Convergent evolution in silico reveals shape and dynamic principles of directed locomotion on the ground

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Resumo

Renata Biaggi Biazzi. **Evolução convergente** *in silico* revela princípios morfológicos da locomoção direcionada no solo. Dissertação (Mestrado). Instituto de Matemática e Estatística, Universidade de São Paulo, São Paulo, 2022.

A locomoção ativa e direcionada sobre o solo está presente em muitas espécies filogenicamente distantes. A simetria bilateral e a modularidade do corpo são traços comuns frequentemente associados à uma boa locomoção direcionada. Entretanto, ambas as características resultam da seleção natural, que é contingente (dependente da história) e multifatorial (vários fatores interagem simultaneamente). Portanto, é difícil mostrar que a simetria bilateral e a modularidade do corpo são traços necessários para uma melhor capacidade de locomoção, pois podem ser resultado do acaso ou estar relacionados a outras funções do corpo. Propomos o uso de simulações físicas evolutivas de robôs feitos de vóxeis maleáveis para testar a necessidade de ambos os traços para uma locomoção direcionada eficiente no solo. Descobrimos que um número intermediário de módulos corporais (apêndices) e alta simetria corporal são selecionados evolutivamente, independentemente dos ambientes gravitacionais, tamanhos de robôs e codificação de genótipos. Portanto, concluímos que ambos os traços são fortes candidatos a princípios universais relacionados a uma locomoção direcionada eficiente.

Palavras-chave: evolução convergente. princípios morfológicos. algoritmo evolutivo. robos maleáveis.

Abstract

Renata Biaggi Biazzi. **Convergent evolution in silico reveals shape and dynamic principles of directed locomotion on the ground**. Thesis (Master's). Institute of Mathematics and Statistics, University of São Paulo, São Paulo, 2022.

Active, directed locomotion on the ground is present in many phylogenetically distant species. Bilateral symmetry and modularity of the body are common traits often associated with improved directed locomotion. Nevertheless, both features result from natural selection, which is contingent (history-dependent) and multifactorial (several factors interact simultaneously). Hence, it is difficult to show that bilateral symmetry and modularity of the body are necessary traits for an improved locomotion ability as they can be a result of chance or related to other body functions. We propose using evolutionary physical simulations of 3D voxel-based soft robots to test the necessity of both traits for efficient directed locomotion on the ground. We found that an intermediate number of body modules (appendages) and high body symmetry are evolutionarily selected regardless of gravitational environments, robot sizes, and genotype encoding. Therefore, we conclude that both traits are strong candidates for universal principles related to efficient directed locomotion.

Keywords: convergent evolution. morphological principles. evolutionary algorithm. soft robots.

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Part I

Evolutionary simulation experiment: looking for morphological principles of directed locomotion on the ground

Chapter 1

Introduction

Exclusive focus on the N=1 example of life provided by Earth's specific phylogenetic tree, with its baggage of frozen accidents, obscures deep principles of life-as-it-can-be. — Michael Levin, 2022

1.1 The existence of animal locomotion principles

Animals have different forms of locomotion due to the complex body-environment relationships developed during their evolutionary history (R. M. ALEXANDER, 2006; BIEWENER and PATEK, 2018). The animal's ability to move in their environments is the base of essential behaviors such as foraging, predator escape, migration, and finding mates to reproduce. Active and directed locomotion - the animal's capacity to intentionally displace themselves continually in a specific direction - is a ubiquitous ability necessary for the survival of several species.

Despite all the animals' diversity and their mechanisms for locomotion, integrative and comparative studies have proposed the existence of locomotion principles based on similarities between very different species (EILAM, 1995; DICKINSON, 2000; R. M. ALEXANDER, 2006; BIEWENER and DANIEL, 2010; BIEWENER and PATEK, 2018). Some examples of shared locomotion features and mechanisms in animals are i. the consistent relationship between muscle function and myocyte composition in animal locomotion revealed by comparative physiology (SCHAEFFER and LINDSTEDT, 2013); ii. form and function relationships studied by functional morphology exposing major patterns related to vertebrate locomotion (HECHT *et al.*, 1977; HILDEBRAND, 1988; P. W. WEBB, 1988) - for example, anatomic body aspects such as limb length and proportion are associated with optimizing locomotion

costs in terrestrial animals (CHRISTIANSEN, 2002; PONTZER, 2007); iii. common locomotion mechanisms of terrestrial animals with different leg numbers and gaits synthesized by a spring-mass monopode system that models energetic and mechanical aspects of legged locomotion (R. BLICKHAN and FULL, 1993); iv. the kinematic synergy of limb movement control shared by mammals and birds (CATAVITELLO *et al.*, 2018); v. animal's typical use of central pattern generators to generate rhythmic locomotion behaviors (KATZ, 2016); vi. mechanisms of mode switching in locomotion shared in limbless and legged animals (Kuroda *et al.*, 2014).

However, there is an entanglement between the body principles behind animals' locomotion ability with all other body functions and needs for survival. It is not straightforward to identify the necessary conditions only for improved autonomous locomotion in the evolution of species. The body's necessary locomotion features are entangled and constrained by other bodies' functions and survival needs (R. M. ALEXANDER, 2006; SHUBIN *et al.*, 2009). An example of this entanglement is the fins-to-limbs transition of tetrapod, a process understood as the result of multiple and interconnected selection pressures (HECHT *et al.*, 1977; PANGANIBAN *et al.*, 1997; DICKSON and PIERCE, 2018; MOLNAR *et al.*, 2021). In this transition, body modifications allowing locomotion on land intertwine with other body needs such as weight support and changes in the respiratory and circulatory systems. Beyond this entanglement, the shared locomotion features and mechanisms exemplified above as principles are from different organization levels. Although they may be considered law-like solutions, some are homologous, and others have different convergence robustness (POWELL and MARISCAL, 2015).

Thinking about animals convergence, the biologist Stephen Jay Gould proposed a thought experiment about the contingency of natural evolution outcomes observed on Earth (POWELL, 2020). Gould hypothesized that if we could replay the tape of life, there is the possibility that we would observe very different outcomes in each repetition. This divergence would be because natural evolution is essentially a historical and contingent process, dependent upon a series of stochastic events (such as asteroid collisions) and their non-predictable effects on species survival and diversification. For example, paleoecological studies of the Cambrian period are usually insufficient to explain why some numerous and dominant species go extinct while others with apparently lower potential manage to thrive (POWELL, 2020). The survival of some features and the disappearance of others have a contingent component and are not just explained by what seems to be a direct fitness advantage. Thus, we cannot be sure about the replicability of the evolutionary outcomes we see today in other "tapes of life" or in potential extraterrestrial life forms (POWELL and MARISCAL, 2015). We can find major trends in Earth's single evolutionary history by studying the current species and its locomotion solutions. However, if we are

interested in universal and necessary principles robust to other replays of life or other planets' evolution, the actual animal outcomes are not a sufficient sample.

1.2 Contingency of symmetry and body modularity for directed locomotion on the ground

Bilateral symmetry and body segmentation are two fundamental body plan features shared by most modern animals. The pathway by which these two features evolved is an open area of debate (ERWIN and DAVIDSON, 2002; X. ZHANG *et al.*, 2014; CHEN *et al.*, 2019). There are different hypotheses about the last common bilateral ancestor and how the modifications of ancestral conserved genetic regulatory networks and developmental constraints led to the evolution of animal body plans (DE ROBERTIS, 2008; BAGUÑÀ *et al.*, 2008; COUSO, 2009; MANUEL, 2009).

The evolutionary origin of bilateral symmetry is mainly attributed to a gain in directed locomotion (Holló and Novák, 2012). However, it can also be associated with other functions such as internal transport in the body (FINNERTY, 2005). Although symmetric structures are a small subset of all the possibilities, they would prevail by best satisfying the restrictions imposed by the physical laws acting in a body (Holló, 2017) - and not by being a contingent result of natural evolution on Earth. Likewise, the correlation between mobility and metamerism (Couso, 2009) and the evolution of appendages with its possible locomotion and sensory functions (PANGANIBAN *et al.*, 1997; SHUBIN *et al.*, 1997) are examples of the undeniable role that a body divided in parts with relatively movement independence (as joint-based segmented limbs) has to locomotion (ALEXANDER, 1982; R. M. ALEXANDER, 2006; HILDEBRAND, 1988; BIEWENER and PATEK, 2018). Besides the macroscopic functional causes (as locomotion), the evolutionary pressure for solutions that minimize descriptional complexity could also be a selective bias to genotype–phenotype maps with symmetric and modular structures (JOHNSTON *et al.*, 2022).

Using the ground - on land or inside the water - to support and propel the body is one of the most typical forms of animal locomotion (R. M. ALEXANDER, 2006; BIEWENER and PATEK, 2018). Examples of this type of locomotion are animals that live outside water without being able to fly and non-sessile crustaceans. Beyond them, ground locomotion occurs in fishes that evolved limb-like adaptations like frogfish (Figure 1.1A), batfish, and mudskippers (DICKSON and PIERCE, 2018) and even in unexpected cases such as octopuses walking (AMODIO *et al.*, 2021). Thus, locomotion on the ground is present in phylogenetically distant species and depends upon one of the essential features of Earth and other planets on which life might appear - the presence of a floor. Here we investigate whether external symmetry and modularity (defined as the division of the body in connected units that move together with relative independence of the rest of the body) are body features that an organism's shape *need* to have for an improved directed locomotion performance on the ground (Figure 1.1B). In other words, we want to know the convergence level of these two features given a selection pressure for locomotion.



Figure 1.1: The convergent evolution of animals and robots makes it possible to find principles of locomotion without contingent dependence. (A) A maned wolf and a frogfish. Besides being very different, both species use the ground for locomotion in their environments. (B) Schematic illustration showing the symmetry and modularity of the maned wolf and frogfish bodies. The modules (blue outlined in red) are connected body parts that move together during locomotion. The symmetry plan (green) indicates the bilateral symmetry of the body. Modularity and symmetry are present in phylogenetically distant species. Therefore, they are candidates for being necessary features (principles) of directed locomotion on the ground. (C) Convergent evolution of organisms with no common ancestor (i.e., animals and robots) and just one shared function (i.e., locomotion) can be used to find principles of this function. It allows differentiating a necessary feature for enhanced locomotion from features resulting from the other animal's functions or contingent on Earth's evolutionary history. (D) The circles filled in green and blue represent, respectively, the shape features of terrestrial and aquatic animals with directed locomotion on the ground. The green, orange, and blue unfilled circles represent, respectively, the shape features of robots with directed locomotion on the ground subject to $9.81 m/s^2$ (Earth's gravity), $3.721 m/s^2$ (Mars's gravity), and $0.1 m/s^2$ (gravity plus buoyancy inside the water) acceleration towards the floor. The red intersection at the center represents the convergent features that indicate principles expected to be valid in different gravitational environments and organisms as different as animals and robots.

1.3 Computationally addressing shape principles of locomotion

There are two requirements to address how necessary symmetry and modularity are for the active and directed locomotion of animals on the ground. The first one is to separate locomotion from other animal needs and functions. Second, we need to access locomotion solutions that are not contingent on having N=1 evolutionary history. The solution for these requirements is to simulate an evolutionary process using robots (Figure 1.1C). Robots allow us to test hypothesis about animals and look for principles of locomotion (Aguilar *et al.*, 2016; GOMEZ-MARIN and Y. ZHANG, 2022).

In robot simulation, we can have N>1 evolutionary histories, a necessary condition to study the contingency level of the outcomes. Also, in robotic implementations we can choose *which* biological process and physical constraints will be emulated, a controlled uncoupling of animal's complexity that is usually difficult to obtain (Auke Jan IJSPEERT, 2001; B. WEBB, 2002; B. WEBB, 2009; Auke J. IJSPEERT, 2014; FUKUHARA *et al.*, 2020; SCHWAB *et al.*, 2021; WENGUANG *et al.*, 2021; GOMEZ-MARIN and Y. ZHANG, 2022).

With the simulations, we can control gravity, a crucial environmental parameter. It allows us to study the effects of different body gravitational loads in locomotion on the ground. This way, we can address the question if external symmetry and modularity are robust principles of locomotion valid on the ground either inside the water $(0.1 m/s^2 - \text{almost}$ no body load caused by buoyancy), on Earth's surface $(9.81 m/s^2)$, or in an imaginary martian life form $(3.72 m/s^2)$. The convergent evolution of shape traits evolved independently in very different systems that have just the directed locomotion ability in common (animals and robots) would justify calling them principles of directed locomotion on the ground (Figure 1.1C).

Chapter 2

Methods

The artist painted this bison with eight legs, suggesting movement Werner Herzog, Cave of Forgotten Dreams

2.1 Overview

For the simulation of an evolutionary process using robots, we used 3D Voxel-based soft robots as our organisms (Figure 2.1B). We used the simulation engine proposed on HILLER and LIPSON, 2014 (Voxelyze). Voxelyze is a software that efficiently and accurately simulates soft bodies' interaction with an environment based on physics laws. The body unit is the voxel. Voxels have features like mass, density, and stiffness and connect to other voxels as mass-spring systems forming the body shape (Figure 2.1A). The volume of each voxel oscillates cyclically and in an independent moment given by its oscillation phase (Figure 2.1A). The connected voxels are a proxy for muscle units as they can expand, contract, and are deformable. Robots are constructed by connecting voxels inside a space dimension of $4 \times 4 \times 4$ possible voxel positions. The robots simulations happen inside a physical environment (Figure 2.1C) that models effects like gravity, floor stiffness, and friction to properly simulate collisions and damping between voxels and the environment (HILLER and LIPSON, 2014). The design and locomotion behavior of evolved simulated robots using Voxelyze successfully transferred to organisms made of biological tissue (KRIEGMAN *et al.*, 2020). We based our simulation parameters on these previous works.

An artificial evolutionary process that selects for better locomotion ability generates the robots. This process contain the fundamental elements of natural evolution: i.reproduction, ii.passage of information through generations (hereditary inheritance), iii.phenotype



Figure 2.1: (A) The voxel is the unit that constitutes the robots. The voxels are connected in different configurations (defining the body shape) and oscillate their volume independently (defining the body control), forming a mass-spring oscillating system. (B) Example of a Voxel-based Soft Robot. The maximum dimension that a robot can occupy is the 4³ voxel's space. (C) The robot simulation occurs in a physical environment that evaluates effects like gravity, friction, and floor stiffness in the mass-spring system of voxels. (D) The generation cycle is the unit of the robots *in silico* evolutionary process. The phenotype evaluation is the average speed of the robot in its environment calculated in the 30s of simulation (directed locomotion ability). The best robots are selected, and their genotypes are mutated to produce a new generation of robots that will constitute the next initial population. (E) In each environment (water, mars, and earth), an evolutionary process of 1500 generation cycles results in a sample of robots with different bodies (shape and control) and performances. The shape and control features of the robots are analyzed, looking for principles.

variation by mutation in genotype and iv.selection of the fittest (Figure 2.1D). Three independent evolutionary process of 1500 generations where simulated, one for each gravitational environment - 0.1 (water), 3.72 (mars), and $9.81 m/s^2$ (earth). Each evolutionary process is a search in the space of shape and control solutions. After 1500 generations, we had a sample of robots with different bodies and directed locomotion abilities (average speed). We repeated this process 30 times (seeds) for each environment, and in the end, we had big samples of different robots for each of the three gravitational environments. In each environment, we classified every robot inside one of the five fitness layers (100%-80%, 80%-60%, 60%-40%, 40%-20% or 20%-0%) according to its fitness ratio relative to the best robot in that environment (100% fitness). With this sample, we investigate whether symmetry and body modularity are principles of the robots' maximum locomotion performance (Figure 2.1E).

In the following sections, we will explain each of the elements of the simulation experiments - the robots (representation and material properties), the virtual environment (physic engine and simulation conditions), and the evolutionary algorithm (a population optimization process). The source code necessary for reproducing the computational results reported here is in GitHub https://github.com/biagzi/locomotion_principles.

2.2 Robot representation

The robots used in this work are 3D Voxel-based soft robots, which means that robots are structures of cubic deformable and oscillating units (voxels). Voxels are combined inside a 4x4x4 bounding box (design space) to form the robot's body shape (Figure 2.1A). We choose to analyze 4³ design space because we consider it is the minimum coarse grain to start approaching the biological question about the contingency of shape outcomes pressured for locomotion. However, we did control experiments with robots within 6³ and 8³ dimensions to check for dimension size effects. Each robot of the simulation is represented both by genotype and phenotype representations. The phenotype consists of the robot shape (voxels configuration), control (voxels phase), and the voxels material properties. The genotype is the encoded information used to construct the phenotype, and it was structured using Compositional pattern-producing networks (CPPNs) (STANLEY, 2007) and Direct Encode.

2.2.1 Phenotype

The phenotype is the virtual realization of the robot in the Voxelyze physics engine (HILLER and LIPSON, 2014). The phenotypic space of possibilities for each robot consists of i. voxel presence or absence in each lattice position (shape), ii. the phase offset of each present voxel (control), and iii. the global stiffness, a unique stiffness value (Young's modulus) for all voxels in the robot. Each voxel *i* has a real value $\phi_i \in [-1, 1]$ defining its phase offset in relation to the environment global signal $\sin 2\pi (f t + \phi_i)$ that controls volumetric actuation in each time *t*. The volumetric change of the oscillating voxels is \pm 50% of their rest volume. We used a fixed frequency oscillation of f = 2Hz (KRIEGMAN *et al.*, 2020).

For each robot, the possible global stiffness values are 5e4, 5e5, 5e6 or 5e7 Pa. We based this range of values on biomechanical properties of muscle, tendons, and limbs of different aquatic and terrestrial species (BENNETT *et al.*, 1986; HE *et al.*, 1991; MCHENRY and PELL, 1995; LONG, 1998; VINCENT, 2012). After the evolution, we noticed that for the water (mars and earth) environment, all the best robots had necessarily the stiffness value of 5e5 Pa (5e7 Pa). Thus, we considered these values the best stiffness for each environment. For all the analyses, we selected just the robots with the best stiffness for each gravitational environment, so we do not have a stiffness variability in the results. The other material properties were kept constant during all the experiments and were based on KRIEGMAN

et al., 2020 work that succeeded in transferring both morphology and behavior from *in silico* to *in vivo* organisms.

2.2.2 Genotype

We used three independent genotype structures: shape, control, and global stiffness. For the global stiffness of the body, we always used a Direct Encode that randomly chooses one of the four possible values for all the voxel's Young's modulus. The Direct Encode genotype is a structure that directly encodes the necessary information for generating a phenotype feature. For the shape and control, we performed experiments both with the Direct Encode and the CPPN. In the cases using a Directed Encode, a matrix of size N^3 (N = 4, 6, or 8) associated with each position of the N^3 cartesian 3D lattice receives a random Boolean value indicating the presence or not of a voxel (shape case) or a random real value $\phi \in [-1, 1]$ indicating the phase offset (control case).

The CPPNs were proposed in STANLEY, 2007 as an indirect encoding that facilitates the generation of spacial regularities. It consists of a directed network with weighted edges that multiplies the signal passing through it. The directed edges connect nodes with activation functions $(\sin(x), \pm |x|, \pm x^2, \pm \sqrt{x})$ that receive the input signal and produce as output the continuous and symmetric patterns given by their functions. Thus, a fixed initial input signal passes through all the possible paths through the nodes, gets into the sigmoidal function of the output node, and gives a value in the [-1, 1] interval. In the case of the control genotype, this value maps directly to the phase offset values. In the case of shape genotype, a map function transforms the output to boolean values defining the presence and absence of the voxels. Using CPPN in the genotype speeds up the optimization of locomotion. However, there was the possibility that configurations that were less intuitive and regular would be as good as the common expected regular solutions. Doing independent simulation with CPPN and Direct Encode - a structure that does not favor regularity - allowed us to compare the results of these two search strategies.

2.3 Virtual environment simulation

We used the Voxelyze physics engine to do the simulations. (HILLER and LIPSON, 2014). It quantitatively models non-linearly deformed soft body dynamics using a mass-spring lattice. Each voxel has mass and rotational inertia values and is a lattice point with three translational and rotational degrees of freedom. Voxels are connected by beam elements with translational and rotational stiffness, thus forming the mass-spring system. The

software efficiently simulates collisions between voxels themselves and voxels with the environment (ground or obstacles) without self-penetration.

We did all the simulations with the same environmental conditions except for gravity. The floor has no slope, and no fluidity effect was enabled. We used a Coulomb friction model with 1.0 (static) and 0.5 (kinetic) coefficients to simulate friction between the voxels and the floor. Other environment parameters were based on KRIEGMAN *et al.*, 2020.

Each robot simulation took 32s, in which 2s are for settling under gravity and 30s for behavior evaluation. We tested different time intervals for evaluation to check if it could affect the final results. When using small evaluation intervals, the robots with a faster launch that fall or trace a highly curved path sometimes had a higher linear displacement than robots with stable and straight trajectories. We concluded that the 30s was enough to differentiate curved and unstable from stable straight trajectories. Time intervals longer than that made no significant difference in the results and significantly delayed the experiment's duration.

2.4 Evolutionary algorithm

We used an evolutionary algorithm based in KRIEGMAN et al., 2020. The algorithm starts generating 101 random robots that constitute the initial population. Each robot of this population has its phenotype evaluated, and 50 are selected, forming the reproduction population (parents). Then, a copy of each robot of the parent group is made with a mutation in the genotype, generating a new robot (offspring). The group of 50 parents, 50 offspring, and one new random individual will constitute the next new initial population of 101 robots. This process completes the first generation cycle (Figure 2.1D). The evolution of the robots is the repetition of this cycle for 1500 generations. After testing other population sizes P_s and numbers of generation G, we found that $P_s = 50$ and G = 1500 are sufficient values to do an extensive search that, after a while, converges to optimal solutions. For each gravitational environment, we performed 30 independent runs (seeds) of the evolutionary process for the 4³ and 6³ CPPN experiments, 20 for 4³ Direct Encode, 10 for 6³ Direct Encode, and 5 for 8³ CPPN and Direct Encode. The different choice of seeds was due to the computational time cost. In all the cases, the number of experiments was sufficient to check our result's robustness. Each step of the algorithm will be detailed and explained next.

2.4.1 Phenotype evaluation and selection

The phenotype evaluation consists of calculating the average speed \bar{s} of the robot after the 30s of simulation in the Voxelyze.

$$\bar{s} = \frac{\sqrt{(x_{final} - x_{initial})^2 + (y_{final} - y_{initial})^2}}{30}$$

The average speed measures the directed locomotion ability of the organism and is its fitness value. The robots with the highest fitness are the ones that maximize displacement and have robust dynamics (they will not tumble with time). Selecting for bodies that maximize speed is a common locomotion bias in natural selection, as both predators and preys and thus fecundity and mortality depend on it (R. M. ALEXANDER, 2006).

The method used for selection was an Age-Fitness-Pareto Optimization (AFPO) (SCHMIDT and LIPSON, 2011). AFPO is a multi-objective method that uses fitness and age as a criterion to select the robots that will survive and constitute the reproduction population. A new randomly created robot starts at age 0. The offspring, created by mutating a robot of the reproduction population, inherit its parent's age. Before adding a new random robot, the age of the 100 robots in the population is incremented by one. This way, age measures how much time passed searching a specific region of the space of possibilities. Then, the robots are classified in dominance levels using the Pareto fronts of multi-objective optimization, maximizing fitness and minimizing age. Using an AFPO method for selection allows young and different solutions to survive (and have a chance to be more optimized) when competing with old and very optimized solutions.

2.4.2 Genotype mutation

In each generation, a copy and mutation of each robot of the population produce a new offspring. To increase the impact of mutations on shape variability inside the population, we used a diversity filter that actuates with a probability of 1/2 in each generation. If applied, the filter ensures that the offspring group of this generation does not contain robots with shape similarity \geq 95%. Each parent will be repeatedly mutated until it generates an offspring not \geq 95% similar to any other offspring. If the diversity filter is not applied, there is no restriction for offspring inclusion. This way, mutations that have both detailed (for body optimization) and significant effects (for keeping shape exploration broadening) can happen. In each parent mutation, the shape, control, and global stiffness genotype structures have a probability of 1/2, 1/2, and 1/5 of being selected for mutation. Thus, the type of mutations can differ in each new offspring.

The mutation in the global stiffness genotype (Direct Encode) is simply a random choice of one of the four options (5e4, 5e5, 5e6, or 5e7 Pa) as long as it is not equal to the previous stiffness. The mutation in shape and control using Direct Encode is a change of values in randomly chosen places of the lattice. In the case of shape and control genotypes using CPPN, it happens by adding, modifying, or removing a randomly chosen node or edge of the network. There is a 1/6 probability of independently selecting each of the six kinds of network mutation (add node/edge, modify node/edge, or remove node/edge) - one of them is applied if none is selected. If the phenotype has not changed (neutral) after a network mutation, another one is applied until 1500 attempts. If the 1500 attempts fail to change the phenotype, all 1500 neutral mutations are applied.

2.5 Environment Transference

After running experiments with the evolutionary algorithm in different environments, we did the environment transference of the best robots of size 4³ and CPPN genotype (Figure 4B). First, we sorted all robots generated in all the 30 seeds by their fitness. Then, we select the 50 best robots with different shapes for each environment. Shapes are different if they have at least four different voxels when compared with each other. Therefore, for the comparison, we first reflect and rotate one of them in all the possibilities concerning the z-axis. The possibilities are i. rotations of the original position in the z-axis (0, 90, 180, 270°), ii. reflection in the x-z plane and its four rotations on the z-axis, and iii. reflection in the y-z plane and its four rotations on the z-axis. Counting all of them (4+4+4) results in 12 possibilities. Thus, we count the number of different voxels between a robot and the 12 possibilities of the other robot. Two robots are different if their closest comparison (their minimum difference of voxels value between the 12 possibilities) is greater than 4.

For each original gravitational environment, we transferred all the 50 best shapes to the other two gravities and their original one (control trial). The transference consisted of optimizing each shape's phase offset (control of the body) in the new gravitational environment. The optimization consisted of evolving the robot, with fixed shape and stiffness, in the evolutionary algorithm described in Section 2.4. The optimization used initial populations of 10 robots with five new random controls added in each cycle and took 200 generations. We checked that this generation number was sufficient to find the best way to move the body (there is a fitness converge). We did not use the diversity alternation filter, as its function is to increase shape diversity, and in this optimization we fixed the shapes. We used a fixed voxel stiffness value of 5e5 Pa for water and 5e7 Pa for mars and earth. After the 200 generations, we choose the best control (phase offset solution) for analyzing the performance in the new environment.

2.6 Shape measurements

2.6.1 Modularity measurement by clustering

We used an algorithm to cluster the neighboring voxels with similar phase offset values inside each robot's body to measure their modularity. We used DBSCAN (PEDREGOSA, F. *et al.*, 2011) as it uses parameters (minsample, eps) that have a meaning in our system and do not need to be blindly guessed. The points with more than minsamples neighbors are core points - the distance used to define neighbors is the eps value. The DBSCAN uses distances between the nearest points to define the density regions in the sample space that constitutes the clusters. Points that are not core points nor are inside a core points radius are outliers. Each point of our sample is a four-dimensional array that represents the position and phase information (x_i , y_i , z_i , ϕ_i) of each voxel *i*. After several tests, we developed an algorithm with three clustering steps and a choice of parameters that kept the clustered robot performance similar to the originals by more than 95% on average.

The first step of the algorithm clusters just the phase offset. It uses *minsample* = 2 (two voxels are sufficient to be considered a cluster) and *eps* = 0.2 (10% of the total range, [-1, 1], of phase offset values). After the first clustering, the algorithm checks if there is no cluster with a phase offset difference larger than 0.2 inside its members before passing to the next step. If there is, it stays in a coarse grain clustering that repeatedly uses *eps* = *eps* - 1/100 until the cluster results pass the check. It ensures that clusters with very different phase offsets inside it will not occur without the risk of wrongly fragmenting too much the clustering.

After the first step, the voxels receive the average phase offset value of the cluster that they belong $\langle \phi_i \rangle$. The second step has a similar structure of the first one, but it clusters position and mean phase offset using the sample of four dimension arrays $(x_i, y_i, z_i, 10 \times \langle \phi_i \rangle)$ and initial eps = 1.2. We multiply the $\langle \phi_i \rangle$ by 10 to bring it to the same order of magnitude of position, as eps = 1.2 apply equally to the four dimensions. This step uses eps = eps - 1/10 to do the coarse grain clustering if the result does not pass the check (the same as in step 1). After the second step, the third step checks for outliers (noisy samples). If there are outliers, each one is independently considered a cluster of 1 voxel or grouped in one of their direct neighbor clusters if they have a phase offset similar enough ≤ 0.3 .

The robot's modular representation uses the cluster's members' average phase offset and position. The modules are linked if they have directed connected voxel members.

2.6.2 Module connectivity

Let *M* be the number of modules (nodes) of the robot and c_i the number of connections (edges) of each module *i* with i = 1, ..., M. Then, we defined average degree as:

AvgDegree =
$$\frac{1}{M} \sum_{i=1}^{M} c_i$$
 (2.1)

Chapter 3

Results

The fewer species there are and the fewer species we know about, the fewer questions we even know to ask. Lynn Margulis

Body modularity and symmetry are considered advantageous features for an organism's locomotion based on extant animal morphology (R. M. ALEXANDER, 2006; HOLLÓ, 2017). However, we cannot guarantee by studying only the existing animals that these features are necessary for a good locomotion performance. Modularity and symmetry could also result from another evolutionary constraint unrelated to locomotion, or they could be the contingent result of the N = 1 evolutionary history. For example, if an organism with a different genome and developmental process had evolved to move on Mars's surface, would it also have a body with bilateral symmetry and modularity? Our study approaches this question by considering the direct locomotion pressures on the shape and dynamic of a body that moves on the ground.

3.1 An intermediate number of modules sparsely connected are necessary to increase directed locomotion on the ground

To study body modularity, we clustered the robot's voxels based on their proximity and synchronization. Connected voxels with similar phase offsets are members of the same module (cluster) (Figure 3.1A). A module has the average position and phase of its voxels members. The modules that have directed connected voxels are linked. We constructed a topological representation - consisting of the robot's modules and connections - for each

3.1 | AN INTERMEDIATE NUMBER OF MODULES SPARSELY CONNECTED ARE NECESSARY TO INCREASE DIRECTED LOCOMOTION ON THE GROUND



Figure 3.1: An intermediate number of modules sparsely connected is necessary for achieving higher directed locomotion performance. (A) The modules are the connected and synchronized grouped voxels of a robot. Using the modules, we created two topological representations of the robot (TP1 and TP2). TP1 has information about each module's mean phase (represented by the color) and position. The size of each module is relative to the number of voxels it contains. Modules that touch the ground are represented as triangles, while those that do not are circles. TP2 representation shows the modules and their connections without further information. (B) Robot's modularity examples with the number of modules and a measure of its connectivity (AvgDegree). (C) Illustration of the hypothesized impact of the number of modules on the directed locomotion ability. The robots with the 20% top directed locomotion ability (red area) have an intermediate number of modules that can maximize both the body's degree of freedom and coordination capacity. (D) The results of the three environments confirm the hypothesis: the best robots (100-80% fitness layer in red) typically have an intermediate number of modules (more than one but less than 17). The module number range increases as the fitness layers get worse. (E) Illustration of the hypothesized impact of the module's connectivity (measured by the network average degree defined in Equation 1) on the directed locomotion ability. The robots with the top 20% directed locomotion ability (red area) maximize both the body's degree of freedom and coordination capacity by having sparsely connected modules. (F) The results of the three environments confirm the hypothesis that robots with better 20% directed locomotion ability (100-80% fitness layer) typically have an average degree between 1.2 and 4 (sparsely connected). Robots with modules densely connected (more than four connections per module on average) do not have good performances.

robot (Figure 3.1A). The topological representation has two visualizations. The first one (TP1) colors the modules depending on their phase value and places them using their mean positions. The size of the module depends on the number of voxels belonging to it. The modules that touch the ground are represented as triangles, while those that do not are circles (see Figure 3.1A). The second type of visualization (TP2) shows the modules and their connections without adding any other information (Figure 3.1A). The average degree measures how connected the network nodes are. Figure 3.1B exemplifies some different robots' modularity and average degree value.

We hypothesized that the robot locomotion ability would be higher when it maximizes both body's degree of freedom and its coordination capacity (Figure 3.1C). The number of possible movements of the body increases with the number of modules (red dotted line in Figure 3.1C). However, more movement possibilities will not necessarily add to a better locomotion performance. Increasing the number of modules reduces the chance of finding suitable coordination for locomotion (Figure 3.1C blue dotted line). Thus the robots with the top fitness value (red) are expected to have an intermediate number of modules to maximize both body's degree of freedom and coordination capacity. Supporting our hypothesis, Figure 3.1D shows that the robots that belong to the top 20% fittest ones (100-80% fitness layer) have exclusively a small to an intermediate number of modules (from 3 to 17, approximately), indicating low tolerance of the best robots to have one or two modules and to increase their number of modules indefinitely. On the other hand, as the fitness layers worsen, they often include robots with lower and higher amplitudes of the number of modules (light and dark blue). This pattern is robust for different gravities and repeats in all three environments (water, mars, and earth).

Additionally to the number of modules, the robot's body dynamics depend on the module's connectivity. Here, we used the network average degree, defined in Equation 2.1, to measure the body's connectivity. Modules more connected make a more tied structure, implicating a decrease in the body's degree of freedom. Furthermore, as the modules' movement affects their neighbors, a strongly tied structure will have higher coordination in its movement (Figure 3.1E). Thus, we hypothesized that the robots with the top performance (red area in Figure 3.1E) will maximize both body's degree of freedom and its coordination capacity by having an intermediate degree of connectivity (*i.e.*, a sparsely connected body). Figure 3.1F shows that in the three environments, the 20% fittest robots (100-80% fitness layer) have, as expected, an intermediate average degree between 1.5 and 4. On the other hand, as the fitness layers worsen (see 20-0% fitness layer in dark blue), they include robots with lower and higher average degrees.

If the hypothesis of balance between the body's degree of freedom and coordination

is correct, we expect that the same pattern of an intermediate number of modules and average degree should hold for different robots' genotypes and sizes. The results presented in Figure 3.1D used CPPN's genotype, a structure that accelerates the search by biasing the bodies to structures with continuities and regularities. To test if our findings are a byproduct of this specific genotype, we repeated the experiments using a Direct Encode a genotype structure where the presence or absence of a voxel is independently chosen from each other, resulting in less bias. We also tested the effect of different dimension sizes evolving robots using a 6^3 and 8^3 design space with CPPNs as genotype.



Figure 3.2: The results of the three experiments (6³ CPPN, 8³ CPPN, 4³ DE) confirm the results of 4³ CPPN that the best robots (100-80% fitness layer in red) typically have an intermediate number of modules and average degree compared to the other layers. Thus, the principles found seem to hold for different genotypes and sizes of robots.

Figure 3.2 shows the number of modules and the network average degree distributions for each fitness layer in water, mars, and earth for the different experiments. As with the 4³ CPPN experiment (Figure 3.1), the best robots (100-80% fitness layer) concentrate in an intermediate range of modules and average degree comparative to the other layers. Therefore, to achieve higher locomotion performance, it is necessary to have an intermediate number of modules sparsely connected (intermediate number of average degree)

independently of the genotypes, sizes, and gravitational environments.

In all the plots showed in Figure 3.1 and Figure 3.2, the layers are normalized together. Thus, we can observe that the worst fitness layers (40-20% and 20-0%) constitute a larger sample of robots than the best fitness layers (100-80% and 80-60%) in all the experiments and all the environments. This difference in sample sizes is expected, as the higher fitness results from the specialization of a small subset of survivor robots given a large number of bad trials that are extinct. In the specific case of the number of modules analysis, the layers distributions have a similar shape except for a tail present in a minimal density. Thus, we checked if the amplitude difference between the layers was significant or was due to extremely rare outliers present in the worst layers because of their bigger sample sizes. For that, we did a bootstrap of the sample for each environment and each experiment, with N = 10000. In Figure 3.3, we plotted the difference of the extreme values (amplitude) for each layer distribution. The points are the mean value of the distribution of amplitude values after N=10000 bootstrapping. The results confirm that there is a difference between layers not explained just by sample size. The best layers (100-80%) average restricts to a specific range of the possibilities (smaller amplitude) of the number of modules explored in all the environments and experiments. As the fitness layers worsen, the amplitude increases. We expect the layers' amplitude difference to intensify even more with more optimization in the 4³ DE and 8³ CPPN experiments. In these experiments, 1500 generations were insufficient to get a fitness value as high as in the 4³ CPPN, which indicates a significant potential for more optimization.



Figure 3.3: The results of the three experiments (6^3 CPPN, 8^3 CPPN, 4^3 DE) confirm the results of 4^3 CPPN that the best robots (100-80% and 80-60% fitness layers) restricts to a small amplitude of values compared to the worst layers (40-20% and 20-0%). The points are the mean values of each layer distribution of amplitudes after a N=10000 bootstrapping.

3.2 Highly symmetric body shape and a break of total symmetry in control are necessary conditions to increase directed locomotion on the ground

To quantify the robot's symmetry, we defined two separately symmetry measures for its shape and control (Figure 1.1E). The shape symmetry is the percentage of symmetric voxels after mirroring the robot on the x and y-axis - see an example of voxels shape symmetry in Figure 3.4A. The XY shape symmetry value is the mean of these two values (the percentage of x-y symmetric voxels in their positions). To calculate the control symmetry, we considered the symmetry of the voxel's position and phase (Figure 3.4A). Thus, the XY control symmetry value is the percentage of x-y symmetric voxels in their positions with equal oscillation phases. Figure 3.4B shows two examples of robots with their shape and control symmetries calculated for the x-axis (X), y-axis (Y), and their mean value (XY).



Figure 3.4: Symmetry measurement. (A) Illustration example of voxels with shape and control symmetry in the y-axis. (B) Examples of robot's shape and control symmetry measures in the x-axis (X), y-axis (Y), and their mean value (XY).

There are three significant types of locomotion sequences: i. tumbled body and no significant trajectory (stands in the same place), ii. tilted body and curved trajectory, and iii. stable body and straight trajectory. The symmetry of the shape impacts the probability of having one of these locomotion sequences by changing the distribution of body weight. We hypothesized that the robots with the best direct locomotion ability must have a highly symmetric body shape. A robot with a low XY shape symmetry (XY shape symmetry < 0.5) will have a poor weight balance, leading it to a lousy locomotion performance (blue dotted line in Figure 3.5A). As XY shape symmetry increases (XY shape symmetry > 0.5), the locomotion performance increases and starts to saturate when the XY shape symmetry approaches 1. A body does not need to be 100% symmetry in the x and y-axis to have a good balance for locomotion. Values of XY shape symmetry larger than 0.5 allow bilateral symmetry in the body. Supporting our hypothesis, the results show that in the three

environments, the robots with top 20% fitness have their distribution shifted to higher values of XY shape symmetry (red areas in Figure 3.5B). The region of low shape symmetry (XY shape symmetry < 0.5) contains mostly robots from the smaller fitness layers (40-20% in light blue and 20-0% in dark blue areas in Figure 3.5B). Thus, bodies with low shape symmetry cannot acquire a locomotion performance as good as the ones with high shape symmetry.

Beyond the shape symmetry, the body's dynamic symmetry (measured by the XY control symmetry) will also impact the locomotion ability. We hypothesized that increasing the XY control symmetry impacts fitness positively as it describes the body synchronicity of movement (blue dotted line in Figure 3.5C). Nonetheless, locomotion in a direction requires a minimum instability in this same direction to generate the necessary forward displacement. The instability will be higher the more asymmetric the XY control (red dotted line in Figure 3.5C). Thus, we expect a break of total XY control symmetry to be a necessary condition for the robots with the top best 20% fitness (Figure 3.5C). Supporting this hypothesis, our results show that in the three environments, the distributions of the best robots (red in Figure 3.5D) have their peaks shifted to higher symmetry values (XY control symmetry > 0.6) but do not reach total symmetry (XY control symmetry = 1). In contrast, the 20-0% (dark blue) and 40-20% (light blue) fitness layers distributions occupy most of the [0,1] interval of possible XY control symmetry values. Thus, we see the requirement of XY control symmetry < 1 for optimizing locomotion.

Animals that use directed locomotion on the ground exhibit bilateral symmetry often, which biases the locomotion to a specific direction (in contrast to radial symmetry) (HoLLÓ, 2015). We asked whether the top best robots also have a preferred shape direction (bilateral symmetry). We classified as bilaterally symmetric the shapes and controls that are 100% symmetric in only one of the axis (X or Y) and as biradially symmetric the ones that are 100% symmetric both on the X and Y axis. We classified as "other" the bodies that did not fit into either of these two categories. Figure 3.5E shows the shape symmetry classification and Figure 3.5F shows the control symmetry classification of the robots from the 100-80% fitness layer. Bilateral symmetry is the most common type of shape and control symmetry between the robots with the best locomotion performance. Biradial symmetry, a symmetry found in corals (sessile animals) and hydras (SAVRIAMA and C. KLINGENBERG, 2011; WATANABE *et al.*, 2014), is a kind of shape symmetry present in a small portion of the top robots (Figure 3.5E).

We tested if our shape and control symmetry hypotheses are also robust to the other genotypes and robot sizes. Figure 3.6 shows that the best robots are shifted and restricted to higher shape and control symmetry values than the other layers. Thus, the bodies with



Figure 3.5: A highly symmetric shape and symmetry breaking in the dynamics are necessary for achieving higher displacements. (A) Illustration of the hypothesized impact of XY shape symmetry on the directed locomotion ability. A higher body weight balance prevents the body from falling or making a curved path. (B) In the results of the three environments, the robots with 20% better direct locomotion ability (100-80% fitness layer in red) typically have a shape symmetry higher than 0.5. The lower fitness layer contains a higher range of symmetry values. (C) Illustration of the hypothesized impact of XY control symmetry on the directed locomotion ability. The body synchronicity between its parts is higher with increased XY control symmetry. However, locomotion depends upon instability (break of symmetry) in the direction of the movement. Thus, the robots with top 20% performance (red) maximize synchronicity but necessarily keep a break of total control symmetry in the body. (D) In the results of the three environments, the robots with 20% better performance (red) have a peak shifted to higher values of symmetry and a break of total control symmetry (XY control symmetry<1). (E) The bilateral symmetry is the type of shape symmetry most frequent in the top robots (100-80% fitness layer). Biradial symmetry is also present. (F) The bilateral symmetry is also the most frequent type of control symmetry in the top robots (100-80% fitness layer). Biradial control symmetry is not present in this layer.

higher symmetry and a break of total symmetry in control emerge as necessary traits for



best performance in robots regardless of the genotypes and sizes.

Figure 3.6: The three experiments (6³ CPPN, 8³ CPPN, 4³ DE) confirm the results of 4³ CPPN that the best robots (100-80% fitness layer in red) typically are shifted to higher shape and control symmetry values compared to the other layers. Besides, in all the cases, there is a break of total symmetry in the control symmetry. Thus, the principles found are true even using different genotypes and robot sizes.

3.3 Shapes are specialized to their gravitational environment

The best robots in the three environments have similar modular and symmetry features (Figure 3.1 and Figure 3.5) - thus justifying calling these features gravity-invariant. Nevertheless, bodies submitted to different gravities might still require distinct features for their optimized locomotion. To test this requirement, we verified if a body shape optimized to one gravity value will keep its performance in another gravitational environment (Figure 3.7A). We selected the best 50 shapes (just voxel arrangement) of each environment and transferred them to the other two environments (Section 2.5). In the new environment, the robots could test different control patterns for their fixed shapes until finding the dynamics that maximize their displacement (Figure 3.7B). One possibility is that the shapes have



Figure 3.7: Robots from different gravitational environments require distinct features for good locomotion performance. (A) Will the best robots in water be the best when transferred to mars or earth? (B) Transference protocol. We optimized the control of the best 50 body shapes of each original environment in the new environments. In each new gravitational environment, the fixed shapes could test different ways of moving their bodies and keep the best. (C) Illustration of a hypothetical transference outcome in which the quality of transference (the ability of directed locomotion in the new environment) will depend on the gravitational difference between the new and original environments. (D) The transferred robots' average new environment performance (directed locomotion ability). Robots originally from water (blue) cannot acquire a performance as good as the best robots originally from mars (orange) and earth (green) in the mars and earth new environment. Robots from mars and earth have worse locomotion when transferred to water and cannot move as well as a robot originally from water.

specializations selected to work well in their original environments but not in the others. In this case, we expect that the transference quality will decrease with the increase of gravity difference between the original and the new environment (Figure 3.7C). Figure 3.7D shows that the robots originally from water (blue) when in other environments do not have a performance as good as the robots originally evolved in mars (orange) or on earth (green). Similarly, the robots from mars and earth do not perform as well in water as those that originally evolved in water. Thus, we conclude that the shapes have specializations to optimize locomotion in their specific gravitational environments.

3.3.1 Different gravity selects different body structures

The shape's lack of transference to other gravitational environments is due to the robot's shape traits specialization for their original environments. A natural question is

whether the robots in each environment have shared traits due to their specializations. For example, one crucial component of the robot's locomotion is the modules that touch the floor (Figure 3.8A). We posit that the relative size of the modules that touch the floor compared to the rest of the body has a different effect depending on the gravity. We found that the robot's feet proportion distribution is different for each environment (*ANOVA test with p < 0.01, Figure 3.8B). The robots that originated from a lower gravity tend to have proportionally heavier feet (modules that touch the ground) than robots that originated from higher gravities (Figure 3.8B). To check if the feet's proportion is related to the lack of transference between environments, we analyzed if there is a correlation between each individual's feet's proportion and its transference capability. We measured the transference capability as the difference in performance between the new and original environment. There is a negative correlation between the proportion of feet voxels and the robot's locomotion transference capability when the robots go to an environment with higher gravity, *i.e.*, water to mars (dark blue in Figure 3.8C), water to earth (light blue), and mars to earth (red). This result implies that lighter feet are usually better in higher gravity environments when compared to heavier feet.



Figure 3.8: The relative volume of the feet affects robot performance in higher gravitational environments transferences. (A) The voxels belonging to modules touching the ground during the robot's movement are called *feet voxels*. (B) The distribution of feet voxels proportion in the body differs between the environments (*p < 0.01, ANOVA) and tends to smaller values when gravity increases. (C) In the environmental transitions that gravity increases - water to mars (dark blue), water to earth (light blue), and mars to earth (red) - the robots with a small proportion of feet voxels better maintain their performance (smaller difference between the new and the original environment). Spearman correlation coefficients of r = -0.39 (water to mars), r = -0.43 (water to earth), and r = -0.32 (mars to earth), all with p < 1e-08.

Chapter 4

Discussion

...is not whether we are alone in the universe, but how common we should expect our cosmic companions to be and whether there is anything biologically meaningful we can say about them from our blinkered vantage point on Earth. — Rachell Powell, Contingency and Convergence: Toward a Cosmic Biology of Body and Mind

Directed locomotion on the ground is present in phylogenetically distant species. We used evolved robots to study which animal's shape features are necessary to maximize this ability and which could be different without disrupting locomotion capacity. We found that the number of modules should be small and sparsely connected. In addition, the body's shape should be highly symmetric, and the body control should exhibit symmetry breaking. Bilateral symmetry showed to be the most successful type of symmetry. We also found that different gravitational environments require different shape structures to optimize locomotion. Finally, we found that the feet's proportion in the body is related to how well the bodies adapt to a higher gravitational environment.

4.1 Morphological computation principles of directed locomotion on the ground

Biological systems carry out computations with their physical bodies to successfully interact with their environments - a concept called morphological computation (Hillel J. CHIEL and BEER, 1997; TYTELL *et al.*, 2011; HAUSER *et al.*, 2014; Y. S. ZHANG and Asif A GHAZ-ANFAR, 2018). In this work, we investigated the existence of morphological computation principles relevant to directed locomotion on the ground. We used a population analysis of

different synthetic organisms not restricted to the known biological solutions. Knowing the shape principles behind an organism's behavior is necessary to understand the coupling between shape, biomechanics, and nervous system in animals (or their counterpart in robots) that interacts with the environment producing behavior (Hillel J. CHIEL and BEER, 1997; H. J. CHIEL *et al.*, 2009; TYTELL *et al.*, 2011).

Biological systems have morphological modularity - a segmentation of the body related to its functional roles (WILLIAMS and NAGY, 2001; C. P. KLINGENBERG, 2008; LAROUCHE et al., 2018). The number of modules, the size, and the position are major features defining the types of locomotion of an animal (NEIL H. SHUBIN and MARCUS C. DAVIS, 2004). We defined the modules as connected body portions with little or no internal relative motion. The robot's number of modules represents the number of dynamical parts of an animal's body - the trunk structure and its number of appendages and limb segments. We found that the optimization of locomotion necessarily requires a small to an intermediate number of modules. A three-segmented limb structure, for example, is already sufficient to allow an organism to displace itself (RITZMANN et al., 2004). Indefinitely increasing the number of modules will saturate and possibly worsen their contribution to locomotion. The modules also need to be sparsely connected, a type of connectivity that generate extremities. This way, our results are consistent with what we observe in different animal species with directed locomotion capacity - the presence of appendages (extremities) and a relatively small number of limbs and limb segments - both usually smaller than ten (FISCHER and Reinhard BLICKHAN, 2006; BRUCE, 2021). This consistency is evidence that a small number of sparsely connected modules is a morphological computation principle for an organism's optimized locomotion.

Animals have different types of symmetry - some examples are asymmetry (demosponges), spherical (adult sponge), cylindrical (sponge and cnidarian larvae), and n-radial (adult echinoderms) and bilateral (bilaterian animals) (MANUEL, 2009). Our work shows that optimizing directed locomotion performance on an organism requires a high shape symmetry and a control (dynamic actuation) with a break of total symmetry. Specifically, bilateral symmetry was the most frequent type of symmetry among our top best robots. In animals, the bilateral symmetry type is present in more than 99% of the species (HOLLÓ, 2015). An argument for the presence of bilateral symmetry is its equal favoring of both sides of the body in rectilinear motion in water (where life originated in the presence of drag forces) and its facilitating action in maneuverability by rapid changes of direction (HOLLÓ and NOVÁK, 2012). Our results point out that shapes with bilateral symmetry are the best solution, even without maneuverability and the presence of drag forces. This type of symmetry establishes a preferential direction in the organism's body, which is a morphological computation contribution to directed locomotion. Furthermore, legged
locomotion requires a dynamic asymmetry (instability) in the direction of movement (HOLMES *et al.*, 2006). A biradial symmetric shape achieves this instability only if it has an asymmetrical control pattern in the axis of movement. Meanwhile, a bilateral symmetric shape acquires it by its shape asymmetry in the displacement axis. Thus, bilateral symmetry also simplifies and even enlarges the control effects on the body's locomotion by its asymmetry in the direction of movement.

We found morphological principles that are robust to different gravitational environments. However, an organism subject to different gravitational loads still needs to modify its limbs coordination to have efficient locomotion - examples are some vertebrate changes of locomotion in aquatic and terrestrial environments (GILLIS and BLOB, 2001) and human astronauts walking on the Moon compared to when on Earth (MINETTI, 2001). Beyond requiring different types of gait, gravity is an evolutionary force that influences the shape outcomes during an evolutionary process (RAYNER, 2003; MIRAS and EIBEN, 2019). We found that the robots have shape specializations to their gravitational environments as they cannot equally transfer to other environments, even being able to modify their movement coordination. Specifically, we found that a smaller feet's proportion in the body correlates with better adaptability in higher gravitational environments. A possible explanation for this effect is that robots with a smaller feet's proportion operate similarly to a Spring-Loaded Inverted Pendulum (SLIP) template (R. BLICKHAN and FULL, 1993; HOLMES et al., 2006). In the SLIP dynamics, the body center of mass (CM) is farthest from the ground and is propelled by a small foot connected to a longer leg, reducing friction effects and amplifying the CM horizontal impulse. On the other hand, robots with proportionally heavier feet result in more body friction and a CM closer to the ground. This way, they will have other types of dynamic propelling, like crawling, that are less suitable for higher gravitational loads.

4.2 Contingency of evolutionary outcomes

An animal's body has functions and needs beyond locomotion for its survival. The body results from an evolutionary process, defined by historically dependent selection factors and genetic heritage. In general, we cannot separate these factors. An interesting situation in which we can study the relevance of each factor is to study the non-functional and teratological outcomes that we observe in nature (ALBERCH, 1989). This way, we can understand the body's internal properties of genetic and developmental interactions that define the phenotypic space of possibilities. Another possible approach (used here) is to investigate how a functional cause - optimization of directed locomotion on the ground - externally defines the phenotypic space of shape possibilities. This approach

allows evaluating the contingency level of shape outcomes (POWELL and MARISCAL, 2015), impacting our expectations about the robustness of Earth's animal morphology inside and outside water, other planets' life forms, and robot applications outside Earth (RUDIN *et al.*, 2022).

Limb pattern formation - a decisive factor for locomotion - can be addressed by the study of gene expression during development (*i.e.*, Hox genes implications in the number of fingers and limb evolution (TABIN, 1992) and limb regression in whales and snakes (BEJDER and HALL, 2002)). Complementary, our work shows that a small to an intermediate number of modules should be a robust evolutionary outcome for organisms with directed locomotion on the ground. This result means that the current shape's modularity of animals (FISCHER and Reinhard BLICKHAN, 2006; LAROUCHE *et al.*, 2018; BRUCE, 2021) is probably not contingent on the unique Earth's life evolution and would consistently repeat in other planet's life or repetitions of the tape of life on Earth (POWELL, 2020). However, our results show that the shape's configuration is to have one leg in each opposite extreme of the anterior-posterior body axis and two others positioned bilaterally symmetrical in the transverse axis (see Figure 4.1). Our results point out that this limb configuration for a quadruped would be as good as the traditional one for directed locomotion on the ground with no obstacles.



Figure 4.1: Alternative leg configuration of a robot belonging to the best fitness layer (100-80%) of 4^3 CPPN experiment in mars.

The conditions that lead to the abrupt explosion of bilaterally symmetric animals and its evolutionary robustness (POWELL, 2020) are still open questions (BUDD and JENSEN, 2017; CHEN *et al.*, 2019; HEGER *et al.*, 2020). For example, internal transport and not directed locomotion could be the original force selecting for bilateral symmetry (FINNERTY, 2005). Thus, the symmetry outcomes of evolution we see today could have been different, including the absence of any type of symmetry. Contributing to these considerations, our study reinforces the thesis that bilateral symmetry is a necessary (law-like) pattern in animal evolution for efficient directed locomotion purposes (HOLLÓ, 2017). More than gene regulatory networks or physical forces (HOLLÓ, 2017), the function would be essential to explain the current

dominance of bilateral symmetry in animal species. In our work, without considering other body functions (such as the digestive system) that would naturally bias a body to bilaterality and not other types of symmetry (FINNERTY, 2005; YOSHIMURA and MOTOKAWA, 2008; MANUEL, 2009), bilateral symmetry showed to be the most robust outcome for bodies selected to directed locomotion.

4.3 Computationally replaying the tape of life

The biologist Stephen Jay Gould proposed a thought experiment about the contingency of natural evolution outcomes observed in Earth (POWELL, 2020). He hypothesizes that if we could replay the tape of life, there would be very different outcomes in each repetition. Widely present biological solutions (*i.e.*, two eyes) might not appear or be exceptions. The difficulty in testing the level of contingency in biological outcomes is that we do not have access to alternative evolutionary histories on Earth or other planets.

Here we propose that evolutionary physical simulations of robots can be a partial realization of Gould's thought experiment about replaying the tape of life. This approach allows the reproduction of N>1 evolutionary process and the study of animal bodies using embodied in silico organisms. With proper choices of the simulation environment, evolutionary algorithm, and encoding structures, it is possible to study the contingency level of a biological outcome given specific selection pressures. There are already evolutionary simulation studies in robots that analyze the effects of development (CORUCCI, Nick CHENEY, KRIEGMAN, et al., 2017), environment (MIRAS and EIBEN, 2019), material properties (Corucci, Nick Cheney, Giorgio-Serchi, et al., 2018), representation (Medvet et al., 2021) and control (Nicholas CHENEY et al., 2014) on morphologies and behavior. Environment's parameters as gravity - a constant variable on Earth that is difficult to test experimentally and affects life's evolutionary outcomes - can be tested in simulation studies (MOREY-HOLTON, 2003). The simulation consistency between our results with a different simulation study that also investigated the relationship of locomotion and symmetry (C. BONGARD and PAUL, 2000), the behavioral transference from in silico to in vivo organisms (KRIEGMAN et al., 2020), and other previous biologic studies using robots and simulations (MILLER et al., 2012; Auke J. IJSPEERT, 2014; AGUILAR et al., 2016) are evidence of the potential of approaching Gould's and other biological questions computationally. This way, we propose associating in silico experiments with biological questions and designs to approach Gould's thought experiment.

Part II

Theoretical and methodological considerations

Chapter 5

Theoretical considerations

A process cannot be understood by stopping it. Understanding must move with the flow of the process, must join it and flow with it. — Frank Herbert, Dune

5.1 Using function to discern between convergent (law candidates) and contingent outcomes

Animal features are context-dependent outcomes that are products of the historydependent evolutionary process of the Earth (GOMEZ-MARIN and Asif A. GHAZANFAR, 2019; POWELL, 2020). Based on this historicity and context-dependence, we can consider an extreme theoretical scenario where any replay of the tape of life would lead to radically different evolutionary outcomes from the one we know on Earth. POWELL and MARISCAL, 2015 defines this thesis as the radical contingency thesis (RCT). The RCT can be thought of as a proposal to consider the sensibility of Earth's macro-evolution outcomes for factors such as the Earth's initial conditions, life's internal constraints (by the specific phylogeny's path taken on Earth), and big and non-predictive events (like asteroids impacts). In Pow-ELL and MARISCAL, 2015, the authors introduce three dimensions that help to evaluate the robustness of evolutionary regularities when discussing pieces of evidence for the RCT.

Adding to this discussion, our results show that the function is an essential criterion that should also be considered when evaluating the robustness of evolutionary regularities. In Part I of this work, we found that selection pressure for a locomotion function is sufficient to produce a repetitive appearance of morphological traits, even using different genotype structures and environments. The morphological principles were present inside the diversity of functional shape solutions typical of the many-to-one mapping of form to function (WAINWRIGHT, 2005) - thus, we called it convergence. We performed experiments that always selected for a higher average speed but varied on the stochastic iterations, gravitational environment, organism size, and genotype structure. The existence of convergent features in these different scenarios is an example that between genetic, developmental, and environmental explanations (VOLKMANN and BALUŠKA, 2006; LALAND, ULLER, et al., 2015), the function is also essential in driving the outcomes. Based on that, a requisite to evaluate the convergence of evolutionary iterations should be to consider if all of the compared outcomes have the same functions, a teleological top-down approach (PEZZULO and LEVIN, 2016). There is no reason to expect that some outcome in two types of life (whether on Earth or another planet) should converge if their functional roles are different. Neither should we explain by contingency the lack of convergence of outcomes with different functional roles. Outcomes with different functions are, exactly by their functional roles, different without the need to use historical contingency explanations to justify their divergence. Thus, we postulate the following situations when comparing independently generated outcomes:

- same functional role (True) & same feature/solution (True) \rightarrow convergence
- same functional role (True) & same feature/solution (False) \rightarrow contingency
- same functional role (False) & same feature/solution (True) \rightarrow contingency
- same functional role (False) & same feature/solution (False) \rightarrow no significance

A critical last consideration is that function is *a posteriori* attribution given by us, humans, when studying or body or other animals (MACDOUGALL-SHACKLETON, 2011). An evolutionary algorithm is programmed by a human and thus will have a fitness-selection artificial definition based on criteria that depend upon our Umwelt and scientific models (TRIANNI, 2014).

5.2 Bridging the gaps between different evolutionary scales - a framework proposal

Based on the algorithm design used in Part I of this work and on the results it allowed to obtain, here we propose a framework that allows evaluating the effects on the evolutionary outcomes given the different ways of integrating biological scales. Animals are complex biological systems that evolved by the conjunction of the different spatial and temporal processes (molecular and cellular, physiological, developmental, behavioral, ecological, and species evolution on Earth) (LEWONTIN, 1970). As humans studying other biological systems, we have limitations and cannot deal with all the biological scales and variables simultaneously. Thus, simplifying the problem and reducing the system complexity to some aspects of interest is necessary. For that, researchers usually focus on one or a few of the processes listed above, as we need to confine the research to well-defined spatial and temporal scales (GOMEZ-MARIN and Asif A. GHAZANFAR, 2019). However, biological systems exist by integrating all the scales. So, after the reduction, the hypothesis and results of one scale need to be connected with the other. This union requires the integration and organization of diverse biological knowledge in a sufficient scope to explain both the specific biological phenomena and the whole (PEZZULO and LEVIN, 2016). This crucial and difficult task of biological research led to definitions of different levels of analysis and ways of viewing its integration (MAYR, 1961; BOLHUIS, 2005; MCNAMARA and HOUSTON, 2009; LALAND, STERELNY, *et al.*, 2011; MACDOUGALL-SHACKLETON, 2011).

Different theoretical frameworks, reductionist and non-reductionist, guide the understanding of the biological scales and their relationships that result in the evolution and development of animals. Based on some of them, - an autopoietic framework (RAIMONDI, 2021), the extended evolutionary synthesis proposal (LALAND, ULLER, *et al.*, 2015), and the developmental systems theory (GRIFFITHS and TABERY, 2013) - Figure 5.1A and Figure 5.1B show a possible representation of an evolutionary process structure. This representation is a proposal to make explicit the theoretical assumptions made in the evolutionary algorithm designs. Thus, we have the possibility of simulating the integration of different scales and testing different theoretical hypotheses about the scales' mutual influences. With these two ingredients, we have a way of testing the effects of different hypotheses on evolution outcomes and exploring alternative types of life not covered in Earth's evolutionary history.

The representation of the evolutionary process proposed here is a sequence (generations) of groups of life cycles (population) (Figure 5.1A). Each life-cycle looping is composed of four fundamental structures (selection, genotype, phenotype development, and behavior) that both create and happen within the unit organism-environment (Figure 5.1B). The structures are inside a block with dashed lines to make explicit that, in principle, they can change and be changed by the organism-environment interaction (QUELLER and STRASSMANN, 2009). The arrows connecting the structures are also bidirectionally to make explicit the possibility of modeling the reciprocal causation and conditional dependence between them (LALAND, STERELNY, *et al.*, 2011). The theoretical relationships presented on Figure 5.1B are just a basin possibility. This base can (and should) be modified in different implementations of evolutionary algorithm designs. With each implementation, it should be possible to computationally test the different hypotheses about causation and



Figure 5.1: The ingredients of a methodological framework to computationally test the effects of the different evolutionary hypotheses.

the mutual influence of the structures involved on the evolution of some trait.

In the Part I of this work, we used the specific design represented on Figure 5.1C. It uses a fixed selection criterion, the average speed, to select the individuals' genotypes that would constitute the next generation of parents. The genotype structures are fixed and static (no influence of the organism-environment interaction). After the parent mutation, a unidirectional map from the genotype creates a fixed phenotype for each new individual. The behaviors, the different ways of locomotion on the ground, emerge with the phenotype interaction with the environment. The fitness is the average speed of this behavior, and then the cycle repeats. Figure 5.1D shows another design example in which the organism's phenotype develops in a dynamic environment. For example, an aquatic environment changes to a terrestrial one while the organism develops and tries to adapt to it. This design could be useful in studying how the need to adapt to different environments affects morphological solutions (VERMEIJ and DUDLEY, 2000; GILLIS and BLOB, 2001; JOACHIMCZAK, SUZUKI, et al., 2016; CORUCCI, Nick CHENEY, GIORGIO-SERCHI, et al., 2018). Another design proposition is shown in Figure 5.1E. In this case, the selection criteria changes with the behavior, which also changes with the phenotype development. An example would be organisms that increase in body size during development - with variated ways of distributing this increase in the body depending on its developmental process. This increase could also depend on the organism's displacement - if the intent is to simulate a proxy for finding food and spending energy. The selection criteria could be a function of the organism's displacement and size change. This design (or a similar one) could be used to investigate, for example, how the need to displace itself with a changeable body size affects the morphological solutions, locomotion strategies, and developmental paths (CORUCCI, Nick CHENEY, KRIEGMAN, *et al.*, 2017).

This framework proposal aims to simultaneously bridge the gaps between different evolutionary scales in one experiment (BLACKISTON, D. *et al.*, 2022). We gave some examples, and there are already a lot of different approaches and designs using evolutionary algorithms that can be a source of inspiration (TRIANNI, 2014). The design will depend on the research question. Beyond that, as it is a simulation study based on tremendous simplifications, a researcher using it should be careful about the actual biological implications that one can assume from it (B. WEBB, 2009; BONGARD and LEVIN, 2021). Therefore, basing the algorithm design on biological references and theories and, when possible, associating it with experimental biology is the way to make it biologically significant (GOMEZ-MARIN and Y. ZHANG, 2022). This way, it is possible to address questions about the robustness of evolutionary outcomes and how evolution's different elements and scales influence each other and create different possibilities for life.

5.3 Animals & Animats - embodied organisms

Animat is the name given to autonomous robots or simulations of *in silico* organisms for which we can attribute behaviors (MEYER and WILSON, 1991). At the end of the 80s and the beginning of the 90s, researchers in fields such as ethology, ecology, neurobiology, robotics, cybernetics, and artificial intelligence gathered around this concept in an attempt to advance the understanding of animal behavior, intelligence, and robot's applications (MEYER and WILSON, 1991; BRAND *et al.*, 1995; STRICKLIN *et al.*, 1995; WATTS, 1998). Since its beginning, animat research has used evolutionary algorithms (TRIANNI, 2014) and discussed the need (and the role) of assuming that the animats have a body when modeling animals' behavior (*i.e.*, situatedness, embodiment, morphological computation) (MEYER and WILSON, 1991; BRAND *et al.*, 1995; DEAN, 1998; MITRI *et al.*, 2013; GOMEZ-MARIN and Asif A. GHAZANFAR, 2019). The recent advances in soft robots have now opened the possibility of more accurate simulation and construction of muscles and other animals' soft tissues (CRADDOCK *et al.*, 2022). The original animat proposal of modeling animals and their behaviors can now properly include its soft structures and the nonlinear effects of soft bodies on morphological computation (H. J. CHIEL *et al.*, 2009; JOACHIMCZAK and

WRÓBEL, 2012).

However, the actual contributions of animat models to biology have been questioned in cases where there is no sufficient biological grounding or connection to real animals (B. WEBB, 2009). Animals and animats have significant differences (BONGARD and LEVIN, 2021). In this work, using evolutionary simulation of animats is not because of its easy feasibility compared to physical robots or animal studies. Instead, it is the theoretical necessity of having other samples than our N=1 Earth's evolution that justifies its use to study the life's solutions known to us and its other possibilities (POWELL, 2020; BLACKISTON, D. *et al.*, 2022). The evolutionary simulation of embodied soft animats is a solution (maybe the only one for now) to approach the contingency of animal morphological outcomes given some function by comparing truly independent samples.

Chapter 6

Methodological considerations

Whether we call them robots or organisms, and whether or not they become chimeras or cyborgs, designing and optimizing such systems is not only strange but extremely non-intuitive. (...) Computational tools (old and new) are poised to help. Sam Kriegman

6.1 Scale and design space constraints

The design space (or workspace) is the lattice defined for a genotype-to-phenotype mapping construction of the robot's phenotype. In the experiment described in Part I of this work, we did simulations using cubic workspaces $(4^3, 6^3, and 8^3)$ with the constraint of having at least 25% of the workspace occupied. The phenotype construction also has the constraint of producing a unique and continuous body. If the genotype maps two separated bodies inside the design space, the smallest one is pruned. As locomotion is a directional function, we expect that the choice of a non-cubic workspace can strongly influence the type of morphologies and behaviors of robots pressured for our locomotion function. For example, if we used an (10, 10, 2) design space, we would probably bias all the robots to snake-like morphologies with crawling behaviors; if we used an (3, 3, 10) design space, we would bias the search for long legs solutions. Our choice of a cubic design space was to not bias the bodies to any specific axis. However, this choice is still biased because it facilitates the creation of cubic and not cylindrical or other types of bodies.

Before the experiment described in Part I, we did an extensive search of smaller cubic design spaces (2^3 and 3^3) (BIAZZI *et al.*, 2021). After that, we considered that the 4^3 was the minimal design space to start analyzing appendices structures - trunk and appendices

structures are easy to separate from this dimension. We also checked that using workspaces with even dimension sizes did not prevent the creation of robots with odd dimensions - there are both cases of even and odd body size lengths between the best robots of 4^3 , 6^3 , and 8^3 workspaces. We consider that simulations of robots with more degrees of freedom ($\geq 10^3$) and with different units of voxel size (we used 1cm as the size unit of the voxels lateral) would be relevant to ensure the robustness of our results in different scales.

6.2 Considerations on behavior simulation time

An important aspect of evolutionary simulations is the appropriate choice of behavior simulation time. This choice will depend on the function - the simulation time has to be sufficient to measure the function of interest - otherwise, the fitness meaning can be different from the expected. For example, in our experiment (Part I), we noted that using 10*s* as simulation time was insufficient to distinguish between straight from curved trajectories. However, the behavior simulation time is one of the biggest bottlenecks of evolutionary simulations, as it cannot be parallelized and significantly increases with the robot's scales. Thus, it is also essential to avoid unnecessarily long simulation intervals. We tested that 30*s* was a sufficient time interval to characterize the robot's directed locomotion behavior that, at the same time, did not extensively increase the total simulation time. An interesting aspect we noted in the simulation videos was that the robots with more degrees of freedom (from the 8³ workspace) sometimes had gaits with longer duration. This difference in gait duration implies that it can be necessary to use behavior simulation intervals $\geq 30s$ when simulating robots of $\geq 10^3$ workspace.

6.3 Considerations on evolutionary simulation time

In all the experiments of this work, we simulated the evolution of 1500 generations. For the robots of the 4³ workspace, there is a significant distance between the fitness (average speed) of the top robots (100% percentile in red) and the second best group (75% percentile in green) in the 1500 generation (Figure 6.1). This difference indicates sufficient simulation time for finding and optimizing the best solutions. However, the space of possibilities is larger for the other design spaces (6³ and 8³). Thus, we think it could still be beneficial to evolve the robots for more than 1500 generations (especially in the 8³ case). We can observe in Figure 6.1 that for 6³ and 8³ design spaces, the difference between the 100% percentile and 75% percentile is small, especially in the 8³. This small difference indicates that the search still has the potential to find more specialized solutions. Using

1500 generations was sufficient to check if the principles of the 4³ workspace also hold in larger dimensional-sized robots. However, we expect that the patterns found for the principles would be even more evident if we continued to simulate more generations, as probably more specialized solutions would appear. For other types of analyzes in the 6³, 8³, and \geq 8³ workspaces, we think that it could be necessary to simulate more than 1500 generations to ensure a robust search of the space.



Figure 6.1: Evolution of average speed value in the three workspace sizes.

6.4 Diversity in the offspring population

After some preliminary simulation tests, we noticed we were using a CPPN genotype encoding with a phenotype map that tended to create mostly fully cubic phenotypes. The morphological outputs were usually cubic phenotypes subtly carved, so there was no actual shape diversity inside the population. The problem was that the mutations did not create a significant difference in the phenotype output. This problem happened because the genotype to phenotype mapping, in most cases of the genotype outputs, created a complete cubic phenotype. A slight modification in the genotype to phenotype mapping made it less easy to create a fully cubic phenotype. Besides that, we increased the impact of mutations on shape variability inside the population using the diversity filter explained in Section 2.4.2. When applied, the filter ensured a shape diversity in the offspring group in that specific generation. This event is noteworthy because it shows how the genotype and its mapping to the phenotype can strongly bias (and disturb) the search space of possibilities of an evolutionary algorithm. The mapping can generate preferences not predicted by the programmer that will strongly impact the algorithm results. A solution for it is to ensure, before the actual experiments, that the algorithm can quickly generate the kind of diversity that the question requires.





Figure 6.2: The caricature representation keeps a significant percentage of the original robot's fitness. This result is approximately robust even when using different parameters in the clustering algorithm.

As described in Section 2.6.1, we clustered the voxels inside the robots to obtain their modularity. To check if our choice of algorithm and parameters was reasonable, we evaluated the difference in fitness between the original robots and their clustered caricatures. In a caricature, each voxel had its original individual phase offset substituted by the phase offset of the cluster it belongs (the phase offset of the cluster is the mean phase offset of its voxels). As the modularity measurement depends on the caricatures, its significance depends that the caricature's fitness is not very different from the original fitness. So, after the clustering, we created caricatures and simulated them in the same conditions as the original robot to calculate its average speed value. Figure 6.2 shows the ratio (in %) between the caricature and the original robot fitness (average speed) for the three gravitational environments of workspace 4^3 . In the x-axis, there is a sweep of the parameter values (see *eps* and *eps*_{po} in Section 2.6.1). We see that the mean of the caricatures percentage of the original fitness is higher than 70% for all the parameter values. In some cases, the similarity between the fitness is around 100%. The cases bigger than 100% are the ones where the original fitness was minimal and the caricature got better than the original. This result gave us the confidence to use our clustering module's measurement as caricature representation still significantly keeps the fitness of the robot.

6.6 Body material stiffness

As explained in Section 2.2.1, we noticed that for each gravitational environment, there was a different value for the voxel's stiffness that allowed the robots to acquire the best fitness, independently of the size. For the water robots, the best stiffness value was 5e5 Pa, and for the mars and earth robots, the best stiffness was 5e7 Pa. In Figure 6.3 we can see that for robots from water of 4³ and 8³ sizes, the best fitness (average speed) are obtained first with 5e5 Pa and second with 5e4 Pa as the voxel's stiffness. The worst cases are the robots with 5e7 Pa stiffness. Observing some simulation videos, we see that the robots with 5e7 Pa seem to be too strict and cannot acquire a body undulation sufficient to move. In mars and earth, the best robots need to have a stiffness value of 5e7 Pa. The ones with 5e4 and 5e5 Pa collapse in themselves because robots made of voxels with these values do not have enough strength to resist their body weight in these higher gravitational environments. It would be interesting to map for more values of gravity which is the best stiffness value and to check how smooth is the relationship between body weight and stiffness. Another interesting experiment would be to allow different values of voxel's stiffness inside the same robot. There would probably be body locations less robust to a change of stiffness (such as the leg) and others in which small stiffness values could be beneficial (as in the superior part of the trunk).



Figure 6.3: Average speed (fitness) distribution by voxels stiffness. In water, the best stiffness is 5e5 Pa, regardless of size. In mars and earth, the best stiffness is 5e7 Pa.

Chapter 7

What is still lacking?

In a forbidden recess of the cave, there's a footprint of an eightyear-old boy next to the footprint of a wolf. Did a hungry wolf stalk the boy? Or did they walk together as friends? Or were their tracks made thousands of years apart? We'll never know. Werner Herzog, Cave of Forgotten Dreams

7.1 What happens when the locomotion function becomes more complex?

A natural question following this work is if the principles found here will also keep accurate in an evolutionary process that selects for more complex forms of locomotion. For example, we could add obstacles, ground inclination, holes on the ground, and different types of ground material. We also could evaluate the shape outcomes of the evolutionary process with other forms of locomotion such as swimming and flying. Based on the agreement between what we observe in nature, our results, and some theoretical arguments (HOLLÓ and NOVÁK, 2012), we expect that bilateral symmetry and intermediate modularity sparsely connected should persist as the better solutions also in these other tasks.

7.2 Finding different species by clustering between organisms

Besides clustering within organisms, another possibility is to cluster between organisms. This clustering could be a way of grouping the organisms into species, analyzing the degree of morphological modification during a lineage evolution, or quantifying how much diversity a specific evolutionary design generates (MEDVET *et al.*, 2021). It could also be used to associate the types of phenotypic change between generations that result in the most significant changes in fitness. For example, we expect that the fitness will be approximately robust to changes in the dorsal part of the body. However, changes in the ventral part of the body have a higher probability of significantly impacting the organism's locomotion ability. Thus, having an organism classification could help to understand how the types of organism change with the increase of fitness during evolution. Besides, it could help to classify the diversity of possible solutions in the expected many-to-one mapping of form to function (WAINWRIGHT, 2005).

7.3 Analysis of convergence in different evolutionary scales

In this work, we measured the body shape and dynamic convergence given a constant selection pressure on a simple locomotion function of the organism. The pressure was indifferent to the types of bodies that were explored in the evolutionary process. This indifference was the reason that allowed us to look for convergent features in the sample of morphologies. However, there are other scales of the organisms in which the selection pressure is also indifferent during the evolutionary process. Thus, it is also possible to look for convergent principles in these other scales (genotype, behavior, and the lineages sequences). We will briefly describe other questions and analysis possibilities in each one.

One of the genotype encoding used in the experiments described in this work was the CPPNs (STANLEY, 2007). This genotype structure creates a network that processes input and gives as the output the information used to construct the phenotype. The functions used in the network's nodes and the structure and weights of the connections will define the output information used to construct the phenotype. Thus, there is the possibility that when selecting the function, the evolutionary algorithm will select classes of genotype structure. An analysis of the genotype features and organizational structure can reveal convergent features in genotype related to the organism's fitness on the locomotion function.

When selecting the function, we are not specifying the types of behavior that will compete for accomplishing it. For example, our robots can have any type of locomotion strategy, such as jumping, crawling, and running on legs in different gaits. There is the possibility that one of these strategies (behavior) could be consistently better than the others. An analysis and classification of each robot's behavior could reveal a convergent behavior given a locomotion selection pressure, even using different morphological solutions.

Our robots have history - they are a product of a specific lineage succession and carry a specific exploration path. There is the possibility that there is a class of exploration paths better than the others and that fitness success will depend on the type of path taken in the organism's exploration. An analysis of the paths can reveal if there is convergence on the exploration paths associated with the best fitness.

If we found principles (convergent features) in these other scales of evolution, we can ask about the fitness predictability of each one of them - and compare if some of them are more predictive of fitness than the others. This measurement could be a possible way of assessing how much information each scale of the evolutionary process (genotype, phenotype, behavior, lineages) has about the function. For example, based on a traditional biologic view, we could expect that the genotype is a major force defining the function, as the other scales would be considered just a consequence of it (MAYR, 1961). On the other hand, based on the functional morphology paradigm, one could predict that the phenotype would be indeed the better predictive of fitness (WAINWRIGHT, PETER C, 1994; GATZ, 1979; VIOLLE *et al.*, 2007; SOBRAL, 2021) - a testable hypothesis using the framework presented here.

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