

A Retaliatory Role for Algal Projectiles, with Implications for the Mechanochemistry of Diatom Gliding Motility

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It is shown that the projectiles ejected by discobolocysts in the single-celled Chrysophyceae alga *Ochromonas tuberculatus* travel at speeds of up to 0.26 km/s, as fast as a bullet from a low power rifle. They may thus inflict damage to a would-be predator. Their Reynolds number is high, around 100, far from the low Reynolds numbers presumed typical of cellular events. Hydration of the mucopolysaccharide in discobolocysts, by one to three hydrogen bonds per monomer, is shown to be a sufficient source of energy for this mechanochemical reaction. The hydrogen bonding appears to induce a conformational change, rather than swelling of the mucopolysaccharide. It is also shown that the same degree of hydration of mucopolysaccharides would provide sufficient motive force to explain the gliding motility of raphid diatoms, when incorporated into the capillarity model for diatom locomotion. The efficiency of the diatom's mechanochemical raphe system may be as high as 99%. The microfilament bundles adjacent to the raphe inside the cell may control forward, stop and reverse functions by a sliding mechanism.

Introduction

The projectiles of single-celled Chrysophyceae move the cell to one side when they fire. Their purpose is unknown (Hibberd, 1970), although one might simply assume that projectiles provide an escape mechanism from predators. I would like to show that the initial velocity of a projectile is comparable to that of a bullet and that we may thus entertain a more startling hypothesis: at close range, as on contact during ingestion, a projectile may actually be able to damage a would-be predator. This is a form of counterattack or retaliation, rather than mere escape. Such injuries or their avoidance may play a role in the selective ingestion of microflora by zooplankters, which has hitherto been attributed to temporal separation and "algal unpalatability, . . . expressed as unmanageability, toxicity, and undigestibility" (Porter, 1977).

Observations indicate that the release of a single projectile from a discobolocyst in *Ochromonas tuberculatus* (Hibberd, 1970; Lee, 1980) displaces the cell suddenly by a distance of 5 μm . Let this distance be d_c . I will derive a formula for d_c in terms of other measurable and estimable parameters. The conservation of momentum will then be invoked to calculate the initial velocity of the projectile, and the conservation of energy to estimate the mechanochemical energy involved. Since the reaction releasing this energy is thought to be hydration of mucopolysaccharides, an estimate of that chemical energy can be made.

Similar, though more controlled capillary releases of mucopolysaccharide by diatoms are probably responsible for their gliding motility (Gordon & Drum, 1970). The data from discobolocysts permits a hitherto unobtainable explanation of the dynamics of diatom motility to be put forward.

Velocity of the Chrysophyceae Cell after Projectile Release

Let the velocity of the cell be $v_c(t)$, where t is the time after discharge. The cell of *O. tuberculatus* is roughly an ellipsoid of revolution, with a long radius averaging $7.5 \mu\text{m}$ and the short radius averaging $6.5 \mu\text{m}$ (Hibberd, 1970). For the sake of the order of magnitude argument given here, I will replace these by an average spherical radius of $7 \mu\text{m}$, designated by r_c , and will ignore any drag or momentary assist of the flagella.

The force F on the cell can be written in two ways. By Newton's second law, the force equals the product of the cell's mass m_c and its acceleration a

$$F = m_c a \quad (1)$$

but once the projectile leaves the cell, the only force on the cell is that due to the viscosity of the medium, which is given by Stoke's law

$$F = -6\pi\eta r_c v_c(t) \quad (2)$$

where η is the viscosity of the medium. The negative sign indicates that this force acts in the opposite direction of the motion. Equating eqns (1) and (2), we have

$$m_c dv_c/dt = -6\pi\eta r_c v_c(t) \quad (3)$$

where I have noted that the acceleration is the time derivative of the velocity. Equation (3) may be rearranged and integrated from the velocity $v_c(0)$ at time 0 to velocity $v_c(t)$ at time t

$$\int_{v_c(0)}^{v_c(t)} v^{-1} dv = \int_0^t (-6\pi\eta r_c / m_c) dt \quad (4)$$

or

$$\ln v_c(t) - \ln v_c(0) = \ln [v_c(t)/v_c(0)] = -6\pi\eta r_c t / m_c \quad (5)$$

Using both sides as exponents of the natural base e , we get

$$v_c(t) = v_c(0) e^{-6\pi\eta r_c t / m_c} \quad (6)$$

Since the velocity is continually changing, to calculate the distance the cell moves, we must integrate

$$d_c(t) = \int_0^t v_c(t) dt = v_c(0) \int_0^t e^{-6\pi\eta r_c t / m_c} dt \quad (7)$$

The result is

$$d_c(t) = [v_c(0) m_c / (6\pi\eta r_c)] (1 - e^{-6\pi\eta r_c t / m_c}) \quad (8)$$

If we consider the limit as t approaches infinity, then we get the total distance the cell moves in response to firing one projectile as

$$\lim_{t \rightarrow \infty} d_c(t) = v_c(0) m_c / (6\pi\eta r_c) = d_c \quad (9)$$

We thus obtain

$$v_c(0) = 6\pi\eta r_c d_c / m_c \quad (10)$$

The mass of the cell can be estimated as the volume times the cell density ρ_c , or

$$m_c = (4/3)\pi r_c^3 \rho_c \quad (11)$$

Thus

$$v_c(0) = 9\eta d_c / (2\rho_c r_c^2) \quad (12)$$

Using the values for the parameters above, $\eta = 0.01$ poise for water, and assuming a neutrally buoyant cell ($\rho_c = 1 \text{ g/cm}^3$), I estimate that $m_c = 1.4 \times 10^{-9} \text{ g}$ and $v_c(0) = 0.45 \text{ m/s}$.

Velocity of the Projectile

To obtain the initial velocity of the projectile, $v_p(0)$, I apply the conservation of momentum to the combined system of cell and discharged discobolocyst, assumed to be initially at rest

$$m_c v_c(0) + m_p v_p(0) = 0 \quad (13)$$

where m_p is the mass of the projectile. Thus

$$v_p(0) = -m_c v_c(0) / m_p \quad (14)$$

with the negative sign indicating motion of the projectile in the direction opposite that of the cell. As in eqn (11), we have

$$m_p = 4\pi r_p^3 \rho_p / 3 \quad (15)$$

where r_p and ρ_p are the radius and density of a discobolocyst. Then eqn (14) becomes

$$v_p(0) = -r_c^3 \rho_c v_c(0) / (r_p^3 \rho_p) \quad (16)$$

If we estimate $\rho_p = 1.53 \text{ g/cm}^3$ (the density of starch, a condensed plant polysaccharide), and take $r_p = 0.875$ to $1 \mu\text{m}$ (Hibberd, 1970, which justifies my tacit assumption that $m_p \ll m_c$), then the mass of a discobolocyst is $m_p = 4.3$ to $6.4 \times 10^{-12} \text{ g}$ and $v_p(0) = -(224 \text{ to } 335) v_c(0) = -(100 \text{ to } 150) \text{ m/s}$. This is nearly as fast as the bullets from 0.22 calibre plinking rifles (200 to 450 m/s) (Derendorf, 1985). Direct contact with a just ejected projectile could thus cause considerable damage to the cell it strikes in the feeding apparatus of a zooplankter (unless it has evolved defences, such as chitin barriers).

