

Optimisation of Biological Transport Networks

Yuankai Lu and Dan Hu*

*School of Mathematical Sciences, Institute of Natural Sciences, and MOE-LSC,
Shanghai Jiao Tong University, Shanghai 200240, China.*

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Abstract. Transport networks such as blood vessel systems and leaf venation are universally required for large-size living organisms in order to overcome the low efficiency of the diffusion in large scale mass transportation. Despite substantial differences in living organisms, such networks have many common patterns — viz. biological transport networks are made up of tubes and flows in tubes deliver target substances. Besides, these networks maintain a tree-like backbone attached with small loops. Experimental and mathematical studies show many similarities in biological mechanisms, which drive structural optimisation in biological transport networks. It is worth noting that the structural optimisation of transport networks in living organisms is achieved in the sense of energy cost as a consequence of natural selection. In this review, we recall the exploration history and show mathematical structures used in the design of biological transport networks.

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1. Introduction

Transport networks play important role in natural and industrial systems. Rivers carry water to oceans and lakes, highways and railways transport people and goods all around the world, telecommunications networks transmit information, and blood vessels and leaf veins transport substances in living organisms.

However, the transport capacity of various networks is limited by the flow processing capacity of network nodes (aviation networks), by the conductance and width of network edges (rivers and blood circulation systems), or by both factors mentioned (internet). In general, the conservation of matter leads to constraints on the flow in different edges. If there is no node capacity, the flow constraints are instantaneously satisfied. Otherwise, a delay is allowed to satisfy the flow constraints. For information networks, such constraints are weakened greatly by a possible information replication on nodes. The limitations in transport capacity and constraints in flows determine the main geometrical and topological

*Corresponding author. *Email address:* hudan80@sjtu.edu.cn (D. Hu)

characteristics of the networks — e.g. biological transport networks usually contain various loops while maintaining an impression of a tree-like backbone [23, 29]. Here, we review the exploration of the designing principle of biological transport networks.

The first breakthrough in biological transport networks was the experimental finding of an approximate cubic law in blood vessel bifurcation — viz. $D^3 = D_l^3 + D_r^3$, where D , D_l , and D_r are the radii of the parent vessel and its left and right daughter vessels, respectively [71]. This law is now referred to as Murray's law due to Murray's deep insight between the bifurcation relation and the optimisation principle in energy cost. According to Murray explanations, this is a consequence of another cubic relation between blood flow Q and vessel radius D , $Q \propto D^3$. In Murray's theory, the latter cubic relation is obtained by the optimisation of the total energy cost — i.e. the fluidic cost in driving blood flow in the vessel and the biological cost in metabolism and material, which includes the material cost in producing blood cells and building the blood vessel wall and the energy consumption in functioning of these cells [54]. Murray's law is also observed in plant vessels and leaf venation [49].

Murray's law provides the deep understanding of the local structure of biological networks. Following the idea of energy-cost optimisation, mathematical models have also been used to understand the geometrical and topological characteristics of an entire biological transport network. For different transport networks, a power law relation $E_m = C^\gamma$ can be generally introduced for the metabolic and material cost E_m and flow resistance C . This relation is used to show that for fixed flow sources (sinks) a network has a tree-like structure if $\gamma < 1$ [5, 6, 14]. In general, there are many loops attached to the tree-like backbone in biological transport networks [9, 11, 29, 34, 55]. Animals and plants can benefit from such loop structures in various ways. By incorporating the risk tolerance in network damages [29] or the effects of fluctuating flow distributions [9, 29, 30], optimal structures are shown to be loopy networks while maintaining a major structure of a tree-like backbone. Such a structure is also believed to afford great benefits to living systems for their mechanical robustness [34].

Optimisation of the energy cost can be viewed as the consequence of natural selection. Highly efficient and robust transport networks, which optimise the energy cost while satisfying tissue demanding, bring tremendous competitive advantages to species. Nevertheless, in order to achieve such an optimisation, life systems have to find special mechanisms such as an adaptation dynamics driven by specific stimuli (which means signals sensed by cells and modulate their cellular dynamics).

The Murray's law also suggests that the wall shear stress, which is proportional to Q/D^3 , is a constant in the entire circulation system at optimal state. This implies that the wall shear stress should be an important stimulus that drives blood vessel adaptation to achieve the optimisation of the network structure. Indeed, experimental studies verified that the wall shear stress in a circulation system lies in a relatively narrow range [19, 23, 25, 58–60]. Further studies have shown that endothelial cells, which form the inner layer blood vessel walls, can really sense the wall shear stress [31–33]. The wall shear stress acts as a key stimulus for both blood flow regulation in the short term response and blood vessel adaptation in the long term response [19, 23, 25, 31–33, 58–60].