Insects Separate Diffusing Particles In Parallel

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ABSTRACT

The circulation of insects and other invertebrates transfers heat, mass, and momentum within micro-fluids through phase interfaces of complex geometry at size ranges important for developing compact energy and chemical systems. Pump size and vascular resistance limit tubular transport of vertebrate systems shrunk to insect volumes. Within bodies <3-4 mm long, flies, beetles and bees disperse and separate diffusing substances in a large body cavity. Body movements and an open tubular pump stir fluid over organs that absorb and contribute substances in parallel. This robust exponential network is most efficient at the smallest dimensions when a 3D volume of blood converts to a 2D surface, increasing transmission probability from 0.34 to 1.

Keywords: hemolymph, networks, miniaturization, dynamical systems, topology

1 INTRODUCTION

From a "law" based on mammalian pulmonary and cardiovascular systems, West et al. (1997) derived a ¾ power allometric scaling relationship for metabolic rates describing distribution through linear space filling fractal networks of branching tubes suggesting such distribution systems characterized all organisms [1, 2, 3, 4].

However, vertebrate generalizations do not work well for invertebrates. Insects are masters of miniaturization. Before shrinking human engineered systems towards insect dimensions, we must learn how insects do it, because an insect's world is far different from ours.

The smallest insects operate in ranges of fluid flow substantially different from those of other animals and larger insects. For example, gravity is of little consequence to most insects; they fall without damage and alight on walls and ceilings. Water's surface tension, however, drowns them, necessitating specialized mouth-parts and long legs to keep them from the dangers of drink.

Insect bodies contain novel morphologies and mechanisms within thin cuticles. A fly's thorax contains asymmetric muscle machinery bathed in blood (hemolymph) beating the wings in excess of 100 Hz at 20% efficiency. Hemolymph transfers the other 80% of this energy to the abdomen dissipating it as heat. Cool hemolymph returns to the thorax [5]. These physiological mechanisms, together with their regulators and suppliers of energy, control bodies and wings in volumes less than half a millimeter cubed.

Insect miniaturized systems are incredibly successful. They function well in all climates at atmospheric pressures. One indicator of how successful insects are, is that global insect biomass is $10 \wedge 12^{th}$ kg worldwide, and insect numbers may be $10 \wedge 18^{th}$. Each insect has a mean mass of 1 mg. In contrast, the biomass of the world's people is only $2x10 \wedge 11^{th}$ kg assuming $\sim 5X10 \wedge 9^{th}$ individuals, each having a mean body mass of 40 kg averaged over all the human ontogenetic stages [6]. There are 5-10 million species of insects and only 42 thousand vertebrate species; consequently, insects provide an incredibly rich source of ideas for miniaturizing engineering innovations.

For all animals, systems generating and transferring mass and energy are integrated into a seamless network of anatomical parts and metabolic processes. We understand the roles of the structures of the cardiovascular systems of vertebrates in these networks, but we know very much less about how substances circulate within invertebrates.

This paper compares topological graphs for the vertebrate circulation network and the insect network and contrasts their scaling properties. Shrinking a vertebrate circulation reveals the lower limits for its size. The smallest insects may reduce what is a three dimensional fluid volume of hemolymph in a larger insect into a two-dimensional surface, facilitating transport that may be further augmented by the movements of locomotion.

2 NETWORKS

The robustness of any pattern of connections for a circulation is rooted in how well its constituent parts supply a maximal number of metabolic interactions. Any circulatory design must insure connection of all cells with nutrients, fluids, gases and other substances while removing wastes and conserving or removing heat. Because circulatory networks are so very complex, mapping connections specific to any individual organism provides little insight into understanding the organizational principles underlying these networks.

Simplified metabolic graphs may help, but the large-scale structure of metabolic graphs, even for

microorganisms, is mostly unknown [7]. Upon learning the generic properties of insect networks, quantitative analysis should follow. Then insect circulatory systems can reveal new principles of design for robust and error tolerant exponential networks, and insects may become common blueprints for systems yet to be formulated upon random or almost random networks.

One must first determine what type of graph- a random, uniform exponential graph, a heterogeneous scale free graph, or a combination of these- best describes the insect system. The nodes in each graph depict spatially separated metabolic sites. Depending on scale and the resolution of the graph, nodes may be cells or organs. Nodes connect by links representing actual or imaginary conduits for moving fluids. The uniquely distributed dynamical system of an insect's circulation undergoes changes in volume that locally rearrange couplings between nodes to produce large changes in the system's global dynamical properties. In vertebrates the links are highly directed, but in insects they appear to be non-directed.

2.1 Vertebrate Circulation Plan

In the well-known model for a mammalian circulation, a central heart of two pumps (ventricles) in parallel creates a head of pressure driving flow. Flow equals the mean difference in pressure between the arterial and venous ends of each circuit. An ohmic relation exists between pressure, flow and resistance; the quotient between the pressure head and the regional flow resistance determines the flow in each circuit. The left heart ejects blood into the systemic vessels supplying the body. These vessels form many regional circuits serving liver, brain, muscle, bone etc that are separately controlled, specialized in design, and arrayed in parallel. The right heart pumps blood under lower pressure into the vascular beds of the lungs. These beds, more uniform in design, are where oxygen and carbon dioxide exchange between blood and air in the alveoli across the walls of lung capillaries [8].

A scale-free graph best represents the vertebrate circulation. In this model the circulatory network is built up of nodes, or sites of metabolism, that connect with each other through links, that are the actual vessels. Blood flows in one direction (from the heart, to the arteries, to capillaries, and then through veins back to the heart), so we distinguish incoming and outgoing links for each node. The probability that a node receives blood from k distal flows equals the probability that this same node feeds k different downstream flows. Both inflows and outflows have similar distributions, because blood is neither consumed nor created in most nodes. P (k) ~ k ^ -γ in equals P (k) ~ k ^ -γ out. Gamma is the probability that two nodes are connected. This scale free network also displays small world character, as any two nodes may connect along existing links by relatively short paths, for example, all blood leaving the left heart traverses the aortic arch [9].

The diameter of a network spanned by a graph characterizes the degree of interconnectivity within a network, defined as the shortest path for blood flow averaged over all pairs of nodes, indicating the rate at which information spreads throughout the graph. If all nodes were fixed, the diameter of a scale free network would increase logarithmically as new nodes joined the network [9]. The diameter of the network of a larger animal comprising a larger number of metabolic sites might exceed that for a smaller animal. A graph of log P (k) vs. log k for the vertebrate circulation has no well-defined peak, and for large k decays as a power law, P (k)~k ^ -γ, appearing as a straight line with slope –γ on a log-log plot, because the heart, lungs, kidneys and brain each have a large number of links. Important nodal organs (hubs) are vulnerable to attacks on the system, as a heart attack or brain infarct can knock out the entire system [10].

2.2 Invertebrate Circulation Plan

Unlike vertebrates, most animals (echinoderms, annelids, arthropods, some mollusks, and some minor phyla) possess a body cavity (hemocoel) filled with hemolymph that is stirred by an open heart, cilia and body movements [11]. Organs remove nutrients and deposit wastes into this moving mixture of substances in large volumes of fluid in open cavities. In adult mosquitoes, for example, an open tubular heart and aorta contract rapidly washing hemolymph over the brain. As hemolymph, now free in the cavity, percolates rearward, heaving contractions of the viscera mix the hemolymph as it shunts posteriorly between membranes (diaphragms) that divide the hemocoel into smaller compartments.

Substances move in all directions within hemolymph by Browninan motion and mechanical dispersion. Except when they pass through the open tubular heart and aorta, substances are free to circulate. Because connections between locations within the hemocoel are unspecified and, therefore, nondirected, and hemolymph is not confined to tubes, a graph of the links and nodes of the hemocoel must show paths taken by metabolites through the moving hemolymph.

Exponential graphs represent the circulations of many invertebrates. Here, again, nodes represent metabolic sites. Because there are no tubes linking nodes, the average connectivity of each node is the same, implying that the diameter of the network increases logarithmically as new nodes are added. The classical random network

of Erdös and Rènyi assumes each pair of nodes connects randomly with probability p, creating a statistically homogeneous network [12]. Despite the randomness of this model, most nodes posses a similar number of links, <k>, so that connectivity follows a Poisson distribution that peaks strongly at <k>, implying that the probability of finding a highly connected node decays exponentially (P(k) ~ e ^ –k for k >><k>). Insects, thus, forgo the disadvantages of hubs of well-connected nodes. Lacking hubs and conduits for moving fluids allows miniaturization of the physical dimensions of the hemocoel while maintaining the network diameter of the graph. Thus, removal of several nodes or changing their connectivity does not disrupt the remaining communication capability of the network. The graph remains stable and connected as the dimensions of the hemocoel shrink or its volume changes.

3 SHRINKING

Shrinking a vertebrate tubular circulation and an insect hemocoel reveals some of the mechanical differences between them. Reducing a vertebrate circulation to mosquito size would make a scale-free closed tubular network more vulnerable to nodal attack. To maintain a closed circulation at minimal dimensions and to keep blood flowing as tube diameters decrease and vascular resistance increases, heart rate and work must increase blood pressure to maintain cardiac output. However, as the walls of the heart pump shrink, and ventricular mass falls, heart size and stroke volume decrease, diminishing achievable blood pressure and stroke volume. The size limit for a circulation utilizing tubular transport appears in cold-blooded fish embryos and in warm-blooded pygmy shrews (<2g) and hummingbirds [13, 14, 15].

Reducing an insect's size shortens transport distances for substances moving in hemolymph. Somewhere around mosquito or midge size a 3D volume of hemolymph of a larger insect appears to shrink to a 2D surface layer coating the organs and the interior surfaces of the hemocoel. Volume, osmolality and composition of hemolymph change with feeding, temperature, and hydration [16]. Minimizing hemolymph volume reduces weight and increases the probability of transmission for dissolved substances from 0.34 towards 1.

4 RANDOM WALK IN HEMOLYMPH

In a three dimensional volume there is a 34% chance of reaching any point starting from any other point in a random walk as the number of steps taken approaches infinity (Polya random walk constant 0.3405373296)[17]. However, the probability rises to 1 (certainty) on a two-dimensional surface as the number of a walker's steps approaches infinity [17]. Particles on a 2D surface in a hemocoel traverse 2D Brownian trajectories reaching any point in the hemocoel from any other point when hemolymph is low, and all surfaces connect by capillarity. Because a surface permits a diffusing particle the whole area for its motion, diffusing particles must touch all points through infinitely many paths, so the probability of eventual transit from any point or node on the surface to any other point or node on the surface goes to 1(certainty).

5 DRIVERS AGGITATE HEMOLYMPH

In still hemolymph the random walker, a particle or scalar, travels typically in Brownian motion, the limit occurs as the diffusional step length goes to zero and as the time between steps goes to zero. In accord with these constraints a group of random walkers spreads out as normal diffusion in the films of fluid coating the organs and inner surfaces of the hemocoel.

These dynamics change, however, whenever body movements disturb diffusion or when hemolymph volume changes. Diffusing particles remain for variable times near a center of diffusion and then suffer sudden displacements. Modeling the probability for a displacement leads to a k-distribution, and the corresponding diffusion constant is time dependent.

During activities, as when emerging from a pupa or breathing, walking and flying, movements of the body, (drivers) interact with hemolymph. Movements may alter local coupling between nodes and even change the system's global properties. Drivers include the heart, accessory pulsatile organs that force hemolymph into the antennae, wings and legs from the hemocoel, and muscles of respiration and locomotion.

Because insect bodies are small, and wing-muscles are powerful, and because the center of mass of an insect's body lies behind the wing bases, the long axis of the body rotates vertically during flight about the wing base axis under gravity's influence [18]. Wing movements create aerodynamic and inertial forces that evoke pitching and yawing oscillations of the body's position and angle through articulations of the wings with the thorax. Inertial lag of the body can dampen these oscillations at elevated wing-beat frequencies [19]. Oscillatory movements of the insect may cause erratic flight paths and agitate hemolymph. Mechanical dispersion of the diffusing gradients anomalously spreads the diffusing particles out non-uniformly. Movements also may disrupt the boundary layers of hemolymph or change their thickness, altering frictional resistance that changes flow, deposition and uptake over surface asperities.

6 DRIVERS, GRADIENTS AND LÉVY FLIGHTS

For most random walks, changing the details of the walk alter only the diffusion constant, D.

The equation for variance: D = < L^ 2>/ L^2 describes the walk. L^2 is the average square of the step size, and T is the average time between steps. When taking one-step in a time interval, D depends on the step length. When the step-length is random, D depends on the average squared step size, not on the average step size. Taking one step in every two intervals of time, D is less than when taking one step per interval. Most random walkers spread out in normal diffusion; the variance of a group of walkers grows linearly with time: variance = D x time. The variance denotes the typical size of a group of random walkers, and is the (average of the squares of the distance moved) minus (square of the average of the distance moved). D is the rate at which the variance grows. Diffusion is faster in watery hemolymph (large diffusion constant) than in hemolymph of high osmolality (small diffusion constant). Volume changes of hemolymph complicate these relationships.

When D is infinite and because the sum of numbers 1/N^2 from 1 to infinity is finite, the total probability for steps of random length adds to 1. Following a random walker in a still hemocoel for a very long time, should reveal "normal" behavior. Small steps are invisible. Motion results from the average affect of all steps. Were we to observe a walker in the hemocoel during flight, we might see long steps occurring as flight movements superimpose upon the random walk. These steps are Lévy flights [20].

In a Lévy flight, a walker's position is almost completely determined by the few long, rare steps -- the "flights" -- and thus individual steps do not average out. Lévy flights create anomalous diffusion wherein the variance (variance ~ (time)^ γ) grows faster than linearly with time. The exponent γ equals one for normal diffusion. For Lévy flights, γ is greater than one and typically smaller than two. Comparing a normal random walk (small L) and a Lévy flight (large L) shows each walk having a random step length. In the normal walk the probability of a long step is proportional to L^(-3.8). In the Lévy flight the probability of a long step is proportional to L^(-2.2)[20].

7 CONCLUSIONS

The hemocoel separates particles in parallel at separate locations perhaps relying on differential mobility in part due to diffusion coefficients and could become a model for engineered microfluid systems. The hemocoel adapts to changes of volume that overwhelm tubular transport. Squeezing a 3D volume into a plane might enable "control" of diffusion. The hemocoel eliminates need for sustained blood pressure, requires minimal energy, is not prone to clots, and is most efficient when small. An engineered model of a hemocoel might excel at sorting and distributing scalars, and be incredibly space, and time efficient.

8 REFERENCES

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