Inertial self-propulsion of spherical microswimmers by rotation-translation coupling

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We study swimming of small spherical particles who regulate fluid flow on their surface by applying tangential squirming strokes. We derive translational and rotational velocities for any given stroke which is not restricted by axial symmetry as assumed usually. The formulation includes inertia of both the fluid and the swimmer, motivated by application to large Volvox colonies. Remarkably, we show that inertial contribution to mean speed comes from dynamic coupling between translation and rotation, which occurs only for strokes that break axial symmetry. This effect overcomes the scallop theorem on impossibility of propulsion by time-reversible stroke. We study examples of tangential strokes of axisymmetric travelling wave, and of asymmetric time-reversible flapping. In the latter case, we find that inertia-driven mean speed is optimized for flapping frequency and sphere’s radius which fall well within the range of realistic physical values for Volvox colonies, indicating that this inertia-driven swimming mechanism can be feasible and biologically relevant.

Volvox algae is a unique microorganism whose swimming is described realistically with a theoretically tractable model [1, 2]. Volvox’s interaction with the fluid is described by no-slip boundary condition on nearly spherical time-dependent envelope of the flagella’s tips whose motion is actuated by the swimmer (squirming) [3, 4]. This velocity sets the fluid in motion that applies propulsion force on the swimmer [1, 17]. It simplifies that the Reynolds number is small so that the fluid motion can be described by linear, steady or unsteady, Stokes equations.

Previous treatments mostly neglected inertias of both the fluid and the swimmer and assumed axially symmetric swimming stroke as in the original formulation [3, 4]. This leads to substantial simplifications in the coupled system of the Navier-Stokes equations (NSE) governing the fluid, and the Newton equations of the swimmer. First, the neglect of fluid inertia allows to use Stokes equations of the flow discarding the unsteady term in the NSE [3, 4, 18, 19]. This neglect is invalid for largest Volvox colonies of hundreds of microns in size [1, 10]. Indeed, significance of inertia of the fluid is determined by the Roshko number \( Ro = \frac{\sigma \tau_d}{d} \) where \( \sigma \) is the frequency of the periodic stroke and \( \tau_d \) is the characteristic time of outward viscous diffusion of momentum from the sphere (sometimes \( Ro \) is called oscillatory Reynolds number [6, 20]). If \( Ro \ll 1 \), which holds for small colonies, then momentum redistributes over the fluid before the swimmer moves the flagella significantly. The flow is then steady Stokes flow determined by instantaneous position and velocity of the flagella. However, for large colonies where \( Ro > 1 \), momentum diffusion and swimming stroke are coupled non-trivially. This coupling is described by the unsteady time-derivative term in the NSE whose inclusion is necessary. This term brings memory where the propulsion force is determined not only by instantaneous stroke but also by its past values [21, 24]. Though this sometimes does not influence the time-averaged net propulsion velocity for periodic strokes, it is relevant for nutrient uptake [17] and reaction to external stimuli [25]. In contrast, the convective term in the equations, giving flow derivative along the streamline, is negligible since the Reynolds number is small even for large colonies [10].

Second, the neglect of swimmer’s inertia implies that the motion occurs at zero force and torque. This is also invalid for large colonies where time-scale of viscous drag is comparable with the period of the stroke. In fact, densities of the swimmer and of the fluid are very close so the relevance of fluid and particle inertias is decided by the same parameter \( Ro \). Third, the assumption of axially symmetric stroke allows to use the general solution for axially symmetric flow. This assumption brings zero rotation thus removing the characteristic rotation of Volvox that gave it its name. The three assumptions mentioned above can be misleading as in the case of phototaxis where the assumption of axially symmetric stroke would miss the considered phenomenon [13, 26].

Few previous works relaxed some of the above assumptions. The work [15] studied the limit case of inertial heavy (called dense in [16]) swimmer in inertialess fluid disregarding rotation of tangential squirmer. In [17] the equation of motion for translational velocity of inertial tangential squirmer in inertial flow was developed using the unsteady reciprocal theorem. However the equation was solved only for axially symmetric case where both inertias do not change the time average velocity, only bringing oscillatory terms that cause no net propulsion [6]. On the other hand, stroke’s symmetry assumption was relaxed in [12, 15] where inertial effects were not considered. It is stressed that currently some ingredient is missing for calculation of Volvox velocity that fits the data [10].

In this work, we relax all the assumptions above and demonstrate that interplay of the fluid and swimmer’s inertia with tangential asymmetric stroke gives a previously unstudied mechanism of swimming. It is usually believed that tangential squirmers that keep constant
spherical shape cannot swim by a time-reversible stroke - the time-averaged velocity is zero [6, 16, 17]. However, this conclusion was made only for axially symmetric stroke that involves no rotation. We demonstrate that asymmetric time-reversible tangential stroke that does involve rotation can generate self-propulsion via nonlinear rotation-translation coupling. In the limit of small inertia, $Ro \ll 1$, the net swimming velocity is proportional to the vector product of translational and rotational velocities obtained by neglecting inertia and to the Stokes time. This result is independent of the details of the stroke. We then present a concrete example of time-reversible stroke with non-zero average nondimensional propulsion speed at any $Ro$. The nondimensional speed decays for small and large values of $Ro$, and reaches a maximum at an intermediate value which falls within feasible physical values of large Volvox colonies. Our formulas for translational and rotational velocity of inertial spherical tangential squirmer in inertial fluid in terms of arbitrary swimming stroke reduce for small colonies to those of [27] for inertialess squirmer in inertialess fluid.

We consider tangential squirmers that have constant shape of sphere with radius $a$. Swimming stroke produces in the body-fixed frame tangential motion of the spherical surface at velocity $v_b(x, t)$. We designate the center position and velocity by $x_0(t)$ and $v(t)$, respectively. The flow around the swimmer is $u(x - x_0(t), t)$ which obeys the unsteady Stokes equation with no-slip boundary conditions,

$$\partial_t u = -\nabla p + \nu \nabla^2 u, \quad \nabla \cdot u = 0, \quad u(\infty) = 0, \quad u(x) = v + \Omega \times x + v_b(x, t), \quad u_b(x, t) = Rv_b(R^t x, t),$$

where $p$ is pressure (minus the hydrostatic pressure) divided by the fluid density $\rho$ and $\nu$ is the kinematic viscosity. The surface flow $u_b(x, t)$ in the frame of the fluid derives from $v_b(x, t)$ and is also tangential to the surface. The rotation matrix $R$ transforms the surface velocity from body-fixed frame to the rest frame of the fluid, $R_{ij}(0) = \delta_{ij}$. The time derivative of $R(t)$ is determined from the angular velocity $\Omega$ via $R_{ij} = \epsilon_{ik}n\Omega_{k}\hat{R}_{ij}$. The flow determines the force $F$ and the torque $T$ applied on the swimmer by the fluid via surface integrals of the stress tensor $\sigma$,

$$\frac{\sigma}{\rho} = -pI + \nu(\nabla u + (\nabla u)^t), \quad F = \int_S \hat{r}_s \hat{r}_n ds, \quad T = \int_S \hat{r} \times \sigma \hat{r} \hat{r}_n ds,$$

where the superscript $t$ stands for transpose, $ds$ is infinitesimal element of the swimmer’s surface $S$ and $\hat{r}$ is unit vector in radial direction. We consider the swimmer as a ball having uniform mass density $\rho_s$ neglecting small density changes due to local deformations of the thin surface which represents short cilia or flagella. Thus, the swimmer has mass $m_s = 4\pi a^3/3$ and constant moment of inertia $J = 2m_s a^2/5$. We have,

$$m_s \frac{d\dot{v}}{dt} = F + (m_s - m_F)g, \quad J \frac{d\Omega}{dt} = T,$$

where $g$ is the gravity acceleration and $m_F = 4\pi a^3\rho/3$ is the water mass displaced by the sphere. We construct the flow which solves Eq. (1) as superposition, $u = u^s + u^\nu$, of the flow $u^s$ of inertialess swimmer in inertial fluid and the flow $u^\nu$ of rigid sphere. The former obeys,

$$\rho \partial_t u^s = -\nabla p^s + \eta \nabla^2 u^s, \quad \nabla \cdot u^s = 0, \quad u^s(\infty) = 0, \quad u^s(S) = v^s(t) + \hat{\Omega}^s(t) \times x + u_b(x, t), \quad F^s = T^s = 0.$$

The flow $u^\nu$ is the flow around a rigid sphere that moves with prescribed translational and angular velocities $v - v^s(t)$ and $\Omega - \hat{\Omega}^s$, respectively. Thus, it obeys:

$$\rho \partial_t u^\nu = -\nabla p^\nu + \eta \nabla^2 u^\nu, \quad \nabla \cdot u^\nu = 0, \quad u^\nu(\infty) = 0, \quad u^\nu(S) = v(t) - v^s(t) + [\Omega(t) - \hat{\Omega}^s(t)] \times x.$$

Since $u^s$ imposes zero force and torque on the swimmer then $F$ and $T$ are determined by $u^\nu$. The force $F(t)$ is the force [22, 24] on rigid sphere that moves with velocity $v(t) - v^s(t)$. This is given by Fourier representation,

$$F(t) = -6\pi \eta a \int_{-\infty}^{\infty} f(\delta - i\omega \tau_d) [\hat{\theta}(\omega) - \hat{v}^s(\omega)] e^{-i\omega t} d\omega,$$

$$f(\lambda) = 1 + 3\sqrt{\lambda} + \lambda, \quad \tau_d = \frac{a^2}{2g},$$

where $\delta$ is infinitesimal so $\sqrt{\delta + i\omega} = [\sqrt{\omega}]{2}(1 - i\omega/|\omega|)$. We designate Fourier transforms in time by hats. Similarly the torque $T(t)$ is given by [24],

$$T(t) = \int_{-\infty}^{\infty} T_0(\omega) \left[\hat{\Omega}(\omega) - \hat{\Omega}^s(\omega)\right] e^{-i\omega t} d\omega,$$

$$T_0(\omega) = \frac{5J}{3\gamma \tau_d} \left(1 - \frac{3i\omega \tau_d}{1 + q(\omega \tau_d)}\right), \quad q(\omega) = 3\sqrt{\delta - i\omega}.$$

where $\gamma = \rho_s/\rho$ is the specific gravity. Thus the force and the torque are determined by $v^\nu$ and $\hat{\Omega}^s$, respectively. This way of solution helps separating the effects brought by the inclusion of the inertia of the fluid and of the swimmer.

Including inertia of the fluid.—For finding $v^\nu$ and $\hat{\Omega}^s$ we can circumvent finding $u^\nu$ by using the reciprocal theorem [16, 17, 23, 27, 28].

$$\hat{v}^\nu \cdot \int_S \hat{r}_s \hat{r}_n \hat{d}S + a \epsilon_{irn} \hat{\Omega}^s \hat{d}\Omega = -\int_S \hat{u}_s \hat{v}^\nu \hat{r}_n \hat{d}S,$$

where $\sigma^k$ is the stress tensor of dual flow $u^k$ also obeying unsteady Stokes equations. We find velocity of inertialess swimmer $\hat{\theta}^\nu$ using the dual flows defined by b. c. on the sphere $\hat{v}_b^k(\Omega) = \delta_{bk}$, see [23] and Appendix A

$$\hat{\theta}^\nu = \left(\frac{1 + i\omega \tau_d}{f(\epsilon - i\omega \tau_d)}\right) \hat{\theta}_b^\nu,$$

where $\hat{v}_b^\nu$ is the velocity of inertialess swimmer in inertialess fluid [27] which using definitions in Eq. (1) reads,

$$\hat{v}_b^\nu(t) = -\int_S u_b(x, t) \frac{dS}{4\pi a^2} = -R \int_S v_b(x, t) \frac{dS}{4\pi a^2}.$$
We find performing inverse Fourier transform of Eq. (8),
\[ \mathbf{v}^s(t) = \mathbf{v}_0^s(t) - \frac{d}{dt} \int_{-\infty}^{t} K\left(\frac{t-t'}{\tau_d}\right) \mathbf{v}_0^s(t')dt', \]
where \( K(t) \) is the inverse Laplace transform of \( 1/f(\lambda) \) and \( \lambda \) is the Laplace transform variable, see Appendix B where \( K(t) \) is obtained in terms of the error functions. The behavior of \( K(t) \) is quite different from that of \( t^{-1/2} \) memory kernel of the force [21–24]. We have \( K(0) = 1 \) rather than divergence at \( t = 0 \). In contrast with memory kernel for the force, \( K(t) \) is integrable: \( \int_{0}^{\infty} K(t)dt = 1/f(0) = 1 \). We have at large times \( K(t) \approx 3t^{-3/2}/\sqrt{4\pi} \) which is consequence of the small \( \lambda \) behavior \( f(\lambda) \approx 1 + 3\sqrt{\lambda} + \kappa \lambda \) and the last term is sedimentation velocity. We find using similarity with Eqs. (8)–(10),
\[ \mathbf{v}(t) = \mathbf{v}_0^s(t) - \frac{dx_i(t)}{dt} + 2(\gamma - 1) g \tau_d, \]
where we introduced the inertial displacement \( x_i(t) \),
\[ x_i = \int_{-\infty}^{t} \hat{K} \left(\frac{t-t'}{\tau_d}\right) \mathbf{v}_0^s(t')dt', \quad \hat{K} = \int_{-\infty}^{\gamma \omega t \tau_d} \frac{1}{f(\lambda)} \frac{d\lambda}{2\pi i}. \]
This has the useful consequence.

The propulsion given by Eqs. (14)–(15) reduces to that for inertialess swimmer in Eqs. (8)–(10) by taking \( \gamma \to 0 \) and \( \kappa \to 1 \). This is seen using that \( K(t) \) can be obtained from the memory kernel \( \hat{K}(t) \) by setting \( \kappa = 1 \). For Volvox \( \gamma \approx 1 \), and \( \kappa \approx 3 \) so inertia of the swimmer brings a finite change of the swimmer’s velocity.

The properties of \( K(t) \) and \( \hat{K}(t) \) are very similar and both of them are roughly \( \delta \)–functions smeared over \( t \to 1 \), see the details in Appendix A. Thus we find by performing consideration similar to that after Eq. (10),
\[ \mathbf{v} \approx \mathbf{v}_0^s - \kappa \tau_d \frac{dx_i}{dt}, \quad R \\text{O} \ll 1. \]

The inertial displacement \( x_{in}(t) \) is bounded and does not contribute the time averaged velocity,
\[ \langle \mathbf{v} \rangle = -\frac{1}{4\pi a^2} \int_S \mathbf{R} \int_S \mathbf{v}_b(x, t)dS + 2(\gamma - 1) g \tau_d. \]
where angular brackets stand for time average and we used Eqs. (9), (14). This has the same form as the average velocity of inertialess swimmer in inertialess fluid [27]. Thus inertia can bring the difference only by changing the rotation matrix \( \mathbf{R} \). This has the useful consequence.

**Inertia has no impact on axially symmetric squirmers.**—The case of axially symmetric squirmers is much studied and presents separate interest. In this case translational and angular velocities are parallel so the swimmer propagates as a screw, see [10] for an example. In this case or the case of no rotation at all \( \mathbf{R}_b = \mathbf{v}_b^s \) so classical swimming theory works. Thus inertia axially symmetric tangential squirmers obey the scallop theorem as was observed in [6] [16] [17].

**Metachronal wave.**—Metachronal wave stroke is believed to describe Volvox with good approximation [10]. Similarly to [27] we consider only tangential part described by time \( t \) position of polar angle \( \theta \) as a function of the position \( \theta_0 \) near which the oscillation occurs as \( \theta(t, \theta_0) = \theta_0 + c \cos(k\theta_0 - \sigma t) \). Our consideration disregards radial and azimuthal displacements. The parameters that fit experiment are \( k = 4.7, \sigma = 203 \text{ radian per} \)
the time-average value of \( t \) respectively. It can be concluded that inertia does not change where oscillations of inertia of both fluid and swimmer is, producing result of [27]. The formula for velocity including term which does not oscillate gives, see Appendix C. This is the swimming velocity neglecting inertia. The time-average is determined by the only term which does not oscillate \( \langle \nu_0(t) \rangle = -\frac{\pi a \sigma c k^2}{8} \) reproducing result of [27]. The formula for velocity including inertia of both fluid and swimmer is, \( v(t) = \nu_0(t) + 2(\gamma - 1)g \tau_d - a e \kappa R_s \frac{d}{dt} \left( \frac{2 \sin(\pi k/2)}{k(4 - k^2)} \right) \) \( \Omega(t) = \Omega^s(t) - \frac{d}{dt} \int_{-\infty}^{t} K_r(t-t') \Omega^s(t')dt' \), where \( \Omega^s \) and \( \Omega^r \) stand for imaginary and real part, respectively. It can be concluded that inertia does not change the time-average value of \( v(t) \) for this stroke, whereas oscillations of \( v(t) \) contain an inertial correction, cf. [14].

Rotation.—Fourier transform of \( J \Omega = T \) gives,

\[
\hat{\Omega}(\omega) = \hat{\Omega}^s(\omega) + \frac{i J \omega \hat{\Omega}^r(\omega)}{T^0(\omega) - i J \omega} = \frac{\hat{\Omega}^s(\omega)}{1 - i J \omega T^0(\omega)} (\omega)，
\]

where we used Eq. [6]. This solves for the swimmer’s rotation implicitly with \( \Omega^s \) from Eq. [11]. In time domain,

\[
\Omega(t) = \Omega^s(t) - \frac{d}{dt} \int_{-\infty}^{t} K_r(t-t') \Omega^s(t')dt'，
\]

where using Eq. [6] we introduced the kernel,

\[
K_r(t) = \int_{-\infty}^{\infty} \frac{d\omega}{2\pi} \frac{\exp(-i\omega t)}{5(1 - 3i\omega/|1 + q(\omega)|)} / (3\omega) - i\omega \]

We assume that \( 5/(3\gamma) \sim 1 \) so that this equation gives that the characteristic time of variation of \( K_r(t) \) is \( O(1) \). We observe that \( \int_{t_0}^{\infty} K_r(t)dt \) is finite and given by the Fourier transform at zero frequency which is \( 3\gamma/5 \). We conclude that \( K_r(t) \) decays over time of order one. In the limit of small Roshko number in the leading order we can set \( \Omega^s(t') \approx \Omega^s(t) \) in the integrand finding,

\[
\Omega(t) \approx \Omega^s(t) - \frac{3\tau_s d\Omega^s(t)}{10} dt， Ro \ll 1.
\]

where \( \tau_s = 2 \gamma \tau_d \) is the Stokes time. This formula describes smaller organisms.

One of our main results is that the propagation of inertial swimmer in the inertial fluid is described by Eqs. [14] and [20]. Rotation decouples from translation and can be considered separately. In contrast, translation depends on rotation via the rotation matrix \( R \) obeying

\[
\hat{R}_{ij} = \epsilon_{ikl} \Omega^l R_{ij}， see e.g. Eq. [17]. The system of Eqs. [14] and [20] describing the translation-rotation coupling is non-local in time having memory described by the kernels \( \hat{K}(t) \) and \( \hat{K}_r(t) \). The system becomes local in the limit of heavy swimmers whose density is much larger than that of the fluid, \( \gamma \gg 1 \). It is demonstrated in Appendix that in this case the swimming is described by,

\[
\tau_s \frac{d\nu}{dt} + v = -\frac{1}{4\pi a^2} \int R \nu_0 dS， \frac{dR_d}{dt} = \epsilon_{ins} \Omega_n R_{nl}， 3\tau_s \frac{d\Omega}{dt} + \Omega = -\frac{3}{8\pi a^2} \int R (x_b \times \nu_b) dS.
\]

This system was obtained in [16] from steady Stokes equations. Setting \( \tau_s = 0 \) recovers the often-used formulation of Stone and Samuel [27] where inertia of the fluid and the swimmer is neglected [27]. In this case reciprocal theorem holds telling that if the swimming stroke is time-reversible then no net self-propulsion occurs over the stroke’s period. Other case where Eqs. [14] and [20] become local in time is the limit of small inertia considered below.

Translational-rotational coupling at small inertia.— Inertia of the swimmer, in contrast with the fluid inertia, changes the rotation of the swimmer. Thus inertia changes \( R \) and the net propulsion velocity. This translational-rotational coupling can bring qualitative and quantitative changes in the swimming. We demonstrate in Appendix that to linear order in \( Ro \),

\[
v = v^{ss} - \kappa \tau_d \frac{dv^{ss}}{dt} + \frac{3\tau_s}{10} v^{ss} \times (\Omega^{ss}(t) - \Omega^{ss}(0))，
\]

where \( v^{ss} \) and \( \Omega^{ss} \) are the Stone-Samuel translational and rotational velocities of inertialless swimmer in inertialless fluid, respectively [27]. These velocities are \( v_0^s \) and \( \Omega^s \) in Eqs. [9] and [11] with rotational matrix \( R \) obtained neglecting the inertia. The appearance of \( \Omega^{ss}(0) \) is not because of infinite memory but rather because the rotation matrix that transforms velocities from the body-fixed to the fluid frames has a reference orientation at \( t = 0 \). Thus the leading order correction to the swimming velocity in inertia of both the fluid and the swimmer derives simply from the zero order in inertia velocities. For time-reversible stroke the scallop theorem guarantees that \( \langle \nu^{ss} \rangle = 0 \) so that the average velocity \( \langle \nu \rangle_{tot} \) of swimmer with time-reversible stroke obeys,

\[
\langle \nu \rangle_{tot} = \frac{3\tau_s}{10} \langle v^{ss} \times \Omega^{ss} \rangle.
\]

The RHS is non-zero for asymmetric stroke demonstrating the breakdown of the scallop theorem due to inertia. We demonstrate in Appendix that Eqs. [25]–[26] hold also for heavy swimmers with \( \sigma \tau_s \ll 1 \). Thus we conclude that in this case the scallop theorem breaks down. In contrast, [16] claimed that the scallop theorem holds also for heavy swimmers with time-reversible tangential stroke. This is because they did not consider the rotational-translation-coupling for this system.
Swimming at arbitrary Ro under time-reversible stroke - example. The above observations persist to higher Ro as we illustrate by considering simple asymmetric time-reversible tangential motion,

$$\theta(t, \theta_0, \phi_0) = \theta_0 + c \cos(\sigma t) + c \epsilon \cos(\phi_0) \cos(\sigma t),$$  

(27)

where $c$ is a constant and $\epsilon$ represents small amplitude of this type of cilia motion. The last term induces asymmetry that causes oscillatory rotation about $y$ direction, which, in turn, gives nonzero net displacement. Straightforward calculation (see Appendix E) gives for time-averaged velocity $\langle \mathbf{v} \rangle = 2(\gamma - 1)g_t d + U a \sigma \hat{x}$. The first term is sedimentation velocity, and the nondimensional speed $U$, which interprets as “displacement in body sizes per stroke”, is given by

$$U = \frac{3\pi c^2}{32} \mathcal{R} \left[ \left( \frac{15}{2\gamma \alpha^2} + i + \frac{5i}{\gamma (1 + \alpha + i\alpha)} \right)^{-1} \right],$$  

(28)

where $\alpha = 3\sqrt{Ro/2}$. In the limit of small Ro this becomes $U = \pi c \gamma^2 \alpha^2 / 80$ which using the formulas of Appendix E is readily seen to agree with Eq. (26). Fig. 1 shows a log-log plot of $U$ as a function of Roshko number $Ro$ for $\gamma = 1$ where sedimentation velocity vanishes. Interestingly, the speed $U$ vanishes at the limits $Ro \to \{0, \infty\}$ and attains a maximum at an intermediate value of $Ro \approx 2.8$ (vanishing at $Ro \to 0$ is due to the scallop theorem and at $Ro \to \infty$ due to large mass). This can be interpreted either as an optimal flapping frequency $\sigma$, or as an optimal body radius $a$ for a fixed frequency. Remarkably, setting physical values of $\sigma = 200$ rad/sec and $\nu = 10^{-6}$ m$^2$/sec for Volvox gives an optimal radius of $a \approx 355 \mu m$, which falls well within the size range of large Volvox colonies. This indicates that asymmetric flapping of inertial squirmer is a feasible mechanism for generation of net propulsion, which can be realistic for Volvox colonies. In Appendix E we also analyze the dependence of the swimming velocities on the density ratio $\gamma$ and show that $U = \gamma / (b_2 \gamma^2 + b_1 \gamma + b_0)$, where $b_i$ are functions of $Ro$ only. This implies the existence of an optimal value of $\gamma$ that maximizes $U$. While for physical values of Volvox the optimal value is $\gamma \approx 10$, this value results in a large sedimentation velocity in Eq. (17) which can hardly be overcome by the strokes. Therefore, Volvox typically tend to a density ratio of nearly neutral buoyancy ($\gamma = 1.003$, cf. [1]) for which sedimentation is nonzero but small.

In summary, we have studied the motion of inertial squirmers under unsteady Stokes equation. Using reciprocal theorem, we derived the swimmer’s translation and rotation under any given stroke of tangential deformation. Our analysis extends the well-known work [27] of Stone and Samuel from inertialless to inertial case. It also generalizes previous works on inertial squirmers [17] which considered only axisymmetric strokes where rotation is either zero or decoupled from translation [10]. As a consequence, we show that an asymmetric time-reversible stroke can lead to net propulsion through dynamic coupling between rotation and translation. For small inertia this coupling is described by the vector product of inertialess translational and rotational velocities. If the product has non-zero time-average then the net propulsion velocity is finite even for time-reversible stroke. For a model of asymmetric stroke the normalized swimming speed is maximized for intermediate values of $O(1)$ Roshko number which falls well within realistic range of large Volvox colonies. For $Ro \to 0$, our results reduce to those of inertialess swimmer in [27]. For $Ro \to \infty$, $U$ decays as $1/\sqrt{Ro}$. We conjecture that swimming optimization at $Ro \sim 1$ can be one of the reasons for the cutoff in size of Volvox colonies at $a \approx 500 \mu m$ [1].

Our current work is limited to tangential strokes, whereas Volvox’s strokes involve also radial component, which must be included in the model for realistic description. For axisymmetric strokes, time-reversible deformation with nonzero radial component can lead to net propulsion of inertial squirmers [6][16]. Nevertheless, inclusion of the radial stroke would not destroy the asymmetric swimming mechanism displayed here. We plan to compare these two mechanisms using a full solution of the flow in the vicinity of the deforming boundary for general strokes. The general solution will also enable calculation of mechanical energy dissipation, which will give another criterion for stroke optimization. Finally, a longer term goal is to use these improvements to the theoretical model in order to match it with experimental measurements of swimming Volvox. This will help in quantifying the true contribution of inertial effects to Volvox motion.

Acknowledgments

This work has been supported by the Israel Science Foundation (ISF), under grant no. 567/14.
Appendix A DUAL FLOWS

Here we provide details of the two dual flows used in reciprocal theorem in Eqs. (7), (8) and (11). The use of the theorem requires knowing the values of the stress tensor of the dual flow on the sphere.

The dual flow, used for finding translational velocity of the swimmer, is the solution of unsteady Stokes equations whose Laplace transform obeys on the sphere $u^k = \delta_{ik}$ and decays at infinity. In time domain the flow $u^k$ describes motion of the sphere that starts from rest at $t = 0$ and has impulsive velocity $u^k(|x| = a, t) = \delta(t)\delta_{ik}$ (we do not keep dimensions here since the corresponding dimensional factors disappear from the final formulas). Thus at $t < 0$ there is no flow, then the velocity jump at $t = 0$ creates a flow. At $t > 0$ the sphere is fixed at the origin and the flow caused by initial impulse decays. The Fourier transform is readily inferred from the Laplace transform provided in [23], see also [29]. We have on the surface of the sphere,

$$\frac{\sigma^k_{il}}{\eta} = \frac{i\omega \hat{r}_i \hat{r}_k}{6\nu} - \frac{\delta_{ik}(1+q(\omega \tau_d))}{2a},$$

where $q(\omega)$ is defined in Eq. (9). This flow was used for deriving Eq. (8) from Eq. (7).

The other dual flow, used for finding rotational velocity of the swimmer, is the solution of unsteady Stokes equations whose Laplace transform obeys on the sphere $\hat{u}^k = \epsilon_{ikn}x_n$ and decays at infinity. This is flow which is created by instantaneous rotation of the sphere at $t = 0$ with angular velocity given by unit vector in $k$–th direction: $u^k(x = a, t) = \epsilon_{ikn}x_n\delta(t)$. This flow can be obtained as superposition of flows caused by rotation of the sphere at angular velocity that depends on time as $\exp[-i\omega t]$ found in [24]. We find ($y = |x|/a$ and $q = q(\omega \tau_d)$),

$$u^k(x, t) = \epsilon_{ikn}x_n \int \frac{d\omega}{2\pi} \exp[-i\omega t - q(y - 1)] \frac{1 + qy}{1 + q}.$$  

If we use spherical coordinates with polar axis in $k$–th direction then velocity has the only non-vanishing component $u_\phi = v$ where [24],

$$v = \frac{x \sin \theta}{y^3} \int \frac{d\omega}{2\pi} \exp[-i\omega t - q(y - 1)] \frac{1 + qy}{1 + q}.$$  

The only non-zero component of $\sigma^k_{il}$ on the surface $S$ is [24],

$$\frac{\sigma^k_{il}}{\eta} = \left( \frac{\partial v}{\partial x} - \frac{v}{x} \right) |_S = -\sin \theta \left( 3\delta(t) + \frac{q^2 d\omega}{2\pi(1 + q)} e^{-i\omega t} \right),$$

$$\frac{\sigma^k_{il}}{\eta} = -\epsilon_{ikl} \hat{x}_l \left[ 3 + \frac{q^2}{1 + q} \right].$$

where the last line is written in the form independent of the reference frame. This flow was used for deriving Eq. (11) from Eq. (7).
Appendix B  INVERSE TRANSFORMS

Here we derive the memory kernels $K(t)$ and $\tilde{K}(t)$ defined in Eqs. (10) and (15), respectively. These kernels are found as inverse Fourier and Laplace transforms of the corresponding functions in the main text. We start from inverse Fourier transform of Eq. (8) that involves
\[ \int \frac{i \omega \tau_0 \exp(-i \omega t)}{f(-i \omega \tau_0)} \frac{d \omega}{2 \pi} = -\frac{d}{dt} \int K \left( \frac{t-t'}{\tau_0} \right) v_0(t')dt', \quad (33) \]
where
\[ K(t) = \int \frac{\exp(-i \omega t)}{f(-i \omega)} \frac{d \omega}{2 \pi}. \quad (34) \]
We observe that $f^{-1}(z)$ is analytic in the complex plane with branch cut at negative real semi-axis. Consequently $f^{-1}(\tau_0(-i \omega))$ considered as function of complex variable $\omega$ is analytic outside the branch cut at $(-i \infty, -i \epsilon)$. We find $K(t) = 0$ for $t < 0$ because the integration contour can be closed in the upper half plane producing zero. This is necessary for causality: otherwise instantaneous velocity in Eq. (10) would be determined by future movements of the swimmer. When $t > 0$ we find passing in Eq. (34) to the integration variable $z = \epsilon - i \lambda$ that,
\[ K(t) = \int \frac{\exp(-i \omega t)}{f(-i \omega)} \frac{d \omega}{2 \pi} = \int_{-i \infty}^{+i \infty} \exp(i \lambda t) \frac{d \lambda}{2 \pi i} \quad (35) \]
that is, $K(t)$ is the inverse Laplace transform of $1/f(\lambda)$ (this could be found directly using Laplace transform in the derivations which would have other disadvantages).

Similar considerations hold for the memory kernel $\tilde{K}(t)$ in Eq. (15). We observe that $K(t)$ can be obtained from $\tilde{K}(t)$ by setting $\kappa = 1$. Thus we consider the inverse Laplace transform of $[\hat{f}(\lambda)]^{-1} = [1 + 3 \sqrt{\lambda} + \kappa \lambda]^{-1}$ in Eq. (15). We use that,
\[ \frac{1}{1 + 3 \sqrt{\lambda} + \kappa \lambda} = \frac{1}{\sqrt{9 - 4 \kappa}} \left[ \frac{x_2}{\lambda + x_2 \sqrt{\lambda}} - \frac{x_1}{\lambda + x_1 \sqrt{\lambda}} \right], \]
where $-x_i$ are roots of quadratic polynomial $1 + 3 \sqrt{\lambda} + \kappa \lambda^2$,
\[ x_2 = \frac{3 + \sqrt{9 - 4 \kappa}}{2 \kappa}, \quad x_1 = \frac{3 - \sqrt{9 - 4 \kappa}}{2 \kappa}. \quad (36) \]
We use known integral (cf. similar calculation in [5]),
\[ \int_0^\infty \exp(-\lambda t + x_i^2 t) \text{Erf}c(x_i \sqrt{t}) dt = \frac{1}{\lambda + x_i \sqrt{\lambda}}, \]
where analytic continuation is used for defining $\text{Erf}c(x)$ for complex $x$. We conclude that,
\[ \tilde{K}(t) = \frac{1}{\sqrt{9 - 4 \kappa}} \left[ x_2 \exp(x_2^2 t) \text{Erf}c(x_2 \sqrt{t}) - x_1 \exp(x_1^2 t) \text{Erf}c(x_1 \sqrt{t}) \right]. \quad (37) \]
This can be represented as series,
\[ \tilde{K}(t) = \frac{1}{\sqrt{9 - 4 \kappa}} \left[ x_2 \exp(x_2^2 t) - x_1 \exp(x_1^2 t) \right] + 2x_1^2 \sqrt{\pi} \sum_{k=0}^{\infty} \frac{(2t)^k x_2^{2k}}{(2k+1)!!} \left[ \frac{2 \sqrt{\pi} \sum_{k=0}^{\infty} (2t)^k x_2^{2k}}{(2k+1)!!} \right]. \quad (38) \]
which is useful at small $t$. In contrast to the memory kernel for the force on the rigid sphere, that has square root divergence at zero, $\tilde{K}(t)$ has a finite value of $1/\kappa$ at $t = 0$. When $t$ is large we can use,
\[ \tilde{K}(t) = \frac{1}{\pi \sqrt{9 - 4 \kappa}} \left[ \sum_{k=0}^{\infty} \frac{(-1)^k \Gamma(k + 3/2)}{t^{k+3/2} x_2^{2k+1}} \right], \quad (39) \]
The leading order behavior at large times is given by $k = 0$ term. We find using $x_1^2 - x_2^2 = 3\sqrt{9 - 4 \kappa}$ that $\tilde{K}(t) \sim 3t^{-3/2}/\sqrt{4\pi}$. This behavior is independent of $\kappa$ because the leading order behavior of $\hat{f}(\lambda)$ at small $\lambda$, given by $[1 + 3 \sqrt{\lambda}]^{-1}$, is independent of $\kappa$. Thus it holds also that $\tilde{K}(t) \sim 3t^{-3/2}/\sqrt{4\pi}$ as claimed in the main text after Eqs. (11).

In the case of Volvox the density of the swimmer is approximately the density of the fluid, $\kappa \approx 3$, so that $\sqrt{9 - 4 \kappa} \approx i \sqrt{3}$ and $x_i$ are complex conjugates of each other. We find,
\[ \tilde{K}(t) = \frac{2 \pi}{3} \left[ x_2 \exp(x_2^2 t) \text{Erf}c(x_2 \sqrt{t}) - x_1 \exp(x_1^2 t) \text{Erf}c(x_1 \sqrt{t}) \right], \quad (40) \]
Finally, we find $K(t)$ setting $\kappa = 1$ above which gives,
\[ x_2 = \frac{3 + \sqrt{5}}{2}, \quad x_1 = \frac{3 - \sqrt{5}}{2}, \quad K(t) = \frac{1}{\sqrt{5}} \left[ x_2 \exp(x_2^2 t) \text{Erf}c(x_2 \sqrt{t}) - x_1 \exp(x_1^2 t) \text{Erf}c(x_1 \sqrt{t}) \right], \quad (41) \]
with the corresponding asymptotic forms and series.

Appendix C  CALCULATIONS OF METACHRONAL WAVE

Here we provide details of the calculation of the swimmer’s velocity for the metachronal wave introduced before Eq. (18). We saw in the main text that $v_{\phi}(t, \theta) = \theta(t, \theta_0) = \phi(t, \theta_0)$, setting $\theta_0 = \theta(t_0, \theta_0) - \epsilon \cos(\kappa \theta(t, \theta_0) - \sigma t)$ that,
\[ v_{\phi}(t, \theta) \approx a \sigma \epsilon \sin(\kappa \theta - \sigma \tau - k \epsilon \cos(\kappa \theta - \sigma t)) \] (42)
which neglects terms of order $\epsilon^3$ and higher. Expanding the last line in the same order,
\[ v_{\phi}(t, \theta, \phi) \approx a \sigma \epsilon \sin(\kappa \theta - \sigma \tau - a k \sigma \epsilon^2 \cos^2(\kappa \theta - \sigma t)). \] (43)
The axial symmetry dictates that $v_0^s(t)$ points in vertical direction. We find designating this component by $v_0^s(t)$ and using $v_{BW} = -v_{BW} \sin \theta$,
\[
v_0^s(t) = \frac{1}{2} \int_0^\pi v_{BW} \sin^2 \theta d\theta = \frac{1}{4} \int_0^\pi v_{BW}(1 - \cos(2\theta))d\theta.
\]
We find using Eq. (43) and the integrals
\[
\int_0^\pi \sin(k\theta - \sigma t) \sin^2 \theta d\theta = \frac{4 \sin(\pi k/2) \sin(\pi k/2 - \sigma t)}{k(4 - k^2)},
\]
\[
\int_0^\pi \cos^2(k\theta - \sigma t) \sin^2 \theta d\theta = \frac{\pi}{4} + \frac{\sin(\pi k) \cos(\pi k - 2\sigma t)}{4k(1 - k^2)}.
\]
that Eq. (18) holds giving the swimming velocity neglecting inertia. We consider the inertia correction to this velocity using
\[
\frac{\tilde{v}_0^s}{\alpha \sigma f(\epsilon - i\sigma \tau_d)} = \frac{2i\pi \sin(\pi k/2)}{k(4 - k^2)} \left( \frac{\exp(-i\pi k/2)\delta(\omega + \sigma)}{f(\epsilon + i\sigma \tau_d)} - \frac{\pi \sin(\pi k)}{8(1 - k^2)} \right) - \frac{\pi \sin(\pi k)}{8(1 - k^2)} \left( \frac{\exp(i\pi k/2)\delta(\omega - \sigma)}{f(\epsilon - i\sigma \tau_d)} - \frac{\exp(-i\pi k/2)\delta(\omega + \sigma)}{f(\epsilon + i\sigma \tau_d)} \right),
\]
where we did not write the $\delta(\omega)$ term which does not contribute the correction. We observe that,
\[
\tilde{f}(\epsilon \pm i\sigma \tau_d) = 1 \pm \frac{\epsilon R_0}{\alpha} + \sqrt{\frac{\epsilon R_0}{\alpha} (1 \pm i),}
\]
so that $\tilde{f}(\epsilon + i\sigma \tau_d)$ and $\tilde{f}(\epsilon - i\sigma \tau_d)$ are complex conjugates. Using Eq. (19) and performing inverse Fourier transform of Eq. (44) we find Eq. (19).

**Appendix D: The Limit of Small Roskho Number**

Here we derive the swimming velocity in terms of the swimming stroke $v_0(x, t)$ in the limit of small Roskho number. Our starting point are Eqs. (16) and (23),
\[
v = v_0^s - \kappa \tau_d \frac{dv_0^s}{dt}, \quad \Omega(t) = \Omega^s(t) - \frac{3\tau_s}{10} \frac{d\Omega^s(t)}{dt}.
\]
These velocities depend on inertia directly, through the corrections linear in $R_0 \propto \tau_d$, and indirectly through the rotation matrix, see Eq. (9). We use for studying the rotation matrix that,
\[
\frac{dR_{ij}}{dt} = R_{il}\epsilon_{lpj} \Omega^p, \quad \Omega^b = R^b\Omega(t),
\]
where we introduced angular velocity in the body-fixed frame $\Omega^b$ with $R^b$ the matrix transpose of $R$. This equation can be obtained from $R_{ij} = \epsilon_{ikl}R_{kl}R_{ij}$ using rotational invariance of the Levi-Civita tensor that implies that $\epsilon_{ipq} = \epsilon_{ikl}R_{kl}R_{ij}$ for any orthogonal $R$. Indeed, this identity gives $R_{kl}\epsilon_{lpj} = \epsilon_{ikl}R_{kl}R_{ij}$ which use in $R_{ij} = \epsilon_{ikl}R_{kl}R_{ij}^p$ brings Eq. (47). We find using Eqs. (11) and (46) that in linear order in $R_0$,
\[
\Omega^b = -\int_S \frac{3\sigma}{8\pi a^4} \frac{d}{dt} \int_S \frac{3\sigma}{8\pi a^4} \frac{3\sigma}{10} \frac{d}{dt} \int_S \frac{3\sigma}{8\pi a^4}.
\]
Thus, $\Omega^b$, in contrast with $\Omega$, is completely determined by $v_0(x, t)$ and is independent of $R$. This is why we use it for finding $R$ in Eq. (47). We rewrite the equation as,
\[
\frac{dR}{dt} = R \left( W - \frac{3\sigma}{10} \frac{dW}{dt} \right),
\]
where we introduced the antisymmetric matrix,
\[
W_{ij} = -\epsilon_{ipq} \left( \int_S \frac{3\sigma}{8\pi a^4} v_0^s(r, t) dS \right)_p.
\]
We look for the solution of Eq. (50) to linear order in $R_0$. The zero order solution $R_0$ obeys $R_0 = R_0W$. We look for solution in the form $R = (1 + \delta R)R_0$ where $\delta R \propto R_0$. We have,
\[
\frac{d\delta R}{dt} = -\frac{3\sigma}{10} R_0 \frac{dW}{dt} R_0 - \frac{3\sigma}{10} \frac{d}{dt} \left( R_0 W R_0^t \right),
\]
where we observed that,
\[
\frac{d}{dt} \left[ R_0 W R_0^t \right] = R_0 \frac{dW}{dt} R_0^t,
\]
which is readily verified using antisymmetry $W^t = -W$. We conclude integrating Eq. (52) from 0 to $t$ with $\delta R(0) = 0$ (implied by $R_{ij}(0) = 0$),
\[
\delta R = \frac{3\sigma}{10} R_0 \left( W(t) - W(0) \right) R_0^t.
\]
We observe that $\delta R$ is an antisymmetric matrix as it must be by the orthogonality of $R$. We can write using Eq. (51),
\[
\delta R_{ik} = \frac{3\sigma}{10} (R_0)_{il}(R_0)_{kj}\epsilon_{lpj} \left( \int_S \frac{3\sigma}{8\pi a^4} v_0^s(r, t) - v_0^s(r, t = 0) dS \right)_p,
\]
which gives using $(R_0)_{lpq} = R_0_{il}(R_0)_{kj}\epsilon_{lpj}$ that,
\[
\delta R_{ik} = \frac{3\sigma}{10} \epsilon_{ikk} (\Omega^b_{ij}(t) - \Omega_{ij}^s(0)).
\]
We introduced the Stone-Samuel angular velocity of inertialess swimmer,
\[ \Omega^{ss}(t) = -R_0 \int_S \frac{3\mathbf{r} \times \mathbf{v}_b(r, t) dS}{8\pi a^4}. \] (57)

We find the swimmer’s velocity using this rotation matrix from Eqs. [9] and [46],
\[ \mathbf{v} = \mathbf{v}^{ss} - \mathbf{\kappa} \frac{d\mathbf{v}^{ss}}{dt} + \frac{3\tau_s}{10} \mathbf{v}^{ss} \times (\Omega^{ss}(t) - \Omega^{ss}(0)), \] (58)
where we used Eq. [66] and introduced the Stone-Samuel velocity of inertialess swimmer,
\[ \mathbf{v}^{ss} = -R_0 \int_S \mathbf{v}_b(r, t) \frac{dS}{4\pi a^2}. \] (59)

This recovers Eq. [25] from the main text.

**Appendix E ASYMMETRIC STROKE**

We consider swimming due to the general asymmetric stroke given by,
\[ \theta(t, \theta_0, \phi_0) = \theta_0 + cy(\sigma t) + c\cosh(\phi_0) y(\sigma t). \] (60)

This reduces to Eq. [27] for \( h(\phi_0) = \cos(\phi_0) \) and \( y(\sigma t) = \cos(\sigma t) \). We demonstrate below that the results obtained for any asymmetry function \( h(\phi_0) \) do not differ from those for \( h(\phi_0) = \cos \phi_0 \). In contrast, the use of different \( y(t) \) can give quantitatively (but not qualitatively) different answers. We consider non-gravitational component of velocity including gravity later.

The asymmetry function \( h(\phi_0) \) describes how different the motion of cilia at different azimuthal angles is and it is a periodic function with period \( 2\pi \) and zero average whose Fourier series is,
\[ h(\phi_0) = \sum_{n=1}^{\infty} (a_n \cos(n\phi_0) + b_n \sin(n\phi_0)). \] (61)

We define constant \( c \) in Eq. [60] so that \( a_1^2 + b_1^2 = 1 \). We assume that the modulation is of order one so \( c \) is also of order one. The function \( y \) characterizes periodic swimming stroke and has the Fourier series representation,
\[ y(\sigma t) = \sum_{n=1}^{\infty} (c_n \cos(n\sigma t) + d_n \sin(n\sigma t)), \] (62)
so that \( \sigma \) is the swimming stroke frequency. For motion given by Eq. [60] the swimming stroke \( \mathbf{v}_b \) has only \( \theta \) component given by \( v_{\theta b}(\theta, \phi) = a\sigma (1 + h(\phi) c) y'(\sigma t) \). Thus,
\[ v_{b\theta} = -a\sigma (1 + h(\phi) c) y'(\sigma t) \sin \theta, \]
\[ v_{bx} = a\sigma (1 + h(\phi) c) y'(\sigma t) \cos \phi \cos \theta, \]
\[ v_{by} = a\sigma (1 + h(\phi) c) y'(\sigma t) \sin \phi \cos \theta. \] (63)

It is then found,
\[ \mathbf{v}_s = -\int_S \mathbf{v}_b(x, t) \frac{dS}{4\pi a^2} = \frac{\pi}{4} a\sigma y'(\sigma t) \mathbf{\hat{z}}; \quad \mathbf{\hat{p}}_s = a_1 \mathbf{\hat{y}} - b_1 \mathbf{\hat{x}}, \]
\[ \Omega_s = -\int_S \frac{3\mathbf{r} \times \mathbf{v}_b(r, t) dS}{8\pi a^4} = -\frac{3}{4} a\sigma y'(\sigma t) \mathbf{\hat{p}}_s, \] (64)
where \( a_1, b_1 \) are defined in Eq. [61]. We observe that \( \mathbf{\hat{p}}_s \) is a unit vector aligned with the constant rotation axis in \( x = y \) plane. Using reference frame rotated in the plane so that \( \mathbf{\hat{p}} \) has only \( y \)-component we find,
\[ \mathbf{v}_s = \frac{\pi}{4} a\sigma y'(\sigma t) \mathbf{\hat{z}}, \quad \Omega_s = -\frac{3}{4} a\sigma y'(\sigma t) \mathbf{\hat{y}}. \] (65)

which is identical with what we would obtain using \( h(\phi_0) = \cos(\phi_0) \) in Eq. [60].

We start from considering the case of \( Ro \ll 1 \) where Eq. [26] holds. We observe that,
\[ \mathbf{v}^{ss} \times \Omega^{ss} = R_0 (v_s \times \Omega_s) = \frac{3\pi a\sigma^2 \sigma^2 (y'(\sigma t))^2}{16} R_0 \mathbf{\hat{x}}, \] (66)
where we use definitions of Appendix [E]. In the leading order in \( \epsilon \) we have the matrix \( R_0 \) is unit matrix since \( \Omega_s \propto \epsilon \). We find from Eq. [26],
\[ (\mathbf{v})_{tr} = \frac{9\pi a\sigma^2 \sigma^2 \gamma_4}{80} \left( (y'(\sigma t))^2 \right) \mathbf{\hat{x}}. \] (67)

This gives for the stroke given by Eq. [27] with \( y(\sigma t) = \cos(\sigma t) \) that,
\[ (\mathbf{v})_{tr} = \frac{\pi a\sigma^2 \sigma^2 \sigma^2}{80} \mathbf{\hat{x}}. \] (68)

where we used \( \sigma^2 = 9\tau_{td}/2 \) defined in the main text. This agrees with the small Roshko number limit of Eq. [28].

Returning to the case of arbitrary \( Ro \), we have from Eq. [20] that,
\[ \hat{\Omega}(\omega) = \frac{(R \Omega_s)(\omega)}{1 - iJ\omega T_0^{-1}(\omega)} = -\frac{3\pi a\sigma (y'(\sigma t) \mathbf{R}_s)(\omega)}{4(1 - iJ\omega T_0^{-1}(\omega))}, \] (69)

where in this formula we designate Fourier transform of some function \( q(t) \) by \( (q)(\omega) \). We observe that since the rotation is around \( y \)-axis then \( \mathbf{R}_s \mathbf{\hat{y}} = \mathbf{\hat{y}} \). We find,
\[ \hat{\Omega}(\omega) = \frac{3i\pi a\sigma \omega}{4} \sum_{n=1}^{\infty} \left( \frac{c_n \left( \delta(\omega + n\sigma) + \delta(\omega - n\sigma) \right)}{1 - iJ\omega T_0^{-1}(\omega)} \right) \]
\[ -i\delta n (\delta(\omega + n\sigma) - \delta(\omega - n\sigma)) \] (70)

where we used Eq. [62]. Inverse Fourier transform gives,
\[ \Omega(t) = \frac{3\pi a}\sigma \omega \sum_{n=1}^{\infty} \left( nc_n \frac{\exp(i\omega t)}{1 + iJ n\omega T_0^{-1}(\omega)} \right) \]
\[ -i\delta n \mathbf{R} \left( \frac{\exp(i\omega t)}{1 + iJ n\omega T_0^{-1}(\omega)} \right) \] (71)
where we used $T_0(-\omega) = T_0^\ast(-\omega)$ and $\mathcal{I}$ stands for imaginary part. Introducing rotation angle $\psi(t) = \int_0^t \Omega(t')dt'$ we find,

$$\psi(t) = \frac{3\alpha}{4} \sum_{n=1}^{\infty} \left( c_n R \left( \frac{1 - \exp(i\sigma t)}{1 + iJ_n \sigma T_0^{-1}(-n\sigma)} \right) \right. + d_n \mathcal{I} \left( \frac{1 - \exp(i\sigma t)}{1 + iJ_n \sigma T_0^{-1}(-n\sigma)} \right) \right) \quad (72)$$

We have that up to quadratic order in $\epsilon$,

$$R(t)v_s(t) = \frac{\pi}{4} a \sigma y'(\sigma)\psi(t)\dot{x} + O(\epsilon^3). \quad (73)$$

We find performing time averaging, using that $\langle v \rangle = \frac{\pi}{4} a \sigma \langle y'(\sigma)\psi(t)\dot{x} \rangle$, see the main text, that,

$$\langle v \rangle = -\frac{3\pi a c^2 \sigma \dot{x}}{16} \sum_{n=1}^{\infty} \left( c_n R \left( \frac{\exp(i\sigma t)y'(\sigma)}{1 + iJ_n \sigma T_0^{-1}(-n\sigma)} \right) \right. + d_n \mathcal{I} \left( \frac{\exp(i\sigma t)y'(\sigma)}{1 + iJ_n \sigma T_0^{-1}(-n\sigma)} \right) \right) \quad (74)$$

We find performing time averaging,

$$\langle v \rangle = \frac{3\pi a c^2 \sigma \dot{x}}{32} \sum_{n=1}^{\infty} R \left( \frac{i(c_{n}^2 + d_{n}^2)}{1 + iJ_n \sigma T_0^{-1}(-n\sigma)} \right). \quad (75)$$

We observe that,

$$\mathcal{R} \left( \frac{i}{1 + iJ_n \sigma T_0^{-1}(-n\sigma)} \right) = \mathcal{R} \left[ \left( \frac{T_0(-n\sigma)}{J_n \sigma} + i \right)^{-1} \right] \quad (76)$$

We have from Eq. (60) that,

$$\frac{T_0(-n\sigma)}{J_n \sigma} = \frac{15}{2\gamma^2 \alpha_n^2} + \frac{5i}{\gamma(1+\alpha_n+i\alpha_n)} \quad (77)$$

where we introduced $\alpha_n = 3\sqrt{nRo}/2$. We find that $\langle v \rangle = U a \sigma \dot{x}$ where the velocity per body size per stroke $U$ is,

$$U = \frac{3\pi a c^2}{32} \sum_{n=1}^{\infty} (c_{n}^2 + d_{n}^2) R \left[ \left( \frac{15}{2\gamma^2 \alpha_n^2} + i + \frac{5i}{\gamma(1+\alpha_n+i\alpha_n)} \right)^{-1} \right] \quad (78)$$

This gives Eq. (28) from the main text by setting all $c_n$ and $d_n$ to zero except for $c_1 = 1$. We see that dimensionless swimming velocity depends on the dimensionless parameters of the stroke as $\epsilon^2$ times order one constant $c$ times a numerical factor that depends on $Ro$. This type of parametric dependence is quite universal. We have $U \sim \epsilon^2$ for the stroke $\theta = \theta_0 + \epsilon \cos(n\theta_0 - \omega t)$ considered in [27]. The same stroke combined with small radial deformations is considered to model Volvox, see e. g. [10]. The radial deformations do not bring strong change in the parametric dependence: we have $U \sim \epsilon^2$ with proportionality coefficient depending on $n$ and the ratio of amplitudes of angular and radial motions. We conclude that our flapping stroke prescribed by Eq. (60) gives parametric dependence that is quite similar to that for irreversible strokes and thus theoretically it must be considered on equal footing with those. This is of course because inertia is of order one, $Ro \sim 1$ so that the scallop theorem’s breakdown is of order one. Whether this type of swimming is used by Volvox or other microswimmer for the actual motion is to be decided by future observations.

We study $U$ as a function of the free parameters of the swimming stroke $\gamma$, $\sigma$, and $\alpha$. We consider the case studied in the main text (where all $c_n$ and $d_n$ are zero and $c_1 = 1$). Writing Eq. (28) explicitly as a real-valued function gives (we designate $\alpha_1$ by $\alpha$ here),

$$U = \left( \frac{15}{2\gamma^2 \alpha^2} + \frac{5\alpha}{\gamma(1+2\alpha+2\alpha^2)} + i + \frac{5i}{\gamma(1+2\alpha+2\alpha^2)} \right)^{-2} 3\pi c^2 \left( \frac{15}{2\gamma^2 \alpha^2} + \frac{5\alpha}{\gamma(1+2\alpha+2\alpha^2)} \right) \quad (79)$$

We find that dimensionless velocity factorizes as,

$$U = \frac{3\pi c^2}{32} \tilde{U}(\gamma, \alpha) \quad (80)$$

where the dimensionless function $\tilde{U}$ of two dimensionless numbers $\gamma$ and $\alpha$ is,

$$\tilde{U} = \gamma (1+2\alpha+2\alpha^2) (15(1+1/\alpha+1/(2\alpha^2)) + 5\alpha) / D \quad (81)$$

with the denominator $D$,

$$D = (15(1+1/\alpha+1/(2\alpha^2)) + 5\alpha)^2$$

$$+ (\gamma (1+2\alpha+2\alpha^2) + 5(1+\alpha))^2 \quad (82)$$

Thus the dependence on the density of the swimmer has the form $U(\gamma) = g/b_{2}\gamma^2 + b_{1} \gamma + b_{0}$ with the corresponding definitions of the $\alpha$-dependent coefficients $b_i$ which can be readily obtained from Eq. (78). Elementary calculus of $U'(\gamma) = 0$ gives that $U$ considered as a function of density of the swimmer has a maximum at an optimal density ratio of,

$$\gamma^* = \frac{5 \sqrt{(3/2\alpha^2 + 3/\alpha + 3\alpha)^2 + (1+\alpha)^2}}{1+2\alpha+2\alpha^2} \quad (83)$$

This optimum has less implications for Volvox because of the presence of the gravitational settling velocity not considered so far. They tend to nearly neutral buoyancy, $\gamma \approx 1$.

**Appendix F  HEAVY SWIMMERS**

We consider the limit of heavy (called dense in [16]) swimmers whose density is much larger than the density
of the fluid, $\gamma \gg 1$. In this limit $\kappa \approx 2\gamma \to \infty$ and we can neglect $3\sqrt{\lambda}$ in $f(\lambda) = 1 + 3\sqrt{\lambda} + \kappa\lambda$ (we cannot neglect one that becomes relevant at $\lambda \lesssim 1/\kappa$). Thus Eq. (13) becomes
\[
\hat{v}(\omega) = \frac{\hat{v}_0^s}{1 - i\omega\tau_s} + 2\pi \delta(\omega) g\tau_s,
\]
where we observed that in this limit $\kappa\tau_d$ is the Stokes time $\tau_s = 2\gamma\tau_d$. Inverse Fourier transform gives,
\[
\frac{dv}{dt} = -v - v_0^s + g. \tag{82}
\]
This reproduces the equation for heavy spherical swimmers derived in [16]. The limit of small inertia, $\sigma\tau_s \ll 1$, is found by writing $v = v_0^s - \tau_s \dot{v} + g\tau_s$ and making first iteration of the RHS,
\[
v \approx v_0^s - \tau_s \frac{dv_0^s}{dt} + g\tau_s. \tag{83}
\]
This agrees with Eq. (10). Similar consideration holds for the angular velocity. We have from Eq. (20)
\[
\hat{\Omega}(\omega) = \frac{\hat{\Omega}_s(\omega)}{1 - (3i\omega\tau_d/5) (1 - 3i\omega\tau_d/[1 + q(\omega\tau_d)])^{-1}} \tag{84}
\]
where we used the definition of $T_0(\omega)$ in Eq. (6). We observe that in the limit of large $\gamma$ the characteristic frequency $\omega_c$ that defines the inverse Fourier transform of $\hat{\Omega}(\omega)$ obeys $\omega_c \tau_d \sim \gamma^{-1}$. This is obtained by the demand that the prefactor in the denominator is of order one. We find observing that at these frequencies $(1 - 3i\omega\tau_d/[1 + q(\omega\tau_d)])^{-1} \approx 1$ that,
\[
\hat{\Omega}(\omega) \approx \frac{\hat{\Omega}_s(\omega)}{1 - 3i\omega\tau_s/10}, \tag{85}
\]
where we used $2\gamma\tau_d = \tau_s$. Performing inverse Fourier transform,
\[
\frac{d\Omega}{dt} = -\frac{10 (\Omega - \Omega_s)}{3\tau_s}. \tag{86}
\]
The system of Eqs. (24) is found by combining this equation with Eq. (82). The limit of small inertia, $\sigma\tau_s \ll 1$, for rotational velocity is found by writing $\Omega = \Omega^s - 3\tau_s \Omega/10$ and making first iteration of the RHS. This reproduces Eq. (23).