

Rate invariance and scallop theorem in viscosity gradients

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Purcell’s scallop theorem states that a swimmer deforming in a fluid at low Reynolds number cannot undergo a net displacement if its sequence of shapes is symmetric in time. Motivated by heterogeneous biological environments, here we consider a fluid with broken translational symmetry where the viscosity of the medium varies spatially. We show that, in a prescribed and smooth but otherwise arbitrary viscosity field, the swimmer’s displacement is independent of its deformation rate and thus the scallop theorem continues to hold. Transport of the viscosity by the flow would therefore be key to enabling reciprocal locomotion in heterogeneous media.

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Motile biological microorganisms represent a paradigm for the design of microrobots [1,2]. For example, swimming bacteria such as the well studied *Escherichia coli* can perform complex tasks such as self-propulsion, self-replication, and navigation [3]. Swimming algae such as the genus *Chlamydomonas* can actively reorient in external fields or under the influence of cues such as light [4]. However, the natural environment in which these organisms swim imposes physical constraints that can lead to technical challenges.

Chief among these physical constraints is the time reversibility of the surrounding fluid flow at low Reynolds number, which is described by the incompressible Stokes equations [5]. Such reversibility requires microswimmers to deform their shapes in a manner that breaks time-reversal symmetry; in other words, a movie of the swimming organism needs to be distinguishable from its version played backwards in time [6]. For example, a microswimmer with a single rigid flapping fin cannot swim. Body deformations that look the same under such time reversal symmetry are termed “reciprocal.” The fact that a reciprocal deformation leads to no net locomotion is now known as the scallop theorem, famously introduced by Purcell in his 1977 lecture “Life at low Reynolds numbers” [7]. Purcell himself gave an intuitive demonstration of the theorem and detailed mathematical work has been devoted to it ever since [8–10], including a rigorous proof [11].

In nature, biological organisms break this time-reversal symmetry by deforming their bodies in a wavelike fashion, thereby indicating a clear direction of time [6]. Prokaryotes such as bacteria achieve this using the rotation of rigid chiral structures (flagellar filaments), while eukaryotes actively deform slender filaments (flagella and cilia) [3]. Scientists, often motivated by potential biomedical applications, have tried to mimic these biological wavelike mechanisms to design

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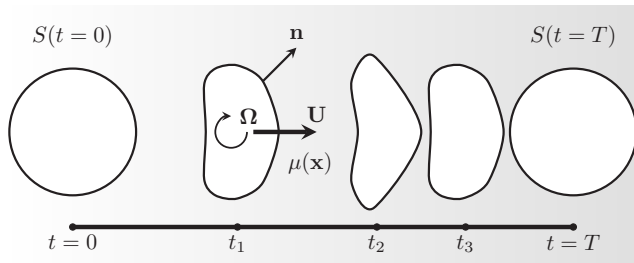


FIG. 1. Body swimming by deforming its surface, $S(t)$, in an otherwise unbounded and quiescent fluid with a prescribed spatially dependent viscosity $\mu(\mathbf{x})$ (the background gray scale gradient schematically represents the variation of viscosity in space). The swimmer moves at each time t with velocity $\mathbf{U}(t)$ and rotates with angular velocity $\mathbf{\Omega}(t)$. We denote by \mathbf{n} the unit vector field normal to the swimmer surface and pointing into the fluid. Reciprocal deformation of the body is represented schematically by the sequence of shapes which show the configuration of the swimmer's body, $S(t)$, at different times. The deformation is periodic and thus $S(0) = S(T)$, with T denoting the period of deformation (the rate of deformation does not need to be constant).

efficient micromachines [2,12–14], for example, by magnetically actuating rotating chiral structures [15–17], flexible synthetic filaments [18], or by integrating biological and synthetic components [19–25].

The fabrication of these bioinspired nonreciprocal devices often involves intricate processes. Fortunately, the scallop theorem only holds under a specific set of conditions and there are several ways in which its constraints can be escaped [26], which in turn facilitates the design and fabrication of microswimmers [27,28]. Physical mechanisms that allow for swimming under reciprocal actuation have been proposed including the use of flow and body inertia [11,29–31], hydrodynamic interactions [32,33], or exploiting nonlinear stresses that arise from non-Newtonian fluid rheology [34–36].

In the natural environment of many swimming microorganisms, the viscosity of the fluid is inherently heterogeneous. For example, pathogenic bacteria that infect the human body find themselves moving in viscous mucus layers that protect the tissues in the respiratory or digestive tracks [37–39]. Similarly, many species of coral release mucus continuously, which accumulates at the surface of the sea and creates an environment of varying viscosity where marine microorganisms swim [40]. Recent experiments have revealed patchiness and spatial heterogeneity of the viscosity field around marine microorganisms [41]. Motivated by these scenarios, work has been devoted by the physics community to the study of microswimmers in viscosity gradients [42–48]. A newly discovered passive reorientation was shown to manifest across viscosity gradients, without the need for active sensing but solely governed by hydrodynamics: when the fluid around a swimmer has a spatially varying viscosity, an imbalance arises between the viscous propulsive force generated by the swimmer and the resisting viscous drag, which in turn leads to a hydrodynamic torque and therefore to reorientation. Since the existence of a viscosity gradient breaks the translational symmetry of the swimmer's environment and leads to new dynamics, it is natural to ask whether it could be also exploited to induce self-propulsion under reciprocal motion. In other words, does the scallop theorem hold in a fluid with spatially dependent viscosity? In this paper, we demonstrate that the answer is yes. When the fluid has a fixed and smooth, but otherwise arbitrary, viscosity, we show using an expansion at any order in the deformation amplitude of the body that the displacement of a periodically deforming body is independent of the rate of deformation and, therefore, that the scallop theorem continues to hold. In order to exploit heterogeneous environments for locomotion, transport of the viscosity field by the moving flow would therefore be the key mechanism to enable reciprocal locomotion.

We consider a deformable body moving in an infinite fluid with variable viscosity at low Reynolds number (Fig. 1). Assuming a generalized Newtonian fluid, we write the stress tensor

as $\boldsymbol{\sigma} = -p\mathbf{1} + 2\mu(\mathbf{x})\mathbf{E}$, where $\mu(\mathbf{x})$ is the spatially dependent viscosity, p is the dynamic pressure, and the strain rate tensor is given by $\mathbf{E} = (\nabla\mathbf{u} + \nabla\mathbf{u}^T)/2$, with \mathbf{u} the incompressible velocity field ($\nabla \cdot \mathbf{u} = 0$). In the absence of external forces, the velocity field \mathbf{u} vanishes at infinity while, on the swimmer surface $S(t)$, it is a combination of deformation with prescribed velocity $\mathbf{u}_s(t)$ and rigid-body swimming motion with instantaneous linear velocity $\mathbf{U}(t)$ and angular velocity $\boldsymbol{\Omega}(t)$, so it satisfies the boundary condition

$$\mathbf{u}|_{\mathbf{x} \in S(t)} = \mathbf{U}(t) + \boldsymbol{\Omega}(t) \times \mathbf{x}(t) + \mathbf{u}_s(t). \quad (1)$$

To derive our results, we use the principle of virtual work [49], which requires the use of an auxiliary flow $\hat{\mathbf{u}}_0$; for this flow, we consider a particle with the same shape, moving in an incompressible Newtonian fluid with constant viscosity μ_0 in rigid body motion with instantaneous linear and angular velocities $\hat{\mathbf{U}}_0$ and $\hat{\boldsymbol{\Omega}}_0$. Assuming that both flow problems follow the inertialess momentum equations, $\nabla \cdot \boldsymbol{\sigma} = \mathbf{0}$, we can contract each momentum equation with the other velocity field, integrate over the whole fluid volume, and use the divergence theorem along with incompressibility and the vanishing of the flows at infinity to obtain the reciprocal identity [49]

$$\int_{S(t)} \mathbf{n} \cdot \boldsymbol{\sigma} \cdot \hat{\mathbf{u}}_0 dS - \int_{S(t)} \mathbf{n} \cdot \hat{\boldsymbol{\sigma}}_0 \cdot \mathbf{u} dS = 2\mu_0 \int_{V(t)} \left(1 - \frac{\mu(\mathbf{x})}{\mu_0}\right) \mathbf{E} : \hat{\mathbf{E}}_0 dV, \quad (2)$$

where \mathbf{n} denotes the unit normal vector to $S(t)$ pointing into the fluid (see Fig. 1). By linearity of the Stokes equations, we may express the stress field in the auxiliary problem in terms of its boundary conditions $\hat{\mathbf{U}}_0$ and $\hat{\boldsymbol{\Omega}}_0$ as $\hat{\boldsymbol{\sigma}}_0 = \boldsymbol{\Sigma}_0^U \cdot \hat{\mathbf{U}}_0 + \boldsymbol{\Sigma}_0^\Omega \cdot \hat{\boldsymbol{\Omega}}_0$, where the tensor fields $\boldsymbol{\Sigma}_0^{U,\Omega}$ only depend on S [50]. Assuming force- and torque-free motion for the swimmer, Eq. (2) finally allows one to express $[\mathbf{U}, \boldsymbol{\Omega}]$ in terms of the auxiliary problem as [49]

$$\begin{bmatrix} \mathbf{U} \\ \boldsymbol{\Omega} \end{bmatrix} = -\mathcal{M}_0 \cdot \begin{bmatrix} \int_{S(t)} (\mathbf{n} \cdot \boldsymbol{\Sigma}_0^U)^T \cdot \mathbf{u}_s dS \\ \int_{S(t)} (\mathbf{n} \cdot \boldsymbol{\Sigma}_0^\Omega)^T \cdot \mathbf{u}_s dS \end{bmatrix} - \mathcal{M}_0 \cdot \begin{bmatrix} \int_{V(t)} \left(1 - \frac{\mu(\mathbf{x})}{\mu_0}\right) \mathbf{E} : \boldsymbol{\Sigma}_0^U dV \\ \int_{V(t)} \left(1 - \frac{\mu(\mathbf{x})}{\mu_0}\right) \mathbf{E} : \boldsymbol{\Sigma}_0^\Omega dV \end{bmatrix}, \quad (3)$$

where \mathcal{M}_0 is the instantaneous mobility matrix of a rigid body with shape S . Importantly, the volume integral on the right-hand side of Eq. (3) is a nonlocal term containing information about \mathbf{U} , $\boldsymbol{\Omega}$, and \mathbf{u}_s ; therefore, a closed-form solution for the swimming velocities in terms of the surface deformation does not appear possible. Nevertheless, as we show below, we can still use Eq. (3) to demonstrate that reciprocal motion leads to no net displacement.

To establish rate independence in the case of a varying viscosity, we take inspiration from the Newtonian (i.e., constant viscosity) case, which we solve first. In that limit, $\mu(\mathbf{x}) = \mu_0$ and the volume integral in Eq. (3) vanishes. The dynamics of the swimmer is then totally determined by the boundary conditions at its surface as

$$\begin{bmatrix} \mathbf{U} \\ \boldsymbol{\Omega} \end{bmatrix} = \begin{bmatrix} \int_{S(t)} \tilde{\mathcal{M}}^U \cdot \mathbf{u}_s dS \\ \int_{S(t)} \tilde{\mathcal{M}}^\Omega \cdot \mathbf{u}_s dS \end{bmatrix}, \quad (4)$$

where $\tilde{\mathcal{M}}^{U,\Omega} = -\mathcal{M}_0 \cdot (\mathbf{n} \cdot \boldsymbol{\Sigma}_0^{U,\Omega})^T$ are second-rank tensor fields that depend only on the shape of the swimmer $S(t)$.

To proceed, we represent a change of rate of deformation by considering a smooth function $g(t)$ such that the shape of the swimmer is invariant under the mapping $t \mapsto g(t)$, up to a rotation. It is convenient to consider a separate virtual swimmer that performs the same deformation as the real swimmer but in a vacuum. Without any material medium to push on, the virtual swimmer does not translate or rotate, and therefore its shape is invariant under that mapping. Denoting by \bar{S} the shape of the virtual swimmer, we thus have $\bar{S}(t) = \bar{S}(g(t))$. The real swimmer, on the other hand, may translate and rotate. Denoting its rotation at time t by $\mathbf{R}(t)$, we can express any point \mathbf{x} on

the swimmer surface $S(t)$ as $\mathbf{x} = \mathbf{R}(t) \cdot \bar{\mathbf{x}}$, where $\bar{\mathbf{x}}$ is on the virtual swimmer surface $\bar{S}(t)$. Using coordinates on the virtual swimmer, Eq. (4) then becomes

$$\begin{bmatrix} \mathbf{U}(t) \\ \boldsymbol{\Omega}(t) \end{bmatrix} = \begin{bmatrix} \mathbf{R}(t) \int_{\bar{S}(t)} \overline{\mathcal{M}}^U \cdot \bar{\mathbf{u}}_s d\bar{S} \\ \mathbf{R}(t) \int_{\bar{S}(t)} \overline{\mathcal{M}}^\Omega \cdot \bar{\mathbf{u}}_s d\bar{S} \end{bmatrix}, \quad (5)$$

where the variables with a bar are expressed on the virtual swimmer. Since the tensors $\overline{\mathcal{M}}^{U,\Omega}$ only depend on $\bar{S}(t)$, which is invariant under the mapping $g(t)$, we have $\overline{\mathcal{M}}^{U,\Omega}(g(t)) = \overline{\mathcal{M}}^{U,\Omega}(t)$. The linear and angular velocities of the swimmer are determined by the surface deformation velocity $\bar{\mathbf{u}}_s$ and since the shapes are prescribed, with $\bar{S}(t) = \bar{S}(g(t))$, the velocity of deformation $\bar{\mathbf{u}}_s$ transforms under $g(t)$ as $\bar{\mathbf{u}}_s(t) = \bar{\mathbf{u}}_s(g(t))\dot{g}(t)$ (the dot denotes a time derivative). Therefore, under the change of rate of deformation described by the mapping g , we obtain for the Newtonian case

$$\begin{bmatrix} \mathbf{U}(t) \\ \boldsymbol{\Omega}(t) \end{bmatrix} = \dot{g}(t) \begin{bmatrix} \mathbf{R}(t) \int_{\bar{S}(g(t))} \overline{\mathcal{M}}^U \cdot \bar{\mathbf{u}}_s d\bar{S} \\ \mathbf{R}(t) \int_{\bar{S}(g(t))} \overline{\mathcal{M}}^\Omega \cdot \bar{\mathbf{u}}_s d\bar{S} \end{bmatrix} = \dot{g}(t) \begin{bmatrix} \mathbf{R}(t) \cdot \mathbf{R}^{-1}(g(t)) \cdot \mathbf{U}(g(t)) \\ \mathbf{R}(t) \cdot \mathbf{R}^{-1}(g(t)) \cdot \boldsymbol{\Omega}(g(t)) \end{bmatrix}. \quad (6)$$

We next show that the rotation matrix \mathbf{R} is rate independent. First we recall the kinematic equation $\dot{\mathbf{e}} = \boldsymbol{\Omega} \times \mathbf{e}$ for any unit vector \mathbf{e} , from which we can deduce $\dot{\mathbf{R}} = \boldsymbol{\Omega} \times \mathbf{R}$, where the cross product between the vector $\boldsymbol{\Omega}$ and the matrix \mathbf{R} is defined by $(\boldsymbol{\Omega} \times \mathbf{R})_{ij} \equiv \epsilon_{kai} \Omega_k R_{aj}$, with ϵ_{ijk} the Levi-Civita pseudotensor and we use the Einstein notation for summation over repeated indices. From the definition of the determinant, we have

$$\det(\mathbf{R})\epsilon_{ijk} = \epsilon_{pqr} R_{pi} R_{qj} R_{rk} = \epsilon_{pqr} R_{ip} R_{jq} R_{kr} = \det(\mathbf{R}^T)\epsilon_{ijk} = \epsilon_{ijk}, \quad (7)$$

where the last equality follows from the fact that the determinant of a rotation is $\det(\mathbf{R}) = 1$. Using the fact that the inverse of a rotation is its transpose, i.e., using index notation $R_{ji} = (\mathbf{R}^{-1})_{ij}$ and thus $R_{ij}R_{kj} = \delta_{ik}$, where δ_{ij} is the Kronecker delta, we can write

$$\begin{aligned} \dot{R}_{ij} &= \epsilon_{pqr} R_{kp} R_{aq} R_{ir} \Omega_k R_{aj} = \epsilon_{pjr} R_{kp} R_{ir} \Omega_k \\ &= R_{ir} [-\epsilon_{rjp} (\mathbf{R}^{-1} \cdot \boldsymbol{\Omega})_p] = R_{ir} \Gamma_{rj} = (\mathbf{R} \cdot \boldsymbol{\Gamma})_{ij}, \end{aligned} \quad (8)$$

where we have defined the tensor $\boldsymbol{\Gamma}(t) \equiv -\boldsymbol{\epsilon} \cdot \mathbf{R}^{-1}(t) \cdot \boldsymbol{\Omega}(t)$.

Using the chain rule and prime to denote differentiation with respect to g we have

$$\dot{\mathbf{R}}(g(t)) = \dot{g}\mathbf{R}'(g(t)) = \dot{g}\mathbf{R}(g(t)) \cdot \boldsymbol{\Gamma}(g(t)). \quad (9)$$

Noticing that Eq. (6) implies $\boldsymbol{\Gamma}(t) = \dot{g}\boldsymbol{\Gamma}(g(t))$ we find $\dot{\mathbf{R}}(g(t)) = \mathbf{R}(g(t)) \cdot \boldsymbol{\Gamma}(t)$. Therefore, $\mathbf{R}(t)$ and $\mathbf{R}(g(t))$ satisfy the same differential equation and, since $\mathbf{R}(0) = \mathbf{R}(g(0)) = \mathbf{1}$ (the identity matrix), we find $\mathbf{R}(t) = \mathbf{R}(g(t))$ for all t . In other words, the orientation of the swimmer is independent of the rate at which it deforms its body. With this, Eq. (6) implies $\dot{\mathbf{X}}(t) = \mathbf{U}(t) = \dot{g}\mathbf{U}(g(t)) = \dot{\mathbf{X}}(g(t))$. Again, both displacement vectors have the same initial condition, $\mathbf{X}(0) = \mathbf{X}(g(0))$; hence $\mathbf{X}(t) = \mathbf{X}(g(t))$ for all t . Hence both the displacement and orientation of the swimmer are independent of the rate at which it deforms its body.

Now, reciprocal motion is defined as one in which the swimmer deforms its body in such a way that the sequence of shapes it adopts are identical under a time reversal transformation, regardless of the rate of motion (see Fig. 1). In the case of reciprocal motion the function $g(t)$ satisfies $g(T) = g(0) = 0$, where T is the period of deformation. Therefore, $\mathbf{X}(T) = \mathbf{X}(g(T)) = \mathbf{X}(0)$ and $\mathbf{R}(T) = \mathbf{R}(g(T)) = \mathbf{R}(0)$. Thus a microswimmer performing a reciprocal motion in a fluid with homogeneous viscosity undergoes no net translation or rotation; this is Purcell's scallop theorem [7,10,11].

To show that the same result holds in a fluid with a spatially dependent smooth viscosity, we write the prescribed viscosity field as a Taylor series around the position \mathbf{X}_s of a point on the surface of the swimmer as

$$\mu(\mathbf{x}) = \sum_{\alpha \in \mathbb{N}_0^N} \frac{1}{\alpha!} \partial^\alpha \mu(\mathbf{X}_s) (\mathbf{x} - \mathbf{X}_s)^\alpha, \quad (10)$$

where we have used the multi-index notation for a function $f : \mathbb{R}^N \rightarrow \mathbb{R}$. If $\alpha = (\alpha_1, \alpha_2, \dots, \alpha_N)$ is a multi-index, then we define for any vector $\mathbf{x} \in \mathbb{R}^N$: $\mathbf{x}^\alpha = x_1^{\alpha_1} x_2^{\alpha_2} \dots x_N^{\alpha_N}$, $\alpha! = \alpha_1! \alpha_2! \dots \alpha_N!$, $|\alpha| = \alpha_1 + \alpha_2 + \dots + \alpha_N$, and $\partial^\alpha f = \partial_1^{\alpha_1} \partial_2^{\alpha_2} \dots \partial_N^{\alpha_N} f$ with $\partial_i f = \partial f / \partial x_i$.

If we denote by L the typical length over which the viscosity changes and R the typical size of the swimmer, we may define the dimensionless parameter $\epsilon = R/L$. In that case, we have $\partial^\alpha \mu \sim \mu_0 / L^{|\alpha|} = \epsilon^{|\alpha|} (\mu_0 / R^{|\alpha|})$, where we take $\mu_0 = \mu(\mathbf{X}_s)$ as the reference viscosity. When the viscosity varies on a length scale larger than the size of the swimmer, i.e., when the swimmer experiences small relative changes in viscosity over its surface, we have $\epsilon \lesssim 1$ and we can write the viscosity field in Eq. (10) as an asymptotic expansion $\mu(\mathbf{x}) = \sum_n \epsilon^n \mu_n(\mathbf{x})$, where $\mu_{|\alpha|}(\mathbf{x}) = L^{|\alpha|} \partial^\alpha \mu(\mathbf{X}_s) (\mathbf{x} - \mathbf{X}_s)^\alpha / (R^{|\alpha|} \alpha!)$. Physically, we expect in that case that, at every instant, the swimming velocity will be close to that of the same reciprocal swimmer moving in a fluid of constant viscosity μ_0 . We therefore look at the swimming velocity, the angular velocity, and the strain rate tensor field as asymptotic expansions in ϵ , and write $\mathbf{U}(t) = \sum_n \epsilon^n \mathbf{U}_n(t)$, $\boldsymbol{\Omega}(t) = \sum_n \epsilon^n \boldsymbol{\Omega}_n(t)$, and $\mathbf{E}(\mathbf{x}, t) = \sum_n \epsilon^n \mathbf{E}_n(\mathbf{x}, t)$.

We now demonstrate that both \mathbf{U}_n and $\boldsymbol{\Omega}_n$ lead to rate invariant displacement and rotation at *all* orders in n . Substituting the expansion in Eq. (3) and comparing the coefficients of the powers of ϵ we find at order ϵ^0

$$\begin{bmatrix} \mathbf{U}_0 \\ \boldsymbol{\Omega}_0 \end{bmatrix} = -\mathcal{M}_0 \cdot \begin{bmatrix} \int_{S(t)} (\mathbf{n} \cdot \boldsymbol{\Sigma}_0^U)^T \cdot \mathbf{u}_s dS \\ \int_{S(t)} (\mathbf{n} \cdot \boldsymbol{\Sigma}_0^\Omega)^T \cdot \mathbf{u}_s dS \end{bmatrix}, \quad (11)$$

which is the expected solution for a swimmer moving in a fluid of constant viscosity. Higher-order corrections balance the volume integral in Eq. (3) at each time t as

$$\sum_{n=1}^{\infty} \epsilon^n \begin{bmatrix} \mathbf{U}_n \\ \boldsymbol{\Omega}_n \end{bmatrix} = - \sum_{n=1}^{\infty} \sum_{m=0}^{n-1} \epsilon^n \mathcal{M}_0(t) \cdot \begin{bmatrix} \int_{V(t)} \mathbf{A}_{n,m}^U dV \\ \int_{V(t)} \mathbf{A}_{n,m}^\Omega dV \end{bmatrix}, \quad (12)$$

where the tensor fields $\mathbf{A}_{n,m}^{U,\Omega}$ ($n - m \geq 1$) are defined as

$$\mathbf{A}_{n,m}^{U,\Omega}(\mathbf{x}, t) = \frac{\mu_{n-m}(\mathbf{x})}{\mu_0(\mathbf{x})} \mathbf{E}_m(\mathbf{x}, t) : \boldsymbol{\Sigma}_0^{U,\Omega}(\mathbf{x}, t). \quad (13)$$

When comparing the coefficients in the power series on both sides of Eq. (12), care must be taken because, in principle, the volume $V(t)$ where the integration is performed varies with the intensity of the viscosity gradient (since it depends on the swimming motion) and therefore $V(t)$ implicitly depends on ϵ . To incorporate this in the calculation, we note that we can obtain the volume $V(t)$ through a mapping $\mathbf{f} : V_0(t) \mapsto V(t)$, where $V_0(t)$ represents the entire space excluding the volume that the swimmer would occupy in the homogeneous case at every instant in time (see illustration in Fig. 2). Since the shape of the swimmer is prescribed, $V(t)$ is thus obtained by a rigid-body transformation of $V_0(t)$. We label the position of the swimmer in three-dimensional space using the location $\mathbf{X}(t)$ of a point of interest inside the swimmer and a rotation matrix $\mathbf{R}(t)$ that defines the swimmer's orientation. Denoting by \mathbf{X}_0 and \mathbf{R}_0 the position and orientation when the swimmer moves in a fluid of constant viscosity, the transformation \mathbf{f} that maps V_0 into V is given by $\mathbf{f}(\mathbf{x}) = \mathbf{R}\mathbf{R}_0^{-1} \cdot (\mathbf{x} - \mathbf{X}_0) + \mathbf{X}$. Expanding \mathbf{X} and \mathbf{R} in powers of ϵ as $\mathbf{X} = \sum_n \epsilon^n \mathbf{X}_n$ and

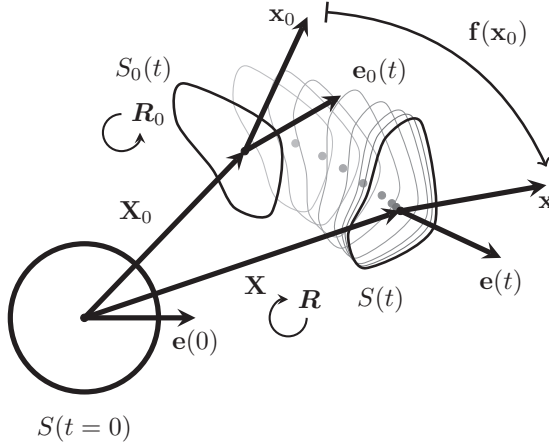


FIG. 2. Schematic representation of the map $f(\mathbf{x})$ in Eq. (14). The shape of the swimmer in the constant viscosity case is denoted by $S_0(t)$, while $S(t)$ denotes the shape of the swimmer when it moves in a viscosity gradient. Similarly, the displacement and rotation of the swimmer in each case is denoted by $\{\mathbf{X}_0, \mathbf{R}_0\}$ and $\{\mathbf{X}, \mathbf{R}\}$, respectively. The unit vector $\mathbf{e}(t) = \mathbf{R}(t) \cdot \mathbf{e}(0)$ denotes the orientation of the swimmer at time t . The gray shades represent the partial approximations of the mapping in powers of ϵ .

$\mathbf{R} = \mathbf{R}_0(\mathbf{1} + \sum_{1 \leq n} \epsilon^n \mathbf{R}_n)$, we have explicitly

$$\mathbf{f}(\mathbf{x}) = \mathbf{x} + \sum_{n=1}^{\infty} \epsilon^n \left[\underbrace{\mathbf{R}_0 \mathbf{R}_n \mathbf{R}_0^{-1} \cdot (\mathbf{x} - \mathbf{X}_0) + \mathbf{X}_n}_{\mathbf{f}_n} \right]. \quad (14)$$

Denoting by \mathbf{x}_0 the position of a point in the fluid in the volume V_0 , we can now evaluate the integrals on the right-hand side of Eq. (12) using the mapping \mathbf{f} to change the volume of integration back to $V_0(t)$ as

$$\int_{V(t)} \mathbf{A}_{n,m}^{U,\Omega}(\mathbf{x}, t) dV = \int_{V_0(t)} \mathbf{A}_{n,m}^{U,\Omega}(\mathbf{f}(\mathbf{x}_0), t) |J| dV_0, \quad (15)$$

where $J = \nabla_{\mathbf{x}_0} \mathbf{f}(\mathbf{x}_0)$ is the Jacobian matrix of the map \mathbf{f} . Since \mathbf{f} is a rigid body motion, it conserves volume and hence $|J| = 1$. Using this, we can formally Taylor expand the integrand in Eq. (15) as

$$\begin{aligned} \int_{V(t)} \mathbf{A}_{n,m}^{U,\Omega}(\mathbf{x}, t) dV &= \int_{V_0(t)} \mathbf{A}_{n,m}^{U,\Omega}(\mathbf{x}_0, t) dV_0 + \epsilon \int_{V_0(t)} \mathbf{f}_1(\mathbf{x}_0) \cdot \nabla \mathbf{A}_{n,m}^{U,\Omega}(\mathbf{x}_0, t) dV_0 \\ &+ \epsilon^2 \int_{V_0(t)} \left(\mathbf{f}_2(\mathbf{x}_0) \cdot \nabla \mathbf{A}_{n,m}^{U,\Omega}(\mathbf{x}_0, t) + \frac{1}{2} \mathbf{f}_1(\mathbf{x}_0) \cdot \nabla \nabla \mathbf{A}_{n,m}^{U,\Omega}(\mathbf{x}_0, t) \cdot \mathbf{f}_1(\mathbf{x}_0) \right) dV_0 \\ &+ \dots \equiv \sum_{\ell=0}^{\infty} \epsilon^\ell \int_{V_0(t)} \mathcal{A}_{n,m,\ell}^{U,\Omega}(\mathbf{x}_0, t) dV_0. \end{aligned} \quad (16)$$

We have introduced the integrands $\mathcal{A}_{n,m,\ell}^{U,\Omega}$ relevant at order ϵ^ℓ and defined in V_0 . We now use Eq. (16) to evaluate the corresponding integrals in Eq. (12). Expanding the sums in m and ℓ and carefully collecting all the terms with the same powers of ϵ , we obtain that the corrections to the linear and angular velocities at order n are given by

$$\begin{bmatrix} \mathbf{U}_n \\ \mathbf{\Omega}_n \end{bmatrix} = - \sum_{m=0}^{n-1} \sum_{\ell=0}^{n-m-1} \mathcal{M}_0(t) \cdot \begin{bmatrix} \int_{V_0} \mathcal{A}_{n-\ell,m,\ell}^U dV_0 \\ \int_{V_0} \mathcal{A}_{n-\ell,m,\ell}^\Omega dV_0 \end{bmatrix}. \quad (17)$$

We can now prove that the corrections to the linear and angular displacements are rate independent at all orders. We start by considering the first-order correction to the swimmer's velocities, given by

$$\begin{bmatrix} \mathbf{U}_1(t) \\ \boldsymbol{\Omega}_1(t) \end{bmatrix} = -\mathcal{M}_0(t) \cdot \begin{bmatrix} \int_{V_0} \mathcal{A}_{1,0,0}^U(\mathbf{x}_0, t) dV_0 \\ \int_{V_0} \mathcal{A}_{1,0,0}^\Omega(\mathbf{x}_0, t) dV_0 \end{bmatrix}, \quad (18)$$

with

$$\mathcal{A}_{1,0,0}^{U,\Omega}(\mathbf{x}_0, t) = \left(\frac{\mu_1(\mathbf{x}_0)}{\mu_0} \right) \mathbf{E}_0(\mathbf{x}_0, t) : \boldsymbol{\Sigma}_0^{U,\Omega}(\mathbf{x}_0, t). \quad (19)$$

Since \mathcal{M}_0 and $\boldsymbol{\Sigma}_0^{U,\Omega}$ depend only on the instantaneous shape of the swimmer, they are invariant under the transformation $t \mapsto g(t)$. The strain rate tensor, on the other hand, transforms as $\mathbf{E}_0(t) = \dot{g}\mathbf{E}_0(g(t))$, by linearity on \mathbf{U}_0 and \mathbf{u}_s . To determine how the viscosity transforms, we note that \mathbf{x}_0 does not depend on the rate of deformation since it is labeled with respect to the position of the swimmer in the homogeneous case, which is rate independent; therefore, $\mu_1(\mathbf{x}_0)$ is invariant under the mapping $t \mapsto g(t)$. We thus get for the integrands in Eq. (18) that $\mathcal{A}_{1,0,0}^{U,\Omega}(\mathbf{x}_0, t) = \dot{g}\mathcal{A}_{1,0,0}^{U,\Omega}(\mathbf{x}_0, g(t))$; hence $[\mathbf{U}_1, \boldsymbol{\Omega}_1](t) = \dot{g}[\mathbf{U}_1, \boldsymbol{\Omega}_1](g(t))$, which leads to $[\mathbf{X}_1, \mathbf{R}_1](t) = [\mathbf{X}_1, \mathbf{R}_1](g(t))$ for all t . The displacement and orientation of the swimmer are therefore rate independent at first order in the viscosity variations.

To proceed and show that the rate independence of displacement and orientation is valid at all orders n , we use mathematical induction. Rate independence has been demonstrated already for $n = 0, 1$, so let us assume it is valid for all orders $n \leq k$ (k is an integer with $k \geq 1$) and show that rate independence is satisfied at order $k + 1$. Since $\mathbf{f}_n(\mathbf{x}_0) = \mathbf{R}_0 \mathbf{R}_n \mathbf{R}_0^{-1} \cdot (\mathbf{x}_0 - \mathbf{X}_0) + \mathbf{X}_n$, we know by the induction hypothesis that $\mathbf{f}_n(\mathbf{x}_0)$ is invariant under the transformation $t \mapsto g(t)$ for $n \leq k$. As argued in the $n = 1$ case, the tensors \mathcal{M}_0 and $\boldsymbol{\Sigma}_0^{U,\Omega}$ are rate independent, and by the induction hypothesis so are the viscosity fields μ_n for $n \leq k$. By induction the strain rate tensors transform as $\mathbf{E}_n(t) = \dot{g}\mathbf{E}_n(g(t))$ for all $n \leq k$. We next observe that the field $\mathcal{A}_{k+1-\ell,m,\ell}^{U,\Omega}$ ($m \leq k$, $\ell \leq k - m$) is a sum of terms that are linear in the strain rate tensors \mathbf{E}_n for $n \leq k$ and that it only depends on the mapping $\mathbf{f}_n(\mathbf{x}_0)$ for $n \leq k$. We thus obtain that under a change of rate $\mathcal{A}_{k+1-\ell,m,\ell}^{U,\Omega}(\mathbf{x}_0, t) = \dot{g}\mathcal{A}_{k+1-\ell,m,\ell}^{U,\Omega}(\mathbf{x}_0, g(t))$, which implies that the linear and angular velocities transform as $[\mathbf{U}_{k+1}, \boldsymbol{\Omega}_{k+1}](t) = \dot{g}[\mathbf{U}_{k+1}, \boldsymbol{\Omega}_{k+1}](g(t))$. Therefore, rate invariance is valid at order $n = k + 1$ and by the induction property it is valid at all orders in the viscosity field. The displacement and rotation of a swimmer undergoing prescribed surface deformation is therefore invariant under the time transformation $t \mapsto g(t)$. As a consequence, for reciprocal swimming we find $[\mathbf{X}, \mathbf{R}](T) = [\mathbf{X}, \mathbf{R}](g(T)) = [\mathbf{X}, \mathbf{R}](0)$, and therefore the scallop theorem holds in a spatially dependent (but prescribed) viscosity field.

Quantifying the physical constraints that lead to the scallop theorem is important for the understanding of biological locomotion and the design of artificial microswimmers. In particular, it is crucial to precisely identify the mechanisms susceptible to suppress the constraints of the theorem. Here, motivated by recent experimental work [42–48], we asked if breaking the translational symmetry of space by allowing the viscosity of the environment to vary in space is sufficient to achieve reciprocal propulsion. We showed that in a prescribed, but arbitrary, viscosity profile the strong condition of rate invariance holds, and therefore so does the scallop theorem.

Naively, this result may appear counterintuitive, since a body undergoing reciprocal action experiences different viscosities during the first and second half of its deformation cycle. However, the key point is that for a given viscosity profile the flow is still instantaneously reversible. This property of the flow ensures that rate invariance, and the scallop theorem, hold for the constant viscosity case, even in the presence of rigid boundaries [10]; we conjecture that this will also be the case in the inhomogeneous-viscosity case.

Throughout our analysis, we assumed that the relevant length scale of viscosity variations, L , was smaller than the typical size of the swimmer, R . This is a reasonable assumption for a viscosity field

that depends on the evolution of a solute concentration C , or on the temperature field T , that diffuses as the swimmer self-propels. Our proof can be extended to show that, for such a viscosity field, both rate independence and the scallop theorem still hold, as long as the Péclet number vanishes and the viscosity field satisfies Laplace's equation [strictly speaking, it is C or T that satisfy the Laplace equation, associated with a constitutive relationship $\mu(C)$ or $\mu(T)$; when C or T vary slowly it is acceptable to assume a linear relationship and therefore $\nabla^2\mu = 0$].

There are, however, biological relevant scenarios in which the viscosity changes abruptly, i.e., over a length scale smaller than the size of the swimmer. For example, this is the case for the gut bacterium *Helicobacter pylori*, which is able to move through the mucus layer that covers the stomach. Recent experiments on low-Re swimmers moving through sharp viscosity gradients [48] revealed that advection plays a significant role in the swimming behavior. Further exploration of the finite-Péclet case will therefore be needed for locomotion through steep viscosity interfaces.

The implication of our work for the design of one-degree-of-freedom swimmers is notable. In order to exploit heterogeneous environments, advection of the viscosity field is therefore key, and it is the only mechanism that could enable reciprocal locomotion. A key question to uncover will then be if the breakdown of the scallop theorem is continuous with the Péclet number or if a finite amount of advection will be required to enable net locomotion—a topic that is reminiscent of the questions raised a decade ago on the impact of fluid inertia on reciprocal swimming [26]. So far viscosity advection has been ignored in the investigation of viscotactic mechanisms. Since locomotion problems associated with finite-Péclet number transport abound in biology, from the dynamics of infectious bacteria to the transport of plankton in the oceans, a key question for future work is the role of viscosity advection in the natural world.

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