A 3-D biomechanical model of the salamander

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Abstract. This article describes a 3D biomechanical simulation of a salamander to be used in experiments in computational neuroethology. The physically-based simulation represents the salamander as an articulated body, actuated by muscles simulated as springs and dampers, in interaction with a simple environment. The aim of the simulation is to investigate the neural circuits underlying the aquatic and terrestrial locomotion of the real salamander, as well as to serve as test bed for investigating vertebrate sensorimotor coordination *in silico*.

1 Computational neuroethology

This article describes the design of a 3D biomechanical model for experiments in *computational neuroethology* [1, 2], a field which studies how behaviors of an autonomous agent (a simulated animal or a robot) arise from neural circuits. A central aspect of computational neuroethology is that it integrates the simulated central nervous system into a body and an environment, and that it investigates behavior as the result of a *sensing-acting loop* within an environment.

Several experiments in computational neuroethology inspired by simpler animals have recently been carried out. Insect locomotion [1, 3, 4], cricket phonotaxis [5], and visual systems of fly [6, 7] have, for instance, been investigated using simulation and/or robots. Vertebrates have also inspired computational models such as Rana computatrix [8, 9, 10], lamprey swimming [11], Artificial Fishes [12], and models of classical conditioning [13].

The interesting features of such computational models are that: 1) they allow hypotheses on central nervous systems to be tested *in silico* within a complete sensing-acting loop, leading to a better understanding of the dynamics and functioning of nervous systems embedded into a body in interaction with the environment, 2) they can potentially give new ideas for neurobiological experiments and measurements, and 3) they provide inspiration for control algorithms which could be useful to other domains such as robotics. In addition, these neuroethological experiments in silico possess all the positive aspects of a computational approach: experiments are reproducible, all parameters of the model are controlled, neural activities can be accurately measured at all levels and simultaneously in all places, and the effect on behavior of altering parameters can readily be investigated (e.g. lesion studies on the real animal can be reproduced).

Computational neuroethology has therefore the potential to bring a significant contribution to neurobiology and neuroethology.

Following these experiments, the aim of our work is to develop a comprehensive computational model of a salamander, with a special emphasis on the physical realism of its body. We are, in particular, interested in the locomotor circuitry underlying the typical locomotion gaits of the salamander. This article describes a 3D biomechanical simulation of the salamander in which potential neural controllers for locomotion will be embedded. This work follows initial experiments in which biologically plausible neural circuits were developed using evolutionary algorithms for controlling the locomotion of a 2D salamander [14, 15, 16]. Although a brief summary of that work is given, this paper focuses on the design of the new 3D biomechanical simulation and presents some preliminary results of locomotion control using algorithmic (rather than neural) controllers.

2 Salamander locomotion

The salamander, an amphibian, is capable of both aquatic and terrestrial locomotion. It swims using an anguiliform swimming gait in which a traveling undulation of the body is propagated from head to tail. On ground, it switches to a trotting gait in which the body makes an S-shaped standing wave coordinated with the movements of the limbs. EMG recordings have shown that two different motor programs correspond to these different gaits, with a traveling wave of neural activity for swimming and a standing wave for trotting [17, 18, 19, 20]. The locomotor circuitry underlying these gaits has, however, not yet been decoded.

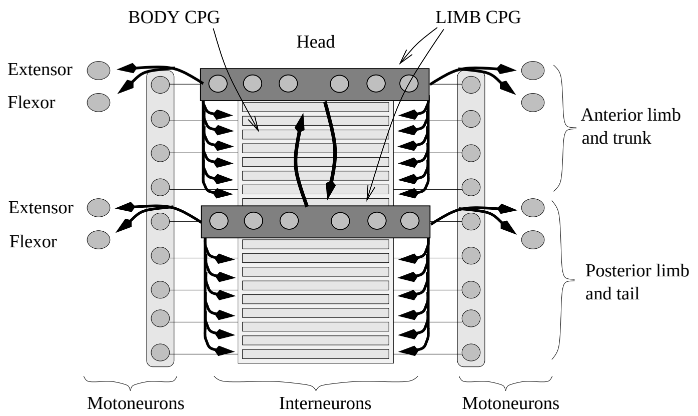

Fig. 1. Structure of the hypothesized salamander locomotor central pattern generator (see [14, 15, 16]). The circuit is based on a lamprey-like body CPG, extended by a limb CPG which unilaterally projects to the body CPG.

In [14, 15, 16], we developed using evolutionary algorithms a potential neural controller for salamander locomotion which was based on a lamprey-like swimming central pattern generator (similarly to what has been hypothesized by neurobiologists [21, 20], Figure 1). When connected to a 2D biomechanical simulation of the salamander, the model, simulated as a leaky-integrator neural network, was capable of exhibiting the typical swimming and trotting gaits observed in the real animal. It produced, in particular, a motoneuronal activity very similar to the EMG recordings reported in [17, 20]. Interestingly, by simply varying the level of tonic input applied to different parts of the locomotor circuitry, the speed and the direction of motion, as well as the type of gait (swimming or trotting), could be modulated.

3 Three-dimensional biomechanical simulation

The new simulated salamander is composed of 18 rigid links, 10 for the body (the trunk and the tail) and 2 for each limb (Figure 2). The links of the trunk and tail are connected by one degree-of-freedom (DOF) hinge-joints, limbs are attached to the pelvis by two DOFs double-hinge joints, and knee-joints have one DOF. Each DOF is actuated by a pair of opposed muscles simulated as springs and dampers (see below). The aim is not to reproduce accurately one specific species of salamander and all its biomechanical properties, but to make an "average" model of salamander which satisfies general characteristics of salamanders such as the range of speeds at which they can locomote. The limb geometry is based on [19].

The acceleration of each link i depends on the torques due to the muscles T, the forces exerted by the environment F_{env}, and the inner forces due to the constraints F_{in}:

$$m_i\ddot{x}_i = F_{env,i,x} + \sum F_{in,i,x} \tag{1}$$

$$m_i\ddot{y}_i = F_{env,i,y} + \sum F_{in,i,y} \tag{2}$$

$$I_i\ddot{\varphi}_i = \sum T_i - \sum F_{in,i,x}\frac{l_i}{2}\sin\varphi_i + \sum F_{in,i,y}\frac{l_i}{2}\cos\varphi_i \tag{3}$$

where m_i and I_i are the mass and the moment of inertia of a link, x_i and y_i are the position of the middle of the link and φ_i is its angle. Table 1 gives the masses and moments of inertia of the different links.

These dynamics equations are solved using MathEngine's Fastdynamics which computes the internal forces keeping the links connected, as well as the forces due to contacts, while the external forces such as the muscles torques and the forces due to the water are given by the user.

Muscle torques A muscle is simulated as a combination of spring and damper. The torques exterted on each joint is determined by a pair of opposed flexor and extensor muscles. These muscles can be contracted by input signals from motoneurons, which increase their spring constant, and therefore reduce their resting length. The torque acting at a particular joint is therefore determined

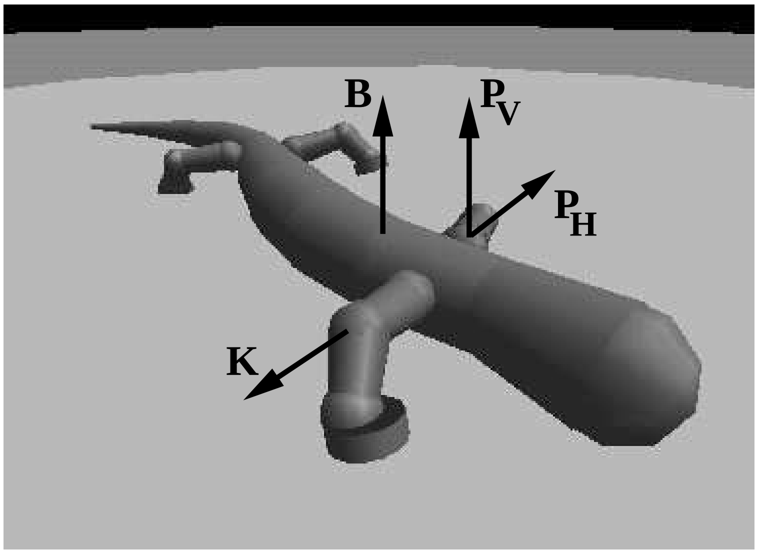

Fig. 2. Biomechanical simulation. The body is composed of 18 rigid links. Body (trunk and tail) links are connected by one-DOF hinge-joints, with vector B as axis of rotation. Limbs are attached to the body by two-DOF joints with one vertical axis of rotation P_V and one horizontal P_H. Finally, knee joints have one DOF and they rotate around axis K.

by the motoneuron activities (M_f and M_e) of the opposed flexor and extensor muscles:

$$T = \alpha(M_f - M_e) + \beta(M_f + M_e + \gamma)\Delta\varphi + \delta\Delta\dot{\varphi} \tag{4}$$

where $\Delta\varphi$ is the difference between the actual angle of the joint and the default angle. The different coefficients α, β, γ, and δ determine, respectively, the gain, the stiffness gain, the tonic stiffness, and the damping coefficient of the muscles. These values vary slightly depending on the type of joints (Table 2).

Forces due to the environment The forces linked with terrestrial locomotion are contact and friction forces. These forces are handled by the Fastdynamics software and are applied to links of the tail and the trunk, as well as to the feet, as soon as these links enter in contact with the (flat) ground. Friction coefficients of 0.8 and 0.1 are used, respectively, for the feet contacts and the body (tail and trunk) contacts. Note that during trotting, the body of the salamander is not supported by the limbs but slides on the ground.

In water, similarly to [11], it is assumed that the speed of the water relative to the body is sufficiently high for the forces exerted by the water to be mainly inertial forces (high Reynolds number). It is also assumed that the water is stationary and that the parallel and perpendicular components of that force on each link can be calculated separately. The components of the force can therefore

Table 1. Parameters for the mechanical simulation. B_i stands for the body links with B1 being the head link, and L1 and L2 stand for the upper and lower part of a limb, respectively. Fore- and hindlimbs are identical.

Link	l_i [mm]	w_i [mm]	m_i [g]	$I_\perp$ [g mm^2]	$I_\parallel$ [g mm^2]	$\lambda_\perp$ [Ns^2/m^2]	$\lambda_\parallel$ [Ns^2/m^2]
B1	30	30	17.7	2319	1988	0.38	0.3
B2	30	25	14.7	1679	1150	0.38	0.2
B3	30	30	17.7	2319	1988	0.38	0.1
B4	30	30	17.7	2319	1988	0.38	0.0
B5	30	30	17.7	2319	1988	0.38	0.0
B6	30	22	13.0	1364	784	0.38	0.0
B7	30	20	11.8	1178	589	0.38	0.0
B8	30	16	9.4	857	301	0.38	0.0
B9	30	10	5.9	478	74	0.38	0.0
B10	30	5	2.9	225	9	0.38	0.0
L1	25	10	2.0	62	20	0.30	0.1
L2	15	10	1.2	29	15	0.30	0.1

Table 2. Muscle parameters.

	α [N mm]	β [N mm]	γ	δ [N mm ms]
Body joint	0.01	0.0015	10.0	0.00010
Pelvis joints	0.01	0.0020	5.0	0.00010
Knee joint	0.01	0.0020	5.0	0.00002

be calculated as: $F_{env\parallel} = \lambda_\parallel v_\parallel^2$ and $F_{env\perp} = \lambda_\perp v_\perp^2$ where $v_\parallel$ and $v_\perp$ are the components of the speed of the link relative to the water and $\lambda_\parallel = \frac{1}{2} C_\parallel S \rho$ and $\lambda_\perp = \frac{1}{2} C_\perp S \rho$ are coefficients which depend on the density of the fluid ρ, the area perpendicular to the movement S and the drag coefficient C dependent on the shape of the link (here $C_\perp$=1, and $C_\parallel$=0 for all links except those close to the head. See Table 1).

The equations for the mechanical simulation are solved with the fourth order Runge-Kutta method with a fixed time step of 1 ms. The simulation is written in C, within the Fastdynamics framework. The OpenGL library is used for graphics.

4 Control of locomotion

In this article, locomotion of the simulated salamander is investigated using simple algorithmic controllers rather than the neural networks developed in [15, 16] which have yet to be extended to control the new DOFs of the articulated limbs.

The outputs of the motoneurons connected to the muscles are computed as simple sinusoidal functions. For the body (trunk and tail) muscles:

$$M_l(t,j) = \text{Max}\{\ \alpha \sin(\omega t - \lambda_j), \quad 0.0\ \} \tag{5}$$
$$M_r(t,j) = \text{Max}\{\ \alpha \sin(\pi + \omega t - \lambda_j), \quad 0.0\ \} \tag{6}$$

where $M_l(t,j)$ and $M_r(t,j)$ are, respectively, the outputs of left and right motoneurons for joint j at time t ($j \in [1,9]$, with $j = 1$ being the head joint). The maximal amplitude of the signal is given by α. ω and λ_j correspond to the frequency of oscillation and the phase of joint j, respectively.

Similarly for the limb joints:

$$M_e(t,d) = \text{Max}\{\ \beta_d \sin(\omega t - \phi_d), \quad 0.0\ \} \tag{7}$$
$$M_f(t,d) = \text{Max}\{\ \beta_d \sin(\pi + \omega t - \phi_d), \quad 0.0\ \} \tag{8}$$

where $M_e(t,d)$ and $M_f(t,d)$ are, respectively, the outputs of flexor and extensor motoneurons for the DOF d at time t. As mentioned earlier, each limb has three DOFs, two at the pelvis and one at the knee, with d=1 being the DOF around the vertical axis in the pelvis, d=2 the DOF around the horizontal axis in the pelvis, and d=3 the DOF of the knee. Note that, by definition, all joints oscillate at the same frequency ω and that the signals sent to opposed muscles (either the left-right muscles in the body or the flexor-extensor muscles in the limbs) are out of phase.

5 Results

Swimming gait The swimming gait is produced by a wave of neural activity traveling from head to tail along the body. Similarly to what has been observed in the real salamander [17, 20], we define the phase between consecutive links such that the body makes a complete wave, with a constant phase lag along the spinal cord: $\lambda_j = j \cdot 2\pi/9$ (i.e. the first and last body joints are in phase). During swimming the limbs are kept against the body through the contraction of the horizontal flexor at the pelvis and the flexor of the knee ($M_e(t,1)$=0.0, $M_f(t,1)$=0.9, $M_e(t,2)$=0.0, $M_f(t,1)$=0.0, and $M_e(t,3)$=0.0, $M_f(t,3)$=0.6).

Figure 3 (top) illustrates a swimming gait with 4Hz oscillations. The neural wave is transformed into a mechanical wave which propels the salamander forward. By keeping the limbs against the body, drag is reduced. The resulting movements are particularly realistic and life-like. The speed of swimming can be varied, and increased, for instance, by increasing either the amplitude of the signals sent to the muscles (α) or the frequency of the oscillations (ω). By simply giving some asymmetry of signal amplitude between left and right sides, turning can also be induced.

Trotting gait On ground the salamander uses a trotting gait in which all joints in the trunk are in synchrony, λ_j=0 for j=2,3,4,5, while being out of phase compared to the joints in the tail, λ_j=π for j=6,7,8,9. The joint of the head

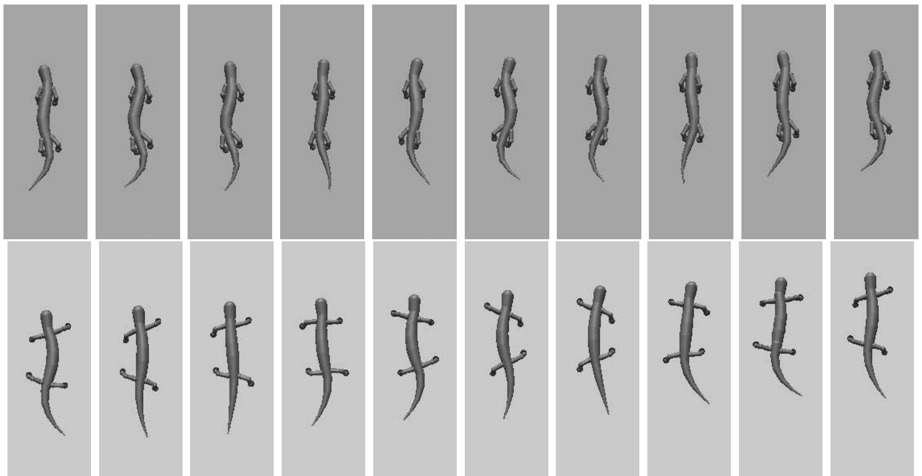

Fig. 3. Top: swimming, Bottom: trotting. Note the traveling wave along the body while swimming, and the standing wave while trotting.

(the neck) also oscillates out of phase compared to the trunk such as to limit head movements, $\lambda_1=\pi$. Crossed limbs oscillate in phase and are out of phase compared to adjacent limbs. Limbs are coordinated with the body movements as follows: muscles in joints d=1 and d=3 oscillate in phase and are also in synchrony with the body muscles on the same side. This means that when, for instance, the left trunk (i.e the upper part of the body) is in contraction, the left forelimb flexors in the knee and in the pelvis around the vertical axis contract such as to pull the limb backwards. Approximate circular movements of the limbs are obtained by having the muscles which create torques around the horizontal axis in the pelvis (i.e. which determine the elevation of the limb) to be ahead by a $\pi/2$ phase compared to the other pelvis muscles.

Figure 3 (top) illustrates a trotting gait with 2Hz oscillations. The biomechanical simulation produces the typical trotting gait of the salamander, with movements of limbs coordinated with those of the body such as to increase their reach during the swing phase. Similarly to swimming, the speed of trotting can be modulated by varying the frequency of oscillations and/or the amplitudes of the signals sent to the muscles. Turning can also be induced, primarily by giving different amplitudes to left and right signals sent to the trunk muscles.

Animated gifs of the different simulations can be found at:
http://rana.usc.edu:8376/~ijspeert/salamander.html

6 Discussion

This article presented a 3D biomechanical simulation of a salamander which extended the 2D model that we had developed in previous work [14, 15, 16]. Our aim is to gain a better understanding of the neural mechanisms underlying behavior in vertebrates by developing a comprehensive model of a vertebrate which includes models of its central nervous system, of its body, and of its environment.

The choice of the salamander as case study is motivated by the following considerations. Firstly, the salamander —an amphibian— is capable of both aquatic and terrestrial locomotion, and represents, among vertebrates, a key element in the evolution from aquatic to terrestrial habitats. Secondly, although its central nervous system has not been decoded for the moment, many data are available characterizing its locomotion, its visual system and its behaviors, which makes the salamander an interesting testbed for the synthetic approach to neurobiology we would like to take [15]. The basic idea of that approach is to use techniques from artificial intelligence such as evolutionary algorithms to automatically generate subparts of neurobiological models whose details are difficult to measure in the real animal. Finally, the salamander is situated at the right level of complexity among vertebrates: it is simple enough for making a comprehensive model of the animal possible (it has, for instance, orders of magnitudes fewer neurons than primates), while the similarities of its central nervous system with more complex vertebrates offers the possibility of general insights into the functioning of vertebrates.

Having a physically-based representation of the body is crucial to understand the dynamics of locomotion and motor control in general. A body has indeed its own dynamics and intrinsic frequencies with complex non-linear properties, to which the frequencies, phases and shapes of motoneuron signals must be adapted for efficient locomotion and motor control. Only a dynamical simulation (rather than just kinematic, as used in most experiments in computational neuroethology) can realistically represents the inertial, elastic, damping, etc. properties of the body. This is not only important for studies of locomotion, but also for investigations of sensori-motor control in general as body dynamics strongly influences sensory inputs (e.g. movements of the head influence visual perception).

The preliminary experiments reported in this article illustrated how the simulation could realistically reproduce the swimming and trotting gaits observed in the real salamander. The motoneuron activity was here produced by a simple sinusoidal function which allowed modulation of the speed, direction and type of gait. Our next step will be to extend the biologically plausible 2D neural networks developed in [15, 16] to control the new DOFs of the articulated limbs.[1] Finally, we are working on the addition of a model of the salamander's visual system to the simulated body and locomotor circuitry in order to investigate the neural mechanisms underlying visually-guided behavior.

While our main interest is to gain a better understanding of the functioning of biological central nervous systems, this type of work may also bring a contribution to graphic animation on one hand —for the generation of like-like animations—, and to biologically inspired robotics on the other. Robots which use animal-like types of gaits are indeed confronted to the same type of control

[1] In the previous biomechanical simulation, a limb was represented by a single rigid link attached to the body with only one DOF.

problems as animals, that is, how to transform simple commands concerning the speed and direction of motion into the complex rhythmic signals sent to multiple actuators. Understanding biological control may prove to be very useful for the construction of a salamander-like amphibian robot, for instance.

7 Conclusion

This article described the design of a 3D biomechanical simulation of a salamander. The physically-based simulation represents the salamander as an articulated body actuated by spring and damper muscles. A simple algorithmic controller was developed to illustrate how the simulation could reproduce and modulate the typical aquatic and terrestrial locomotion of the salamander. This model is currently used for the investigation of potential neural mechanisms underlying the locomotion of the real salamander, and extended with a model of the salamander's visual system for sensori-motor experiments in silico.

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