Detention times of microswimmers close to surfaces: Influence of hydrodynamic interactions and noise

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After colliding with a surface, microswimmers reside there during the detention time. They accumulate and may form complex structures such as biofilms. We introduce a general framework to calculate the distribution of detention times using the method of first-passage times and study how motional noise and hydrodynamic interactions influence the escape from a surface. We compare generic swimmer models to the simple active Brownian particle. While the respective detention times of source dipoles are reduced and of pullers are increased, spanning several orders of magnitude, pushers show both trends. We apply our results to the more realistic squirmer model, for which we use lubrication theory, and validate them by simulations with multi-particle collision dynamics.

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Biological microswimmers such as bacteria are omnipresent in our everyday life. At the micron scale their locomotion in aqueous environment is determined by low-Reynolds-number hydrodynamics and influenced by thermal and intrinsic biological noise\textsuperscript{1,2}. In real environments such as the human body\textsuperscript{3} or the ocean\textsuperscript{4,5} microorganisms swim in the presence of soft or solid boundaries. When bacteria approach surfaces, they accumulate and form complex aggregates such as biofilms\textsuperscript{6}. This letter develops a general approach for investigating the fundamental and biologically relevant question how long microorganisms reside at bounding surfaces.

To develop an understanding for the accumulation and the dynamics of microorganisms near walls, several important aspects have been investigated recently: swimmer-wall hydrodynamic interactions\textsuperscript{7–12}, thermal and intrinsic noise\textsuperscript{1,2,6,7,11}, cilia- and flagella-wall interactions\textsuperscript{13}, bacterial tumbling\textsuperscript{13,14} and buoyancy\textsuperscript{14,11}. Whether either stochastic motion or swimmer-wall hydrodynamic interactions determine the reorientation of microswimmers at a surface and how they both influence the bacterial distribution between parallel plates has been discussed controversially\textsuperscript{7,8,11,13}. Hydrodynamic interactions trap bacteria at surfaces\textsuperscript{8,15}, force them to swim in circles\textsuperscript{16}, or even suppress bacterial tumbling\textsuperscript{13}. However, non-tumbling bacteria\textsuperscript{7,11} or elongated artificial microswimmers\textsuperscript{17} use rotational noise to escape from surfaces.

Artificial microswimmers such as active Janus particles or squirmers, which are driven by a surface velocity field, have been studied in front of a no-slip wall both in experiments\textsuperscript{18,20} and by theoretical models. The latter either include hydrodynamic interactions\textsuperscript{15,21–23} or only consider active Brownian particles\textsuperscript{18,19,26,28}.

An important prerequisite for the observed accumulation near walls are the relatively large times microswimmers reside at a surface before leaving it\textsuperscript{17,19}. In this article we call these swimmer-wall contact times detention times and develop a formalism to calculate their distributions near a plane no-slip surface based on the method of first-passage times\textsuperscript{29}. For generic microswimmers we demonstrate that hydrodynamic interactions, relative to pure motional noise, can either increase the mean detention by several orders of magnitude or also decrease it.

At low Reynolds number the motion of an axisymmetric microswimmer with orientation $\mathbf{e}$ in the presence of bounding surfaces is governed by the Langevin equations

\begin{equation}
\dot{\mathbf{r}} = \mathbf{v}_A + \mathbf{v}_{HI} + \mathbf{v}_N + ..., \\
\dot{\mathbf{e}} = \Omega \times \mathbf{e} \quad \text{with} \quad \Omega = \Omega_{HI} + \Omega_N + ..., \tag{1}
\end{equation}

which account for the stochastic dynamics of position $\mathbf{r}$ and orientation $\mathbf{e}$. Here we only consider the influence of the activity of the swimmer ($\mathbf{v}_A = U\mathbf{e}$ with bulk swimming velocity $U$), hydrodynamic interactions with the surface ($HI$), and noise ($N$). However, our approach can in principle be used for any dynamics which is of the form of Eqs.\textsuperscript{11} and also include, e.g., steric or electrostatic interactions as well as external fluid flow.

In the following, we assume a spherical microswimmer moving at sufficiently large Péclet number $Pe = UR/D_t$, where $R$ is its radius and $D_t$ its translational diffusion coefficient. Moving on a smooth trajectory, the swimmer

![FIG. 1. Definition of coordinate system and sketch of a typical trajectory for a spherical microswimmer approaching a plane no-slip surface (h = h*) at time $t_0$ and leaving the surface at $t^*$. The detention time at the surface is $t^* - t_0$.](image)
reaches the wall at time \( t_0 \) with an angle \( \theta_0 \) against the surface normal (see Fig. 1). For large \( \text{Pe} \) it stays there at a height \( h \approx R \) and the swimming direction \( e \) diffuses on the unit sphere but also drifts with angular velocity \( \Omega_{\text{HI}} = \Omega_{\text{HI}} e_\phi \). Once the swimming direction has reached the escape angle \( \theta^* \), to be defined below for each swimmer type, the microswimmer leaves the surface at time \( t^* \). This stochastic process is described by the Smoluchowski equation \( \partial_t P = \mathcal{L} P = (\mathcal{R} \cdot \Omega_{\text{HI}} + D_r \mathcal{R}^2) P \), where \( \mathcal{R} = e \times \partial/\partial e \) is the rotation operator and \( D_r \) the rotational diffusion constant [20, 30].

Rotational diffusion along the azimuthal angle \( \phi \) does not influence the escape from the surface and it is sufficient to consider the conditional probability \( P(\theta, t^*|\theta_0, t_0) \). To calculate the distribution of detention times at the surface, we use the Fokker-Planck approach of first-passage problems [29]. The integrated probability \( g(\theta^*, t|\theta_0) = \int_0^{\theta^*} P(\theta, t^*|\theta_0, t_0) \sin \theta d\theta \) for finding the swimming direction in the angular interval \([\theta^*, \pi]\) at time \( t = t^* - t_0 \) obeys the adjoint Smoluchowski equation

\[
\partial_t g(\theta^*, t|\theta_0) = \mathcal{L}^+(\theta_0) g(\theta^*, t|\theta_0),
\]

with \( \mathcal{L}^+(\theta_0) = \Omega_{\text{HI}}(\theta_0) \partial_\theta + D_r \partial_{\theta_0}^2 \), where \( \Omega(\theta_0) = \Omega_{\text{HI}}(\theta_0) + D_r \cot \theta_0 \) is an effective angular drift velocity. To solve it, one uses at \( \theta_0 = \pi \) reflective \( \partial_\theta g(\theta^*, t|\theta_0)_{\theta_0 = \pi} = 0 \) and at \( \theta_0 = \theta^* \) absorbing \( g(\theta^*, \theta^*) = 0 \) boundary conditions. Now, we realize that \( -\partial_t g(\theta^*, t|\theta_0) dt \) is the probability to leave the surface with escape angle \( \theta^* \) at time \( t \) in the time interval \( dt \) and we can interpret

\[
f(\theta^*, t|\theta_0) = -\partial_t g(\theta^*, t|\theta_0)
\]

as the distribution of detention times \( t = t^* - t_0 \) for being trapped at the surface (DTD).

To investigate how hydrodynamic interactions compared to pure rotational noise influence the detention time, we calculate the DTD \( f(\theta^*, t|\theta_0) \) for several model microswimmers by numerically solving Eq. (2) and using Eq. (3). From here on, we always rescale time by the ballistic time scale \( \tau_b = R/U \) and introduce the persistence number \( \text{Pe}_r = (2D_r \tau_b)^{-1} \). Since \((2D_r)^{-1}\) is the orientational correlation time, \( \text{Pe}_r \gg 1 \) means directed swimming [11, 31].

First, we consider a spherical active Brownian particle (ABP) without any orientational drift, \( \Omega_{\text{HI}} = 0 \), which only reorients by rotational diffusion near the surface [20, 28]. The escape angle is simply \( \theta^* = \pi/2 \). From the known propagator of free rotational diffusion [31], one can determine \( g(\theta^*, t|\theta_0) \) and ultimately the DTD becomes

\[
f\left(\frac{\pi}{2}, t|\theta_0\right) = \frac{\pi}{2 \text{Pe}_r} \sum_{l=1, \text{odd}}^{\infty} (-1)^{(l+1)/2} e^{-(l+1)^2 t/(2 \text{Pe}_r)} \\
\times \frac{l(2l+1)}{2^{l-1}} \left( \frac{l-1}{2} \right) P_l(\cos \theta_0),
\]

where \( P_l(\cos \theta_0) \) are Legendre polynomials. The DTD is plotted in Fig. 2(a) for \( \theta_0 = 3\pi/4 \) and \( \text{Pe}_r = 10 \). Using the formalism in Ref. [29], one can determine the mean detention time \( T = \int_0^{\theta^*} f(\theta^*, t|\theta_0) dt \) of the ABP at the surface,

\[
T_{\text{ABP}} = 2\text{Pe}_r \ln(1 - \cos \theta_0).
\]

We plot \( T_{\text{ABP}} \) versus \( \theta_0 \) in Fig. 2(b). Note that the most likely detention time \( t_{\text{max}} \) [see Fig. 2(c)] is much smaller compared to \( T_{\text{ABP}} \) due to the slow decay of \( f(\theta^*, t|\theta_0) \).

Second, we consider microswimmers which generate either a force-dipole flow field of strength \( p \) or a source dipole field of strength \( q > 0 \) in the surrounding fluid [2]. Examples for the first case are pushers (\( p > 0 \)) such as bacteria or pullers (\( p < 0 \)) such as the biflagellated algae Chlamydomonas. Source dipoles are realized by active droplets [32] or Paramecia [34]. Each flow field is described by a flow singularity located in the center of the swimmer. For simplicity, we assume that the description by singularities is still valid close to the wall (see also the discussion in [7, 15]) and hydrodynamic interactions with the surface are thus described by their flow fields. These fields generate wall-induced angular velocities \( \Omega_{\text{HI}} \) of the microswimmers, which at the wall (\( h = R \)) read \( \Omega_{\text{HI}} = 3p \sin \theta \cos \theta/8 \) for the force dipole and \( \Omega_{\text{HI}} = -3q \sin \theta/8 \) for the source dipole, respectively [8, 15]. The stable orientations \( \theta_s \) of our swimmer types at the wall in the absence of noise are sketched in the inset of Fig. 2(a). They are calculated from \( \Omega_{\text{HI}}(\theta_s) = 0 \) and \( \partial \Omega_{\text{HI}}(\theta)/\partial \theta|_{\theta_s} \). The deterministic rotation of the swimmers due to hydrodynamic interactions with the wall is perturbed by rotational diffusion.

Hydrodynamic interactions of the source dipole (\( q > 0 \)) always rotate the swimmer away from the surface until it leaves the surface at \( \theta^* = \pi/2 \). Hence, the width of the DTD is much narrower compared to the ABP [see Fig. 2(a)]. The mean detention time \( T \) plotted in

\[FIG. 2. (a) DTD for ABP and source- and force-dipole swimmer with \( \text{Pe}_r = 10 \) and an initial angle \( \theta_0 = 3\pi/4 \). (b) Mean detention time \( T \) versus initial angle \( \theta_0 \). (c) Most likely detention time \( t_{\text{max}} \) (maximum of \( f \)).\]
Fig. 2(b) is much smaller compared to \( T^{\text{ABP}} \) for all incoming angles \( \theta_0 \) and the most likely detention time \( t_{\text{max}} \) is comparable to \( T \) [see Fig. 2(c)]. Clearly, since \( \Omega_{\text{HI}} \propto -q \), the mean detention time \( T \) decreases with increasing \( q \).

The puller \( (p < 0) \) is rotated towards the surface by hydrodynamic interactions if \( \theta > \pi/2 \) and can only escape if angular noise drives it to \( \theta < \theta^* = \pi/2 \). As a consequence, the DTD only has a weakly pronounced maximum and decays very slowly [see Fig. 2(a)]. Therefore, at \( P_e = 10 \) the mean detention time of the puller is by an order of magnitude larger than for the ABP, although their \( t_{\text{max}} \) are comparable and nearly identical for \( \theta < 5\pi/6 \). Now, since \( \Omega_{\text{HI}} \propto p \) the detention time increases with dipole strength \( |p| \) because the trapping at the surface becomes stronger.

The situation of the pusher \( (p > 0) \) is more complex. Due to hydrodynamic interactions it has a stable orientation parallel to the wall \( [\theta = \pi/2, \text{see inset of Fig. 2(a)}] \). Since, in addition, the wall-induced velocity \( v_{\text{HI}}(\theta) \) pushes it towards the wall, a noiseless pusher always swims at the wall and \( T \to \infty \). In the presence of noise the swimmer orientation fluctuates about its stable direction. The pusher stays trapped until the escape angle \( \theta^* < \pi/2 \) is reached, where the total swimmer velocity starts to point away from the wall. Thus, the escape angle is determined by the condition \( |V_\text{A}(\theta^*) + v_{\text{HI}}(\theta^*)| e_z = 0 \), which gives \( \theta^* = \arccos(-4 + \sqrt{16 + 108p^2}/9p) \). Hence, \( \theta^* \) decreases towards \( 55^\circ \) with increasing \( p \).

Hydrodynamic interactions of the pusher with the surface have two counteracting effects. They can either enhance or reduce the detention time compared to a simple ABP. On the one hand, increasing \( p \propto \Omega_{\text{HI}} \) from zero reduces the time to reach the stable parallel orientation and thus the time to get closer to the escape angle \( \theta^* < \pi/2 \). This can reduce the mean detention time compared to ABPs for small \( p \) as illustrated in Fig. 2(b). On the other hand, increasing \( p \) further traps the orientation more strongly at \( \theta_s = \pi/2 \) and also pushes \( \theta^* \) more and more away from \( \theta_s \). Since rotational diffusion has to compensate for both effects, the detention time increases.

Figure 2(a) gives an overview of the force-dipole swimmer by plotting \( T/T^{\text{ABP}} \) in a color code versus \( P_e \) and \( p \). For negative \( p \) the strong increase of \( T \) beyond \( T^{\text{ABP}} \) with increasing \( |p| \) is visible and also documented in the inset for two values of \( P_e \). For small positive \( p \) and for \( P_e \gtrsim 5 \) a clear minimum of \( T \) develops as just discussed (see also the inset). In particular, in region I one finds \( T < T^{\text{ABP}} \). For example, for \( P_e = 160 \) the minimum at \( p = 0.4 \) amounts to \( T/T^{\text{ABP}} = 0.18 \). Interestingly, this minimum occurs at a dipole strength comparable to the one estimated for \( E. \) coli bacteria (\( p \approx 0.16 \)) [7]. In region II, \( T \) grows to \( 10T^{\text{ABP}} \) or well beyond. For example, at \( P_e = 160 \) and \( p = 2 \), one finds \( T/T^{\text{ABP}} = 6 \cdot 10^5 \).

In region II the orientation of the pusher has time to equilibrate about \( \theta_s = \pi/2 \) and then attempts to reach \( \theta^* \) by rotational noise. Indeed, one can rewrite the effective rotational drift in Eq. 2 by introducing an effective angular potential \( \Omega = -\partial V_{\text{eff}}/\partial \theta \) with \( V_{\text{eff}} = V + V_r = 3p \cos^2 \theta/16 - \ln(\sin \theta)/2P_e \). where the second term comes from the 3D rotational diffusion. However, the pusher escaping from the wall at \( \theta^* \) cannot be viewed as a typical Kramers problem since the orientation vector \( e \) does not pass a smooth potential barrier of height \( \Delta V_{\text{eff}} \) when reaching the escape angle \( \theta^* \).

Instead, the swimmer orientation moves up the potential \( V_{\text{eff}} \) by an amount \( \Delta V_{\text{eff}} = V_{\text{eff}}(\theta^*) - V_{\text{eff}}(\theta_s) \) and when the pusher leaves the wall at \( \theta^* \), it also leaves the range of \( V_{\text{eff}} \) [see Fig. 2(b)]. However, using the theory for the mean detention time [29], one can derive an approximate formula for large \( P_e \Delta V_{\text{eff}} \) with the Arrhenius factor reminiscent of Kramers’ mean escape time (see Supplemental Material [35] [36],

\[
T_{\text{pusher}} \approx \frac{\sqrt{\pi}}{2P_e V_{\text{eff}}(\theta_s)} e_{\theta^*} \Delta V_{\text{eff}}. \tag{6}
\]

Interestingly, in case of the puller, the rotational-noise contribution \( V_r \) shifts the most stable orientation to \( \theta_s = \pi - \arcsin[2\sqrt{3P_e}] < \pi \) [see Fig. 2(c)] [33]. Here, we can approximate the mean detention time by Kramers’
The inset of Fig. 3(a) demonstrates that $T$ calculated from Eqs. 6 and 7 at $|p|\text{Pe} \gg 1$ agrees very well with $T$ obtained by numerically solving Eqs. 2 and 3.

While so far we considered generic microswimmer models, we now turn to the spherical squirmer \cite{25}, which serves as a model for ciliated microorganisms such as Paramecium \cite{5, 26} and Volvox \cite{10} but also for active emulsion droplets \cite{33}. The squirmer propels itself by an axisymmetric surface velocity field $\mathbf{v}_s = \frac{1}{2} (1 + \beta \mathbf{e} \cdot \mathbf{r}_s) [(\mathbf{e} \cdot \mathbf{r}_s) \mathbf{r}_s - \mathbf{e}]$, where $\mathbf{r}_s$ is the unit vector pointing from the center of the squirmer to its surface. The neutral squirmer ($\beta = 0$) creates the bulk flow field of a source dipole with $q = 1/2$, while $\beta \neq 0$ adds an additional force-dipole field with $p = -3\beta/4$ \cite{40}. Recent studies with squirmer-wall interactions already exist but without any noise \cite{18, 28, 29, 30}. Using lubrication theory, the authors of Ref. \cite{40} have calculated the hydrodynamic interactions of a spherical squirmer with a nearby plane surface. In the 1D description used here, only the dimensionless friction torque acting on the squirmer in front of a wall is considered \cite{40},

$$M = (6\pi/5)(1 - \beta \cos \theta) \sin \theta (\ln \epsilon^{-1} - c),$$

where $\epsilon = h - 1$ is the small distance parameter and $c = \text{const}$. This gives the wall-induced angular velocity $\Omega_{\text{HI}} = -M/\gamma_r$, where $\gamma_r$ is the rotational friction coefficient near the surface \cite{41, 42}. Note that the neutral squirmer ($\beta = 0$) behaves like the generic source dipole even very close to the wall since $\Omega_{\text{HI}} \sim -\sin \theta$, which rotates the squirmer away from the wall. This might explain why far-field hydrodynamic interactions describe the near-wall swimming of neutral squirmers as shown in \cite{15}. The $\beta$-dependent term in Eq. 3 adds to $\Omega_{\text{HI}}$ the force-dipole term $-p \sin \theta \cos \theta$. This term alone rotates the squirmer pusher ($\beta > 0$) towards the wall and therefore it behaves like the generic puller with increased detention time and vice versa. These results are in accordance with recent simulations at finite Reynolds numbers \cite{24}.

To demonstrate that our 1D model is applicable, we perform full 3D mesoscale hydrodynamic simulations using multi-particle collision dynamics (MPCD) \cite{42, 43}. It solves the Navier-Stokes equations for the fluid around the squirmer and the wall and naturally includes thermal fluctuations \cite{46, 47}. First, we numerically determine $c \approx 0.9$ \cite{35} and then investigate the swimmer-wall interaction in simulations of a neutral squirmer for different incoming angles. Figure 4 shows results for the mean detention time $T$ plotted versus the initial angle $\theta_0$, which agree well with our analytic model. The mean detention time of the deterministic swimmer, $T_{\text{puller}} \approx \frac{\pi}{2|\text{Pe}|} |\text{det}|^{\frac{1}{2}} |\text{Pe}|^{\frac{3}{2}} \left(1 - 1.5|\text{Pe}|^{\frac{1}{2}} + 0.4|\text{Pe}|^{\frac{3}{2}} \right)$

FIG. 4. Mean detention time $T$ of a neutral squirmer plotted versus the initial angle $\theta_0$ for Pe = 110 and $\epsilon = 0.01$ (mean distance from the wall in MPCD simulations) and compared to the analytic 1D model [Eqs. 2 and 3], and the deterministic model (Pe \to \infty). Inset: Distribution of detention times from MPCD simulations and compared to analytic model.

$T_{\text{det}} \propto \ln(\tan(\theta_0/2))$ \cite{35}, deviates from the full model only close to the unstable equilibrium orientation at $\theta = \pi$. Here $T_{\text{det}} \to \infty$, whereas noise renders $T$ finite and helps the swimmer to escape. The inset of Fig. 4 shows a convincing agreement of the DTDs determined from the analytic model and MPCD simulations.

For small Péclet numbers the 1D description is not valid any more. Now, to determine the DTD, one has to include the dynamics of the swimmer height above the surface. For the state variable $y(t) = (h, \theta)$ one defines the probability $g(y^*, t | y_0)$, which includes to find the swimmer below an escape height $h^*$ at time $t = t^* - t_0$ while the initial state $y_0$ at $t_0$ starts at $h_0 \in [1, h^*]$ and $\theta_0 \in [0, \pi]$. The probability obeys the adjoint Fokker-Planck equation

$$\frac{\partial}{\partial t} g(y^*, t | y_0) = \left[ (\mathbf{v}_A + v_{\text{HI}}) \cdot \mathbf{e}_z \partial_{h_0} + D_1 \partial_{h_0}^2 ight. - (\Omega_{\text{HI}} + D_r \cot \theta) \partial_{\theta_0} + \left. D_r \partial_{\theta_0}^2 \right] g(y^*, t | y_0),$$

with the initial condition $g(y^*, t_0 | y_0) = \delta(y^* - y_0)$, and reflecting at $y_0 = (1, \pi)$ and absorbing at $y_0 = (h^*, \theta^*)$ boundary conditions for $g(y^*, t | y_0)$. Then, $f(y^*, t | y_0) = -\partial_h g(y^*, t | y_0)$ is the DTD for detention time $t$. To conclude, based on the method of first-passage times, we developed a formalism to determine the distribution of detention times for micoswimmers near a plane no-slip surface taking into account hydrodynamic interactions and rotational noise. For generic microverssimmers such as source dipoles, pushers, and pullers we demonstrated that the mean detention time can vary over several orders of magnitude relative to the ABP depending on persistence number Pe and swimmer strengths $q, p$. This allows to quantify the relative importance of hydrodynamic interactions and rotational noise. Our method can be extended to include further drift terms, for example, due to non-spherical shape. Therefore, it offers a systematic approach for studying how artificial as well as biological microswimmers behave at surfaces.
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