A Model of Protozoan Movement for Artificial Life.

Alan Dorin, Justin Martin
Department of Computer Science, Monash University, Clayton, 3168, Australia.
e-mail: aland or justinm@bruce.cs.monash.edu.au

ABSTRACT
Perhaps the most important aspect of modelling Artificial Life for computer animation is the accurate portrayal of motion. We introduce a method for the modelling and locomotion of Artificial Life based on the behaviour of single-celled organisms. We describe the means by which protozoa are able to move through fluids using flagella and cilia, and discuss a physically-based model for locomotion in this manner. We then apply this model to the locomotion of evolved artificial organisms.

Keywords: artificial life, locomotion, dynamics, animation, procedural models, genetic algorithm, cilia, flagella.

1 INTRODUCTION

Biological locomotion is an important area of research, with direct application to the study of computer graphics and robotics. Models of legged locomotion are abundant within the computer graphics literature (1, 2, 3), Miller (4) has described a physically based means of modelling the locomotion of makers and worms. Models for motion of fish and large marine life through fluids have also been briefly described by van de Panne and Fiume (5). Most large marine animals rely on the presence of rigid structures within the body of the organism to generate the necessary forward thrust through the generation of lift or fluid accelerations. We present a model for locomotion which relies on viscous shearing of flexible tentacle-like structures through which single celled organisms may obtain mobility.

Protozoa have extremely low masses and must propel themselves through fluids under the influence of high viscous drag. Under such conditions, a microscopic organism cannot successfully propel itself by jet as do the cephalopods, nor can it produce lift by employing aerofoils in the manner of larger marine animals. Conventional rowing motion is also ruled out at this level (see below).

Thrust is generated in single celled organisms by the continuous motion of waves through cellular projections attached to the main structure. We shall refer to these structures as 'tentacles', the two main forms occurring on Protozoan being flagella and cilia. We discuss these and present models for their animation. We then describe a means of controlling the motion of multiple tentacles and examine artificial organisms which employ these techniques for locomotion. We conclude by discussing further areas of research.

2 FLUID DYNAMICS

In order to understand the manner in which a microscopic organism generates thrust, we must examine the behaviour of a fluid / body system at the cellular scale. The Reynolds number (Re) is a dimensionless value representing the ratio of inertial to viscous stresses in a fluid / body system. Systems consisting of a Protozoan and a fluid with the density and viscosity of water have extremely small Reynolds numbers. The interactions between the fluid and solid body are governed almost exclusively by viscous forces. Consequently a single celled organism in water will come to a halt as soon as it ceases to apply thrust. Also at low Reynolds numbers, a slow stroke through the fluid induces the same amount of drag as a more rapid stroke. Should a microscopic organism attempt to execute a recovery stroke symmetrical to its power stroke, even if the recovery stroke occurs at a lower angular velocity, the organism will exactly undo the work done by the power stroke.

The Navier-Stokes equations describe the relationship between force $F$ and flow in a fluid. The solution of these equations for a sphere of radius $a$ moving at velocity $U$ through a stationary fluid of viscosity $\mu$, is given by Tritton (6) as:

$$ F = -6 \pi a U \mu $$

where $C_D = 6 \pi a \mu$ is the drag coefficient.

The bodies and associated drag of many interesting organisms can be approximated using spheres, cylinders or collections of such primitives. For the purposes of this model, we may use cylinders to approximate tentacle sections. An isolated cilium or flagellum may therefore be approximated by a chain of such cylinders. The drag coefficient of a cylinder varies with its orientation to the flow of fluid over its surface. The tangential and normal components of the force acting on a particular flailing tentacle section (of radius $r$ and length $L$) can be calculated as a function of its velocity relative to the fluid:

$$ F_t = -C_{T1} U_L $$

$$ F_n = -C_{T2} U_R L $$

(2)

The coefficients $C_{T1}$ and $C_{T2}$ are the drag coefficients for the cylindrical section tangential and normal to the flow. For a cylinder of infinite length, the normal drag coefficient approaches twice that of the tangential coefficient. We may treat our tentacle elements as infinite cylinders as their movement through a fluid medium is not effected by the presence of end caps. To calculate a value for $C_{T1}$ Holberon (7) gives:

$$ C_{T1} = \frac{2 \pi \mu}{(\ln (2L/r) - 0.5)} $$

(3)

The net force $F$ acting on a length $L$ of tentacle moving at velocity $V$ can then be calculated by summing the vector components of the forces parallel and perpendicular to the element as shown (Fig 1).
3 MODELLING PROPULSIVE TENTACLES

3.1 Flagella

Flagella usually operate by actively propagating a helical or planar wave through the tentacle from base to tip. Some forms of flagella operate purely by rotation at the base. In this case the tentacle is left to drag freely through the fluid. This thrust generated by a flagellum is entirely due to viscous shearing and is generated parallel to the direction of wave propagation.

Flagella are usually few in number, so the hydrodynamic effect each tentacle has on its neighbour may be neglected. We also ignore potential collisions between flagella. In this model we use the approximation given above to calculate the force a tentacle applies to an organism. Integrating the resultant forces generated by each flagellum allows us to find the net propulsive force acting on the organism (fig 2). From this force, we subtract an approximation for the viscous drag encountered by the organism.

The resultant force is used to calculate the acceleration experienced by the organism (\( \mathbf{a} = \mathbf{F}/m \)). This acceleration is then integrated over a fixed time-step to find the velocity. The Euler method is adequate for this purpose. The velocity thus determined will be used for the calculation of drag in the next time interval. Integrating the velocity over the same time-step produces the organism's new position.

The behaviour of a flagellum may be specified kinematically. The wave propagated through the structure is approximated by a sinusoidal function, although some organisms are known to have developed more efficient waves for locomotion. To model a flagellum dynamically, we construct an articulated chain of cylindrical links. Calculation of the dynamics of this chain is carried out using the articulated body method described by Featherstone (8). This method is of linear time complexity in the number of degrees of freedom exhibited by the articulated body and is suitable for the modelling of lengthy articulated chains.

To determine internal forces within the chain, damped springs are attached between links as described by McKenna and Zelazny (2). The force exerted by a spring acting across a link is linearly proportional to the distance of the joint angle from some specific target. By varying the target angle we are able to control the force applied at a joint in the flagellum model. Active contraction and relaxation along a flagellum is simulated in our dynamical system by adjusting the joint target angles using a sinusoidal function. This flexes the chain in the tentacle's bending plane.

Some organisms have evolved flagella with spiny projections, known as mastigonemes (fig 3). These spines are attached along the length of the flagellum and may be either rigid or flexible. In the case of the organism Ochromonas, the presence of rigid mastigonemes appears to be responsible for the reversal of the net thrust produced by its flagellum. The dynamics of this has not yet been convincingly modelled.

3.2 Cilia

Ciliates are typically larger than flagellates although cilia are the shorter tentacle type. Rather than propagating regular wave along their length, cilia act like miniature oars. On the organism Pleurobrachia, the cilia are fused into a series of comb plate which act in the same manner as conventional tentacle-like cilia. Several thousand cilia may exist on the one organism, often arranged in closely packed rows across complete surfaces.

3.2.1 Cilium Movement

As discussed above, at low Reynolds numbers a conventional rowing motion is not suitable for propulsion. Instead, the cilia vary their rigidity during beating. The power stroke is made by pivoting from the base of the cilium. The structure itself remains relatively straight and rigid during this phase. On the recovery stroke, the tentacle is allowed to relax along its length. The cilium is drawn tangentially through the fluid by a bend which rises from the base and passes along until it reaches the tentacle tip (fig 4).
During this phase the drag on the tentacle is caused almost entirely by the tangential flow of fluid across its surface. Consequently the recovery stroke induces less resistance than the power stroke and the organism is able to use the cilia for locomotion by dragging fluid over its surface.

The motion of a cilium may be controlled kinematically, although we have found a full dynamic simulation to be of value in determining the trajectory of the beat. Once a known structure in a particular fluid has been successfully simulated, the generated behaviour can be used to construct kinematic controllers for tentacles in later animations.

We construct such kinematic controllers by storing the angles between adjacent elements of the cilium at predetermined keyframes and interpolating the motion. There is nothing to be gained by dynamically computing the behaviour of each cilium since the structures are identical and act under the same viscous forces.

Cilia are modelled using chains of cylindrical links, as were flagella. Once again, the stiffness of the tentacle is controlled by springs set across each of the chain links. During the power stroke the spring constants along the length of the cilium are kept relatively high in order to maintain the rigidity of the structure.

An internally generated force at the base link of the cilium drives the structure through an arc. At each time step we calculate the drag occurring on the cylindrical elements using equation (2). We then apply this externally generated force to the center of mass of the element. This force is added to the internally generated forces to find the net force acting on the element.

To reduce the rigidity of the cilium during the recovery stroke, the stiffness of the inter-link springs must be reduced. A kink propagates along the length of the cilium during its recovery stroke. This helps to draw the cilium tangentially through the fluid and lowers the normal component of the drag the cilium experiences. The kink is actively induced in cilia and so we likewise pass a wave of contraction along the springs in our linkage. The rate and strength of this flexion determines the efficiency of the individual cilium while recovering for the power stroke.

3.2.2 Metachronism in Cilia

A frequently encountered natural solution to the problem of coordinating multiple limbs is the metachronal wave. This ensures adjacent propulsive structures operate slightly out of phase with one another to minimize interference and allow the continuous generation of thrust. Cilia, occurring as they do in large numbers, are ideal candidates for control by metachronism. The direction and rate of beating may be fixed or may be under the control of the organism to which the cilia are attached (9).

In figure 4 the power stroke occurs in a direction opposite to the direction of travel of the metachronal wave. This is called antisymplectic metachrony. The power stroke in some organisms may travel in the same direction as the metachronal wave. This is symplectic metachrony. In desymplectic metachrony the beat is not planar. During the recovery phase the cilium leaves the plane along which the metachronal wave propagates.

3.2.3 Force Evaluation For Closely Packed Cilia

As was noted earlier, because of hydrodynamic interference between closely packed tentacles we cannot simply sum the effects of individual cilia. Three models predict the force applied by a group of cilia, these being the envelope, sublayer and traction layer models. Details of these are presented by Daniel et al (10).

The envelope model acts as a guide for calculating the thrust generated by closely packed cilia acting in symplectic metachrony. An individual cilium tip sweeps out an approximately elliptical path. This path may divide into components parallel and perpendicular to the surface of the organism. The model treats the envelope across the tips of the cilia as a surface deforming in a metachronal wave. The velocity of travel of an organism is estimated from the speed of this wave and its amplitude. The direction of travel is determined by the component of motion of the cilium tips parallel to the surface of the organism.

The envelope model's predictions are based on two assumptions: natural organisms are typically equipped with a number of cilia far in excess of the ratio of body length to cilium length (2); packing density of cilia does not vary appreciably among organisms. As a consequence, it is acceptable to estimate the velocity of travel of many cilia independently of the number of cilia they possess. Holberton (7) gives the velocity \( U \) of travel as being:

\[
U = 0.5 k^2 (b^2 + 2 \beta b \cos(\phi) - \beta^2) v_w
\]

where \( k \) is the wave number of the metachronal wave and \( v_w \) is its speed, \( \beta \) is the amplitude of the phase swept out by a cilium tip parallel to the surface of the organism and \( b \) is the cilium tip beat amplitude normal to the surface of the organism. (The sign of \( \beta \) is determined by the cilium tip sweep during the power stroke. A cilium tip moving in a transverse direction opposite that of the metachronal wave takes a value of \( \beta \) that is negative.) \( \phi \), the phase difference between parallel and perpendicular cilia tip waves, is the angle of inclination of the ellipse swept out by a cilium tip to an axis perpendicular to the surface of the organism.

Since we have stored the path of the individual cilia on an organism, we are able to evaluate the transverse and longitudinal amplitudes of their beat cycle as well as the phase difference between these waves. The propagation speed of the metachronal wave is determined by the organism as a whole and is governed by the rate at which signals are sent along its internal network (see below).

At present we adopt the envelope model for all forms of metachrony. Thus an organism with closely packed cilia will move with velocity given by (4) regardless of the cilia number or spacing.

3.2.4 Force Evaluation For Widely Spaced Cilia

An organism may arise having only a small set of widely spaced cilia. Clearly it will not do to use the envelope model in such a case. To allow for organisms with few cilia, we make use of our dynamic cilium model. As outlined above, the dynamic model is used to produce a set of keyframes for the animation of the cilium through their power and recovery strokes. Besides storing the angles of the cylindrical elements of the tentacle, we also store the net force the cilium produces at each keyframe as the tentacle forces its way through the fluid. This force is calculated during the dynamic simulation in the same manner as was the net force acting on a flagellum. That is, we sum the forces acting on the individual cylindrical elements of the cilium.

To evaluate the net force acting on an organism with few, widely spaced cilia, we sum the forces (interpolated between keyframes) produced by each cilium individually at the appropriate stage of its beat cycle. From the resultant force we subtract the drag experienced by the cilia and then proceed to find the acceleration, velocity and new position of our organism using the method outlined for flagellates above.

The envelope model is used for organisms in possession of longitudinal rows of cilia (called kineties) of length greater than one metachronal wave length. If there are not sufficient tentacles in the kineties to ensure that at least one set of cilia is currently engaged in the power stroke, then we evaluate the cilia forces individually. All the information needed to determine the appropriate method of force calculation is contained within the organism's gene set and signal propagation network (see below).
4 ARTIFICIAL EVOLUTION

The models we discuss here are produced using object oriented software for the development of Artificial Life. This interactive system provides general purpose class structures for the evolution and animation of artificial organisms. The software also provides tools for the construction and animation of complete virtual environments within which to examine the behaviour of our creations.

4.1 Evolution of Visible Structure

Sims (11, 12) has used an interactive system to evolve procedural models and dynamical systems. This system relies on the user to select attractive phenotypes for cross-breeding in the sense of a conventional genetic algorithm. The fitness function of an organism in such a case is therefore based on its user-specified aesthetic merits. The genotype on which crossover and mutation operate specify parameters of the model such as its colour, shape, texture or the way in which these properties change over time. Extremely beautiful and complex structures can be evolved using such tools.

Koza (13) describes a method of evolving solutions to specific mathematical problems using hierarchies of Lisp expressions. The fitness functions for such problems are predetermined and specified mathematically.

The bodies of our artificial organisms consist of collections of graphical primitives, possibly with attached propulsive structures. A hierarchical genotype specifies the number, position, orientation and scale of the primitives, cilia and flagella. We prefer a hierarchical genotype to the more conventional fixed length bit-string, precisely because of the limited nature of fixed length genotypes. A hierarchical gene set is dynamically constructed and is therefore free to evolve to the complexity required by the problem. Its complexity is not predetermined by the programmer. New nodes to the hierarchy may be easily added and unwanted nodes may be deleted or swapped with nodes from another genotype simply by reassigning pointers.

The nodes of the genotype may be one of a number of functions for applying transformations to their children in the hierarchy in the manner of Todd and Latham's virtual sculptures (14) or they may be simple graphical primitives such as spheres, cones, cylinders etc. The transformation nodes we have found most useful are illustrated (fig 5). We may evolve organisms using either a Blind Watchmaker type interface as described by Dawkins (15), or mathematically defined fitness functions.

Some simple organisms using the above transformation nodes and a spherical primitive are illustrated below (fig 6) illustrate some flagellates and ciliates constructed similarly (fig 7).

Figure 5: Transformation nodes for construction of artificial organisms

Figure 6: Some simple artificial organisms
Included in the genes for each node are 'phase shift' values used to alter incoming signals. These values may also alter the type of signal as it passes from one primitive to the cilium at the current time and is used as an index into a lookup table containing the jenamic model. Signals may also be responsible for reversal of the direction of the power

Metachronism may be implemented along a simple chain of cilia bearing primitives to the node. If the repeat node changes the phase of the signal between repeated adjacent elements, complex hierarchies of primitives may propagate signals with varying le- between adjacent cilia within a single row.

4.3 Explicit Fitness Evaluation

Organisms generate force dependent on the characteristics of the tentacles they employ and thus an equally wide variety of possible forces amongst our population of ciliomites.

The drag induced by an organism may be approximated by summing the effects of isolated sphere will generate drag according to equation (1). For drag computation, a placed by a cylindrical element of length equivalent to the original sphere's diameter. F bers, any blunt object forcing its way through a fluid may be approximated by a sphere object.

Contained within the genes of a transformation node are the orientation vectors for This gives simple access to the orientation of the elements relative to velocity of trace of the drag acting on an element using the methods outlined above.

We limit the evolution of artificial organisms to those which are symmetrical about This imitates the path taken by carbon-based evolution and reduces computation by el on the organism as a whole. Such torques are generated by asymmetrical propulsion, or

Having calculated the net force acting on an organism, we may introduce this value evolution of artificial life. In this case, the fittest organisms are those most adept at lax components of our organisms to allow the genetic algorithm to focus on finding intese rather than just locating organisms with zero body size and extremely lengthy and inst limit on the bending force an organism may apply to its tentacles.

5 FUTU RE RESEARCH

The evolution of organisms with asymmetrical bodies and unbalanced propulsion about the organism's centre of mass. Turning behaviour could, with sensor controls, avoid the manner of Reynolds's boids (16). The organisms could be placed in a mate, eat and fight in order to survive.

The path swept out by a tentacle plays an important role in determining its effici generate different functions to control the inter-link spring constants in our dynamic m
propulsive tugs at low Reynolds numbers. We have used this model to produce artificial organisms which employ such structures for locomotion.

The artificial organisms are capable of employing metacontrol as a means of coordinating multiple propulsive structures. The organisms may be evolved interactively or using a conventional genetic algorithm with externally determined fitness function.

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REFERENCES