Supplemental Information

Motility of Colonial Choanoflagellates
and the Statistics of Aggregate Random Walkers

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Single cells

So-called ‘slow-swimmer’ S. rosetta unicells, similar in morphology to the individual cells that comprise a colony, clearly exhibit random walk behaviour. Fig. 1 shows the mean squared displacement of 32 S. rosetta slow-swimmers, each filmed for ∼1.5 minutes. The behaviour is well-described by the equation for conventional active random walkers,

\[
\langle \Delta r^2 \rangle = \left( \frac{2 v^2}{D_r} \right) \left( D_r t + e^{- D_r t} - 1 \right). \tag{1}
\]

Figure 1: Squared distance moved averaged over 32 S. rosetta single cells. Overlayed fit (dashed) is to Eq. (1). Parameters: \( v = 12.3 \ \mu m/s, D_r = 0.15 \ s^{-1} \).

The active rotational diffusion constants for both single cells and colonies (main text) are on the order of 0.1 \( s^{-1} \). With a beat frequency \( f \sim 40 \ Hz \), this corresponds to a distribution of angular deviations per beat with standard deviation \( \sim \sqrt{D_r / f} = 3^\circ \). The thermal rotational diffusion constant \( D_r^{\text{thermal}} = k_B T / 8 \pi \mu a^3 \) ranges from 0.012 to 0.0014 \( s^{-1} \) for radii 2.5 to 5.0 \( \mu m \), at least an order magnitude below the active one.

Noise induced drift

The Langevin equations

\[
dv(t) = \omega(t) \times v(t) \ dt + \sqrt{2 D_r} \ dW_r(t) \otimes v(t) \tag{2}
\]
\[
d\omega(t) = \sqrt{2 D_r} \ dW_r(t) \otimes \omega(t) \tag{3}
\]
must be interpreted in the Stratonovich sense for the magnitude of \( v \) and \( \omega \) to not grow indefinitely. Using \( dW_r(t) = (dW_1(t), dW_2(t), dW_3(t)) \), Eq. (3) can be written as
\[
d\omega(t) = \sqrt{2D_r} \begin{pmatrix} 0 & \omega_3(t) & -\omega_2(t) \\ -\omega_3(t) & 0 & \omega_1(t) \\ \omega_2(t) & -\omega_1(t) & 0 \end{pmatrix} \circ \begin{pmatrix} dW_1(t) \\ dW_2(t) \\ dW_3(t) \end{pmatrix} \equiv \sigma(t) \circ \begin{pmatrix} dW_1(t) \\ dW_2(t) \\ dW_3(t) \end{pmatrix},
\]
and likewise for Eq. (2). The corresponding Itô equation becomes
\[
d\omega(t) = \sigma(t) \cdot \begin{pmatrix} dW_1(t) \\ dW_2(t) \\ dW_3(t) \end{pmatrix} + \frac{1}{2} \left( (\sigma(t) \cdot \nabla \omega) \sigma(t) \right)^T dt
\]
where \( T \) denotes transpose. The last term is the noise-induced drift, evaluating to
\[
\frac{1}{2} \left( (\sigma(t) \cdot \nabla \omega) \sigma(t) \right)_i = \frac{1}{2} \sum_{k=1}^{3} \sum_{j=1}^{3} \sigma_{ij} \frac{\partial \sigma_{ij}}{\partial \omega_k} = -2D_r \omega_i,
\]
The calculation of \( v(t) \) follows the same procedure, and yields \(-2D_r \bar{v}_i\).

**Derivation of random walker functions**

Since the rotation angles \( \alpha, \beta, \) and \( \gamma \) are Markov processes we can write the probability distribution functions as e.g. \( P(\alpha(t')) = N(\alpha_0, 2D_r t') \) and \( P(\alpha(t)|\alpha(t')) = N(\alpha(t'), 2D_r (t - t')) \) for \( t' < t \), where \( N(\mu, \sigma^2) \) is the normal distribution. Using \( P(\alpha(t), \alpha(t')) = P(\alpha(t)|\alpha(t')) P(\alpha(t')) \) we obtain averages such as
\[
\langle \cos \alpha(t) \cos \alpha(t') \rangle = \int_{-\infty}^{\infty} dx \int_{-\infty}^{\infty} dy \cos(x) \cos(y) N_x(x, 2D_r |t - t'|) N_y(y, 2D_r |t - t'|)
\]
which in the stationary limit can be used to find the velocity autocorrelations, e.g.
\[
\langle \nu_x(t) \nu_x(s) \rangle = \langle \nu_\omega \cos(\beta(t)) \cos(\gamma(t)) \cos(\omega_0 t) + \nu_\varphi \sin(\beta(t)) - \nu_\omega \cos(\beta(t)) \sin(\gamma(t)) \sin(\omega_0 t) \rangle
\]
\[
\quad - \nu_\varphi \sin(\beta(t)) \sin(\omega_0 t) \times \langle \nu_\varphi \sin(\beta(t)) + \nu_\omega \cos(\beta(t)) \sin(\gamma(t)) \cos(\omega_0 t) - \nu_\omega \cos(\beta(t)) \sin(\gamma(t)) \sin(\omega_0 t) \rangle
\]
\[
= \frac{1}{2} \nu_\varphi^2 e^{-D_r |t - s|} + \frac{1}{4} \nu_\omega^2 e^{-2D_r |t - s|} \cos(\omega_0 (t - s)).
\]
The function only depends on the time difference \( t - s \), which is the case for stationary autocorrelations (this is the very definition of a *weakly* stationary process). From
\[
\nu_y(t) = -\nu_\varphi \sin(\alpha(t)) \cos(\beta(t)) + \nu_\omega \sin(\alpha(t)) \sin(\beta(t)) \cos(\gamma(t)) + \cos(\alpha(t)) \sin(\gamma(t)) \cos(\omega_0 t) + \cos(\alpha(t)) \cos(\gamma(t)) - \sin(\alpha(t)) \sin(\beta(t)) \sin(\gamma(t)) \sin(\omega_0 t)
\]
we find in a similar manner
\[
\langle \nu_y(t) \nu_y(s) \rangle = \frac{1}{4} \nu_\varphi^2 e^{-2D_r |t - s|} + \frac{1}{8} \nu_\omega^2 (e^{-3D_r |t - s|} + 2e^{-2D_r |t - s|}) \cos(\omega_0 (t - s)),
\]
and the same for $\langle v_z(t) v_z(s) \rangle$. We project on to a random 2D plane by summing the $x, y, z$ results followed by multiplication of $2/3$ (this gives a different result than simply summing the $x$ and $y$ components due to the asymmetry induced by the approximation). We thus find

$$
\langle v(\Delta t) \cdot v(0) \rangle = \frac{e^{-2D_t|\Delta t|}}{6} \left[ 2v_p^2 \left( 1 + e^{D_t|\Delta t|} \right) + v_\omega^2 \left( 3 + e^{-D_t|\Delta t|} \right) \cos(\omega_0 \Delta t) \right].
$$

(11)

The mean squared displacement is obtained by integrating the autocorrelation twice

$$
\langle \Delta r^2(t) \rangle = \int_0^t \int_0^t \langle v(t') \cdot v(t'') \rangle \, dt' \, dt''
$$

(12)

$$
= \frac{v_p^2 e^{-2D_t t}}{6D_t^2} \left( 1 + 4e^{D_t t} \right) + 4D_\infty t - a_0 \\
+ \frac{v_\omega^2 e^{-2D_t t}}{6D_t^2} \left( \frac{4D_t^2 - \omega_0^2}{(4D_t^2 + \omega_0^2)^2} + \frac{9D_t^2 - \omega_0^2}{3(9D_t^2 + \omega_0^2)^2} e^{-D_t t} \right) \cos \omega_0 t \\
- \frac{v_\omega^2 e^{-2D_t t}}{6D_t^2} \left( \frac{4\omega_0 D_t}{(4D_t^2 + \omega_0^2)^2} + \frac{2\omega_0 D_t}{(9D_t^2 + \omega_0^2)^2} e^{-D_t t} \right) \sin \omega_0 t,
$$

where

$$
a_0 = \frac{5v_p^2}{6D_t^2} + v_\omega^2 \left( \frac{4D_t^2 - \omega_0^2}{(4D_t^2 + \omega_0^2)^2} + \frac{9D_t^2 - \omega_0^2}{3(9D_t^2 + \omega_0^2)^2} \right).
$$

(13)

As $t \to \infty$, $\langle \Delta r^2 \rangle \sim 4D_\infty t$, where

$$
D_\infty = \lim_{t \to \infty} \frac{\langle \Delta r^2 \rangle}{4t} = \frac{v_p^2}{4D_t} + \frac{v_\omega^2 D_t}{4} \left( \frac{1}{9D_t^2 + \omega_0^2} + \frac{2}{4D_t^2 + \omega_0^2} \right).
$$

(14)

The existence of the above (non-zero) limit confirms the diffusive behaviour.

**Comparison of fit parameters**

![Comparison of fit parameters](image)

Figure 2: Comparison of fit parameters of 36 tracks. Tracks where $\omega_0, v_\omega$ could be determined in red and tracks where $\omega_0, v_\omega$ are forced to zero in blue.
Fig. 2 shows scatter plots of fit parameters of the model to 36 different S. rosetta colonies, indicating the high variances of all parameters. We note, however, that the determination of some parameters is difficult in certain regions. For instance, $\omega_0$ and $v_\omega$ are hard to determine when either one becomes small, and accordingly we have forced them to zero in these cases and plotted them in blue. Naturally, these cases will have a higher $v_p$ as is clear in the two plots in the left part of Fig. 2.

Applying the same area estimator as in Fig. 4 of the main text, the parameters can also be plotted as a function of size. Just as with swimming speed, Fig. 3 shows that the model parameters have very high variances and no clear dependence on size. For a subset of the short tracks we were able to fit the model well enough to estimate $\omega_0$ and these are shown as blue crosses. However, the short track colonies for which good estimates could be obtained are biased towards high $\omega_0$ (and $v_\omega$). Nonetheless, there is no clear tendency for larger colonies to rotate slower as is the case for e.g. bacterial clumps [1]. For an interesting example of a big fast-spinning colony see the end of Supplemental Video 2, in which a colony has formed a dumbbell shape.

References

[1] J. Schwarz-Linek, C. Valeriani, A. Cacciuto, M.E. Cates, D. Marenduzzo, A.N. Morozov, and W.C.K. Poon, Phase separation and rotor self-assembly in active particle suspensions, Proc. Natl. Acad. Sci. USA 109, 4052-4057 (2012).