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A simulation study of sperm motility hydrodynamics near fish eggs and spheres

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HIGHLIGHTS

- Sperm motility near a rigid sphere is simulated using boundary element methods.
- Hydrodynamic sperm guidance for fish sperm swimming near an egg is considered.
- Hydrodynamic attraction does not significantly alter egg collision cross sections.
- Hydrodynamic attraction alone does not induce stable fish sperm swimming near an egg.
- With an additional surface repulsion, sperm swimming near an egg is relatively stable.

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ABSTRACT

For teleost fish fertilisation, sperm must proceed through a small opening on the egg surface, referred to as the micropyle. In this paper, we have used boundary element simulations to explore whether the hydrodynamic attraction between sperm and a fish egg can be a sperm guidance cue. Hydrodynamical egg–sperm interactions alone do not increase the chances of an egg encounter, nor do they induce surface swimming for virtual turbot fish sperm across smooth spheres with a diameter of 1 mm, which is representative of a turbot fish egg. When a repulsive surface force between the virtual turbot sperm and the egg is introduced, as motivated by surface charge and van-der-Waals interactions for instance, we find that extended surface swimming of the virtual sperm across a model turbot egg occurs, but ultimately the sperm escapes from the egg. This is due to the small exit angle of the scattering associated with the initial sperm–egg interaction at the egg surface, leading to a weak drift away from the egg, in combination with a weak hydrodynamical attraction between both gametes, though the latter is not sufficient to prevent eventual escape. The resulting transience is not observed experimentally but is a detailed quantitative difference between theory and observation in that stable surface swimming is predicted for eggs with radii larger than about 1.8 mm. Regardless, the extended sperm swimming trajectory across the egg constitutes a two-dimensional search for the micropyle and thus the egg is consistently predicted to provide a guidance cue for sperm once they are sufficiently close. In addition, the observation that the virtual turbot sperm swims stably next to a flat plane given repulsive surface interactions, but does not swim stably adjacent to a turbot-sized egg, which is extremely large by sperm-lengthscales, also highlights that the stability of sperm swimming near a boundary is very sensitive to geometry.

1. Introduction

Flagellated spermatozoa are ubiquitous but ultra-specialised, with the function of propagating a genetic payload toward an egg for fertilization, driven by an active axoneme which induces cell motility via the action of dynein molecular motors, resulting in undulating flagellar oscillations (Lindemann and Leisch, 2010). Such

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a relatively uncluttered relationship between mechanics and biological function is rare and interests not only biologists, but also physicists, hydrodynamicists and applied mathematicians, who study the fluid and filament dynamics associated with sperm propulsion (Lighthill, 1976; Fauci and Dillon, 2006; Gaffney et al., 2011).

A breakthrough in the hydrodynamical understanding of sperm motility mechanics arose from the development of resistive force theory due to the joint work of a biologist and a hydrodynamicist (Gray and Hancock, 1955). While resistive force theory is simple to implement, it is relatively inaccurate and hence slender-body theory was developed in the 1970s and 1980s for mechanical studies of cellular swimming (e.g. Higdon, 1979; Johnson, 1980). Nonetheless the additional complexity of slender-body theory, and the fact resistive force theory is reasonably accurate, at least for small cell bodies and away from surfaces (Johnson and Brokaw, 1979), has entailed that resistive force theory has remained popular in numerous inter-disciplinary studies of cell swimming, for instance the works of Hines, Blum, Katz and Rikmenspoel among others (Hines and Blum, 1978, 1979; Katz and Yanagimachi, 1980; Rikmenspoel, 1984). More recently, there has been a tremendous resurgence of theoretical interest in the field, predominantly driven by advances in computational speed and memory allowing sophisticated simulation studies, extending accuracy beyond slender body theories, for example via the use of boundary elements (Gillies et al., 2013; Ishimoto and Gaffney, 2014), as required for studying the subtle dynamics of boundary accumulation (Ishimoto and Gaffney, 2014). In addition, numerical approaches are now regularly coupled with the digital revolution of video-microscopy, with the latter providing extensive quantitative spatio-temporal data for cell motility studies (Riedel-Kruse et al., 2007; Smith et al., 2009b; Friedrich et al., 2010).

However, with the prime exception of sea urchin sperm, which are often described as the *E. coli* of fertilisers, externally fertilising sperm has been neglected in these interdisciplinary studies. This neglect is despite the fact fish spermatology is a mature field supporting the needs of aquaculture sperm-banking and biotechnology (Suquet et al., 2000). In particular, to improve our understanding of how and why fish sperm cells behave and to improve the characterisation, classification and understanding of reconstituted sperm from cryo-preserved stocks, aquatic reproductive physiology laboratories have exploited the digital revolution of video-microscopy, providing extensive data (see Fig. 1a for example). Furthermore, fish sperm often exhibits behaviour not seen in mammals, such a limited duration of beating, which can be less than a minute after activation (Cosson et al., 2008b).

In particular, the limited beat duration is exhibited by our exemplar of turbot sperm below: the initial flagellar waveform is illustrated in Fig. 1a and persists for approximately 30 s after activation via contact with higher osmolarity solutions (Chauvaud et al., 1995), such as seawater. During this early-stage of active beating, turbot sperm swim at speeds of approximately 150–200 μm/s (Chauvaud et al., 1995; Dreanno et al., 1999), after which the flagellar waveform transitions relatively abruptly to one which is distally subdued and with a slightly shorter wavelength. This late-stage of flagellar beating is illustrated in Fig. 1b, which presents the waveform one minute after activation, with further supporting observations provided by the stroboscopic experiments of Chauvaud et al. (1995). During this period of flagellar beating, sperm swimming speeds are slower, at just under 100 μm/s and many turbot flagella are no longer significantly beating 80 s after activation (Chauvaud et al., 1995; Dreanno et al., 1999). Hence turbot sperm do not progress more than about 1 cm in their motile phase, in distinct contrast to the sperm of many mammals which must progress for at least tens of centimetres. More generally, even our preliminary considerations highlight that there is an enormous wealth of biodiversity and data in studies of fish sperm motility, in turn generating numerous novel modelling questions from the perspective of the physical sciences. Within this larger framework, we will focus on an initial study of how the hydrodynamics of sperm motility can inform our understanding of the interactions between fish sperm and eggs, motivated by a fundamental question of sexual reproduction: how does a sperm find and then penetrate the egg?

To simplify the scope and the hydrodynamics, we will only consider pelagic eggs of teleost fish, which are buoyant, isolated and representative of natural fertilization for numerous commercial fish, such as turbot, sturgeon, carp and salmonids. Furthermore, sperm only enter these eggs via a micropyle opening, highlighted in Fig. 1c, which is small relative to the millimetre scales of the egg, so that simply reaching the egg is not sufficient. Certainly therefore, an ability for sperm to be captured by, and swim close to the egg surface, would be beneficial, in that the initial sperm–egg encounter region need not be limited to the micropyle. Furthermore, the presence of a surface is well-known to influence sperm motility with many species of spermatozoa observed to readily accumulate near a coverslip surface (Rothschild, 1965; Woolley, 2003). This property is known as thigmotaxis and recent simulation studies have revealed that accumulation near a solid plane surface can be explained simply by hydrodynamic interaction between the cell and the surface (Fauci and McDonald, 1995; Smith et al., 2009a, 2011; Elgeti et al., 2010, 2011; Ishimoto and Gaffney, 2014). Furthermore, this behaviour has been reported in fish sperm studies, not only near a solid surface, but also near an air-water interface with reduced surface tension due to surfactant (Cosson et al., 2003; Boryshpolets et al., 2013). In particular, given that the fish egg is approximately flat on the scale

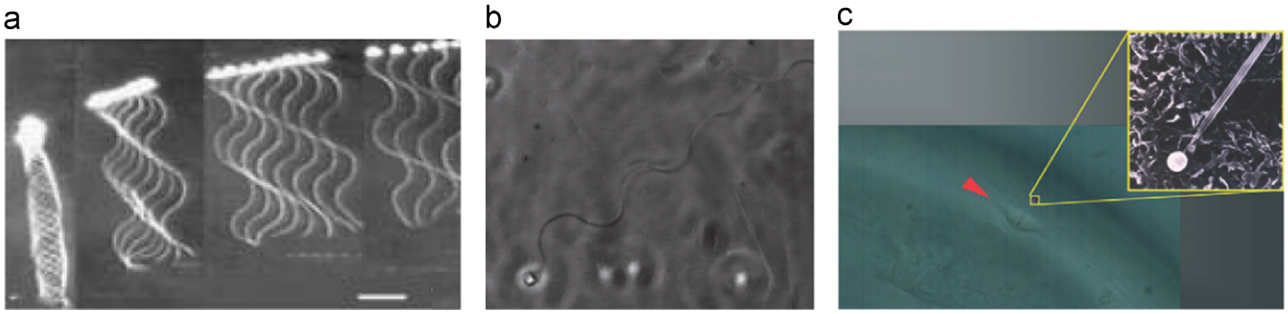

Fig. 1. (a) Successive images of individual turbot spermatozoa obtained every 3 ms (from left to right in each) shortly after flagellar waveform activation; one can estimate the wavenumber is approximately 4π. Scale bar 10 microns. Reproduced from Cosson et al. (2008a), with permission. Copyright, 2008, BioScientifica Ltd. (b) An unpublished image of a turbot sperm waveform observed one minute after activation; note that the distal beat pattern is extensively subdued and the wavenumber is slightly higher. (c) A turbot sperm adjacent to a turbot egg. Red arrow: the micropyle, in which the sperm must reach and enter to fertilise the egg. Yellow box: the turbot sperm; note the difference in scales of the sperm and egg. Reproduced from Cosson et al. (2008b), with permission. (For interpretation of the references to colour in this figure caption, the reader is referred to the web version of this paper.)