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Hydrodynamic evolution of sperm swimming: Optimal flagella by a genetic algorithm

Kenta Ishimoto [a,b,*]

[a] The Hakubi Center for Advanced Research, Kyoto University, Kyoto 606-8501, Japan
[b] Research Institute for Mathematical Sciences, Kyoto University, Kyoto 606-8502, Japan

HIGHLIGHTS

- Optimal sperm beating patterns are obtained by a genetic algorithm.
- Optimal beating is planar or helical, depending on the size of a head.
- Wavenumber, amplitude and head volume are major parameters for efficient swimming.
- Head geometry and wave shape are relatively minor factors for efficiency.
- The genetic optimization distinguishes biologically important flagellar parameters.

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ABSTRACT

Swimming performance of spermatozoa is an important index for the success of fertilization. For many years, numerous studies have reported the optimal swimming of flagellar organisms. Nevertheless, there is still a question as to which is optimal among planar, circular helical and ellipsoidal helical beating. In this paper, we use a genetic algorithm to investigate the beat pattern with the best swimming efficiency based on hydrodynamic dissipation and internal torque exertion. For the parameters considered, our results show that the planar beat is optimal for small heads and the helical flagellum is optimum for a larger heads, while the ellipsoidal beat is never optimal. Also, the genetic optimization reveals that the wavenumber and shape of wave envelope are relevant parameters, whereas the wave shape and head geometry have relatively minor effects on efficiency. The optimal beat with respect to the efficiency based on the internal torque exertion of an active elastic flagellum is characterized by a small-wave-number and large-amplitude wave in a lower-viscosity medium. The obtained results on the optimal waveform are consistent with observations for planar waveforms, but in many respects, the results suggest the necessity of a detailed flagellar structure–fluid interaction to address whether real spermatozoa exhibit hydrodynamically efficient swimming. The evolutional optimization approach used in this study has distinguished biologically important parameters, and the methodology can potentially be applicable to various swimmers.

1. Introduction

The sperm cell is unique; it is produced for a particular purpose, i.e. the fertilization of an egg. The cell is, roughly speaking, composed of a head and a tail, called a flagellum, which is a slender appendage that produces propulsion in fluid by its bending in order to convey the genetic information packed in the head (Gaffney et al., 2011). Human spermatozoa, for instance, are required to travel for a long distance more than thousands of times their cell length in the female body, and only one of the ejaculated hundreds of millions of cells can perform fertilization (Suarez and Pacey, 2006). Thus the cells experience strong selective pressure during its process. This does not mean that the egg is waiting for the fastest sperm, but indicates more complicated fertilization mechanisms. For example, not only the good quality of the cells but also well-timed ovulation and proper capacitation of sperm are also required (Suarez and Pacey, 2006). According to the theory of *sperm competition* in evolutionary biology, which argues for evolutionary selective processes on spermatozoa, the number of spermatozoa in an ejaculation increases and the sperm morphology can be sophisticated, and this tendency is promoted in

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[*] Correspondence address: Research Institute for Mathematical Sciences, Kyoto University, Kyoto 606-8502, Japan.
E-mail address: ishimoto@kurims.kyoto-u.ac.jp

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environments of multiple possible mating partners (Humphries et al., 2008; Simmons and Fitzpatrick, 2012). In particular, the limited functionality of the cell would enhance the evolutionary pressure on swimming in contrast to other microswimmers such as bacteria, algae, and ciliates, which require multiple functions for survival, e.g. nutritional uptake, escape from predators and reproduction (Lauga and Powers, 2009; Guasto et al., 2012). Moreover, the swimming performance of spermatozoa is an important index in clinical diagnosis of *in vitro* fertilization treatments (Mortimer et al., 2013), and this fact emphasizes its significance for fertilization. For these reasons, one may consider whether the sperm waveform and the morphology are mechanically optimized. The optimal sperm morphology and flagellar beat pattern have gathered the particular interest of physicists who study effective swimming based on hydrodynamics. Furthermore, the swimming optimization is important for micro-machine technology, such as artificial flagella and cilia (Sareh et al., 2013).

The flagellum is composed of two inner microtubules and nine outer microtubule doublets, forming a so-called 9+2 structure. The relative sliding of doublet microtubules, caused by the exertion, binding and detachment of dynein arms between neighbors, leads to local flagellar bending. The mechanism for the generation of the flagellar wave is, however, still controversial (Lindemann and Leisch, 2010; Bayly and Wilson, 2015). Nonetheless, most energy induced by the dynein is dissipated by fluid viscosity around the cell, and thus, many studies have focused on sperm swimming efficiency based on the energy output toward the surrounding fluid, and have assumed that the flagellar beat is planar (Pironneau and Katz, 1974; Lighthill, 1975; Higdon, 1979a; Tam and Hosoi, 2011; Lauga and Eloy, 2013) or axisymmetrically helical (Chwang and Wu, 1971; Coakley and Holwill, 1972; Higdon, 1979b; Fujita and Kawai, 2001), though the beating pattern of the spermatozoa can be planar, helical, and even non-axisymmetrically helical, depending on species (Ishijima et al., 1992) and medium conditions such as viscosity (Kantsler et al., 2014). In this paper, for brevity, the medium is assumed to be Newtonian since fluid in the mammalian oviduct is reported to have the same order of viscosity as a watery medium according to some observations (Miki and Clapham, 2013), though mucus in the human reproductive tract can be non-Newtonian (Smith et al., 2009a).

From Lighthill's pioneering work on optimal planar beating (Lighthill, 1975), it has been shown that a sawtooth wave is optimum in terms of swimming efficiency for an infinite swimmer, using the local hydrodynamic theory. Tam and Hosoi obtained optimal planar swimming for a finite length of flagellum using a non-local hydrodynamic theory (Tam and Hosoi, 2011), which shows that a nearly sawtooth traveling wave containing 1–1.5 complete waves per tail provides optimal swimming efficiency based on the hydrodynamic dissipation rate as in Lighthill's paper.

A classic study by Chwang and Wu (1971) considered optimal circular helical swimming, for which some recent computational studies (Fujita and Kawai, 2001; Shum et al., 2010) have obtained the optimal head size. Differences between a planar and a helical beat for swimming efficiency are discussed in Chwang and Wu (1971), arguing that a helical beat can be more efficient than planar swimming for a cell with a larger head by an analysis of spermatozoa with a spherical head.

Nonetheless, comprehensive studies on the difference between planar and helical beating in terms of optimal swimming are required since the ellipsoidal flagellum, the intermediate flagellar beating pattern between the two beat patterns, has not been taken into consideration, although such a beating is widely observed in mammalian spermatozoa in particular (Woolley, 2003). We, therefore, study the optimal flagellar beating for general three-dimensional swimming. However, for characterization of the optimal beat, only a small number of parameters, which are considered to be important and measurable in experiments, will be discussed.

Even in the case of a small number of parameters, numerical optimization is still a challenge when the value function possesses multi-modality, and an evolutionary-optimization method such as a genetic algorithm is commonly used to overcome this difficulty (Simon, 2013), as utilized for some swimming problems (Usami, 2006; Gazzola et al., 2011). Nevertheless, to the author's knowledge, these methods have not been applied to the problem of optimal flagella, for which such algorithms have an affinity because the evolutionary-optimization method models a biological process with evolution and the sperm morphology can also evolve as discussed in the context of the sperm competition theory. In this study, therefore, a genetic algorithm is employed to obtain a global optimum. Also, assuming that sperm morphology is adopted for better hydrodynamic efficiency, as discussed above, such evolutionary optimization would provide a scenario for how the sperm morphology and beating pattern evolve. In addition, comparing the obtained computational results with the observation would enable us to approach the question of whether sperm cell swimming is hydrodynamically sophisticated, which will also be discussed.

2. Models and methods

2.1. Model spermatozoon

The spermatozoon is modeled as a slender flagellum of length L with a prolate spheroidal head of major axis r_a and minor axis r_b. The head is smoothly connected to the flagellum, and this is a reasonable assumption for mammalian spermatozoon with a stiff mid-piece part (Gaffney et al., 2011; Ishimoto and Gaffney, 2014). As illustrated in Fig. 1(a), the head aspect ratio, β, is introduced by $\beta = r_a/r_b$. Let us consider a laboratory-fixed reference frame $\{X_i\}$ $(i = 1, 2, 3)$ and a sperm-fixed reference frame $\{x_i\}$ $(i = 1, 2, 3)$

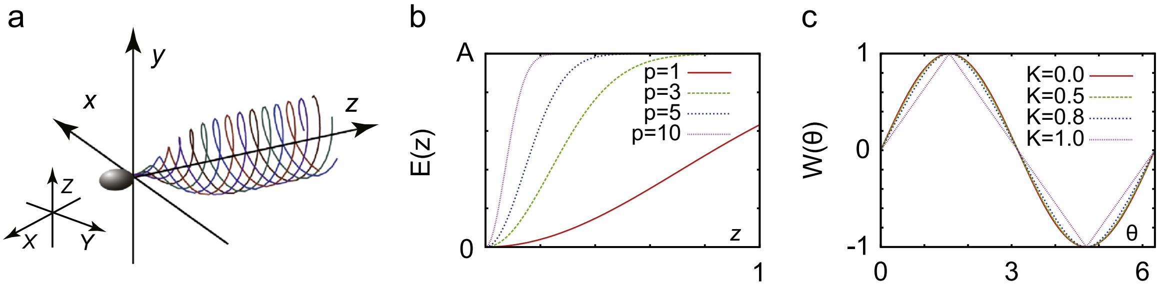

Fig. 1. Schematic of the model sperm beat and the shapes of the functions, $W(z)$ and $W(\theta)$. (a) The superimposed snapshots of the ellipsoidal helical beat at different times are described in color, together with a spheroidal head of the major axis, r_a, and minor axis, r_b. (b) The shape of the envelope function, $E(z)$, with different p. (c) The shape of the function of the wave pattern, $W(\theta)$, with different K. The 2π-periodic function changes from a sinusoidal to a sawtooth wave as K increases from 0 to 1.