

Chapter 1

Scaling in Nervous Networks

Why are biological structures shaped or organized like they are? For example, why is the brain in the head, why is the cortex folded, why are there cortical areas, why are neurons and arteries shaped like they are, and why do animals have as many limbs as they do? Many aspects of morphology can be usefully treated as networks, including all the examples just mentioned. In this chapter I introduce concepts from network theory, or graph theory, and discuss how we can use these ideas to frame questions and discover principles governing brain and body networks.

The first topic concerns certain scaling properties of the large-scale connectivity and neuroanatomy of the entire mammalian neocortical network. The mammalian neocortex changes in many ways from mouse to whale, and these changes appear to be due to certain principles of well-connectedness, along with principles of efficiency (Changizi, 2001b). The neocortical network must scale up in a specific fashion in order to jointly satisfy these principles, leading to the kinds of morphological differences between small and large brains.

As the second topic I consider the manner in which complexity is accommodated in brain and behavior. Do brains use a “universal language” of basic component types from which any function may be built? Or do more complex brains have new kinds of component types from which to build their new functions?

The final topic concerns the nervous system at an even larger scale, dealing with the structure of the nervous system over the entirety of the animal’s body. I show that the large-scale shape of animal bodies conforms to a quantitative scaling law relating the animal’s number of limbs and the body-to-limb proportion. I explain this law via a selective pressure to minimize the amount of

limb material, including nervous tissue (Changizi, 2001a). That is, because we expect nervous systems to be “optimally wired,” and because nervous systems are part and parcel of animal bodies, reaching to the animal’s extremities, we accordingly expect—and find—the animal’s body itself to be optimally shaped.

One feature connecting the kinds of network on which we concentrate in this chapter is that each appears to economize the material used to build the network: they appear to be volume optimal. It is not a new idea that organism morphology might be arranged so as to require the least amount of tissue volume [see, for example, Murray (1927)], but in recent years this simple idea has been applied in a number of novel ways. There are at least three reasons why optimizing volume may be evolutionarily advantageous for an organism. The first is that tissue is costly to build and maintain, and if an organism can do the same functions with less of it, it will be better off. The second reason, related to the first, is that minimizing tissue volume gives the organism room with which to pack in more functions. The third reason is that minimizing tissue volume will tend to reduce the transmission times between regions of the tissue. These three reasons for volume optimization in organisms are three main reasons for minimizing wire in very large-scale integrated (VLSI) circuit design (e.g., Sherwani, 1995); we might therefore expect organisms to conform to principles of “optimal circuit design” as made rigorous in the computer science fields of graph theory and combinatorial optimization theory (e.g., Cormen et al., 1990). ...and we might have this expectation regardless of the low level mechanisms involved in the system.

Y junctions

The first quantitative application of a volume optimization principle appears to be in Murray (1926b, 1927), who applied it to predict the branching angles of bifurcations in arteries and trees (e.g., aspen, oak, etc.). He derived the optimal branch junction angle (i.e., the angle between the two children) to be

$$\cos \theta = \frac{w_0^2 - w_1^2 - w_2^2}{2w_1w_2},$$

where w_0 , w_1 and w_2 are the cross-sectional areas of the junction’s parent and two children. One of the main consequences of this equation is that, for symmetrical bifurcations (i.e., $w_1 = w_2$), the junction angle is at its maximum of 120° when the children have the same cross-sectional area as the parent segment, and is 0° when the children’s cross-sectional area is very small. [Actually, in this latter case, the branch angle falls to whatever is the angle between

the source node of the parent and the termination nodes for the two children.] That is, when trunks are the same thickness as branches the branch angle that minimizes the volume of the entire arbor is 120° . This is very unnatural, however, since real world natural arbors tend to have trunks thicker than branches. And, if you recall your experience with real world natural arbors, you will notice that they rarely have junction angles nearly as high as 120° ; instead, they are smaller, clustering around 60° (Cherniak, 1992; Changizi and Cherniak, 2000). *Prima facie*, then, it seems that natural arbors are consistent with volume optimality. Murray also derived the equation for the volume-optimal angle for *each* child segment relative to the parent, and one of the main consequences of this is that the greater the asymmetry between the two children's cross-sectional areas, the more the thinner child will branch at 90° from the parent. We find this in natural arbors as well; if there is a segment out of which pokes a branch at nearly a right angle, that branch will be very thin compared to the main arbor segment from which it came. Qualitatively, then, this volume optimality prediction for branch junctions fits the behavior of natural junctions. And it appears to quantitatively fit natural junctions very well too: These ideas have been applied to arterial branchings in Zamir et al. (1983), Zamir et al. (1984), Zamir and Chee (1986), Roy and Woldenberg (1982), Woldenberg and Horsfield (1983, 1986), and Cherniak (1992). Cherniak (1992) applied these concepts to neuron junctions, showing a variety of neuron types to be near volume-optimal; he also provided evidence that neuroglia, Eucalyptus branches and elm tree roots have volume optimal branch junctions. [Zamir (1976, 1978) generalized Murray's results to trifurcations, applying them to arterial junctions.]

Although it is generally difficult to satisfy volume optimality in systems, one of the neat things about this volume optimization for natural branch junctions is that there is a simple physical mechanism that leads to volume optimization. Namely, the equation above is the vector-mechanical equation governing three strings tied together and pulling with weights w_0 , w_1 and w_2 [see Varignon (1725) for early such vector mechanical treatments]. If each of the three junction segments pulls on the junction with a force, or tension, proportional to its cross-sectional area, then the angle at vector-mechanical equilibrium is the volume-optimizing angle (Cherniak, 1992, Cherniak et al., 1999). Natural arbors conforming to volume optimality need not, then, be implementing any kind of genetic solution. Rather, volume optimality comes for free from the physics; natural arbors like neurons and arteries self-organize into shapes that are volume optimal (see, e.g., Thompson, 1992). In support of this,

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