Co-evolution of Morphology and Control of Soft-bodied Multicellular Animats

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ABSTRACT

We present a platform that allows for co-evolution of development and motion control of soft-bodied, multicellular animats in a 2-dimensional fluid-like environment. Artificial gene regulatory networks (GRNs) with real-valued expression levels control cell division and differentiation in multicellular embryos. Embryos develop in a simulated physics environment and are converted into animat structures by connecting neighboring cells with elastic springs. The springs connecting outer cells form the external envelope which is subject to fluid drag. Both the developmental program and motion control are encoded indirectly in a single linear genome, which consists of regulatory regions and regions that code for regulatory products (some of which act as morphogens). We applied a genetic algorithm to co-evolve morphology and control using a fitness measure whose value depends on distance traveled during the evaluation phase. We obtained various emergent morphologies and types of locomotion, some of them showing the use of appendages.

Categories and Subject Descriptors

I.2.8 [Artificial Intelligence]: Problem Solving, Control Methods, and Search—*Heuristic methods*; F.1.1 [Computation by Abstract Devices]: Models of Computation— Self-modifying machines; J.3 [Life and medical sciences]: Biology and genetics

General Terms

Algorithms, Design, Experimentation

Keywords

Artificial Embryogenesis, Body-brain co-evolution, Development, Evolution of locomotion, Evolution of morphology,

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Gene Regulatory Networks, Generative and Developmental Systems, Genetic Algorithms, Soft-body animats

1. INTRODUCTION

Co-evolution of morphology and movement control is one of the most active research areas of Artificial Life. Progress in this area is driven by the desire to shed light on how co-evolution of body and control shaped the form of biological organisms, and also by the hope that the creative power of artificial evolution can be used to discover novel morphologies and control methods which would be difficult to conceive using other engineering approaches.

Ever since the landmark paper by Karl Sims [23], there have been many proposals for how to use generative or developmental processes to evolve animats (e.g., [9, 14, 18]), but often with high level abstractions of biological development, and large components (such as parameterized shapes) connected with joints. This is effective from the engineering point of view, but very far from biology. Although a considerable progress has been achieved recently in using lower-level approaches, inspired by biological gene regulatory networks (GRNs), for modeling evolution of development (e.g., [5, 15, 10, 12]), there are only a handful of models for the evolution of multicellular animats with such a low-level approach. For example, Bongard and Pfeifer [1] used artificial GRNs to evolve morphologies and neural networks of animats moving on a plane (cells were connected by rotating joints). Eggenberger Hotz [6] demonstrated how GRN-controlled multicellular animats can move without a neural network, thanks to the adhesive forces between cells reshaping the morphology. Several recent animat models (e.g., [17, 13, 26, 16, 20] are based on spring-massed systems, perhaps drawing inspiration from the landmark work of Terzopoulos et al. [25]. However, some of these models do not use GRNs [17, 13, 26] or are not developmental [26].

The platform described in this work allows for evolution of GRN-controlled development in a 2-dimensional (2-D) simulated physical environment. The final structure of an animat is defined as a spring-mass system in the form of a planar graph, in which nodes represent masses (cells) and edges act as springs. The regions of the body determined by edges are prevented from collapsing through internal pressure. These regions behave like pressurized chambers and form a kind of "hydrostatic skeleton". Each cell in the final structure is capable of actuation by contracting and ex-

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panding its springs, which reduces or enlarges neighboring regions. The resulting soft-bodied, highly flexible structure relies both on the actuators and internal elasticity to generate forces that drive movement. Both the developmental programs and the way movement is controlled are encoded indirectly in biologically-inspired genomes. During evolution animats are selected only for their ability to swim in a virtual environment, so neither the type of morphology nor the controller are externally enforced.

Our work was driven by the desire to create a model of co-evolution of form and function, but the results are relevant for the emerging field of soft-bodied robotics. This field has seen considerable progress in recent years: physical robots with fluid/air filled cavities driven by expanding and contracting actuators [24, 22], robots inspired by caterpillars [19], octopuses [3], and starfish [22], and models of entirely amorphous, locally expanding morphologies [8].

2. EMBRYOGENETIC MODEL

We adopted the model of the genome, GRN, and multicellular development from our earlier work [12]. Our platform strives for biological realism. The animat phenotype is a result of interactions taking place on multiple levels of abstraction. On the lowest level, the interactions between products and promoters, encoded in a linear genome, determine the GRN topology. Products continuously build up and degrade in cells and their level determines cell division and differentiation. The final body shape is the result of physical interactions between cells, which freely move in 2-D space with simulated physics as the embryo develops. Finally, the movement of the animat results from interactions between distributed control, the physical structure of the animat, and the properties of the simulated environment.

2.1 Genome and GRN

Our model of the genome was inspired by the work of Eggenberger Hotz [5], but with some important differences discussed in our previous papers [10, 12, 11]. A genome is a list of genetic elements, divided into three classes: (i) genes, coding for products (transcription factors, TFs), which can act only in one cell or diffuse to other cells (and act as morphogens), (ii) regulatory regions (promoters), and (iii) "special elements" which are used as inputs and outputs of the network (Fig. 1). The genome is parsed sequentially. Regulatory units are formed whenever a series (one or more) of promoters is followed by a series of genes. Regulatory units form the nodes in the GRN. When a unit is active, all genes that belong to it are expressed at the same level.

Each genetic element has several fields (numbers). Affinity between products and promoters is determined using a metaphor of chemical affinity between biological informational macromolecules (proteins and nucleic acids). Two fields (real numbers) specify a point in continuous R^2 "affinity space". Affinities depend on distances between points corresponding to genetic elements. The smaller the distance, the higher the weight (maximum weight, set to 10, for zero distance). The weights decrease exponentially with distance, up to a cut-off value (at which the weight is zero) to prevent full connectivity. Other fields of the genetic elements define their class and their "sign" (the result of multiplication determines if a product-promoter interaction corresponds to inhibition or activation). Since regulatory units can have multiple promoters and multiple products, any two nodes in



Figure 1: The structure of the genetic elements and the linear genome. Each element consists of a type field (the numbers in parenthesis in the descriptions below the graph indicate types), a sign field, and an ordered set of N real values which is used to determine affinity to other elements; N = 2 was used in this paper.

the graph can be connected by several edges. Our approach does not enforce limits on the size of regulatory graph or the number of types of TFs which can be encoded in the genome.

Product concentrations are updated in discrete time steps. First, activation of each promoter of the given regulatory unit is calculated as a weighted sum of concentrations of products which have affinity to this promoter. Then, the sum of the activities of all the promoters is used to calculate the rate at which products of this regulatory unit are produced or degraded:

$$\Delta L = (\tanh \frac{A}{2} - L)\Delta t \tag{1}$$

where Δt is the time step (0.05 was used), L is the current concentration of the product, and A is the sum of activation of all promoters for this regulatory unit. The formula ensures that all product concentrations remain within [0, 1).

Special elements, which encode the inputs and outputs of the GRN, are treated like TFs (for inputs) or like if they were regulatory units with one gene (for outputs). The activation of outputs is determined by the concentration of TFs that have affinity to a particular special element. The model includes six cellular actions, associated with outputs: cell division, cell rotation, modification of cell size (which affect development), and three actions that modify oscillation parameters (which affect movement; explained below). Four inputs can be used: a signal of "1" (a TF with a constant maximum concentration; this is similar to a bias input in neural networks), and three substances ("maternal morphogens") diffusing from three sources in the 2-D physical space in which development occurs. Evolution determines what inputs and outputs are actually used in a given GRN.

2.2 Developmental process

Development starts from a single cell (Fig. 2). All cells have the same GRN, encoded by the genome. Cells occupy real-valued positions in 2-D space and behave as soft circular objects in a simulated fluid-like environment. After each division, physical forces cause now overlapping cells to repel each other and to gradually drift apart. Coherent structure of the embryo is maintained by an adhesive force that makes close-by cells stick to each other.

Development is guided by diffusive substances, which include not only the three maternal morphogens, but also morphogens which can be produced by cells. In our simplified, grid-less diffusion model, the level of a diffusing product at



Figure 2: Example of a developmental process. The panels (a-g) show the development of the animat in Fig. 7b, 6a at indicated simulation time steps, (d) shows cells that have just divided, but were not yet pushed away by physical forces, this process took about 30 time steps (e). Cells are represented as circles, short lines indicate the direction of the orientation vector.

a given location is a function of distance and the historic concentration of this morphogen at its source.

Cell division occurs when the level of a product coded by the special element associated with this action reaches the threshold of 0.9. Each cell maintains its orientation vector, used to determine the direction towards which a new cell will be placed at division. The daughter cells inherit all the TF concentrations and the direction of the orientation vector from their mothers. At division, the daughter is placed in close proximity to the mother, and the orientation vector of the daughter is rotated proportionally to the activation level of the associated GRN output (maximum expression, 1, corresponds to a rotation angle of 2π). If a mother cell expresses the gene responsible for size increase, the radius of a new cell may be up to 50% larger. We enforced a hard limit for the size of the embryo of 32 cells, with the exception of one series of evolutionary runs in which up to 64 cells were allowed. This limitation can be seen as stemming from the strict limits on the resources available to the embryo.

3. PHENOTYPIC REPRESENTATION

After the development ends, the obtained morphology is transformed into the animat structure. The first step of this transformation is the formation of the edges connecting the centers of adjacent outer cells. This outline forms the external surface of the animat (Fig. 3). In our model of a fluid-like environment, it is only the outline that generates drag. The overall shape of an animat is maintained by all of its cells, connected with damped springs.

To obtain the internal structure of an animat, a graph of connectivity between cells is computed. The vertices correspond to cell centers; edges connect neighboring cells. Importantly, only the positions of cell centers in the developed embryo are taken into account, and not cell radii (but the radii determine the final positions of centers during development). Thus, the connectivity graph of the animat structure is determined entirely by cell positions, which are indirectly encoded in the genome.

We use Gabriel graphs [7] as a notion of point proximity. For P points in the plane, any two points a and b are connected by an edge if and only if the disc with the diameter



Figure 3: Algorithmic transformation of a set of points into the structure of the animat: (a) cell centers at the end of developmental phase, (b) a Delaunay triangulation, (c) a Gabriel graph (final structure).

ab does not contain any other point of P. A Gabriel graph can be obtained from a Delaunay graph by removing edges that do not fulfil the above criterion.

Actuation is achieved by modifying the resting lengths of the springs. Each cell (vertex) can contract or extend the length of the springs (edges) connected to it. The result is shrinkage or expansion of the regions around this cell. The effect exercised by two cells connected to the same spring is additive. Each cell is characterized by three parameters describing its pattern of oscillation: amplitude, phase and frequency. These three parameters are influenced by the corresponding GRN outputs. The state of the outputs at the end of development is used to set parameters for each cell. The parameters remain fixed during evaluation of locomotion.

The resting length of each spring is modified according to:

$$L = (1 + a_1 \sin(f_1 t + \phi_1) + a_2 \sin(f_2 t + \phi_2)) \cdot L_0 \qquad (2)$$

where a_1, a_2 are the evolved amplitudes of the two connected cells (scaled to the interval between 0 and 0.2), f_1, f_2 are the evolved frequencies of oscillation, and ϕ_1, ϕ_2 are evolved phase shifts (from 0 to 2π). To prevent sudden changes in resting length for cells with non-zero phase shift at the start of simulation, such cells postpone their activity for up to half of their period, so that the resting length is always modified gradually from its equilibrium value.

4. PHYSICS SIMULATION

The structure of the animat is simulated in the physical environment as a set of small, circular masses (cells) connected by damped springs. All cells have identical mass. Each spring has a resting length determined during creation of the animat. The forces acting on cells connected by springs are calculated according to Hooke's law with damping (with the same values of the elasticity and damping coefficient for all the springs).

The body is divided into regions (polygons formed by edges) which act as pressurized chambers and oppose excessive compression to prevent collisions of internal nodes with springs. The chambers provide the animats with a form of hydrostatic skeleton. At the time of creation of the morphology, the area S_0 for each region is computed and pressure is assumed to be in equilibrium. If during actuation a body region becomes smaller or larger, a pressure force will act along the normal of each edge defining this region:

$$F_p = c_p \cdot L \cdot (1 - \frac{S}{S_0}) \tag{3}$$

where F_p is the pressure force acting outward along the nor-

mal of the edge that is considered, L is the length of this edge, S and S_0 represent the current and original surface area of this region, while c_p is the global pressure coefficient, controlling resistance to compression.

We used a simplified model of fluid drag [20, 21] which assumes that the fluid is stationary and that the force acting on a single edge belonging to the outline of the body is a sum of tangential and normal drag components for the motion of this edge. Thus, to calculate drag, the motion of the edge is split into its normal and tangential components v_T and v_N :

$$F_T = -d_T \cdot L \cdot sgn(v_T) \cdot (v_T)^2 \tag{4}$$

$$F_N = -d_N \cdot L \cdot sgn(v_N) \cdot (v_N)^2 \tag{5}$$

where d_T and d_N are the drag coefficients for tangential and normal drag of unit length edge. Since the animat structure is not rigid and the lengths of the springs change dynamically, the direction of motion of a given edge is understood as the direction of movement of its center. The calculated force is then divided by two and applied to the nodes associated with the given edge. Penetration of an edge by a cell is not allowed and results in an elastic collision. This could happen, for example, when protruding parts of the morphology hit each other or bend to collide with the external surface of the animat.

We used the Bullet library [2] for physics simulation. Because this library is best suited to rigid body simulations, we used it only for the integration of cell movement. Forces related to the damped spring-mass system described above were calculated externally to the library.

5. GENETIC ALGORITHM AND FITNESS EVALUATION

Genetic operators in our system can change element type, sign, or coordinates. The change of coordinates moves the point that corresponds to the element in a random direction in affinity space by a distance drawn from a normal distribution. In addition, duplications and deletions of series of elements are allowed.

We employed a genetic algorithm with a population size of 100, elitism, tournament selection, and multipoint crossover for sexual reproduction (for 20% of the individuals in each generation). Tournament selection was performed on two randomly drawn individuals. To avoid premature convergence, the probability of selection of the fitter individual was initially equal to 0.8 and continuously increased to 1 over the first 1000 generations. The initial populations were generated randomly, by creating individuals with 10 regulatory units, each containing a single promoter and a single product. To assess individual fitness, animats were placed in the simulated physical world and simulated for a fixed number of time steps (4000 or 8000 in some experiments). The fitness awarded to an individual was equal to the straightline distance traveled by the animat's center of mass from its initial location. Evolutionary runs were terminated after no improvement over 500 generations was detected (the total number of generations was usually around 5000, and rarely above 10000).

To promote faster evolution, we introduced criteria which individuals had to meet to take part in the creation of the next generation. The regulatory graph (the GRN) had to contain a path between at least one input and the outputs



Figure 4: Snapshots of a single motion cycle of two undulating individuals propelling themselves in a high drag ($d_N = 10$) fluid environment. Node color indicates whether the cell is contracting or expanding its springs (red: expansion, blue: contraction, green: neutral). Numbers indicate the time steps in the cycle. The direction of movement is rightwards.

associated with division and oscillations. Animats were required to have at least three cells. The last division had to occur at least 100 time steps before the end of development (which was simulated for 400 time steps in total). This condition is necessary to allow the morphology to expand after the last division (see Fig. 2). The initial random individuals were generated until the criteria were fulfilled and then placed in the initial population. Typically, this required a few hundred tries for each random individual.

6. RESULTS: EVOLUTION OF SWIMMING

We evaluated the ability of our approach to co-evolve morphology and control under different environmental conditions, varying the settings for normal/tangential drag coefficients (the latter was always 1/200 of the former). We have run 10 independent evolutionary runs for each setting.

In almost all cases, the factor responsible for an increase of cell sizes during development was found to be expressed at the maximum level, resulting in the largest morphologies possible. This may be because we rewarded the absolute distance traveled, not the distance relative to animat size, so it is beneficial to be large.



Figure 5: Snapshots of a single motion cycle of two individuals propelling themselves through asymmetric contractions in a moderate drag environment $(d_N = 2)$. Node color indicates whether the cell is contracting or expanding its springs (red: expansion, blue: contraction, green: neutral). Numbers indicate the time steps in the cycle. The direction of movement is rightwards.

The best individuals (for all settings) would propel themselves using either waves of contractions traveling through the body or synchronous contractions of the whole structure. The frequency of contractions evolved to reinforce the oscillations coming from the elastic properties of the physical structure of the animat.

We could identify three main strategies of evolved locomotion, but many of the best individuals displayed a combination of two modes. One class consists of animats with bodies elongated in the direction of motion and moving by undulation which results from waves of contractions propagating through the body in a direction perpendicular to the direction of movement (Fig. 4)¹. In 10 independent runs with a high drag coefficient ($d_N = 10$), half of the best individuals in 10 independent runs, including the two best solutions overall, moved by undulation. This strategy appeared, but mostly mixed with other strategies, among the best solutions when the drag was moderate (when $d_N = 2$, four out of 10 used undulation, three mixed it with other strategies, see below), and rarely if at all when the drag was low $(d_N = 0.5;$ only one mixed strategy involved limited undulation, see below).

The second mode of locomotion is also employed by elongated individuals, but instead of undulating, their bodies contract along the direction of motion because the cells oscillate synchronously. An expansion of the animat structure generates asymmetric drag. The front of the body becomes pointy, while the back becomes flat due to drag, which further increases drag because most surfaces are orthogonal to the direction of expansion (Fig. 5). During the contraction, the drag is almost equal at the front and at the back (Fig. 5a; note how the "tail" becomes perpendicular to the direction of motion during expansion while it is aligned during contraction). This type of locomotion was the most successful when drag coefficients were moderate ($d_N = 2$: six best individuals in 10 independent runs, one of them with undulation), but emerged in all environmental settings ($d_N = 0.5$: one out of 10; $d_N = 10$: two out of 10).

Perhaps the most interesting mode of locomotion was obtained in experiments with the lowest drag coefficients: under these conditions, animats often evolved protrusions ("appendages"; in nine out of 10 runs with $d_N = 0.5$, in one of these nine the best strategy was mixed with some undulation). When the drag coefficients were moderate, protrusions appeared, but only in strategies mixed with undulation $(d_N = 2:$ in two out of 10). When the coefficients were high $(d_N = 10)$, protrusions also appeared (in four out of 10), but the movement strategy was less clear or (in one of these four best individuals) mixed with undulation.

The best individuals which use protrusions propel themselves by extending them and generating thrust while the protrusions are pulled backwards (Fig. 6). Although fins sensu stricto cannot exist in 2-D, the overall appearance is similar. Movement results from the fact that the protrusions are fully extended when moving backwards (generating thrust) but are contracted during their return. We have observed a clear tendency to place the protrusions symmetrically. In 32-cell structures protrusions are often built from one cell extending beyond the main outline of the body and become more pronounced only due to dynamic changes in shape during motion. Much more clearly defined protrusions, consisting of multiple cells (Fig. 6b), emerged when the cell limit was increased to 64 cells and the drag was put at an even lower value ($d_N = 0.2$; under these conditions nine out of 10 best individuals used protrusions, but one had a mixed strategy, using a "tail", the remaining one used only the "tail"). In most of 32- and 64-cell individuals employing this mode of locomotion the wave of contractions allowing for movement travels from the back towards the front of the animat.

More detailed analysis of the best individuals revealed that the amplitude and frequency of the oscillations is rarely differentiated between cells. We observed some successful individuals who had cells with slightly different frequencies of oscillations, but the motion of these animats was usually efficient only during a very limited period of time. In particular, their motion would quickly become inefficient when the simulation was extended beyond the lifespan they experienced during the evaluation phase of the genetic algorithm.

The amplitude of oscillation almost universally evolved to be close to maximum for all cells. This could be because there is no cost to actuation. Using maximum amplitudes of oscillations is a way to perform the most work against the fluid drag. Because the whole structure is connected and energy is easily transferred along the springs, even the contractions of internal cells add to the forces acting on external surfaces. On the other hand, the differentiation of phase

¹Supplementary videos of animat behaviors are available at: http://www.evosys.org/gecco12animats



Figure 6: Snapshots of two individuals propelling themselves with the use of symmetric protrusions in an environment with low fluid drag. Panel (a): an individual with 32 cells, evolved under $d_N = 0.5$, (b): with 64 cells (b), $d_N = 0.2$. Node color indicates whether the cell is contracting or expanding its springs (red: expansion, blue: contraction, green: neutral). Numbers indicate the time steps in the cycle. The direction of movement is upwards.

did evolve. For example, the perpendicular wave traveling through the body in Fig. 4a is a direct result of the fact that cells differ in phase in the direction perpendicular to the direction of movement (Fig. 7a). For the individual seen in Fig. 6a, most springs contract and expand in synchrony and there is no smooth phase gradient (Fig. 7b). However, because a line of cells at the back is strongly shifted in phase,



Figure 7: Example of evolved cell oscillation phase shifts. Panel (a): the individual in Fig. 4a, (b): in Fig. 6a, (c): in Fig. 5a. All animats are displayed in their initial, equilibrium states. Color range is normalized on each picture and the maximum value of phase shift in each individual (corresponding to the red node) is indicated.

a wave of contractions travels through the body during locomotion. For the individual in Fig. 5a, the phase differences are small, and springs contract and expand almost at the same time (Fig. 7c, note the low maximum phase shift).

7. RESULTS: EVOLUTIONARY HISTORY

The fitness function we employed implicitly rewards size, so the best individuals we obtained always had the maximum number of cells that was allowed. Early generations were populated by animats in which all springs contracted and expanded in synchrony and with similar amplitude. Combined with asymmetries in the morphology, these oscillations would allow for some movement.

Analysis of the best fit individuals over generations suggests that initially the winning morphology changes rapidly. In all the runs, entirely new combinations of morphology and control sweep through the population for the first hundreds of generations, until the winning mode of locomotion emerges. For most of the remaining evolutionary history, small improvements of control and morphology would prevail (this stage would often take more than 10 000 generations). Only rarely would the best morphology change after many thousands of generations (this was the case for the history of the individual shown in Fig. 4a, whose mode of locomotion became the best after generation 8914, replacing an individual in the class of motion shown on Fig. 5). Whenever a significant morphological change would occur, it was quickly followed by a steep improvement in fitness, spanning about 100 generations. Some of these improvements corresponded to refinements of morphology, but mostly to adjustments of control to exploit new body structures.

For example, the history of the run that gave rise to the individual in Fig. 4b (Fig. 8) reveals that after two thousand generations, a large change in the winning morphology occurred. This morphology was quickly refined to its final state in less than 200 generations. The path for a final series of improvements was initiated around generation 3100, by modifying the control to a non zero, non uniform phase shift among cells. Further refinements took over 3500 generations, without any morphological change.

A fragment of another evolutionary history (Fig. 9) shows that the most radical improvements after generation 200 were driven by morphological changes. The winning morphological type appeared very early, about generation 340. Along the way, the final winning morphology already seen in generation 250 would be at least once out-competed by a related morphology in generation 263, only to reappear as the winning solution in generation 292.



Figure 8: Fitness of the best individuals in the evolutionary run that ended with the animat in Fig. 4b. The last two individuals (which were the best around generation 3000) are shown enlarged and with cells colored to illustrate the change in oscillation phase shift among the cells, which was no longer zero afterwards.

7.1 Conclusions and future work

We present in this paper a model of the evolution of GRNcontrolled development of multicellular bodies which form soft-bodied animats able to move in a fluid-like environment. Our model has similarities with the one presented by Schramm et al. [20], who evolved GRNs which controlled development of 2-D animats (with springs and masses) promoting elongated shape in the fitness function. In contrast to this previous work, we do not promote any particular morphology nor the type of locomotion. Both are encoded indirectly, in one linear genome. We have shown that various combinations of morphology and control, with various modes of locomotion, emerge in environments with different drag coefficients. We observed that high drag promotes movement employing undulations while lower drag promotes symmetric appendages. We found that our method of converting the multicellular embryo into a mass-spring structure with a hydrostatic skeleton generates a wide range of interesting and relatively complex morphologies with different methods of locomotion despite the use of low numbers of cells. Importantly, the approach we employed to generate the final animat structure is based only on a set of points which is later outlined with an external "skin" and divided into elastic regions. This method provides a simple and useful approach to generate animat morphologies in other generative multicellular systems. It could also be easily extended to 3-D.

The observation that most changes in morphologies occur during initial generations suggests that most of the later morphological changes are highly detrimental. We have also observed that novel morphologies quickly improve in fitness thanks to the readjustments to control. Our observations suggest that the genetic algorithm might benefit from niching. Protecting novel morphologies until evolution has the time to adjust the control could prevent the loss of some morphologies with potential for supporting even better locomotion than we observed, but which were lost because our simple genetic algorithm did not allow their lineages enough time to adjust control.

One clear direction for future work is to allow for active control of the animats during locomotion. In the present version of our system, the GRN controls only the develop-



Figure 9: Fitness of the best individuals in the evolutionary run that ended with the animat in Fig. 6a. Multiple changes to the winning morphology occur during about 100 generations.

ment. If the GRN continued to function beyond development, direct control of spring contractions would be possible. The cells could also communicate during that time through diffusive factors (similar to morphogens acting during development). It would be interesting to investigate if such communication influences the sustainability of behavior over time or its robustness to external disruptions and if the addition of sensors would allow for directional swimming. The relative ease with which the GRN model used here could actively control behavior of unicellular organisms sensing food gradients has been evaluated in our earlier work [11].

We chose Gabriel graphs as our initial approach to specify animat internal structure because they are a fast and non-parametric way to generate non convex structures and because they allow the generation of interesting patterns of connectivity which are not limited to triangle meshes. Obviously, this is just one of many possible notions of point proximity. Computational geometry provides many comparable methods that might be worth exploring in further work. For example, connections could be generated between nodes only if they are within a certain distance. Another approach would be to compute the outline of the body through α -shapes [4], a method that would additionally allow the generation of hollow structures. Alternative methods may become useful when the number of cells is increased and a more fine-grained definition of shape becomes possible.

In future work, the stiffness of the springs could also be put under genetic control, so that some parts of the animat would be more soft and some more rigid. We also plan to investigate evolution of locomotion in an environment with a surface with ground friction and gravity. Our preliminary results show that such an environment promotes evolution of primitive appendages. We would also like to introduce the notion of energy efficiency as a part of the fitness function. We hope that introducing the cost of actuation will introduce an evolutionary pressure to employ only some of the cells as actuators and to leave others to be passive but elastic elements of the structure which allow energy transfer along the body.

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