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Gait transition from swimming to walking: investigation of salamander locomotion control using nonlinear oscillators

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Abstract

This article presents a model of the salamander's locomotion controller based on nonlinear oscillators. Using numerical simulations of both the controller and of the body, we investigated different systems of coupled oscillators that can produce the typical swimming and walking gaits of the salamander. Since the exact organization of the salamander's locomotor circuits is currently unknown, we used the numerical simulations to investigate which type of coupled-oscillator configurations could best reproduce some key aspects of salamander locomotion. We were in particular interested in (1) the ability of the controller to produce a traveling wave along the body for swimming and a standing wave for walking, and (2) the role of sensory feedback in shaping the patterns. Results show that configurations which combine global couplings from limb oscillators to body oscillators, as well as inter-limb couplings between fore- and hindlimbs come closest to salamander locomotion data. It is also demonstrated that sensory feedback could potentially play a significant role in the generation of standing waves during walking.

1. Introduction

The salamander, a tetrapod capable of both swimming and walking, offers a remarkable opportunity to investigate vertebrate locomotion. First, as an amphibian with a sprawling posture and axial locomotion, it represents, among vertebrates, a key element in the evolution from aquatic to terrestrial habitats [1]. Second, the salamander has orders of magnitudes fewer neurons than mammals and is therefore at a level of complexity which is more tractable from a comprehension and modeling point of view. Finally, the central nervous system of the salamander shares many similarities with that of the lamprey, and many data and models of the lamprey's swimming circuitry are therefore available to guide the understanding of the salamander's locomotor circuitry.

This article investigates the mechanisms underlying locomotion and gait transition in the salamander. We develop computational models of the spinal circuits controlling the axial and limb musculature, and investigate how these circuits are coupled to generate, and switch between, the aquatic and terrestrial gaits. In previous work, one of us developed neural network models of the salamander's locomotor circuit based on the hypothesis that the circuit is constructed from a lamprey-like central pattern generator (CPG) extended by two limb CPGs [2]. In that work, a genetic algorithm was used to instantiate synaptic weights in the models such as to optimize the ability of the CPG to generate salamander-like swimming and walking patterns. Here, we develop models based on coupled nonlinear oscillators, and extend that work by systematically investigating different types of couplings between the oscillators capable of producing the patterns of activity observed in salamander locomotion. The use of nonlinear oscillators instead of neural network oscillators allows us to reduce the number of state variables and parameters in the models, and to focus on a systematic study of the interoscillator couplings.

We address the following questions: (1) how are body and limb CPGs coupled to produce traveling waves of lateral displacement of the body during swimming and standing waves during walking? (2) how is sensory feedback integrated into the CPGs? (3) does sensory feedback play a major role in the transition from traveling waves to standing waves? (4) to what extent is the inter-limb coordination between fore and hind limbs due to inter-limb coupling and/or the coupling with the body CPG? Clearly most of these questions are relevant to tetrapods in general.

2. Neural control of salamander locomotion

The salamander uses an anguiliform swimming gait very similar to the lamprey. The swimming is based on axial undulations in which rostrocaudal waves with a piece-wise constant wavelength are propagated along

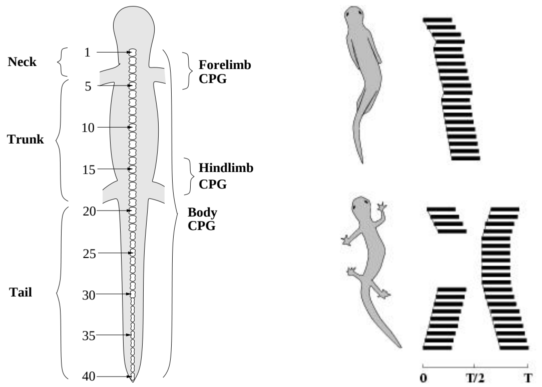

Figure 1: Left: Schematic dorsal view of the salamander's body. Right: Patterns of EMG activity recorded from the axial musculature during swimming (top) and walking (bottom), adapted from Delvolvé et al. 1997.

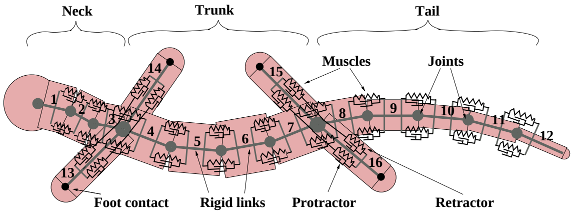

Figure 2: Mechanical model of the salamander's body. The two-dimensional body is made of 16 rigid links connected by one-degree-of-freedom joints. Each joint is actuated by a pair of antagonist muscles simulated as spring and dampers.

the whole body with limbs folded backwards (Figure 1, right). As in the lamprey, the average wavelength usually corresponds to the length of the body (i.e. the body produces one complete wave) and does not vary with the frequency of oscillation [3, 4].

On ground, the salamander switches to a stepping gait, with the body making S-shaped standing waves with nodes at the girdles [3, 4]. The stepping gait has the phase relation of a trot, in which laterally opposed limbs are out of phase, while diagonally opposed limbs are in phase. The limbs are coordinated with the bending of the body such as to increase the stride length in this sprawling gait. EMG recordings [3, 4] have confirmed the bimodal nature of salamander locomotion, with axial traveling waves along the body for swimming, and mainly standing waves coordinated with the limbs for walking (Figure 1).

The CPG underlying axial motion —the body CPG— is located all along the spinal cord. Similarly to the lamprey [5], it spontaneously propagates traveling waves corresponding to fictive swimming when induced by NMDA excitatory baths in isolated spinal cord preparations [6]. Small isolated parts of 2 to 3 segments can be made to oscillate suggesting that rhythmogenesis is similarly distributed in salamander as in the lamprey.

The neural centers for the limb movements are located within the cervical segments C1 to C5 (Figure 1 left) for the forelimbs and within the thoracic segments 14 to 18 for the hindlimbs [7, 8, 9]. Evidence from spinal sections [7] shows that these regions can be decomposed into left and right neural centers which independently coordinate each limb.

Finally, independent oscillatory centers for upper limb extensor and flexor motoneuron pools have been identified by intracellular recordings in the mudpuppy [9]. The centers are located in cervical segments C2 (elbow flexor center) and C3 (elbow extensor center), and can be made to oscillate independently with electrical and chemical stimulation. This interesting finding suggests that the walking CPG is decomposed into even small oscillatory units than Grillner's hypothesized "unit burst generators" for each limb and joints [10].

3. Mechanical simulation

The two-dimensional mechanical simulation of the salamander is an extension of Ekeberg's simulation of the lamprey [11]. The 25 cm long body is made of twelve rigid links representing the neck, trunk and tail, and four links representing the limbs (Figure 2). The links are connected by one-degree-of-freedom joints, and the torques on each joint are determined by pairs of antagonist muscles simulated as springs and dampers. The signals sent by the motoneurons contract muscles by modifying (increasing) their spring constant.

The accelerations of the links are due to four types of forces: the torques due to the muscles, inner forces linked with the mechanical constraints due to the joints, contact forces between body and limbs, and the forces due to the environment. The forces due to the environment depend on whether the salamander is in water or on the ground. In water, it is assumed that each link (limb included) is subjected to inertial forces due to the water (with forces proportional to the square of the speed of the links relative to the water). On ground, all body links are subjected to a friction force, representing the fact that the trunk and the tail of the salamander slides on the ground when the salamander is trotting. As only the accelerations in the horizontal plane are calculated, we represent the contact of a limb with the ground as a friction force applied to the extremity of the limb link. We assume that the contact in itself is determined by the signals sent to the horizontal protractor and retractor muscles. The limb is assumed to be in the air (i.e. without friction) when the signal of the protractor is larger than that of the retractor, and on the ground otherwise. The motoneurons for the retractor and protractor therefore not only determine the torque of the limb, but also its stance and swing phases. The mechanical simulation is described in more detail in [2].

4. Locomotion controller

4.1. Nonlinear oscillator

The building block of our model of the CPGs is the following nonlinear oscillator:

$$\begin{aligned} \tau\dot{v} &= -\alpha\,\frac{x^2+v^2-E}{E}\,v - x \\ \tau\dot{x} &= v \end{aligned}$$

where τ, α, and E are positive constants. This oscillator has the interesting property that its limit cycle behavior is a sinusoidal signal with amplitude $\sqrt{E}$ and period $2\pi\tau$ ($x(t)$ indeed converges to $\tilde{x}(t) = \sqrt{E}\sin(t/\tau+\phi)$, where ϕ depends on the initial conditions, see also Figure 3).

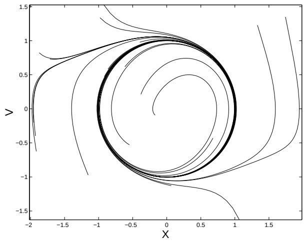

Figure 3: Limit cycle behavior. Time evolution of the nonlinear oscillator with different random initial conditions.

We assume that the different oscillators of the CPG are coupled together by projecting to each other signals proportional to their x and v states in the following manner

$$\begin{aligned} \tau\dot{v}_i &= -\alpha\,\frac{x_i^2+v_i^2-E_i}{E_i}\,v_i - x_i \\ &\quad + \sum_j (a_{ij}x_j + b_{ij}v_j) \; + \; \sum_j c_{ij}s_j \\ \tau\dot{x}_i &= v_i \end{aligned}$$

where a_{ij} and b_{ij} are constants (positive or negative) determining how oscillator j influences oscillator i. In these equations, the influence from sensory inputs s_j weighted by a constant c_{ij} is also added, see next sections for further explanations.

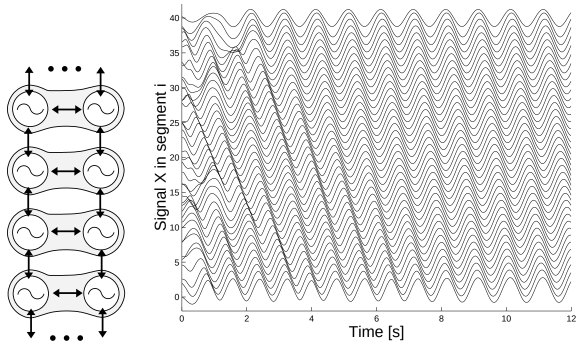

Figure 4: Left: Configuration of the body CPG. Right: oscillations in a 40-segment chain (only the activity in a single side is shown).

4.2. Body CPG

We assume that the body CPG is composed of a double chain of oscillators all along the 40 segments of spinal cord. The type of connections investigated in this article are illustrated in Figure 4 (left). For simplicity, we assume that only nearest neighbor connections exist between oscillators. In our first investigation, the oscillators are assumed to be identical along the chain (with identical projections), as well as between each side of the body. The connectivity of the chain is therefore defined by 6 parameters, two (the a_{ij} and b_{ij} parameters) for each projection from one oscillator to the other (i.e. the rostral, caudal, and contralateral projections). Of these 6 parameters, we fixed the couplings between contralateral oscillators to $a_{ij} = 0$ and $b_{ij} = -0.5$ in order to force them to oscillate in antiphase. We systematically investigated the different combinations of the four remaining parameters (the rostral and caudal projections) with values ranging from -1.0 to 1.0, with a 0.1 step.

Traveling wave Experiments on isolated spinal cords of the salamander suggest that, similarly to the lamprey, the body CPG tends to propagate rostrocaudal (from head to tail) traveling waves of neural activity. During (intact) swimming, the wavelength of the wave corresponds approximately to a bodylength. We therefore systematically investigated the parameter space of the body CPG configuration to identify sets of parameters leading to stable oscillations with phase lags between consecutive segments approximately equal to 2.5% of the period (in order to obtain a 100% phase lag between head and tail). The goal is to obtain traveling waves which are due to asymmetries of interoscillator coupling, while maintaining the same intrinsic period (the same τ) for all oscillators.

We found that several coupling schemes could lead to such traveling waves. The coupling schemes can qualitatively be grouped in three different categories: dominantly caudal couplings, balanced caudal and rostral couplings, and dominantly rostral couplings.[1] By dominant, we mean that the sum of the absolute values of the weights in one direction are significantly larger than in the other direction. While all groups can produce traveling waves corresponding to salamander swimming, solutions which have balanced caudal and rostral couplings need significantly more cycles to stabilize into the traveling wave (starting from random initial conditions) than the solutions in which one type of coupling is dominant. It is therefore likely that the salamander has one type of coupling which is dominant compared to the other. A very similar conclusion has been made concerning the lamprey swimming controller [12].

Figure 4 (right) illustrates the traveling waves generated by one of the dominantly caudal chains. As can be observed, starting from random initial states, the oscillations rapidly evolve to a traveling wave. Since the period of the oscillations explicitly depend on the parameter τ, the period can be modified independently of the wavelength. The wavelength of one-body length is therefore maintained for any period, when all oscillators have the same value of τ (i.e. the same intrinsic period). This allows one to modify the speed of swimming by only changing the period of oscillation, as observed in normal lamprey and salamander swimming.

Interestingly, while the connectivity of the oscillators favors a one-body length wavelength, it is possible to vary the wavelength by modifying the intrinsic period of some oscillators, the oscillators closest to the head, for instance. Reducing the period of these oscillators leads to an increase of the phase lag between consecutive oscillators(a reduction of the wavelength), while increasing their period leads to a decrease of the phase lag, and can even change the direction of the wave (i.e. generate a caudo-rostral wave). This type of behavior is typical of chains of oscillators [12].

Piece-wise constant wavelength We identify at least four potential causes for the small changes of wavelength observed along the body at the level of the girdles: (1) differences of intrinsic frequencies between the oscillators at the girdles and the other body oscillators, (2) differences in intersegmental coupling along the body CPG (with three regions: neck, trunk, and tail), (3) effect of the coupling from the limb CPG, (4) effect of sensory feedback. Recent in-vitro recordings on isolated spinal cords showed that a change of wavelength is also obtained during fictive swimming. It therefore seems that the phenomenon is mainly due to the CPG configuration rather than to sensory feedback (explanation number four is therefore the less likely). We tested these different hypotheses with the numerical simulations. For the hypothesis 2, it meant adding 8 parameters for differentiating the intersegmental couplings in the neck, trunk and tail regions.

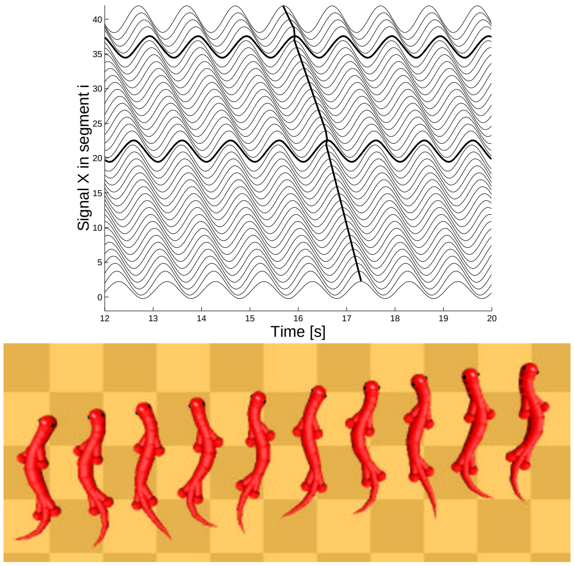

Figure 5: Top: Piece-wise constant wavelength. The oscillations at the level of the girdles are drawn with thicker lines. Bottom: resulting swimming behavior (in steady state).

The results suggest that, in our framework, the most likely cause of the three-wave pattern is a combination of differences in intersegmental coupling and of intrinsic frequencies of the oscillators at the girdles. The differences in intersegmental coupling lead to variations in the wavelength of the undulation along the spinal cord. But they do not explain the abrupt changes of phases at the level of the girdles. These are best explained by small differences in intrinsic frequencies of the oscillators of the body CPGs at the two girdles (these could also potentially be due to the projections from the limb CPG, see next sections).

We can furthermore tell that the effect of variations of the intrinsic frequencies depend on which coupling is dominant in the body CPG. The patterns observed in the salamander are best explained with either a combination of dominantly caudal coupling and higher intrinsic frequency at the girdles, or dominantly rostral coupling and lower intrinsic frequencies at the girdles. The resulting activity in the latter configuration is illustrated in Figure 5 top.

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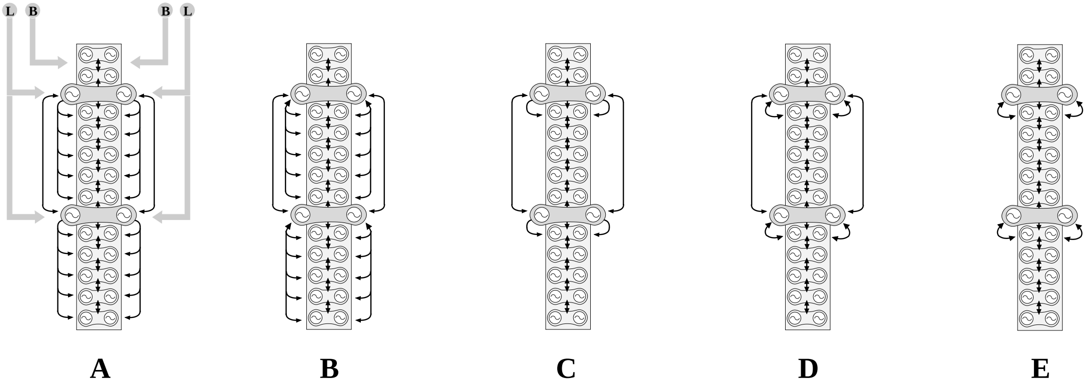
[1] Dominantly caudal and rostral couplings are essentially equivalent since each coupling type which is dominant in one direction has an equivalent in the other direction by inverting the sign of some weights. However, that equivalence is lost when the intrinsic frequencies of some oscillators are varied, see the “Piece-wise constant wavelength” paragraph.



Unilateral
Global
With interlimb c.

Bilateral
Global
With interlimb c.

Unilateral
Local
With interlimb c.

Bilateral
Local
With interlimb c.

Bilateral
Local
Without interlimb

Figure 6: Different potential CPG configurations.

Swimming We tested the body CPG in the mechanical simulation for controlling swimming. Since the mechanical simulation has only 11 joints along the body, 11 pairs of equally-spaced oscillators were picked from the body CPG to drive the muscle models, such that the oscillators in one pair project to the muscle on their respective side. A “motoneuron” m_i signal is obtained from the states x_i with the following equation $m_i = \beta \max(x_i, 0)$, where is β a positive constant gain. This motoneuron signal controls how much a muscle contracts by essentially changing the spring constant of the spring-and-damper muscle model (see [2]). An example of the swimming gait is shown in Figure 5 (bottom). The speed of swimming can be modulated by changing the frequency of all oscillators (through the parameter τ), while the direction of swimming can be modulated by applying an asymmetry of the amplitude parameter E between left and right sides of the chain. The salamander will then turn toward the side which receives the highest amplitude parameter.

4.3. Different body-limb CPG configurations for gait transition

One of the goals of this article is to investigate different types of couplings between the body and limb CPGs, and how these couplings affect the gait transitions between swimming and walking. There are currently too few biological data available to indiquate how the different neural oscillators in the body and limb CPGs are interconnected. Our aim is to investigate which of these configurations can best reproduce some key characteristics of salamander locomotion.

We tested five different types of coupling (Figure 6). These couplings differ in three characteristics: *unilateral/bilateral* couplings, in which the limb CPGs are either unilaterally or bilaterally (i.e. in both directions) coupled to the body CPG, *global/local* couplings, in which the limb CPGs project either to many body CPG oscillators, or only those close to the girdles, and *with/without* interlimb couplings between fore- and hindlimbs. In our previous work [2], we tested configuration A (unilateral, global, with interlimb coupling) using neural network oscillators. The unilateral projections from limb to body CPG essentially means a hiearchical structure in the CPG for that configuration.

In all configurations, we assume that two different control pathways exist for the body and the limb CPGs, in order words, that the control parameters τ and E can be modulated independently for the body and limb oscillators. In particular, we make the hypothesis that the gait transition is obtained as follows: swimming is generated when *only* the body CPG is activated (*Ebody* = 1.0 and *Elimb* = 0.005), and walking is generated when *both* body *and* limb CPGs are activated (*Ebody* = 1.0 and *Elimb* = 1.0).

The simulation results show that only configurations A and B, i.e. those with global coupling between limb and body CPG can produce standing waves (in the absence of sensory feedback). For these configurations, the global coupling from limb oscillators to body oscillators ensures that the body CPG oscillates approximately in synchrony in the trunk and in the tail when the limb CPG is activated (Figure 7). For the other configurations (C, D, and E) the fact that the couplings between limb and body CPGs are only local means that traveling waves are still propagated in the trunk and the tail, despite the influence from the limb oscillators. Configurations E, which lacks interlimb couplings can still produce walking gaits very similar to those of configurations C and D, because the coupling

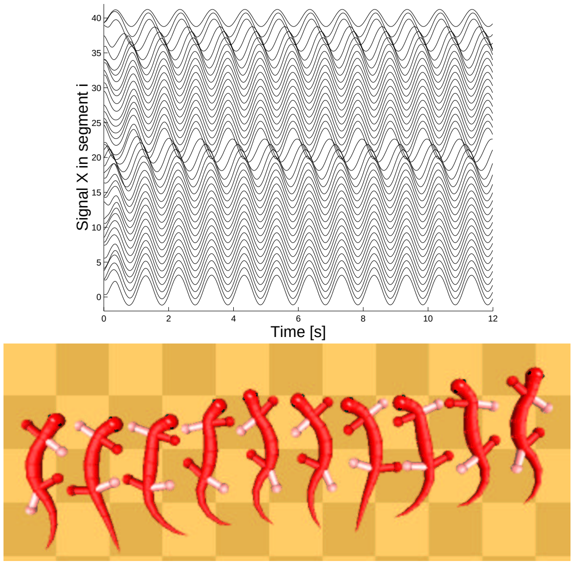


Figure 7: Top: oscillations along the body in a CPG of type A (only the activity in a single side is shown). Bottom: resulting walking behavior (in steady state).

with the body CPG gives a phase relation between fore- and hindlimbs of approximately 50% of the period (because fore and hindlimbs are separated by approximately the half of one body-length).

Having bilateral couplings between limb and body CPGs does not affect the walking pattern in a significant way. However, if the coupling from body CPG to limb CPG is strong, it will affect the swimming gait. In that case, even if the amplitude of the limb oscillators is set to a negligible value (*Elimb* = 0.005), the inputs from the body CPG will be sufficient to drive the limb oscillators which in return will force the body CPG to generate a wave which is a mix between a traveling wave and standing wave. It is therefore likely that the couplings between limb and body CPG are stronger from limb to body CPG than in the opposite direction.

Note that the fact that CPG configurations B, C and D can not produce standing waves, does however not exclude the possibility that these configurations produce standing waves when sensory feedback is added to the controller. This will be investigated in the next section.

Effect of sensory feedback When a lamprey is taken out of the water and placed on ground, it tends to make undulations which look almost like standing waves because the lateral displacements do not increase along the body but form quasi-nodes (i.e. points with very little lateral displacements) at some points along the body [13].

Interestingly, the same is true in our simulation. When the swimming gait is used on ground (without

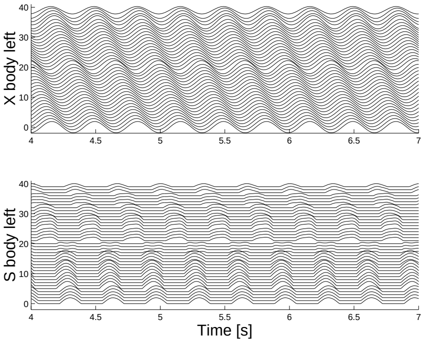


Figure 8: Walking gait produced by configuration D, **without** sensory feedback. Top: output of the body CPG, Bottom: output of the stretch sensors.

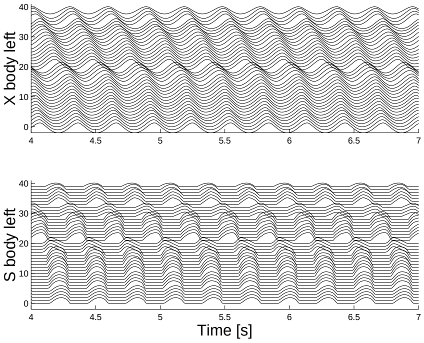


Figure 9: Walking gait produced by configuration D, **with** sensory feedback. Top: output of the body CPG, Bottom: output of the stretch sensors.

sensory feedback), the body makes a S-shaped standing wave undulation instead of the traveling wave undulation generated in water. This is due to the differences between hydrodynamic forces in water (which have strongly different components between directions parallel and perpendicular to the body) and the friction forces on ground (which are more uniform). The sensory signals from such a gait are then reflecting this S-shaped standing wave, despite the traveling waves sent to the muscles.

Sensory feedback is therefore a potential explanation for the transition from a traveling wave for swimming to a standing wave for walking. We therefore tested the effect of incorporating sensory feedback in the different CPG configurations described above. Sensory feedback to the salamander's CPG is provided by sensory receptors in joints and muscles. We designed an abstract model of sensory feedback by including sensory units located on both sides of each joint which produce a signal proportional to how much that side is stretched: $s_i = \max(\phi_i, 0)$ where ϕ_i is the angle of joint i measured positively away from the sensory unit. For simplicity, we only consider sensory feedback in the body segments (i.e. not in the limbs), and assume that a sensory unit for a specific joint is coupled only locally to the two (antagonist) oscillators activating that joint.

Figure 8 shows the activity of the body CPG and the sensor units produced during a stepping gait with a controller with configuration D. Without sensory feedback (Figure 8), this controller produces a traveling wave during walking because the limb oscillators have only local projections to the body CPG. Despite this traveling wave of muscular activity, the body (in contact with the ground) makes essentially an S-shaped standing wave as illustrated by the sensory signals (synchrony in the trunk and in the tail, with an abrupt change of phase in between). When these sensory signals are fedback into the CPG (Figure 9), the body CPG activity is modified to approach the standing wave (i.e. the phase lag between segments decrease in the trunk and in particular in the tail). Note that if the sensory feedback signals are too strong, the stepping gait becomes irregular. Interestingly, the sensory feedback leads to an increase of the oscillation's frequency, something which has also been observed in a comparison between swimming with and without sensory feedback in the lamprey [14].

5. Discussion

The primary goal of this article was to investigate which of different CPG configurations was most likely to control salamander locomotion. To the best of our knowledge, only three previous modeling studies investigated which type of neural circuits could produce the typical swimming and walking gaits of the salamander. In [15], the production of S-shaped standing waves was mathematically investigated in a chain of coupled non-linear oscillators with long range couplings. In that model, the oscillators are coupled with closest neighbor couplings which tend to make oscillators oscillate in synchrony, and with long range couplings from the extremity oscillators to the middle oscillators which tend to make these coupled oscillators oscillate in antiphase. It is found that for a range of strengths of the long range inhibitory coupling, a S-shaped standing wave is a stable solution. Traveling waves can also be obtained but only by changing the parameters of the coupling. In [2], one of us demonstrated that a leaky-integrator neural network model of configuration A could produce stable swimming and walking gaits. Finally, in [16], it was similarly demonstrated that a neural network model of the lamprey swimming controller could produce the piece-wise constant swimming of salamander and the S-shaped standing of walking depending on how phasic input drives (representing signals from the limb CPGs and/or sensory feedback) are applied to the body CPG. The current paper extends these previous studies by investigating more systematically different potential body-limb CPGs configurations underlying salamander locomotion.

The simulation results presented in this article suggest that CPG configurations which have global couplings from limb to body CPGs, and interlimb couplings (configurations A or B) are the most likely in the salamander. These configurations can indeed produce stable swimming and walking gaits with all the characteristics of salamander locomotion. Our investigation does not exclude the other configurations, but suggest that these would need a significant input from sensory feedback to force the body CPG to produce the S-shaped standing wave along the body. These results suggest new neurophysiological experiments. It would, for instance, be interesting to make new EMG recordings during walking without sensory feedback (e.g. by lesion of the dorsal roots). If the EMG recordings remain a standing wave, it would suggest that configurations A or B are most likely, while if they correspond to a standing wave if would suggest that configurations C, D, or E are most likely.

To make our investigation tractable, we made several simplifying assumptions. First of all, we based our investigation on nonlinear oscillators. Clearly, these are only very abstract models of oscillatory neural networks. In particular, they have only few state variables, and fail to encapsulate all the rich dynamics produced by cellular and network properties of real neural networks. We however believe they are well suited for investigating the general structure of the locomotion controller. To some extent, some properties of interoscillator couplings are universal, and do not depend on the exact implementation of the oscillators. This is observed for instance in chains [12], as well as rings of oscillators [17]. Our goal was therefore to analyze these general properties of systems of coupled oscillators. Taking this study as starting point, we intend on one hand to use our results to guide new neurophysiological measurements, and on the other hand to gradually make the oscillators more realistic using neural network simulations based on the new data.

An interesting aspect of this work was to combine a model of the controler and of the body, since this allowed us to investigate the mechanisms of entrainment between the CPG, the body and the environment. We believe such an approach is essential to get a complete understanding of locomotion control, since the complete loop can generate dynamics that are difficult to predict by investigating the controller (the central nervous system) in isolation of the body. The transformation of traveling waves of muscular activity into standing waves of movements when the salamander is placed on ground is an illustration of the complex dynamics which can results from the complete loop.

Finally, this work has also direct links with robotics, since the controllers could equally well be used to control a swimming and walking robot. Especially interesting is the ability of the controller to coordinate multiple degrees of freedom while receiving very simple input signals for controling the speed, direction, and type of gait.

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