

Elastohydrodynamic Scaling Law for Heart Rates

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Animal hearts are soft shells that actively pump blood to oxygenate tissues. Here, we propose an allometric scaling law for the heart rate based on the idea of elastohydrodynamic resonance of a fluid-loaded soft active elastic shell that buckles and contracts axially when twisted periodically. We show that this picture is consistent with numerical simulations of soft cylindrical shells that twist-buckle while pumping a viscous fluid, yielding optimum ejection fractions of 35%–40% when driven resonantly. Our scaling law is consistent with experimental measurements of heart rates over 2 orders of magnitude, and provides a mechanistic basis for how metabolism scales with organism size. In addition to providing a physical rationale for the heart rate and metabolism of an organism, our results suggest a simple design principle for soft fluidic pumps.

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In living organisms, a characteristic scale determined by the balance between diffusion and uptake rate is typically of the order of 1 mm. On scales larger than this, active devices are necessary to guarantee uniform access to oxygen and efficient elimination of carbon dioxide or excreta. Soft fluidic pumps such as the heart are an evolutionary innovation that solve this problem by enabling internal fluid transport in large multicellular organisms [1,2]. As organism size varies over many orders of magnitude, so does their metabolism [2,3], suggesting a natural question: what are the scaling principles behind the dynamics of the largest and most powerful pump in organisms, the heart [4,5]? A biological argument for the heart rate starts with Kleiber's law [2], i.e., the metabolic rate $\sim (\text{body mass})^{3/4}$. Balancing the metabolic rate with the energy consumption rate $\sim (\text{heart rate}) \times (\text{heart blood volume})$ yields the power law: $(\text{heart rate}) \sim (\text{body mass})^{-1/4}$, in reasonable agreement with experimental data [2–4]. However, one may question the fundamental premise of this argument, as the theoretical assumptions underlying Kleiber's law remain under debate [6,7].

Here, we start with a physical argument based on the idea that mechanical resonances in biological systems lead to energy economy [4,8–12]. We will see that this leads to experimentally testable predictions for the heart rate of organisms, from mice to blue whales, that have hearts of different sizes but similar geometries [13], as exemplified in Figs. 1(a) and 1(b). Furthermore, we show that the resulting scaling law provides an alternative basis for Kleiber's law.

The pumping motion of the heart, and particularly that of the left ventricle which pumps oxygenated blood into the body, is driven by the twisting-untwisting dynamics of the

cavity which relies on the helical configuration of the ventricular myocardial band [15–17] as shown in Fig. 1(c). Ventricular motion is driven by cardiac muscle cells which contain thick myosin filaments that pull on thin actin filaments during ventricular contraction [18,19]. This results

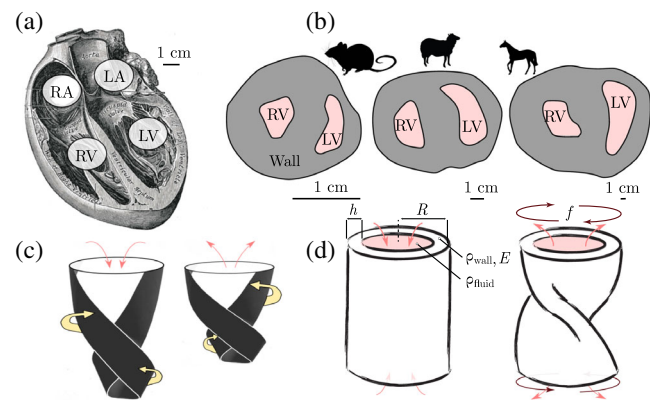


FIG. 1. (a) Structure of a four-chambered heart. LA, LV, RA, and RV denote the left atrium, left ventricle, right atrium, and right ventricle, respectively (drawing adapted from [14]). (b) Transverse section of the ventricles of a rat, sheep, and horse (schematics adapted from [13]). The sections have been enlarged to emphasize their close resemblance. (c) Schematic of the apical loop of the ventricular myocardial band. Adapted from [15]. Periodic twisting and untwisting of the ventricle driven actively by myocardial band contraction leads to fluid pumping. (d) Simplified ventricle geometry, reduced to an elastic shell of thickness h , radius R , density ρ_{wall} , elastic modulus E , and containing a fluid (blood) of density ρ_{blood} . Passive end-twisting of the cylinder causes it to buckle and pump fluid.

in contraction driven stresses within the cardiac muscular tissue that lead it to bend and buckle [20–22], reducing the internal volume of the chamber and forcing the ejection of blood through the aortic valve. Since muscles are only capable of generating contractile stresses, a passive mechanical rebound at the end of ejection would enhance the efficiency of pumping. This is therefore suggestive of an elasto-hydrodynamic resonance of a fluid-loaded soft elastic shell that is capable of bending and twisting as it ejects fluid over a contraction cycle.

To understand the principle determining the heart rate f_t , we start by assuming that the anatomy of the ventricle can be approximated by that of an elastic shell of radius R and thickness $h < R$, as shown in Fig. 1(d). For relatively thin plates and shells, the bending energy scales as $O(h^3)$ while the stretching energy scales as $O(h)$, so that it is relatively easier to deform a shell by bending it [23]. Thus, it is reasonable to expect that the active stresses induced by muscles will excite the softer bending modes of deformation more easily than the stiffer stretching modes. At a scaling level, the active muscular work required to bend such a shell scales as $Eh^3\kappa^2R^2$, where E is the elastic modulus of the walls and $\kappa \sim A/R^2$ is the wall curvature for a small amplitude of deformation A . This work is converted into kinetic energy of the blood (density ρ_f) that is pushed out of the aorta, and scales as $\rho_f R^3 (Af_t)^2$, where we have assumed that the fluid velocity scales as $f_t A$. Equating the muscular work with the kinetic energy of blood over a cycle yields an estimate for the frequency of a fluid-loaded soft elastic shell as

$$f_t \approx \frac{c_{\text{shape}}}{2\pi} \sqrt{\frac{E}{\rho_{\text{blood}}} \frac{h^{3/2}}{R^{5/2}}}, \quad (1)$$

where c_{shape} is a dimensionless constant that is determined by the shape of the ventricle ($c_{\text{shape}} \simeq 1/2$ for a sphere, and $c_{\text{shape}} \simeq 1/\sqrt{6}$ for a cylinder), first suggested theoretically by one of us in [24]. For a human heart, $h \sim 10$ mm, $R \sim 30$ mm, $E \sim 10^4$ Pa [25,26], and $\rho_f \sim 10^3$ kg/m³, which gives an elasto-hydrodynamic resonance frequency $f_t \sim 1$ Hz, in agreement with the observations [27]. For comparison, we also addressed the case of a soft pump dominated by stretching deformations (see Supplemental Material [28]), which leads to different scaling law and a resonance frequency much higher than that measured experimentally.

To further test the idea of the heart as an elasto-hydrodynamically resonant pump, we now turn to numerical simulations. Our approach builds on and complements the large number of studies on the fluid-structure interaction in coronary flows, heart valve dynamics, and ventricular flows [46–53]. We do this in a simplified setting by starting with an elastic cylindrical shell immersed in a fluid which can deform by bending, shearing, and

stretching. For thin and even relatively thick shells, the dominant modes of deformation are those associated with twisting and bending as these are energetically cheaper and thus easier to activate using muscles, consistent with observations of deformation of the heart ventricle [15,54]. Indeed, observations with a rubber cylindrical shell (see Supplemental Material [28] for details and experimental realization for such a model), confirm that twisting leads to a spontaneous buckling instability of the cylinder into a wrinkled tube (with a wavelength that scales with the radius of the cylinder) that also shrinks axially. This mode of deformation reduces the internal volume of the cylinder and thus can be easily harnessed to pump fluid. A full cycle is complete when the cylinder is then brought back to its initial position by untwisting it. The geometry of the shell is characterized by its aspect ratio L/R and thickness ratio R/h , where L , R , and h are the length, radius and thickness of the shell, respectively. In the simulations, we fix the aspect ratio to $L/R = 3$ and vary the thickness ratio h/R , and the shape of the shell is controlled by twisting at one end while keeping the other fixed. A total twist of 90° is imposed at one end and the shape evolution is computed in a quasistatic way by minimizing the bending and stretching energy of the surface [55]. The surface of the cylinder is discretized using approximately 10 000 triangular elements and the material is assumed to be incompressible. The cylindrical shell is immersed in a Cartesian box of size $4L \times 4L \times 4L$ filled with a fluid of kinematic viscosity ν . The boundary conditions imposed on the faces of the Cartesian box perpendicular to the cylindrical axis allow the free flow of fluid into and out of the domain, while free-slip boundary conditions are imposed on the other four faces [37,38]. Through domain dependency tests, we ensure that the boundary conditions and domain size do not influence the final results (see Supplemental Material [28] for details of our numerical model).

In Fig. 2(a), we show snapshots of the shape evolution of the shell from the numerical simulations for a thickness ratio of $R/h = 10$. In Fig. 2(b), we show the net ejection fraction as a function of the driving frequency, in scaled form defined as $\langle \dot{V}_f \rangle / \Delta V_s$ where \dot{V}_f is the net volume of fluid pumped along the axis of the cylinder and ΔV_s is the difference between the initial and final inner volumes of the shell during deformation. The driving Reynolds number, characterizing the ratio of the inertial to viscous forces is defined as $\text{Re} = \pi(2R)^2 f / \nu$, where f is the frequency of the twist-untwist cycle physically imposed on the open face of the cylindrical shell. For each of four different cylinder thickness ratios $R/h \in [5, 20]$, one can clearly observe a nonmonotonic dependence of the pumping efficiency on the driving Reynolds number. At low Re , due to the dominance of the viscous forces over inertial forces, any fluid pumped out during twisting comes back into the shell during untwisting thus leading

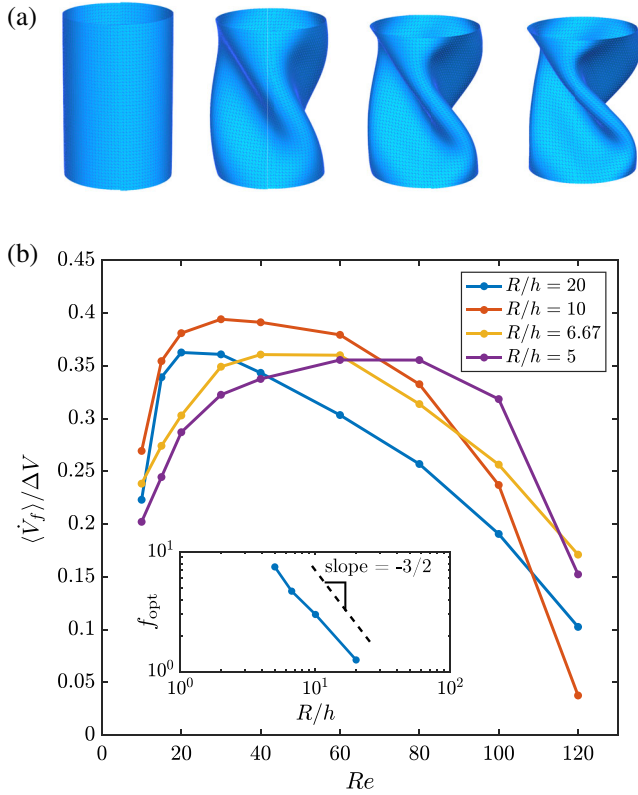


FIG. 2. (a) Snapshots from numerical simulations of a cylindrical shell buckling under twist. The bottom end is kept fixed while the top end is rotated by $\pi/2^c$. The rotation step between each picture is $\pi/6^c$. As the shell buckles into a low-order mode that has an internal volume that is smaller than that of the straight cylinder, it ejects fluid during the process. (b) Net ejection fraction versus the driving Reynolds number for different thickness ratios computed using direct numerical simulations of a deforming elastic shell coupled with a Navier-Stokes solver (see Supplemental Material [28] for details). Inset shows dependence of the frequency with the highest ejection fraction for each thickness ratio versus the thickness ratio which roughly follows a scaling $f \sim (R/h)^{-3/2}$ for fixed $L/R = 3$, consistent with (1).

to a near-zero net pumping rate. As the driving Re increases, inertial effects come into play which leads to symmetry breaking and net pumping of fluid in one direction along the cylinder axis. When Re is further increased, excessive viscous dissipation from high intensity vorticity regions near the buckles of the cylindrical shell significantly reduces the pumping efficiency. This leads to a nonmonotonicity in the pumping efficiency as a function of Re , and the driving frequency, as seen in Fig. 2(b). Furthermore, despite the relatively small bending strains (which are of the order of $Ah/R^2 \sim 5\%$), we see that a combination of buckling instabilities working in tandem with elasto-hydrodynamic resonance can lead to ejection fractions of the order of 35%–40%, explaining a long-standing puzzle in heart physiology [54,56].

These numerical simulations confirm that there is an optimal frequency of pumping to maximize ejection

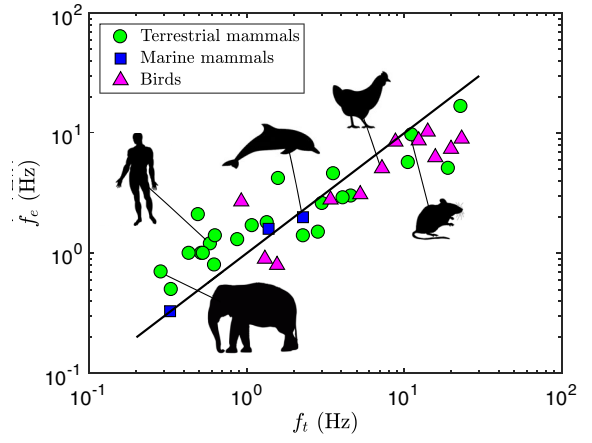


FIG. 3. Comparison between experimentally measured animal heart rates f_e (see Supplemental Material [28]) and the theoretical law for elastohydrodynamic resonance f_t ; the straight line is the linear relation (1) $f_e = f_t \approx c_{shape}/(2\pi)\sqrt{E/\rho_f}h^{3/2}/R^{5/2}$, with $c_{shape} \approx 1/\sqrt{6}$ (for cylindrical shapes).

fraction in an actively driven elastic cylindrical shell, and that the optimal frequency varies with varying thickness ratio. In the inset of Fig. 2(b), we plot the optimal pumping frequency versus the thickness ratio and observe that the frequency roughly follows a scaling $f \sim (h/R)^{3/2}$, consistent with the scaling law (1). The frequency of pumping for a cylindrical shell of a given thickness is optimal when the driving is strong enough to overcome time reversibility in the low Reynolds regime, but not so strong as to produce intense viscous dissipation of the fluid near the buckling regions during the twist-untwist cycle.

To test the theoretical scaling law for the heart rate f_t given by (1), we now compare it with experimental measurements of heart rate f_e across different species [57]. Using data for the average radius and thickness of 38 mammalian and avian left ventricles (see Supplemental Material [28] for details), Fig. 3 shows the experimentally observed heart rate versus the theoretical frequency. We see good agreement between the two in terms of both the trend and, equally importantly, the actual numerical values. Our results are also quantitatively consistent with recent experiments on a tissue-engineered heart ventricle [24] and show that the maximum ejection fraction is achieved when the heart is resonantly forced. Delving deeper into the experimentally observed values of the ventricle radius and its thickness, which together determine the geometrical factor in (1), we find that the typical wall thickness h of the left ventricle is nearly proportional to its typical radius R , with a scaling $h \sim R^\alpha$ where $\alpha = 1.15 \pm 0.06$ (see Supplemental Material [28] for details). This implies that $f_e \sim f_t \sim R^\beta$, where $\beta = -0.78 \pm 0.09$, in good agreement with experimental data (see Fig. S3 of the Supplemental Material [28]).

We now turn to discuss the implications of our elasto-hydrodynamic scaling law on metabolic demands in organisms and across species. Since the red blood cell size ($\sim 10\ \mu\text{m}$) and the hemoglobin density in the cells ($\sim 100\ \text{g/L}$) are approximately constant in mammals [2], the volume of oxygen transported within one heartbeat universally scales as the volume of the heart, which itself scales as the volume of the animal [57,58]. The metabolic rate, which is proportional to the rate of oxygen transport, therefore scales as $Q_{\text{metabolic}} \sim R^3 f_t \sim M^\gamma$, where M is the animal body mass and $\gamma = 1 + \beta/3 = 0.74 \pm 0.03$. This combination of structural, dynamic, and functional constraints thus provides an alternative physical basis for Kleiber's law [2], based on the geometry, elasticity, and dynamics of the soft fluid pump that powers organisms. All together, these laws provide a physical basis for the scaling of heart rates and metabolism as a function of body size, consistent with the matching of (heart) form, dynamics, and (physiological and metabolic) function in organisms [61].

Finally our results also suggest a design principle for soft fluidic pumps [24,59,60]: by taking advantage of elasto-hydrodynamic resonance, they can operate far more efficiently than otherwise. This is consistent with numerical simulations of the coupled elasto-hydrodynamic problem linking the elastic buckling of thin shells to viscous fluid flow, showing how relatively large ejection fractions can be achieved when the pump is resonantly driven. How this design might have arisen during the evolution of fluidic pumps in natural and engineered systems is a question for the future.

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