Journal of Theoretical Biology 360 (2014) 187–199

Contents lists available at ScienceDirect

Journal of Theoretical Biology

journal homepage: www.elsevier.com/locate/yjtbi

A study of spermatozoan swimming stability near a surface

Kenta Ishimoto [a,*], Eamonn A. Gaffney [b]

[a] Research Institute for Mathematical Sciences, Kyoto University, Kyoto 606-8502, Japan
[b] Wolfson Centre for Mathematical Biology, Mathematical Institute, University of Oxford, Oxford OX2 6GG, UK

HIGHLIGHTS

- Sperm motility near a no-slip surface is studied using boundary element methods.
- Dynamical systems theory is used to explore and classify surface swimming stability.
- A wide range of cell head morphologies and flagellar waveforms are considered.
- Sperm accumulation heights are sensitive to flagellar wavenumber but not head shape.
- Limited focal depth may bias observed wavenumbers in sperm flagellate microscopy.

ARTICLE INFO

Article history:
Received 25 March 2014
Received in revised form
25 June 2014
Accepted 26 June 2014
Available online 8 July 2014

Keywords:
Sperm motility
Low Reynolds number flow
Boundary element method
Cell accumulation
Hyperactivation

ABSTRACT

The swimming stability of spermatozoa with a specified planar beat pattern in the presence of a no-slip flat surface is explored in a modelling study exploiting direct numerical computation via the boundary element method and dynamical systems theory. Parameter sweeps varying the sperm head morphology and flagellar beat pattern wavenumber are conducted and reveal that stable surface swimming is a robust hydrodynamical phenomenon across extensive parameter values, emphasising that diverse sperm will readily swim adjacent to a surface without detailed feedback. There is little sensitivity to the details of the sperm head morphologies considered and, in particular, cells with human sperm head geometries are well approximated by those with prolate ellipsoid heads. However, surface accumulation is predicted to be inhibited by changes associated with mammalian sperm hyperactivation and quantitative aspects, such as the accumulation height associated with surface swimming, are sensitive to the flagellar beat pattern wavenumber and even to the asymptotically small modelling approximations of slender body theory. In particular, the predicted sensitivity of the accumulation height of swimming sperm to the beat pattern wavenumber is sufficient to suggest the possibility that the limited focal depth of typical microscopy studies analysing flagellar patterns with a fixed focal plane may inadvertently bias the wavenumber of the sperm that are observed.

1. Introduction

The spermatozoon is unique: certainly in humans it is the only cell which is flagellated and evolutionary selected to function inside a genetically distinct body. It also carries a payload of highly condensed genetic material, confined to 10% or less of the somatic cell nucleus volume (Miller et al., 2010). This extreme compaction is associated with the presence of protamines rather than histones in DNA packing and is perhaps sufficient to indicate that physical constraints influence the selection pressure, structure and morphology of sperm cells in their fundamental function of fertilisation. These cells have been studied in ever-increasing detail ever since van-Leewenhoek first documented his observations of sperm in the 17th century and since that time observations have typically been conducted close to a microscope cover-slip to keep sperm in focus despite a finite focal depth of microscopy. In particular, observing sperm trajectories in three-dimensional detail is highly challenging, due to the relatively high speed and small size of the cell; this is highlighted by the fact that detailed studies on human sperm behaviour away from surfaces have only been reported in the past few years (Su et al., 2012). Consequently, the presence of a surface is implicit in almost all sperm motility microscopy studies to date, emphasising the importance of understanding how sperm and other cells swim near boundaries, motivating many observational studies (Rothschild, 1963; Woolley, 2003; Cosson et al., 2003; Denissenko et al., 2012; Boryshpolets et al., 2013), which demonstrate that sperm can swim stably near a

* Corresponding author.
E-mail addresses: ishimoto@kurims.kyoto-u.ac.jp (K. Ishimoto), gaffney@maths.ox.ac.uk (E.A. Gaffney).

http://dx.doi.org/10.1016/j.jtbi.2014.06.034
0022-5193/

surface and thus accumulate near boundaries. In addition, for mammalian sperm, there is a distinct flagellar waveform corresponding to hyperactivation (Ohmuro and Ishijima, 2006) which takes place in the oviducts and is critically important in the final stages of the sperm's approach to the egg, as shown by Cat-Sper gene knock-downs (Suarez and Pacey, 2006), but the impact of hyperactivation on the prospect of sperm swimming near a surface and boundary accumulation have not been explored in detail.

Regardless of observational studies, understanding whether sperm boundary accumulation is a consequence of physical hydrodynamics or requires detailed biological feedback is a difficult task, complicated by the fact that the fluid dynamics of swimming sperm occurs at low Reynolds number flow, due to the domination of viscosity over inertia (Gray and Hancock, 1955; Fauci and Dillon, 2006; Gaffney et al., 2011). Thus, fluid dynamicists have also been attracted to this area, demonstrating that hydrodynamics is sufficient to attract and maintain sperm and other swimmers near a surface (Fauci and McDonald, 1995; Smith et al., 2009a; Smith and Blake, 2009; Elgeti et al., 2010; Ishimoto and Gaffney, 2013), with predictions of sperm accumulation heights consistent with microscopy observations (Fauci and McDonald, 1995; Smith et al., 2009a; Smith and Blake, 2009). However, the complexity of the problem entails that the theoretical studies of sperm boundary accumulation and surface swimming to date have been limited by both small parameter spaces despite extensive biological diversity and use of approximations, such as two-dimensional flows (Fauci and McDonald, 1995) or asymptotic slender body theories (Smith et al., 2009a; Smith and Blake, 2009).

Consequently, our fundamental aim is to use direct numerical simulation via boundary element methods to study sperm behaviour near surfaces to a much greater extent than previous theoretical studies, using parameter sweeps and a dynamical systems classification to explore the impact of different sperm head morphologies and flagellar waveform properties. This will enable us to explore numerous questions, for instance, the accuracy limitations of the numerical algorithms used in previous studies and whether any special features are required for surface swimming sperm which might in turn exert selective pressure on sperm. We will also assess the impact of flagellar waveform changes associated with hyperactivation and whether the ubiquity of stable surface swimming and boundary accumulation by sperm from many different species can be explained hydrodynamically or requires detailed biological regulation or selection. Finally, we will assess whether detailed morphologies of sperm need to be considered to understand the details of how sperm behave hydrodynamically near a surface and whether the limited focal depth of 4–6 μm in representative sperm flagellum video-microscopy studies (Gillies et al., 2009; Smith et al., 2009b) selects for specific features of sperm swimming in observational studies.

Despite considering direct numerical simulations and parameter space sweeps in this first application of boundary element techniques to the study of the interactions of sperm with surfaces, we still need to consider approximations and restrictions. In particular, we consider a specified flagellar waveform, albeit based on observations of waveforms for sperm swimming near surfaces (Dresdner and Katz, 1981). In particular, this waveform does not respond to its local mechanical microenvironment and hence there is an absence of feedback between the forces and the torques experienced by the flagellum and its subsequent waveform. This feedback is certainly present when sperm cells experience relatively large mechanical stimulation, for instance, the induction of a calcium spike in sea urchin sperm on crashing into an obstacle, which in turn induces significant flagellar waveform changes (Kambara et al., 2011). In contrast, in our modelling study it is taken that the relatively weak interactions between a sperm and a surface when it is swimming above the surface do not alter the waveform. This assumption is supported by observational evidence presented in Appendix A and entails that a kinematic model of the flagellum, with a specified waveform based on observation, is sufficient to classify the accumulation height and linear stability of boundary accumulating sperm. We also briefly consider swimming far from stable accumulation heights but now with caution over the assumption of a non-adaptive, specified, flagellar waveform. We further restrict ourselves to planar flagellar waveforms, as required to simplify the parameter space of possible flagellar beat patterns and as justified by the fact that sperm swimming adjacent to surfaces are regularly observed to possess essentially planar flagellar waveforms, as seen in Appendix A and Woolley's detailed study (Woolley, 2003).

We also do not consider rheological complexities. Thus, our simulations are not applicable in the isthmic and cervical regions of the mammalian female reproductive tract where highly viscoelastic physiological media is encountered (Jansen, 1978). Nonetheless, the oviductal fluid upstream of the isthmus is observed in rabbit to have a viscosity within 25% of water (Hamner and Fox, 1968) and thus is anticipated to be potentially approximated by a Newtonian fluid and numerous laboratory studies of mammalian sperm motility utilise Newtonian media motivating our restriction to such media even for mammalian cells. In contrast, external fertilisers typically swim in essentially water, further motivating the restriction to Newtonian fluids.

To explore the impact of diverse sperm morphologies and flagellar waveform parameters on sperm swimming near surfaces and boundary accumulation, we firstly describe our model of the virtual sperm in Section 2 detailing the sperm head geometries and flagellar waveforms that we consider. This is supplemented by details of the numerical algorithm and how dynamical systems' concepts can be used to classify the behaviour of swimming sperm near a surface. Comparisons with algorithms using asymptotically accurate slender body theories are briefly presented in Section 3 prior to parameter sweeps and the associated results for sperm dynamics near a surface, with an interpretation and discussion of the results in the context of sperm behaviour and model limitations in Section 4.

2. Models and methods

The kinematic problem for predicting the trajectory of a sperm requires a specification of (i) the sperm head geometry and (ii) the flagellar waveform, including the details of how the waveform is oriented relative to the sperm head. These are described below, prior to detailing the fundamental biophysical equations governing the spermatozoan trajectory and the numerical algorithm used to solve these equations.

2.1. The virtual kinematic sperm

2.1.1. The sperm head and flagellum

For future reference, we define a cell-fixed reference frame with coordinates $\boldsymbol{\xi}' = (\xi_1', \xi_2', \xi_3')$, with origin at the head–flagellum junction and ξ_3' directed along the axis containing the head centroid and the head–flagellum junction, increasing away from the junction towards the centroid, as illustrated in Fig. 1a. We will in general consider an axisymmetric ellipsoidal sperm head and a human-shaped sperm head in the studies below. The ellipsoidal sperm head will have a default volume of

$$V_h^* = \frac{4}{3}\pi r^{*3}, \quad r^* = 1.56\ \mu\text{m}, \tag{2.1}$$

which matches a typical human sperm head volume, and an aspect ratio of c such that $c > 1$ is a prolate ellipsoid and $c < 1$ is