liters, nor about cerebral cortex thickness averaging 2 mm or more (with mean thickness running lower at folds). But then

$$1,000,000 \text{ mm}^2 \text{ cortex area} \times 2 \text{ mm thickness}$$
$$= 2,000,000 \text{ mm}^3$$

That is, such a 1 m^2 "all-cortex brain" alone requires around 2 liters, considerably more than the 1.4 liter total available brain volume. Not much refinement of such calculations is needed to exclude some of the lower cortical sheet estimates: A 400,000 mm^2 cortex 2 mm thick requires 800,000 mm^3; on the assumption that all other brain structures combined required a similar volume (in fact, all other cerebral structures alone should require a corresponding volume), total brain volume would again exceed actual cranial volume. If volume of the cerebral hemispheres, minus estimates of the volume of white matter, major vascular system, thalamus, and major nuclei, is considered, the upper end of the cortical sheet estimates can be further constrained.

Therefore, the explanation for such very large and unacknowledged area discrepancies does not appear to be only "gray-area" indefiniteness regarding what counts as cortical surface in the sulci, or differences in definition or criteria or measurement techniques for cortical surface (e.g., how allowance has been taken for shrinkage of tissue during fixation), or practical difficulty of the measurements, or differences in populations sampled, or in natural variation of cortex area as opposed to brain volume. Something more basic may also be involved, a way of seeing—or tending to fail to see—the cerebral cortex as part of a physical structure, the brain, with dimensional magnitudes that ought to cohere with each other. [The estimates reported in Blinkov & Glezer (1968, pp. 172–173, 346, 374) of around 160,000 mm^2 appear the most likely to be in the correct range (Blinkov and Glezer do not note the diversity of estimates discussed here); they agree well with the recent measurements of Jouandet, Tramo, Herron, Hermann, Loftus, Bazell, & Gazzaniga (1989, p. 95).]

Simple but pervasive quantitative consistency slips elsewhere in neuroanatomy contribute to the mystification of the cortex. Shepherd (1979, p. 347) had to write, "It is a commonplace to cite an estimate of 10 billion neurons contained within the human neocortex as evidence for the fantastic overgrowth and therewith unprecedented capabilities for complex functions of this region. Those who cite this figure invariably fail to recall that the number of granule cells in the cerebellum is probably several times this number." It is as if there is some tension between cortical imperialism and the idea that the neurons in the seat of higher cognition could be outnumbered by the cell population of an area commonly pictured as merely mediating walking and chewing gum, so to speak. As another instance of flawed arithmetic that fits with the idea of an *idée fixe* of cortical imperialism, Nauta and Feirtag (1979, p. 96) state that neocortex "is estimated to contain no fewer than 70 percent of all the neurons in the central nervous system" of man and other primates. Shepherd's discussion of the cerebellar granule cells makes clear that even qualitatively, this is not a fair claim. Individually, cases such as these illustrate only the uninteresting point that nobody and nothing (including, inevitably, the present discussion) is perfect; together, they begin to suggest an intriguing pattern of higher level nonquantitativeness.

MICROCONNECTIVITY RESOURCES

The examples occupying the rest of this paper focus on small-scale cortical connectivity. Some of the most interesting directions of recent investigation in mind/brain science involve exploration of models of massively parallel and massively interconnected computation in the brain (see, e.g., *Cognitive Science* 1985, and Rumelhart & McClelland 1986). Attention has only just begun to turn to the fundamental question of the actual neural realizability of these avowedly neural-metaphor models.

As mentioned earlier, a number of the connectionist constructs seem in fact to be cognitive impossibility engines. Surely a quantitatively coherent neuroanatomy becomes crucial here; the above inconsistencies in simple estimates of cortical sheet area do not bode well for current approaches to more complex anatomical questions. The most local connectivity constraint is synaptic density, particularly in cerebral cortex. What are the available cortical microconnectivity resources? Again to shift the perspective, a truism contrary to Cartesian anatomy: Real synapses are not infinitesimal, dimensionless geometrical points or junctions; each has a small but finite volume. They are not "everywhere-dense" (in the topological sense that, between any two points on the real number line, another can always be interpolated), nor comparable to the dimensionless spheres representing molecules in the classical ideal gas laws. Actual synapses have a maximum packing density. We need to check how many synapses can fit on the head of a pin.

What is the volume of a synapse? It is easier to raise such a question than to settle it. Synapse structure epitomizes the stunning diversity of the nervous system; one can get a sense of the brain as ultimate Rorschach blot, with no typical or representative cases, and few perceivable central tendencies. Synaptic junctions—often not well-defined—include not only end enlargements in the form of knobs, but also spines, claws, mossy terminals, and many other intricate shapes. To constrain this diversity somewhat, we will tend to concentrate on primate primary visual cortex. In addition, we will proceed by "qualitative arithmetic," where we seek only rough approximations of the volumes of the complex structures involved. That will suffice for some simple bookkeeping review.

Cragg's (1967) electron microscopic study of cortical synapses yielded average diameters of the order of 0.6 μm for mouse and monkey visual and motor cortex, with monkey visual cortex synapse mean diameter of 0.72 μm. (Cragg reported E. G. Gray's similar unpublished results, that rat visual cortex synapses had an average profile diameter of 0.73 μm.) In Cragg (1975), one of the most often cited electron microscopic studies of human cortex synapse density, the dimensions of the synapse structures (and synaptic appositions alone) in the plates and tables seem to agree with this quantitative picture. These dimensions are also confirmed by Gray (1959), and Peters, Palay, and Webster's ultrastructure atlas (1970). [For recent studies supporting these results, see also Colonnier's review (1981) of synaptic types in cat and rat neocortex, and Peters' review (1985) of rat visual cortex synapse anatomy.]

Therefore, visual cortex synapse volume—including both pre- and postsynaptic structures—by itself should fall at least in the 0.2–0.4 μm³ range. Measurements from Valverde's (1985) remarkably vivid Golgi-method camera lucida drawings of macaque primary visual cortex suggest as much as a mean 1 μm³ per synapse estimate.

Similarly, in their horseradish peroxidase studies of macaque striate cortex, Blasdel and Lund (1983) report 0.5–2 μm diameter boutons. [Carpenter & Sutin's (1983, p. 119) single choice for a micrograph of a presumably typical axodendritic synapse from human cerebral cortex yields a volume in excess of 2 μm³.] It should be emphasized that estimates of overall synaptic volume overhead must include not only the volume of the junction structures themselves in isolation, but in addition the volume of other cell structures that are dedicated exclusively to a particular synapse. For example, one can calculate the average length of fiber associated uniquely with each synapse of a given type; Valverde's (1985) camera lucida drawings suggest a figure of as high as 5 μm of dendrite and/or axon (see also Blasdel and Lund, 1983, pp. 1398, 1407) per synapse for macaque visual cortex. We can thus suppose that the volume of each synapse plus its uniquely associated structures will average around 1 μm³.

A table of synaptic density estimates can be assembled that begins to resemble the set of cortical sheet estimates of Table 1. Most importantly, there is again the danger signal of estimates ranging over more than an order of magnitude. Toward one extreme, Hubel (1979, pp. 45–46) gives total human neuron and synapse populations that entail roughly 1000 synapses/neuron; this is for the entire brain, but therefore also includes the extremely high synapse densities observed for cerebellum. Toward the other extreme, Cragg (1975, p. 85) reported 39,000 synapses/human cortical neuron in frontal, temporal, and parietal areas.[2] In between fall estimates such as Colonnier's (1981, p. 127) of 15,000–30,000 synapses/cortical neuron. Ten thousand synapses/neuron is a rather typical claim for cerebral cortex. Of course, complexity of synaptic structure, and its variability for different human brain regions, makes comparison of different synapse density estimates much more difficult than comparison of cortical area estimates.[3]

Nonetheless, some natural questions of quantitative coherence emerge. (See Table 2 for a summary of the following calculations.) To begin, what is the total volume of the average cortical neuron—synapses, dendrites, soma, axons, and all? This crucial constraint on modeling of real-world cortical connectivity is not very readily available. Despite difficulties of generalizing across vast diversity, there seems to be rather good agreement that mean human cortical neuron density is about 50,000 neurons/mm³ of cortical tissue. The range is from 30,000 neurons/mm³ for motor cortex (Brodmann area 4) to over 100,000/mm³ for primary visual cortex, a variation of a factor of 3 (e.g., Blinkov & Glezer 1968, pp. 203, 398, which includes data from Shariff 1953; see also Pope 1978, p. 16; Peters 1987, pp. 269, 273; O'Kusky & Colonnier 1982). Therefore, mean available volume per human cortical neuron would be around 20,000 μm³.

Of course, an all-neuron brain would be another impossibility engine. The brain is commonly characterized

Table 2. Estimating the Volume-Budget of an Average Human Cortical Neuron: Soma, Dendrites, Axons, and Synapses

Mean density: ~50,000 neurons/mm³ cortical tissue   Hence, total available volume/neuron = ~20,000 μm³

Fine-scale vascular system of cortex: ~5% total volume
   Extracellular spaces in cortex: ~20%
   So, remaining cortical volume: ~75%

Volume of neurons < volume of glial cells   Hence, neuron volume = ~30% total cortical volume
Therefore, actual mean volume/neuron = ~6000 μm³

Mean soma volume estimate: ~1600 μm³
   So, volume of dendrites, axons, and synapses of "typical"
   cortical neuron = ~4400 μm³

See text for explanation and references.

as over 10 times more metabolically active than the mean rate for the human body. Neurons cannot be dense packed as a pure matrix, burning immaterial ectoplasm; they require a vascular system, glial cells, and extracellular spaces. As a start on a large issue, let us attempt an estimate of this volume overhead. Blinkov and Glezer (1968, pp. 252, 267) cite measurements that suggest the intracerebral vasocapillary system alone (as distinct from larger intracerebral arteries and veins) occupies about 7% of the volume of gray matter. (Cortical capillaries have an internal diameter of about 7 μm, with a volume 2 to 3 times larger than in the white matter. These terminal vessels are supplied by intracerebral arteries with diameters of 8 to 20 μm, in turn fed by radial arteries with a diameter of 10 to 42 μm that sink into the cortex at intervals of around 500 μm.) Then there is a corresponding venous system (we exclude major extracerebral arteries and vessels). Let us suppose that the finer-scale vasculature of the mature cortex by itself could occupy 5% of its volume.

On extracellular spaces in adult cerebral cortex: Carpenter and Sutin (1983, pp. 22, 134) note that estimates by electron microscopy run lower than estimates from neurochemical techniques, but give a range of recent values consistent with 10% or greater volume. After reviewing conflicts between different techniques, Pappius (1982) concludes that a consensus has emerged, that interstitial space in cerebral cortex tissue constitutes 15 to 25% of total tissue volume. We will assume 20% volume. On glia: Blinkov and Glezer (1968, pp. 239, 252) concluded that neurons occupy a smaller proportion of brain tissue than neuroglial cells and their processes; Carpenter and Sutin (1983, p. 135) state that mammalian neuroglial cells alone may comprise almost half of total brain volume. With 5% vessel volume and 20% extracellular volume, 75% of brain volume would remain available for neurons and glial cells, which suggests neurons might occupy less than 40% of total brain volume. In

fact, ion-uptake studies of Vernadakis (1968, p. 397) give the neuronal space for adult rat cortex as 35%, which turns out to agree fairly well with Pope's (1978, p. 18) estimation of the neuronal compartment of human neocortex at 35–40% of the fresh volume. Adjusting the latter estimate in light of Vernadakis' study, plus the hypothesis that species with larger brains have a larger glial volume proportion (Tower 1973, 1978), let us suppose as an approximation that neurons constitute about 30% of adult human cortical volume.

With 20,000 μm³ of cortical volume available per neuron, it would follow that the actual mean volume of a human cortical neuron falls in the range of about 6000 μm³. Of course, within this average value there is room for enormous variance. For instance, Blinkov and Glezer (1968, p. 387) give calculations of the volume of cell bodies alone of pyramidal cells from seven Brodmann areas that range from 297 μm³ to 2953 μm³, about an order of magnitude of variation. [Calculations from data compiled by Blinkov & Glezer (1968, pp. 394, 396) suggest mean volume of the soma only of cortical neurons in general might be around 1660 μm³.] A basic coherence question for most customary synaptic density estimates can now be glimpsed. Even just 10,000 synapses, each requiring 1 μm³ volume, per average neuron would result in something worse than an "all-synapse cortex," for there simply does not seem to be enough room in the cortex for 10,000 μm³ of synapses per neuron, even if the rest of the neurons' structure were crowded out entirely. The main conclusion here is that a priori, only the lower range of synaptic density estimates for human cerebral cortex appear to be realistic candidates. Once the above soma volume estimate is subtracted from the mean total neuron volume, less than 4400 μm³ remains for dendrites, axons, and specifically synaptic structures. Therefore, it would be difficult to explain a mean synaptic density per cortical neuron that ran much above 4000. At 4000 synapses per neuron, hardly any volume would remain for dendrite or axon trunks.

LOCAL AND MID-RANGE CONNECTIVITY

The next stage in a connectivity analysis of the cortex is to proceed to extrasynaptic but still relatively local connections—in the 5 to 1000 μm distance range from a given neuron. And a natural first step is to ask, what is the maximum connectivity capacity of a single average cortical neuron? In particular, what is the total length of dendritic and axonic fiber available for an average-volume neuron? If a neuron's processes were infinitely thin wires, to go with geometrical points as synapses, its connectivity could be unlimited; but that is only another impossibility engine. We need first to determine some mean values for diameters of feasible fibers.

Of course, there is a great range. (1) Generally, considering the entire nervous system: Shepherd (1979, p. 343) describes apical dendrite trunks of sensory cortex

pyramidal cells, at 5–10 μm diameter, as among the thickest dendrites in the nervous system. At the other extreme, thin axons can be found in the cerebellum, such as unmyelinated parallel fibers of granule cells, with a smallest diameter of only 0.2 μm, gradually increasing to 1 μm (1979, p. 219); or again, unmyelinated afferent axons of receptor cells in the olfactory mucosa are "extremely thin," approximately 0.1–0.3 μm in diameter (1979, p. 153). Blinkov and Glezer (1968, p. 170) cite studies of long-range fiber densities in human corpus callosum and anterior commissure that indicate a mean cross-section of 1 μm diameter or more, and a recent study of monkey cerebral commissures by Lamantia and Rakic (1989) reveals fine axon diameters of about 0.3–0.7 μm. (See also Feldman 1984, p. 161; Bullock & Horridge 1965, p. 150; Fulton 1949, p. 323.) Hillman (1979, p. 480) reports mean minimum diameter attained by dendrites, across a range of cell types, as 0.76–1.1 μm. (2) Specifically for the primate visual system: Blasdel and Lund (1983, p. 1400) found that afferent axon trunk diameters in the white matter of macaque primary visual cortex range between 2 and 5 μm. The very smallest processes in the visual cortex, in the vicinity of synaptic terminals, generally might not go much below 0.3 μm diameter; see the high-magnification light micrographs in Shkol'nik-Yarros (1971, Chap. 2) for rabbit, cat, dog, monkey, and man (no correction appears to have been made for tissue-fixation shrinkage). For electron micrographs of rat cortex, see Gray (1959) and Peters et al. (1970). Valverde's (1985) camera lucida drawings suggest a rough estimate of near 1 μm mean diameter for macaque visual cortex longer range fibers.

A fairly safe, as well as computationally convenient, guess therefore might be to begin by exploring the supposition that *average* fiber cross-sectional area in adult visual cortex (areas 17, 18, and 19), with axon generally smaller than dendrite, approaches approximately 1 μm². With about 4000 μm³ available for the dendrites, axons, and synapses of the average cortical neuron, it would seem that such a neuron could have no more than 4000 μm of 1 μm² fiber, or 6000 μm of 0.75 μm² fiber. The fact that there might be only half a centimeter or so of intracortical connectivity per neuron in turn has other anatomically interesting implications.

The mid-scale range of cortical connectivity is 1–10 mm, still within one Brodmann area. According to the classical picture, the most salient structural feature of the cortex with respect to connectivity is extremely limited "horizontal" connections within the cortex beyond about 1 mm length. Anatomical work of Lorente de No (1949) suggested a predominantly vertical organization of fibers in the neocortex, from layer to layer. Physiological studies by Mountcastle (1957) for motor cortex and Hubel and Wiesel (1962) for visual cortex added the idea of a columnar cortical organization, with segregated cylinders or arrays of neurons less than 1 mm diameter having common functional roles, such as edge-orientation de-

tection. What emerges, then, is the prospect of most mid-range cortical connectivity having to proceed relatively indirectly via the deeper white matter, with a potential for some puzzling connectivity bottlenecks there.

However, more recent studies (Gilbert & Wiesel 1983; Rockland & Lund 1983; Blasdel & Lund 1983) with intracellular injection of horseradish peroxidase (HRP) reveal a different picture, of intrinsic horizontal cortical connections over long distances, up to 4 mm or more. [In fact, considerably earlier, Sholl (1955), using conventional Golgi techniques, had reported tangential fibers in the cat visual cortex that extend for "several millimeters."] From the perspective of a connectivity analysis of cortex, a basic issue is the density of these longer range connections. Can they provide a relatively major proportion of cortical connectivity, or is their role apparently more limited? Gilbert and Wiesel (1983, pp. 1116, 1118) provide some information: They report neurons that form widespread clustered axonal projections occur in all layers of area 17 of the cat cortex, with at least half of the pyramidal and spiny stellate cells studied of this giant-arbor type. Pyramidal and spiny stellate cells together constitute the preponderance of cortical neurons. In effect, giant-arbor neurons are therefore observed to be distributed on the two orthogonal dimensions of cortical layer and cell type.

The quantitative question here is, what is the maximum feasible density in the human primary visual cortex for longer range axonal arborizations? What is the highest proportion of area 17 neurons that could have such long connections? (Table 3 summarizes the following calculations.) The half-dozen cells shown in Gilbert and Wiesel (1983) have axon arbors alone with mean total length exceeding 20 mm. (In addition, it seems a presently open question whether even current HRP techniques typically fill more than about 80% of a neuron's complete giant arborization.) Starting with the earlier idea of an average 1 μm² fiber cross-section, the giant axon arbor by itself of such a cell would occupy an average volume of over

Table 3. Estimating the Total Gray Matter Connectivity-Budget of an Average Neuron in Human Primary Visual Cortex

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Density in area 17 > 100,000 neurons/mm³

Hence, all-cortex neuron volume estimate of Table 2 yields mean volume/area 17 neuron <3000 μm³

Less soma and dendrite volume (and afferent arbors) yields mean axonal connectivity volume <~2000 μm³

For mean 1 μm³ cross-section fiber[a] yields ~2000 μm of axon length for average area 17 neuron

On these assumptions, if even 10% of area 17 neurons had giant arbors of 20 mm total length, no volume would remain for axons of the other 90% of neurons

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See text for references.

20,000 μm^3. As previously discussed, neuron packing density in area 17 is the highest in the human cortex, over 100,000 cells per mm^3; our 6000 μm^3 cell volume estimate was for the all-cortex mean of 50,000 cells per mm^3, and so would be lowered for average area 17 neurons to less than 3000 μm^3. [Glial cell counts/mm^3 (Blinkov & Glezer 1968, pp. 416, 420) and capillary lengths/mm^3 (Blinkov & Glezer 1968, pp. 432, 433, 436) for different cortical areas are consistent with a supposition that glial and vascular overhead in area 17 is comparable to other areas of the cortex.] After soma and dendrite arbors are taken into account, the average axonal connectivity available per human neuron would fall below 2000 μm, around a tenth of the giant axon arborization mean. Also, area 17 tissue must include afferent axons from the lateral geniculate nucleus and elsewhere. This suggests that if even one-tenth of the primary visual cortex neuron population had such giant arborizations, no volume would remain for axons of the other 90% of the cells. Thus, based on the above argument, giant axon arborizations could occur in only a proportion of the cell population below 10%. If the actual proportion of giant-arbor neurons numbered anything like the reported 50%, their dense web would entirely dominate the anatomy of the primary visual cortex—yielding, in effect, an "all-axon cortex."[4] This seems to open questions about the role of the giant axon arborizations in visual processing.

A rather elementary sampling model would explain the high observed ratios of neurons with large arborizations. In the conventional HRP procedure a micropipette electrode is first inserted into the cortical area being studied until a single cell is penetrated, as indicated by recorded potentials; the cell's receptive field properties are then electrophysiologically mapped (the great majority of striate cortex neurons appear to have classically characterizable receptive fields, so there is not much electrophysiological prescreening), after which the cell is injected with HRP. The probability of such a virtually random microelectrode penetration intersecting a cell of a given size would be a function of the area of the profile of the neuron in the plane perpendicular to the microelectrode track. In this way, a population of giant neurons with, for example, a mean 10 times the profile area of the average neuron would, other things being equal, be 10 times more likely to be randomly sampled. In fact, this skewness could be affected by the character of the typical distribution of a given cell type's processes—e.g., whether they are densely compacted and overlapping or spread out (as the giant arborizations are). It should also be noted that finer fibers are less likely to be successfully impaled by a micropipette; this will reduce the effective profile area of the giant axonic arborizations. (However, it also appears likely that these cells have larger than average cell bodies.) Thus, with the observed ratio of electrophysiologically characterized giant-arbor neurons of 50%, and a proposed sampling

correction of around 10:1, the estimated actual ratio of giant cells would be only in the range of 5% of the total population, yielding, of course, a much more feasible volume of these cells.

In interpreting this quantitative discussion, it is interesting to consider some lesion experiments by Sperry and co-workers, in which monkey motor cortex (Sperry 1947) and cat occipital–parietal cortex (Sperry & Miner 1955; Sperry, Miner, & Myers 1955) were cut vertically in a cross-hatched pattern. These studies appear to have stood the test of time so far (e.g., Berlucci & Sprague 1981, p. 416). In the cat visual cortex, the slices extended 2 mm deep and so severed intracortical connections while leaving underlying white matter tracts largely intact. (Postmortem micrographs indicated no regrowth of intracortical fibers; in some cases mica "insulating" strips had been inserted.) The lesions formed an approximate grid of less than 1 mm spacing—roughly columnar dimensions. It is as if an arbitrary and "impermeable" columnar structure had been imposed on primary and association visual cortex. Yet, after recovery, the cats retained the ability to make fine and complex global visual pattern discriminations at close to the upper limits of their original preoperative capacity. Complete ablation of these cortical areas does destroy these discrimination abilities, so these "micro-ablation" experiments suggest that longer range direct intracortical connections—such as those revealed in the recent HRP studies—may in fact not be necessary at all for high-level visual performance. There is thus some convergence with the above quantitative analysis of the giant arborizations.

The final stage of a connectivity analysis of the cortex concerns long-range fibers; the mean 170 mm length × 140 mm width of the total human cerebrum (Blinkov & Glezer 1968, p. 109) gives some idea of the maximum possible connection lengths. Here attention must turn from traditional cortical imperialism to constraints imposed by the cerebral white matter. Long-range connections each cost more in volume than shorter range ones, and so have to be particularly sparse. An analysis of global connectivity bottlenecks requires, as well as the above quantitative results on local connectivity, some of the formalisms of combinatorial network optimization from graph theory and computational complexity theory, and can be found in another study (Cherniak 1990).

ETIOLOGY OF CARTESIAN ANATOMY

The above discussion suggests that when impossibility engines appear in neuroanatomy, they exceed actual available resources by about an order of magnitude or two. Relative to higher level models, this is a moderate overshoot—but nonetheless an impressive one, given the unavoidable concreteness of anatomy, as opposed to, for example, philosophy of mind. The more concrete the model, the less extreme the idealization of resources; but tacit idealization continues, with required resources

generally overestimated, not underestimated. The picture of prevalent quantitatively incoherent neuroanatomy sketched here seems sufficiently puzzling to invite questions regarding its proper interpretation. In making sense of scientific practice, it is natural, and proper, to appeal to some "principle of (moderate) charity": A methodological account of the behavior should make it at least minimally reasonable from the practitioner's perspective. Thus, it is no explanatory digression to inquire into the etiology of the idea of brain as impossibility engine. There are, of course, important reasons for the lack of higher level consistency analysis that arise from actual practice—for instance, techniques diverging so widely that comparisons become difficult. However, we focus here instead on some of the theoretical presuppositions that also seem to drive this pervasive inattention to quantitative coherence checking; the rationale for concentrating on the latter etiology is that sometimes basic shifts of conceptual perspective can lead to posing usefully different types of internal questions. There seem to be several distinct philosophical origins of quantitative incoherence here.

1. The picture of an unbounded mind/brain was introduced earlier as joining "the myth of the ghost in the machine," and indeed perhaps arising by a kind of cognitive momentum from Cartesian mind–brain dualism. Hence, a so-called "Cartesian anatomy" of the brain, on the model of the mind, as an only quasi-spatial substance, with dimensions—and questions of their mutual consistency—lacking or tending to be overlooked.

2. The notion of an algorithm as something like an abstract mathematical structure, hence without spatial location or magnitudes, can also carry over to the conception of brain as algorithm-follower. In this way, another source of the picture of cognitive resource unboundedness is the idealizations of classical computation theory: A basic unifying framework of cognitive science is computational psychology—mind conceived of on the model of a hardware-independent Turing machine, with potentially infinite available time and space. A tendency to leap to a corresponding tacit notion of the brain is then perhaps understandable. The main insight of computational psychology, that program, not physical realization, is supposed to be the basic structure, the essence of mind, would thereby reinforce predilections to overlook quantitative anatomy. When, for example, the classical Pitts–McCulloch "neuron" idealization is overextended and reified, taking on a life of its own—with dimensionless, infinitesimal cell bodies and synapses, one-dimensional axons and dendrites—its "anatomy" does indeed suggest unlimited spatial resources.

3. Yet another diagnosis of the source of a quantitatively incoherent anatomy might be characterized as the *qualitative heuristic*, a theoretician's quick and dirty strategy of simplification by retaining basic qualitative proportions, but intentionally avoiding and discarding

quantitative information. Given the distinctive—indeed, putatively unrivaled—complexity of mind–brain phenomena, the drive toward this simplifying strategy should be uniquely powerful here. The remarkably ubiquitous human tendency to reject event base rate information in probabilistic reasoning, extensively examined by Tversky and Kahneman (1982), for example, in their studies of the "representativeness" and "vividness" heuristics, seems a special case of this qualitative heuristic. Another would be the human tendency to simplify quantitatively by "thinking linearly"—that is, treating exponential curves as if they were the more cognitively manageable straight lines of linear functions. We thereby arrive at impossibility engines through our failures to perceive threats of exponential explosion, and limits to their growth. Nonetheless, sound rationales for some use of the qualitative heuristic must be emphasized—in fact, the methodology of qualitative arithmetic employed throughout the quantitative anatomy of the present discussion is just another instance of this heuristic.

4. Attention to matters of bookkeeping in neuroanatomy can seem mean-spirited or beside the point when the human brain is viewed as microcosmos or monad, reflecting—indeed, comparable to—the entire universe. Neuroscientists like to assert that our brain (setting aside that of the elephant or whale) is the most complex natural physical structure we now know of in the universe. They also like to point out that although our brain has 100 billion neurons, our galaxy has about the same number of stars (and the entire known universe contains about the same number of galaxies). Toward a purely quantitative demystification of the brain, one can reply that, as noted earlier, the cerebellum—concerned with posture, muscle tone, etc.—contains at least four times the neuron population of the cerebral cortex, putative seat of higher mental function. Similarly, the lymphocytes alone of the human circulatory system outnumber the neurons of our nervous system by at least an order of magnitude (Jerne 1985). Indeed, a few tablespoons of yogurt contain more than 100 billion lactobacillus bacteria. Furthermore, the apparent information-representation capacity of the cortex is in fact by no means unrivaled, much less unbounded (Cherniak 1988). On the usual assumption that the synapse is the necessary substrate of memory, supposing very roughly that (given anatomical and physiological "noise") each synapse encodes about one binary bit of information, and a thousand synapses per neuron are available for this task: 10^{10} cortical neurons x 10^3 synapses = 10^{13} bits of arbitrary information (1.25 terabytes) that could be stored in the cerebral cortex. But the Library of Congress contains 80 million volumes, which (with an average book of 300 typed alphanumeric pages) is

$$8 \times 10^7 \text{ volumes} \times 300 \text{ pages} \times 16 \times 10^3 \text{ bits/page}$$
$$= 3.84 \times 10^{14} \text{ bits}$$

that is, 48 terabytes. On this type of rough estimate, the

cerebral cortex could not even contain all the information in the 25 million volume Lenin Library.

5. Finally, we must turn to a motivation for the idea of an unconstrained mind/brain that appears to originate in concerns about the relation between the scientific world view and human values. The issue can be couched as the question of what is the essence of personhood or humanity, traditional answers including rationality, the capacity for language, or a type of functional/computational organization. We can now add another candidate for an answer, that human beings are quantitatively distinct—it is our unbounded complexity of mind and brain that is unique, that puts us on top. What is at stake here is not only the analytic matter of what it is to be a person, but also what it is that gives persons any distinctive moral worth. This is not just species snobbery, but rather a matter of preserving our distinctive moral value in view of a perceived encroachment of the naturalistic view of the universe and our species' place in it. In such a context, quantitatively romanticizing the brain is understandable and, in a sense, admirable: The problem of the human mind's place in nature is solved by making the brain into microcosmos, comparable to the entire universe. But even as subtext, this still seems incorrect; the puzzle remains of finding sound bases for humanity toward humanity.

CONCLUSION

This discussion has attempted to show how a type of methodological self-awareness—a bounded-resource philosophical framework—can shift point of view so that different internal neuroscientific issues are considered. A quantitatively self-conscious perspective suggests, surprisingly, that even the most concrete level of mind-brain science, neuroanatomy, like more abstract explanatory levels, needs to focus more attention on questions of quantitative coherence. Analysis of published figures has also in fact yielded a few approximate estimates—with ample but indefinite margins of uncertainty—relating to human cortical connectivity resources that constitute basic constraints on models of massively parallel and interconnected computation in the brain: (1) Total cortical sheet area falls in the 100,000–200,000 mm^2 range. (2) Mean cortical synapse density should not run higher than about 4000/neuron; at 4000/neuron, an average of approximately 200 million synapses/mm^3 of cortex would be available. (3) The mean total gray-matter connectivity available per cortical neuron will be around half a centimeter of dendrite and/or axon—yielding about 1/4 km of connections/mm^3 of cortex. These estimates, as emphasized earlier, can only be a provisional starting point. In this way, some redefinition of research agenda emerges, toward a quantitatively coherent, and therefore computational, neuroanatomy.

Notes

1. The figures in Rakic (1981) and Mountcastle (1978) are for neocortex only; Blinkov and Glezer (1968, p. 374) state that neocortex occupies over 95% of the total cerebral cortex surface.

2. Cragg's influential estimate of cortical synapse density is so high that it begins to approach some of the synapse densities cited for cerebellar Purkinje cells, among the highest in the human nervous system. Some conjecture seems in order regarding just what the source of the apparent internal disparity between Cragg's synapse size and density estimates is. One part of a possible explanation is the fact that Cragg's (1975, p. 85) mean neuron density of 15,600 neurons per mm^3 of normal cortex is about two to four times lower than conventional estimates (e.g., Blinkov & Glezer 1968, p. 398). However, even if neuron volume is adjusted upward for Cragg's neuron density range, his synapse density still seems to leave no volume for the rest of the neuron. [Cragg (1975, pp. 85 and 88) also unaccountably gives somewhat different synapse densities.]

3. Uncertainties about the extent of tissue fixation shrinkage, and whether or not it has been taken into account, contribute considerably to the divergence of synapse density estimates. For instance, for tissue fixation techniques for light microscopy, cited estimates of volume reduction range from 45 to 83% (Cragg 1967, p. 639; Blinkov & Glezer 1968, p. 17; Konigsmark 1970, p. 318). See also O'Kusky and Colonnier (1982, pp. 281, 286). There are also questions concerning non-uniformity of shrinkage, and the extent of shrinkage of specimens for electron microscopy.

4. As a perturbation analysis, the maximum feasible population of giant arbor neurons should be recalculated for axon diameter ranges that are significantly finer than cortical fiber diameters previously reviewed. If *mean* diameter were assumed to be around 0.5 μm, yielding a cross-sectional area of 0.25 μm^2, then if 50% of the population of neurons had these slimmer giant arborizations, still no volume ("negative volume," actually) would be left for the axons of any other neurons. Even for this different regime of diameter assumptions, a question remains regarding the very great proportion of available cortical volume that so dense a web of giant arborizations would occupy.

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