

Sensory Feedback to Improve and Simplify a Neuromechanical Network

In Adult *Drosophila Melanogaster*

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Abstract

A substantial part of scientific research and in particular scientific experimentation is nowadays relying on *in vivo* experiments conducted on animals, or on *in vitro* experiments using cell culture or small organisms. The high complexity of certain processes and environments, which makes them hard to record *in vivo* or to reproduce *in vitro*, along with the rise of computing technologies, have kept on pushing experimentation to renew itself and to try to complement the current experimentation techniques with computational models. *Drosophila melanogaster* is widely used as a model organism for research in various fields such as genetics and physiology, therefore making the development of an *in silico* model for it particularly useful. The goal of this project was to review the mechanisms of sensory feedback in insect locomotion both on an intra-leg and on an inter-leg coordination level, and to incorporate them to the simulation with the aim to reduce the complexity of the network and to improve the efficiency of the simulated gait. With the added contribution of the implemented sensory input, the current neuromechanical model of the *Drosophila melanogaster* (Figure 1) is able to produce a realistic and adaptive locomotion pattern while reducing the number of oscillators required to generate the gait.

The simulation is able to adapt its sequence of events and its locomotion pattern to the sensory information coming from the other leg joints and from the other legs. Even when perturbations are applied to the inter-leg phases, the model tends to converge to a tripod-like gait within a few gait cycles. The current implementation provides the tool necessary for the future development of more complex and realistic mechanisms of insect locomotion, such as the elevator reflex necessary to locomote on uneven terrain.

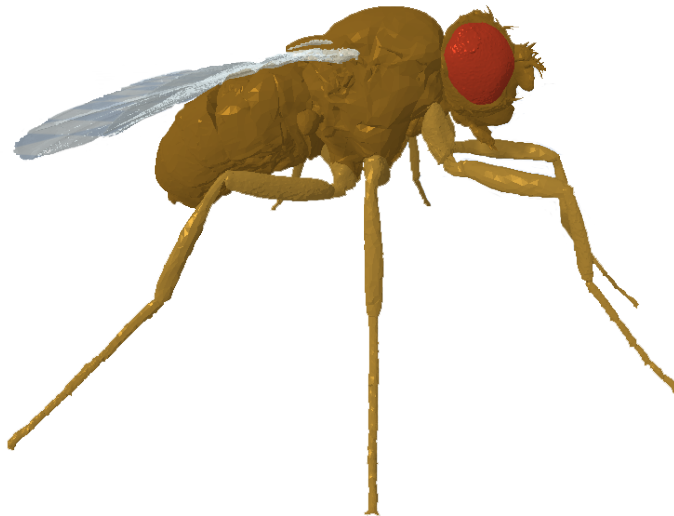


Figure 1: Visual aspect of the simulated *Drosophila melanogaster*

1 Introduction

Locomotion is one of the most primary and basic mechanisms for an animal and already a substantial challenge in the development of an *in silico* model, due to the intricate neural pathways involved in the process. The already implemented *Drosophila* model successfully manages to reproduce some form of rhythmic gait. However, evidence suggests that sensory feedback significantly contributes to the generation of locomotion in insects and its implementation is believed to help with reducing the complexity of the current network and provide the model with the ability to adapt to some sensory events.

Flies have 6 legs, each composed of several joints and muscle couples. Each leg segment is given the ability to rotate around an axis thanks to a pair of muscle fibres, each time pairing a flexor muscle with an extensor muscle, the contraction of the former inducing flexion of the joint, while contraction of the latter results in extension of the joint. Three joints per leg are considered in the current model, allowing the leg to rotate along three axes : Retractor/Protractor on the Thorax-Coxa joint (ThC) making the leg go backwards or forwards, Depressor/Levator on the Coxa-Trochanter joint (CTr) to lower or lift the leg, and Flexor/Extensor on the Femur-Tibia joint (FTi) to bend or distally extend the leg.

Within a leg, these different fibres are activated following a sequence of events in order to produce a certain gait pattern. In the present model, each of these joints' activity is governed by a distinct oscillator, making it to a total of 36 independent oscillators. Shifting the activity of the different muscles in time allows for a sequenced activation of the fibres and thus causes the generation of a specific locomotion pattern. All of these oscillators are connected and shifted with phases to form an organised neural network, whose architecture is depicted on Figure 2.

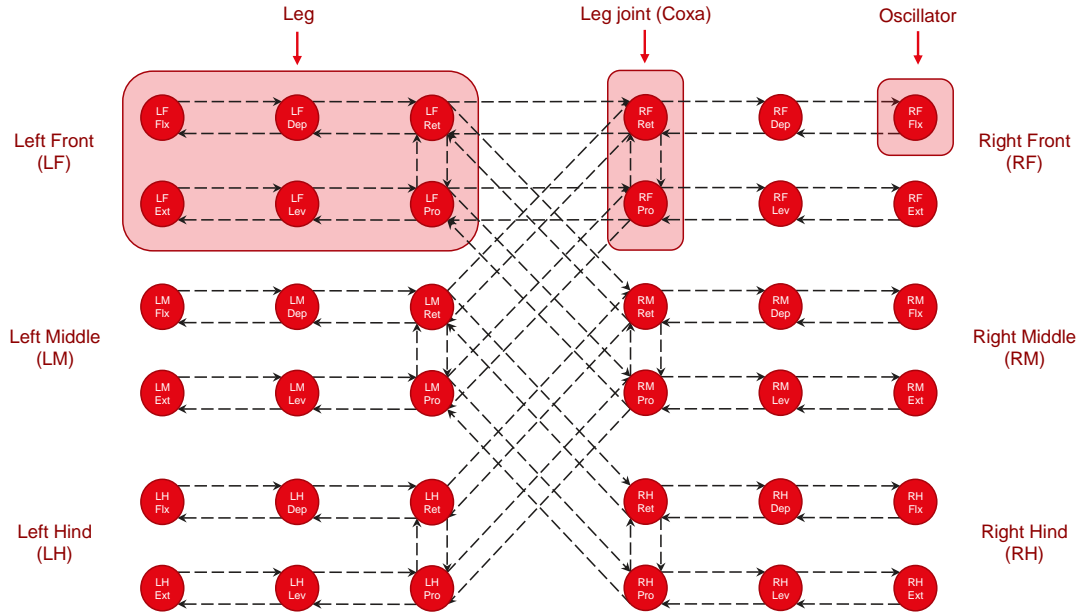


Figure 2: Neural network architecture. Each small red dot represents an oscillator, there are two of them for each of the leg joints, one generating the flexor oscillation, the other one for the extensor oscillation. Each arrows shows the connectivity between the joints, represented by a phase shift between the connected oscillators. There are phase shifts between the different joints of a leg, as well as a shift between flexor and extensor activity, and a phase shift between each leg.

It is well accepted that there are such neural networks in the central nervous system of walking animals, and that these units are able to generate a rhythmic output delivered by the motoneurons responsible for muscle activation (Grillner, 2006). These oscillators don't require an input to generate such patterns, but there is strong evidence that, in animals, these oscillations highly rely on ascending input to adapt and coordinate the legs in a more efficient and convenient way (Akay, 2020). Sensory signals seem to be integrated by the nervous system to generate a more coordinated and robust walking pattern able to adapt to more variable environments, such as inclined walking, or walking on uneven terrain. Applying that thought process to computational modelling, incorporating this sensory component to a simulation has been shown to result in a more robust and adaptive simulation in robots (Yu et al., 2020). In addition, the current project aims at finding out how, using the knowledge available on leg coordination, the complexity of the network used in the previous model can be reduced. Involving the output of numerous oscillators, the previous network is believed to be significantly complex, and the available literature leads us to the hypothesis that a similar gait can be generated using a restricted number of oscillators.

The current simulated fly consists of a shell composed of many segments and sections that can move freely from one another, yet still connected. One way to assess the quality of the gait is by displaying the fly on a freely-moving ball, whose rotation magnitude and deviation will give out information about the efficiency of the gait. Without the implementation of the sensory feedback, the simulated fly is able to generate movements and articulate the different segments of the legs in a certain manner based on pre-defined phase shifts between the oscillators. However, both on a single-leg level and on an inter-leg coordination level, incorporation of sensory feedback is finally believed to help with the generation of an efficient and more stable tripod-like gait.

2 State-of-the-art

Sensory feedback has been previously shown to play an essential role in gait transitions and in the coordination of the legs, be it on fairly simple animal models such as cockroaches (Zill et al., 2009, studying load sensing and onset of stance), or on bigger models such as salamander (Harischandra et al., 2011, investigating sensory feedback and gait transitions) or cats (Duysens and Pearson, 1976, analysing the sensory stimulation of decerebrate cats and resulting muscle activity changes). There is therefore strong evidence that there are such mechanisms that input on the locomotion of most animal species to make it more effective and more adaptive to its environment. To this day, there's no clear research in *Drosophila* in particular regarding the sequence of sensory events that lead to the modulation of the locomotion pattern and how specifically they act on the activation of the muscles. The pattern of muscle activation relying on the integration of sensory signals has been more extensively studied in the stick insect (detailed in section 3.3). However, it is believed that the middle legs of a fly behave similarly to those of a stick insect, and that for the current simulation, the implementation of those findings can be generalised to the six legs of a fly following slight adaptations for the hind and the front legs.

The implementation of sensory feedback was already shown to be effective and to improve the adaptability of locomotion in a simulation (Owaki and Ishiguro, 2017), where the implementation of feedback sensing led to the ability to trigger gait transitions (from walking to trotting)

simply by modifying the speed of the robot. That ability being ensured by the inter-limb coordination resulting from the implementation of a sensory input measuring the load acting on the legs. As there is extensive literature on the different types of sensors that are physiologically expressed in the *Drosophila melanogaster*, it makes sense to assume that the implementation of such mechanisms in the current model could improve the performance of the simulation. The sensing activity of the two main types of sensors is implemented in the proposed model.

2.1 Chordotonal Organs

The chordotonal organs (CO) are stretch receptors, similar to muscle spindles in humans. Their mechanisms is based on neurons expressing mechanically gated ion channels, which get activated upon stretching of the sensory neurons. These sensors are expressed in *Drosophila*, and in particular at the proximal end of the femur, forming a cluster accountable for most of the chordotonal sensing, called the femoral chordotonal organs (fCO, see Figure 3).

These sensors are able to detect variations in the movement of the involved leg joints, variations in speed, acceleration, vibrations and to detect position. These proprioceptors, in particular the fCO, are able to detect the position of the tibia relative to the femur (Mamiya et al., 2018) and act as a measurement of the angle separating two joints, here the Femur-Tibia angle (FT angle). Monitoring the FT joint angle in the simulation is therefore a way to model the fCO.

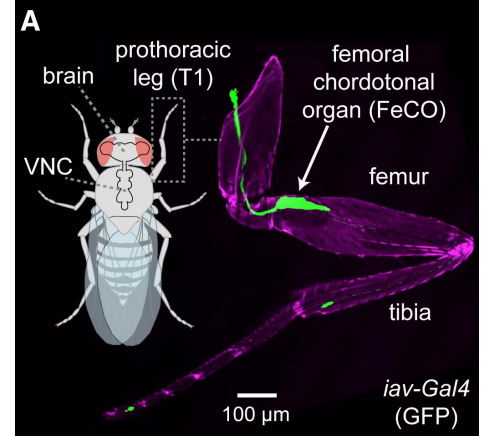


Figure 3: Location of the fCO on a *Drosophila* leg (illustration taken from Mamiya et al., 2018).

2.2 Campaniform Sensilla

The campaniform sensilla (CS) are mechanoreceptors that are similar to Golgi tendon organs (GTOs) in humans, and that take the form of a neuron connected to a small socket. That specific neuron fires when the socket edges are deformed, meaning that a significant strain is being applied on its structure. These neurons act as the physiological sensors that measure the load and force applied on the muscles. When these are activated, they can eventually have an impact on the magnitude and the timing of muscle activation (Dinges et al., 2020). A possible way to measure the muscle load is to sum up all activity on a muscle, which can be monitored in the model by adding the extensor and the flexor activity of muscle in the model.

In addition to sensing muscle load, these mechanoreceptors provide flies with tactile sensing. In particular, a fly is then able to detect when their legs come in contact with the ground and campaniform sensilla therefore also act as ground reaction force sensors. Implementing the detection of ground contact events in the simulation is the last kind of sensory feedback whose contribution is added to the previous model. The round-up contribution of these two sensors is thought to be enough to model the signal events that are detailed in section 3.3.

3 Methods

As mentioned earlier, implementation of the sensory feedback is expected to let room for improvement in two specific areas : first the single-leg coordination, in order to improve the sequence of events generating the locomotion of each single leg separately, and second, the coordination of all the legs together to produce a coherent and adaptive locomotion.

Before digging into how the current project is dealing with these two issues, basic knowledge on how the model is built and understanding on the architecture of the simulation is useful.

3.1 Model Environment

The model is based on the implementation of an object, the fly, modelling all the dynamical characteristics of a *Drosophila* that are necessary for the current neuromechanical model. In particular, the animal has 18 joints as attributes each of them being implemented as a couple of antagonist muscles (a flexor and an extensor). Figure 4 displays a simplified diagram of what happens during the simulation. The generation of the motion of the fly is based on processing the output of the many oscillators making up the model. The dynamical properties of the fly are continuously updated based on the computation of the torque applied on every joint. That torque itself relies on the integration of the output coming from the oscillators as detailed in the next section.

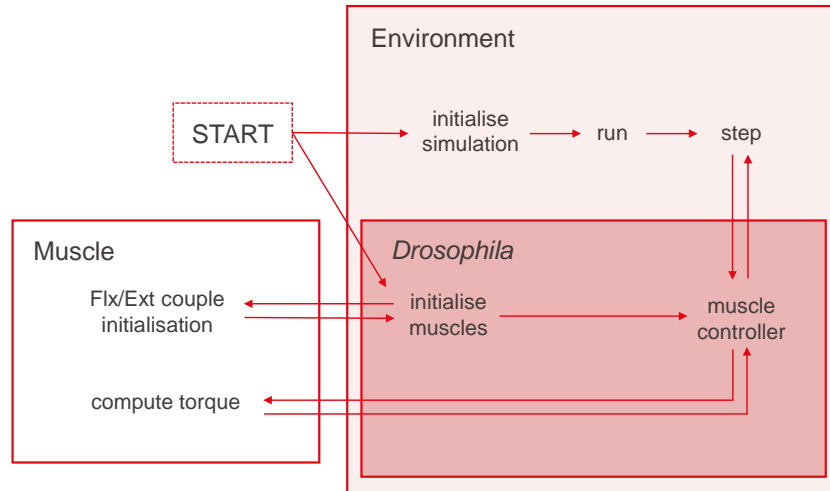


Figure 4: Diagram of the 3 main classes of the program : the simulation environment, the fly and its muscles, and a simplified scheme of what happens during the simulation.

The main goal of sensory feedback implementation is to have the ability to modify and act on the motion of the animal in real time depending on some ascending signals. Considering the current architecture and how the motion is computed, acting on the oscillations defining the torque applied on the leg joints will allow us to modulate the activity of the legs and drive the motion towards a set direction.

3.2 Torque Computation

The torque is computed based on an equation following the mechanical model detailed in the article (Ekeberg, 1993). The expression (1) of the muscular torque τ can be derived from the muscle properties after assuming the muscles from our model behave like a spring :

$$\tau = \alpha \cdot (A_{flexor} - A_{extensor}) + \beta \cdot (A_{flexor} + A_{extensor} + \gamma) \cdot (x_{rest} - x_{joint}) - \delta \cdot v_{joint} \quad (1)$$

Here, α , β , γ and δ are some constants, whose physical significance is further detailed in the aforementioned article. x represents the position of the joint, A_{flexor} and $A_{extensor}$ are respectively the activity of the flexor and extensor component of the muscle couple. These activities are themselves relying on the input coming from the oscillators that is computed solving the equations of the oscillators. The activity of the flexor and the extensor is related to the output of the oscillators with the following relation :

$$A_{flexor} = R_{flexor} \cdot (1 + \sin(f_{mn_flexor})) \quad (2)$$

$$A_{extensor} = R_{extensor} \cdot (1 + \sin(f_{mn_extensor})) \quad (3)$$

$R_{flexor/extensor}$ are constants, and $f_{mn_flexor/extensor}$ represent the input of the motoneuron on the muscles, which is the output calculated from the oscillators as mentioned above. These activities display the rhythmic component that we expect from the oscillators, and by acting on these sine functions, we can therefore modify the output of the torque. For instance, if we shift the activity of the levator/depressor couple by a phase of π while the leg is lifted up, the activity of this muscle couple will be reversed and the leg will tend to lower down. Implementing the specific events that trigger modifications in the activity of the joints is how sensory feedback is modelled in the current project. The sensory feedback is incorporated into the model by applying some changes to the previous equations (2) and (3), as detailed in the next section.

3.3 Single-leg Coordination

On a single-leg level, we can take the effects of the sensory feedback by playing with the amplitude, the frequency and the phase of the activity curves. We can rewrite the equations (2) and (3) including the sensory input terms :

$$A_{flexor} = Amp_{flexor} \cdot R_{flexor} \cdot (1 + \sin(f_{mn_flexor} \cdot \nu_{flexor} + \phi_{flexor})) \quad (4)$$

$$A_{extensor} = Amp_{extensor} \cdot R_{extensor} \cdot (1 + \sin(f_{mn_extensor} \cdot \nu_{extensor} + \phi_{extensor})) \quad (5)$$

These additional amplitude, frequency and phase terms are all modulated by the sensors mentioned earlier, and each of these 3 terms are computed every iteration based on the output of the methods *GRF_coeff*, *fCO* and *CS*. These methods all return modified amplitude, frequency and phase depending on the sensory input. What particular data is read as an input by the 3 feedbacks is further detailed in sections 3.3.1 to 3.3.3. Previous research conducted on *Carausius Morosus*, a species of stick insect, analysed the correlation between sensory signals and activity

patterns (Rosenbaum et al., 2010), and is put together in the form of a table in a literature review released a few years later (Bidaye et al., 2018). The sensory signals listed in the bottom of Figure 5 are the signals implemented into the current model. For instance, when the FT joint extends, meaning when the angle between the femur and the tibia goes above a certain threshold, the depressor muscle is activated, while the levator muscle activity is reduced. Two ways are used and can be combined to enhance the activity of a specific muscle : increasing the amplitude ($Amp_{flexor/extensor}$) and/or shifting the phase ($\nu_{flexor/extensor}$) by a small amount to jump to a point in the oscillation when the activity is higher. The same process can be applied for the inhibition of a muscle.

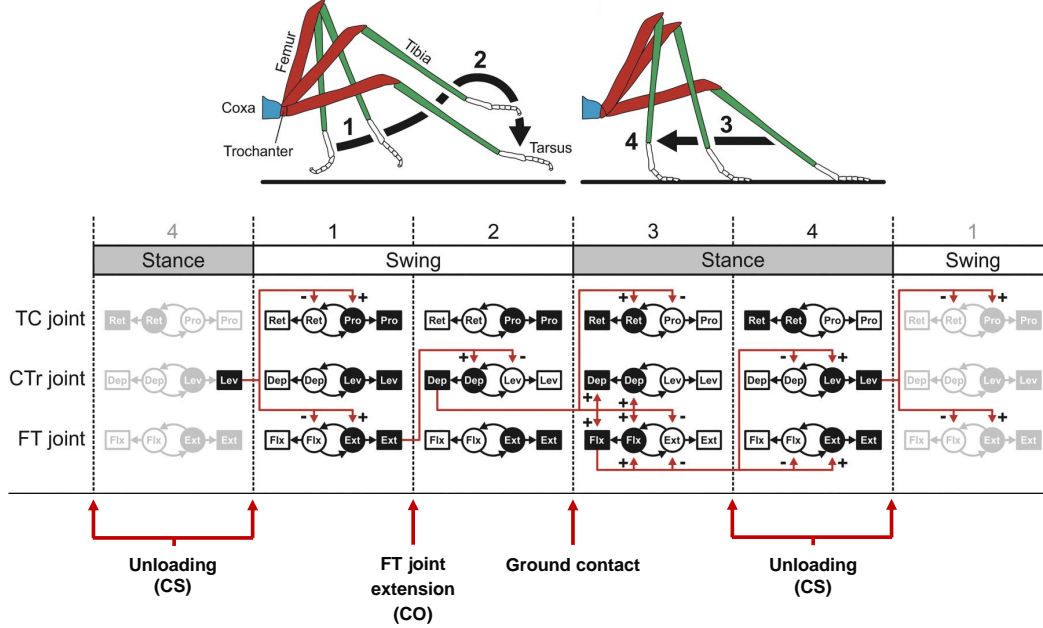


Figure 5: Diagram showing the sequence of sensory events and what flexor or extensor muscles they specifically activate or inhibit in the stick insect single-leg stepping. Each joint is represented by its own oscillator (circles) and the associated leg muscles (squares). The red arrows show the pattern of activation/inhibition and the filled circles or squares show which joints are active at a specific point in time. The sensory signals taken into account in the current model are displayed in the bottom. Diagram taken and adapted from (Bidaye et al., 2018).

3.3.1 GRF Feedback

The first feedback implemented in the simulation is the ground reaction force feedback. That feedback is activated at the start of stance when the leg hits the ground, and it modulates the activation of the femoral and tibial muscles (as depicted on Figure 5). In particular, the GRF feedback becomes active when the output of the GRF sensor is strictly positive and if the leg is at the start of stance. The GRF sensor is reading the output of the ground reaction force applied on the five tarsal segments of the leg and averaging them. This is believed to be an accurate way to have an idea of the overall ground reaction force applied on a leg. This feedback increases the amplitude of activation of the flexor and depressor muscles and decreases the activation of the associated extensor muscles (namely the extensor and the levator). The

GRF feedback has to only be active for the first half of the stance in order to avoid limitation of the levator activity that is supposed to come in the second half of the stance. No frequency or phase shift is introduced with this feedback. The opposite was applied to the FTi joint for the hind legs, as flexion during the swing and extension during the stance is preferred due to the orientation of the legs (further detailed at the end of section 3.3)

3.3.2 fCO Feedback

The second sensing used is the fCO feedback. The value of the FTi joint angle, meaning the joint angle value retrieved from the FTi joint in the model, is used as a sensory signal for that feedback. Once that angle goes over a certain threshold, represented by the leg extending past a certain angle, the feedback is activated. It acts on the levator/depressor muscle couple. It introduces a phase shift and modulates the amplitude of the activity so as to shift to a later stage in the oscillation when the conditions are met. That means that when a leg is in swing and is sufficiently extended, the oscillation will straight jump to a later configuration where levator activity has already terminated and depressor activity will be higher, resulting in the leg to lower down earlier than without the feedback. The feedback signaling depression of the leg during the swing is terminated when the leg strikes the ground.

3.3.3 CS Feedback

The last feedback is using the joint load, which represents the total amount of activity applied on the joint muscles. The CS feedback acts in particular during the second half of leg stance. Its main function is to enhance the transition to swing, and for that it causes enhanced protractor, levator and extensor activity, while it decreases the associated flexor activity. To do that, it introduces a positive phase shift in all of the 3 leg joints so as to shift the leg to a later stage in the oscillation, and make it switch to swing earlier than it would without the feedback. That shift is introduced following a specific order, first activating in the levator/depressor couple, then in the extensor/flexor couple, and finally in the protractor/retractor couple. The shift is progressively going back to 0 while the leg is in swing to make it go back to the normal oscillation. On top of that, specific changes in the amplitude of the muscle activities are applied, for instance to make sure that the hind legs, which struggle at lifting off the ground without feedback, exhibit a high and consistent swing. A clear swing is necessary to avoid some unwanted events of the leg getting in touch with the ball during protraction which could mislead to the activation of certain feedbacks.

In the previous model, all the phase shifts represented by the black arrows on Figure 2 are obtained through a process of optimisation that maximises the ball rotation, which ultimately satisfies the goal of having an efficient gait. However, there is no guarantee that the optimisation will converge towards a solution that displays a setting that could be observed in real flies. When using the joint phases obtained through the optimisation, the pattern of muscle activation does not match the sequence of activation that is physiologically observed in flies. Indeed, in stick insects the muscles activate following a specific order with for example the levator, the extensor and the protractor activating in that relative order shortly before swing (Rosenbaum et al., 2010). There is no constrain on that sequence through the optimisation, and the proposed implementation of the sensory signals is not possible if the sequence of muscle

activation differs from what is physiologically observed. The joint phases (*opti_joint_phases*) were therefore hand-tuned in the *update_parameters* method to match a physiological pattern of muscle activation. Moreover, the literature mentioned above only holds for stick insects, and it makes sense to consider that the middle legs behave like stick insect legs. Nevertheless, the hind legs in particular do not display the same orientation as the ones from a stick insect and are more oriented towards the back. The extension during the retraction is therefore preferred over extension during the protraction for the middle legs, as more force can be generated to push the fly frontwards, and the used joint phases are consequently adapted to take that into account. Figure 6 shows an example of the activity of the muscles for all three joints of the left middle leg. We can observe the hand-tuned offset mentioned above between the three flexor or extensor muscle oscillations. We also see the flexor/extensor offset between the left and the right plot, which corresponds to a phase of $\pi/2$ and represents one of the vertical arrows on the network architecture (Figure 2). As implemented in the program, the oscillations are clipped accordingly to some physiological measurements of muscular activity, as shown on Figure 6 the activity of the left middle leg depressor muscle is clipped very high, meaning that the activity of this muscle does not physiologically drop past the threshold used here.

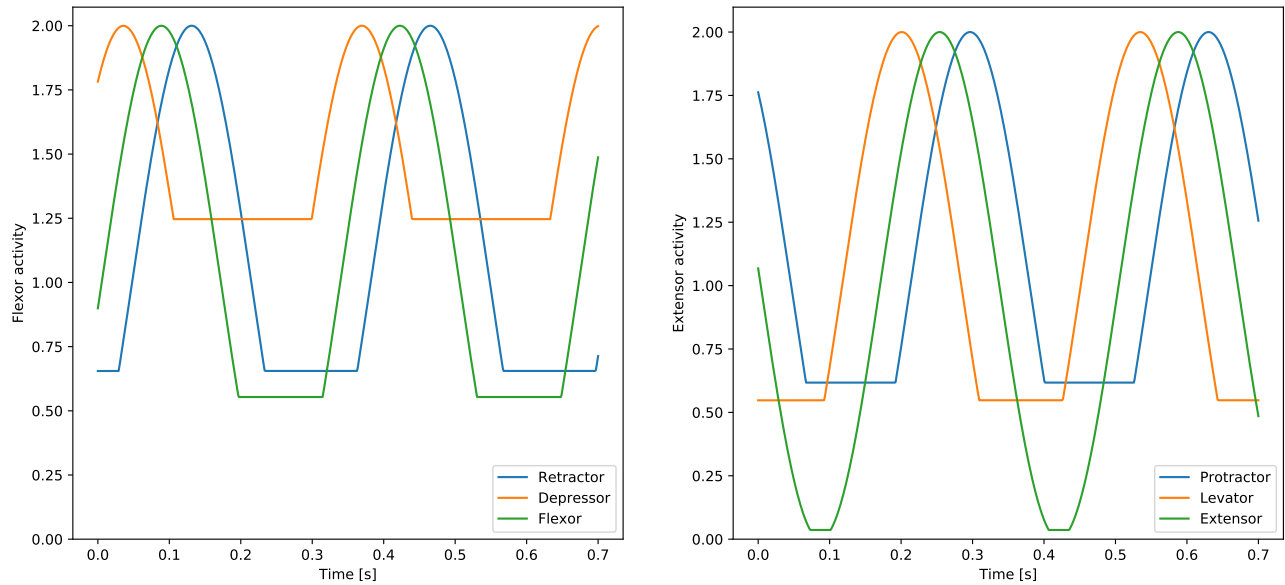


Figure 6: Example of flexor (left) and extensor (right) activity for all the muscles of the left middle leg (LM) without sensory feedback

3.4 Inter-leg Coordination

The behavioural mechanisms giving rise to inter-leg coordination in stick insects have long been studied and reviewed, especially by Holk Cruse, who published many papers attempting to decipher the mechanisms of action of the coordination between legs. A list of the rules governing these effects named "Cru(i)se control" has been drawn up based on his many publications, e.g. in Cruse (1990) or Cruse et al. (2007). Before digging into what coordination rules are used in the current model, it is important to note a change in the hierarchy of the network that is made necessary to implement the effects of inter-leg coordination. As shown on Figure 2, the neural

network is based on having one independent oscillator working for each muscle, and if we wish to implement inter-leg coordination, we want to have the ability to act on the oscillations of a leg as a whole unit, for example to pause or shift its activity. That means that somehow the oscillators within a same leg have to be related and coordinated. With the previous model, a shift in the activity of the Left Front Coxa joint will for instance only result in a phase shift in the oscillations of that particular joint, which will mess with the pattern of synchronisation with the other oscillators within that same leg. The introduction of hierarchy of oscillators helps with that issue.

In order to model all the joints of a leg as being part of the same unit, we build a network with master/slave-oscillator hierarchy. The activity of a slave oscillator being directly related to the one of its master, minus an offset ϕ necessary to model the offset separating the activation of the muscles from the different joints. Equation (6) shows the expression of f_{mn_flexor} for the slave joints (ϕ is 0 for the master joint) :

$$f_{mn_flexor} = master_{mn_flexor} - \phi \quad (6)$$

Here, the oscillation of each Coxa joint is the one accounting for the oscillation of the other two remaining leg joints, meaning that the Femur oscillators and the Tibia oscillators are simply using the output of the Coxa oscillators minus the associated offset. These offset phases were hand-tuned as explained in section 3.3 to match a physiological pattern of locomotion. Figure 7 provides an example of the master/slave relationship acting on the flexor muscles of a leg.

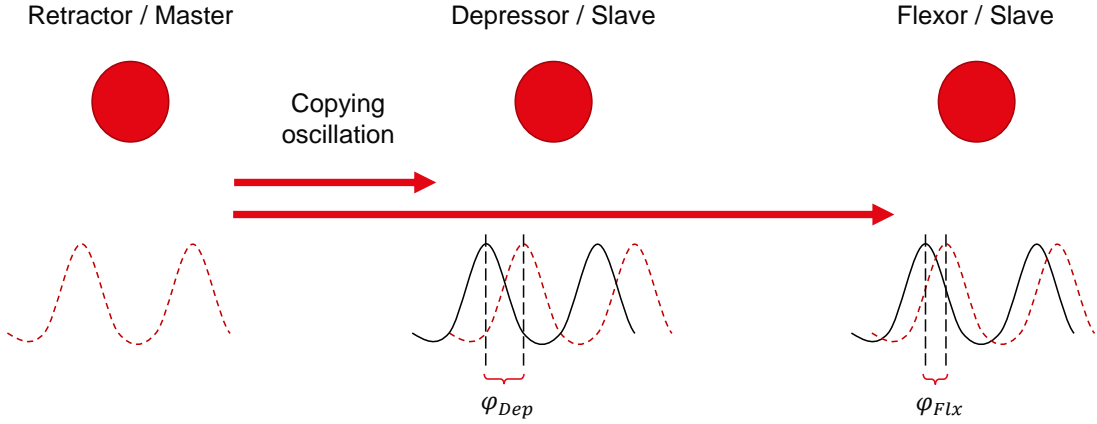


Figure 7: Diagram showing how the 3 flexor oscillators of a leg are copying the oscillation of the Coxa oscillator minus an offset that is specific to each joint. The red circles represent oscillators and the red dotted sine represents the master oscillation

With that modification of the motoneuron output, we're making sure that any modification of the oscillation of the master oscillator will be carried out to the two downstream oscillators, so the flexor/extensor muscle activity equation for the slave oscillators becomes :

$$A_{flexor} = Amp_{flexor} \cdot R_{flexor} \cdot (1 + \sin(master_{mn_flexor})) \quad (7)$$

Then, the inter-leg coordination can be incorporated into the model by directly acting on the input of the master activity oscillation. As explained in the rules detailed below, we wish to either increase the frequency of a leg (of the Coxa/master oscillator), or pause that leg depending on some signal retrieved from the other legs (later see Figure 8).

$$master_{mn_flexor} = f_{mn_flexor} \cdot \nu_{interleg} - \phi_{interleg} \quad (8)$$

Equation (8) shows the computation of that input. f_{mn_flexor} is obtained through the solving of the equations of motion, and its computation remains unchanged for the duration of the simulation. A copy of that value additionally taking the inter-leg coordination effects into account is then computed, and $master_{mn_flexor}$ is set to that value. $\nu_{interleg}$ and $\phi_{interleg}$ represent the inter-leg sensory input that can vary depending on the other legs' activity and the values they take are developed in the next subsections 3.4.1 to 3.4.3.

The specific sensory events that can trigger transitions or pausing in the activity of other legs were described by Holk Cruse. The diagram shown below on Figure 8 depicts the mechanisms of actions of each of the rules that were implemented in the current project, the arrows representing the direction of action and pointing towards the leg whose activity will be affected by the sensory event.

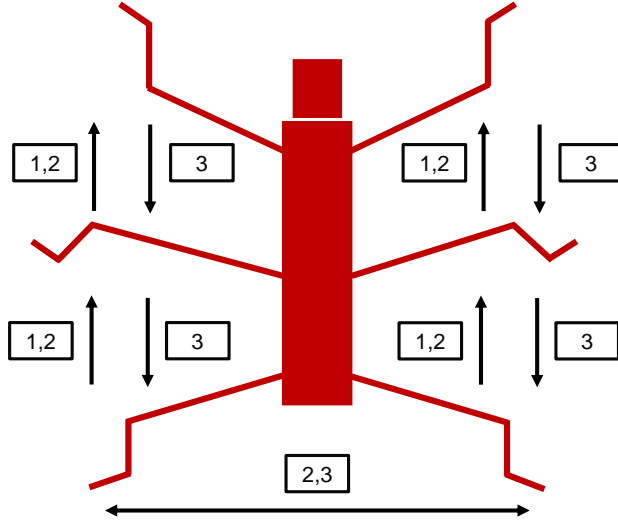


Figure 8: Diagram of the ipsi- or contralateral effects of each rule. Each arrow represents the direction of action of a rule. It points from the leg that is signaling a sensory event to the target leg whose activity will be modulated. Rule 2 and 3 are acting contralaterally between the 3 leg pairs.

3.4.1 Rule 1

Rule 1 is only working ipsilaterally and is active on a target leg when its posterior leg is still in swing. Rule 1 causes the lift off of the target leg to be suppressed, meaning that the leg will be locked in stance. To implement that rule in the program, the information on the swing of the posterior leg is retrieved, and rule 1 is active when the two following conditions are met :

- The ground reaction force acting on the posterior leg has been zero for some iterations and the leg is going forward, meaning that the posterior leg is in swing
- The target leg is still in stance and reaching the end of stance

If these two conditions are met, the target leg will be locked in stance by setting the amplitudes of the muscle activities to 0 while the rule is still active. Some of the activities like the Tibia joint flexor activity are not set to 0 but simply reduced to prevent the legs from flattening on the ground, which is what happens when no torque is acting on a leg. Rule 1 induces a lasting phase shift, $\phi_{interleg}$, that keeps the oscillation in the state at which it is when the rule is activated, and that ultimately delay the oscillation by a shift representing the duration of the pause.

3.4.2 Rule 2

Rule 2 is working both contralaterally and ipsilaterally. It is active when the two following conditions are met :

- An anterior or contralateral leg just touched down, i.e. reached the end of swing
- The target leg is at the end of its stance

The activation of rule 2 results in the facilitated onset of protraction in the target leg. To model that, the end of the stance phase is accelerated in the target leg. $\nu_{interleg}$ is increased as soon as the rule is activated (for example to 2), and goes back to a normal frequency of 1 after inactivation, which means when the target leg starts swinging. With the implementation of the master/slave organisation detailed in section 3.4, the increased frequency will be carried out to all the other slave oscillators of the same leg, causing that leg to half the duration of the remaining stance if the frequency is doubled.

3.4.3 Rule 3

Rule 3 is similar to rule 2 in its implementation in the way that it is shortening the stance phase of a target leg upon certain signals coming from the other legs. It is active contralaterally and ipsilaterally, and is active when :

- A posterior or contralateral leg is in stance
- The target leg is still in stance but at a later stage in its stance phase as compared to the signaling leg

For this rule again, the interleg frequency $\nu_{interleg}$ is increased for the whole duration of the rule activation.

Combining these rules together, the simulation is expected to be able to correct inefficient coordination of the legs and converge towards a more efficient and more stable gait. Indeed, the combination of these rules should be shifting the phases between the legs so as to approach a tripod-like gait pattern, which is what we most commonly observe in a physiological fly.

Extra caution has to be taken when modifying the frequency of the oscillators. According to (8), when $\nu_{interleg}$ increases, $master_{mn}$ does too, but as the frequency goes straight from 1 to another higher value, continuity of the oscillation has to be ensured. Using the example of the $\sin(2\pi x)$ function, which has a frequency of 1, if the frequency is increased to 2 at $x = x_0$, we do not have that $\sin(2\pi x_0)$ is equal to $\sin(4\pi x_0)$. Indeed, as shown on Figure 9, we need

to add a phase shift to avoid the jump of the sine and to ensure continuity of the oscillation. To deal with that, each rule induces a phase shift upon activation and inactivation, as there is a frequency change back to a frequency of 1 as well, and these phase shifts are put together as $\nu_{interleg}$ to compute the $master_{mn}$ of the leg.

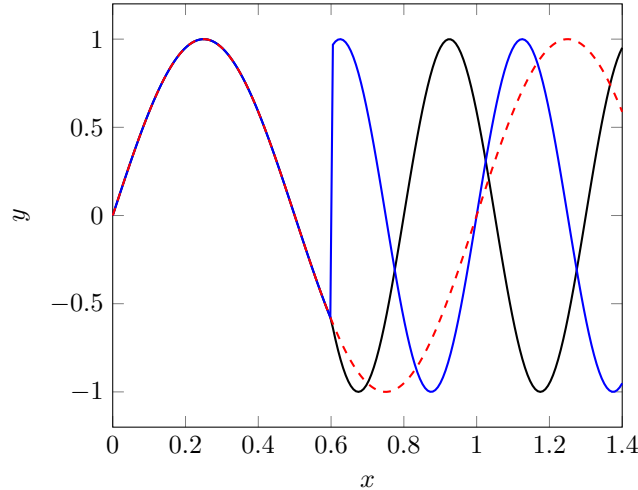


Figure 9: Plot of $\sin(2\pi x)$ in red, and of $\sin(4\pi x)$ with and without the introduction of the phase shift (respectively in black and in blue) for $x > 0.6$. The curve in black ensures continuity while the blue one does not. The expression of the black curve for $x > 0.6$ becomes $\sin(2\pi(2x - 0.6))$ and effectively fixes the jumping issue.

One last issue has to be addressed : the order of priority of activation of the rules. Rule 1 is given the priority, as it is important to keep the anterior leg in stance in order to avoid having two ipsilaterally neighbouring legs in the air at the same time. That means that when rule 1 is activated, rule 2 and rule 3 are inactivated and $\nu_{interleg}$ is reset to 1 (and the phase shift adapted as it represents the opposite scenario as the one depicted on Figure 9). For the order of priority of rule 2 and rule 3, if one of the two rules is already active on a leg, that rule stays active and the other one can not activate for the duration of the other rule. Same goes for the activation of the same rule ipsilaterally and contralaterally : only one can be active at a time and priority is given to the condition that is met first. That still means that some rules can become activated back to back on successive iteration and the induced phase shift has to take that into account. Indeed, the phase shift to ensure continuity is itself proportional to the differential of the frequency before and after the sensory event. For instance, if a specific leg has rule 2 active at $t = t_0$ and then rule 3 active at $t = t_0 + 1$ (following the inactivation of rule 2), and both rule result in increasing the frequency to 2, no phase shift has to be added, as there is no change in the frequency of the oscillation.

4 Results

The effects of sensory feedback on both single-leg and inter-leg levels can be easily observed by running the simulation and by picking the options of interest. The contribution of each of the 3 sensors can be independently selected to analyse the effects of a feedback in particular, same goes for the inter-leg coordination rules.

4.1 Single-leg Coordination

This section details the contribution of each single-leg sensory feedback to the simulation.

4.1.1 GRF Feedback

When the GRF feedback is switched on, it increases the flexor and the depressor activity for the first half of stance. Figure 10 shows what effects the feedback has on the activity of the flexor and of the extensor muscles. We observe an increase in the depressor and the flexor activity scaled on the amount of ground reaction force as the leg strikes. The increase in amplitude is not completely smooth as it is calculated based on the amount of GRF applied to the tip of the leg, and the profile of the GRFs is not very smooth in itself. Scaling the GRF is important as it still lets the levator activity increase when the amount of GRF decreases, e.g. when approaching the end of the front legs stance, if the levator activity is too significantly contained, the elevation of the leg during the swing will be reduced.

The GRF feedback provides an interesting contribution for the gait generation for each leg. It increases the amount of pull that the middle and hind legs can generate as additional depressor activity is expressed when needed, which ultimately improves the rolling of the ball. For the front legs, the flexor activity increase is important to counterbalance the heavy strike amplified by the fCO feedback. The fCO feedback causes the front legs to speed up as they hit the ground and they tend to overextend, and the GRF feedback seems to reduce the extent of that effect.

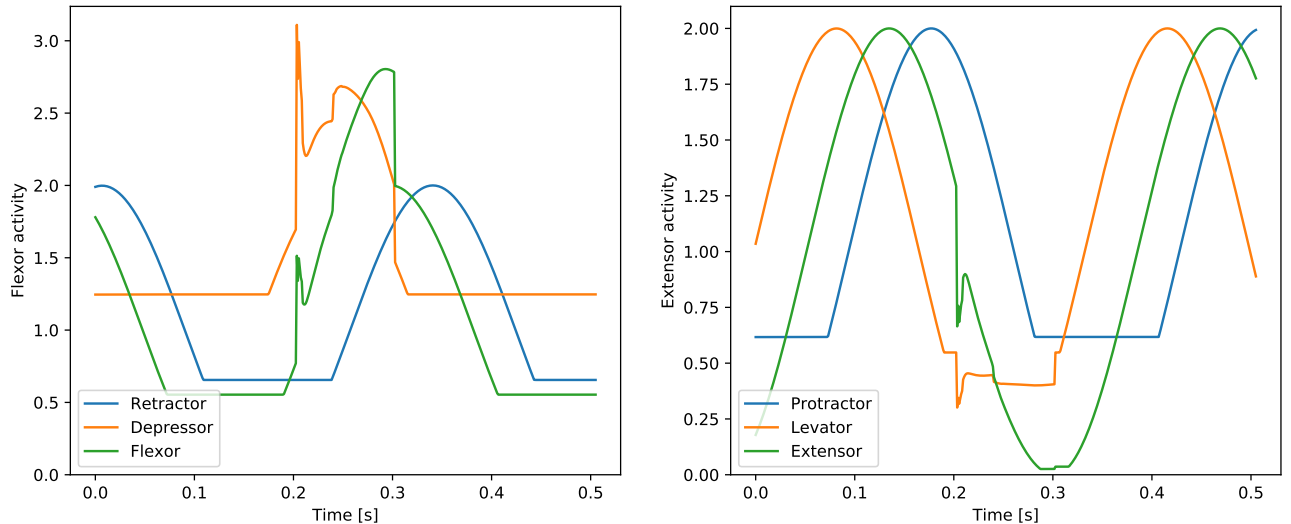


Figure 10: Flexor (left) and extensor (right) activity of the LM leg with the activation of the GRF feedback when the leg strikes at around $t = 0.2s$ up until $t = 0.3s$.

4.1.2 fCO Feedback

Figure 11 shows the modification in the oscillations caused by the fCO feedback. Once the FTi angle threshold is reached, the feedback is activated and a phase shift occurs in the Dep/Lev oscillation. This feedback is only necessary and used in the middle and the front legs. The main issue with the hind legs is to try to lift them up and keep them high during swing, so an increased drive to lower down the hind legs at the end of swing is not useful. fCO is interesting as it helps with shortening the front legs' swing. One essential feature for the efficient working of the inter-leg coordination (as detailed in section 4.2) is to have legs that display similar lengths of swing and stance, otherwise the inter-leg timing of the legs will have to be constantly updated. The fCO feedback forces the front legs to start their swing depression phase instead of lifting higher up and then spend that additional spare time of the oscillation in stance as the shift is reset to 0 when the leg strikes (fCO feedback condition). For the middle legs, that feedback is essential to deal with the end of action of the CS feedback in particular. It avoids the middle legs to stay in the air for longer when their protraction has already come to an end, and that unexpected event is especially emphasised when CS feedback is turned on. The fCO feedback also counterbalances the shortening of stance caused by the CS feedback-induced early swing transition, as it brings the middle legs to the ground faster.

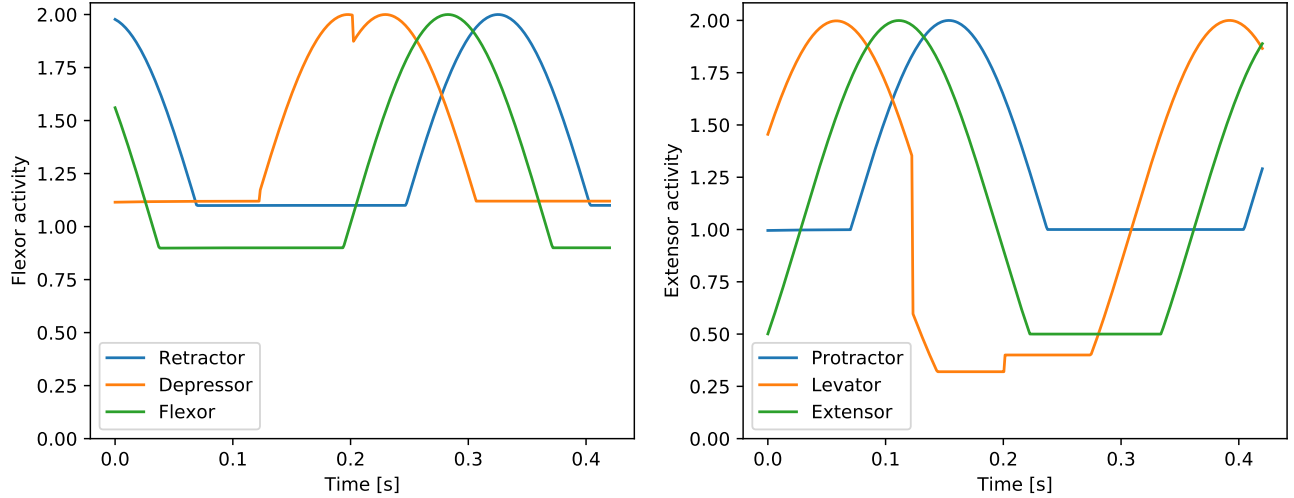


Figure 11: Flexor (left) and extensor (right) activity of the LF leg with the activation of the fCO feedback at around $t = 0.12s$ and until $t = 0.20s$. We observe the phase shift of the Dep/Lev oscillations, not noticeable in the Depressor curve, as the changes occur below the clipping value. The shift back to the normal oscillation, however, is clear on both plots.

4.1.3 CS Feedback

The CS feedback is switched on at the very end of stance and successively acts on the Dep/Lev, Flx/Ext, and Ret/Pro muscle couples. A small delay of 10 time steps is introduced between their inactivation/activation. All the activities from the flexors are set to 0 as shown on Figure 12 until the end of the feedback activation. The activity of the extensors is shifted later in the oscillation at a point representing a swinging leg, the levation is therefore increased. Some changes in amplitudes are also applied to control the extent of the levation and of the extension,

hence the jump in the oscillation when the feedback ends. The phase shift is linearly going back to normal as the feedback reaches the end of its set activity duration time, but that is not made noticeable on the plot due to the jump in amplitude. The CS feedback is particularly useful on the hind legs, as they are now clearly able to generate a lasting swing phase. That feedback also acts as a modulator of the stance duration, lowering the load threshold is a simple way to trigger the feedback earlier and shorten the stance.

The CS feedback has to be used in combination with the fCO feedback in the middle legs in particular to counterbalance what is happening when the amplitudes jump back to normal and lower the leg to the ground without having to wait for all levator activity to come to an end. Finally, the CS feedback was not used in the front legs, as it is a way to trigger the transition to swing, and the issue with the front legs has continuously been to lengthen stance as much as possible, not to cut off the end of the phase. Using it was therefore not necessary to have similar stance and swing duration as detailed below.

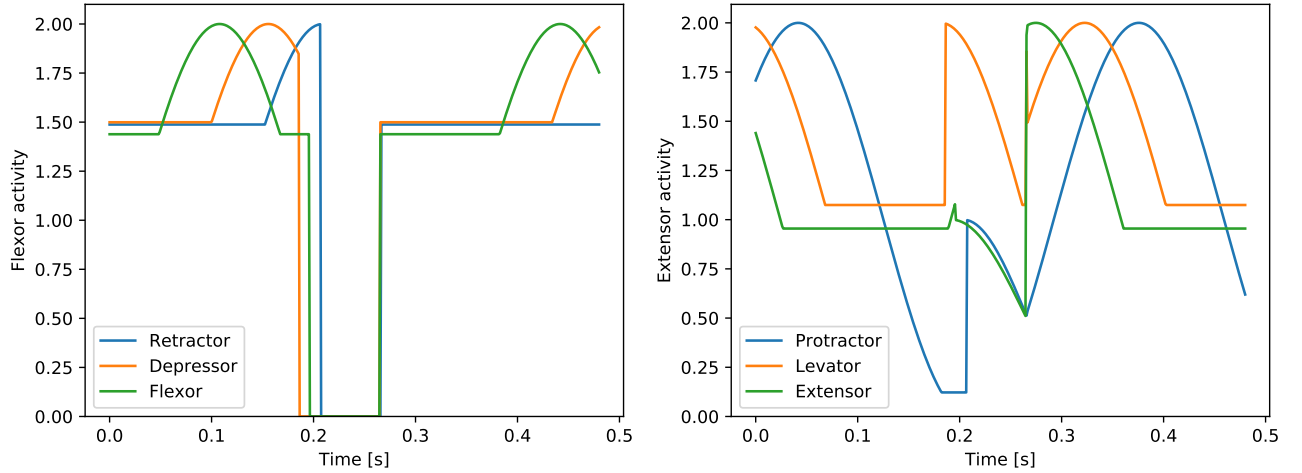
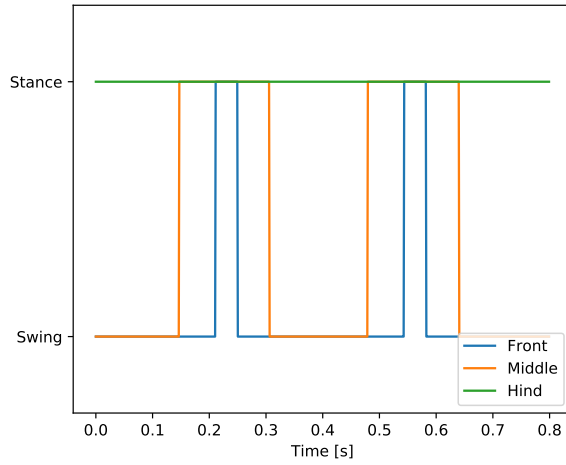


Figure 12: Flexor (left) and extensor (right) activity of the LH leg with the activation of the CS feedback at around $t = 0.185s$ and until $t = 0.265s$.

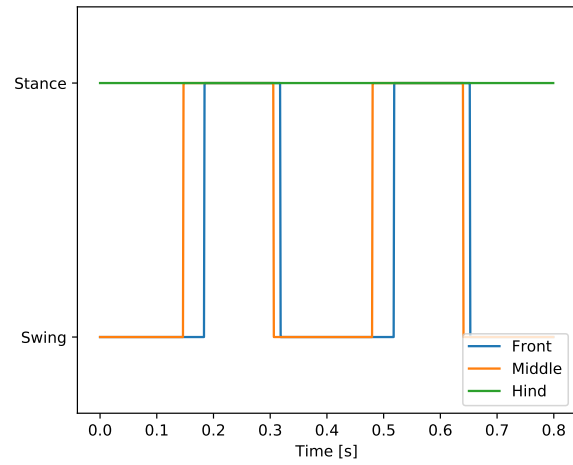
In order to reach stability and to maximise the chances to have three legs on the ground at a specific time, it is essential to have legs that display similar stance and swing duration. Without the work done on the feedbacks and on the clipping of the legs, large differences were observed, especially regarding the duration of stance for the front legs. That is particularly essential in order to have an efficient inter-coordination of the legs and to not be forced to constantly shorten the stance of other legs by increasing their oscillation frequency. That could keep on happening as an attempt by the inter-leg rules to compensate the potential delays that can be introduced for example by rule 1 with a leg staying in swing longer in average than its target leg. Tuning the contribution of the 3 feedbacks together along with applying some modifications to the clipping of the front legs were necessary to achieve that goal.

Figure 13 shows three plots comparing the stance and swing duration for the three left-sided legs in three configurations : before any changes were made, after the unclipping work on the front legs, and after implementation of intra-leg sensory feedback. We observe that the stance period was almost non-existent for the front legs before, and that does not let much time for the inter-leg coordination rules to act during stance. The hind legs are kept in stance for their whole cycle without the implementation of sensory feedback, and the duration of the front leg's

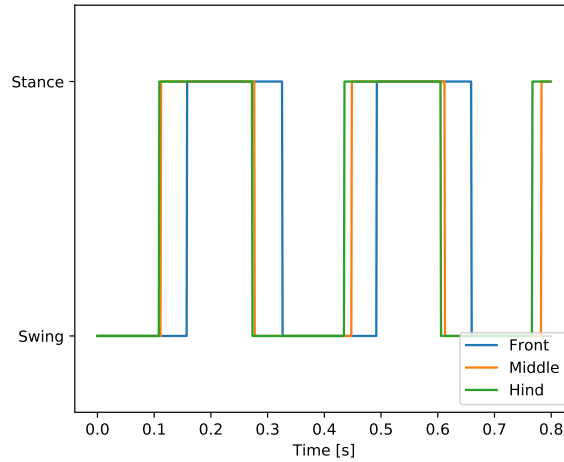
stance is still significantly different than the one of the middle legs (stance/swing duration of $0.160s/0.173s$ and $0.133s/0.200s$ respectively for the middle and the front legs). Eventually, the relative duration of stance and swing are almost even for all legs after implementation of the sensory feedback. From the plots, we get a stance/swing relationship of $0.168s/0.162s$ (hind legs), $0.165s/0.170s$ (middle legs) and $0.168s/0.165s$ (front legs). Reducing the gaps in stance duration between the legs can help with minimising the amount of time the inter-leg coordination rules will have to be called to ensure convergence and even maintenance of a tripod gait.



(a) Without both unclipping and sensory feedback



(b) Without sensory feedback



(c) Final model

Figure 13: Comparison of the stance and swing respective duration of the three left-sided legs in three different settings. These plots were obtained using the binary output of the ground reaction force sensor.

4.2 Inter-leg Coordination

Figure 14 shows the effects of rule 1 on the level of the oscillations. The activity is not completely set to 0 for the duration of the rule, but the leg activity is maintained constant and significantly reduced as compared to its normal activity. Some of the amplitude is preserved to maintain the legs in a flexed position when locked in at the end of stance, as we wish to avoid that the legs start extending at the end of their stance when being locked in that state through the activation of rule 1. We observe that the activity starts at the same stage in the oscillation after the pause as it was before the activity was stopped, which means that continuity of the muscle activation is ensured through the use of rule 1.

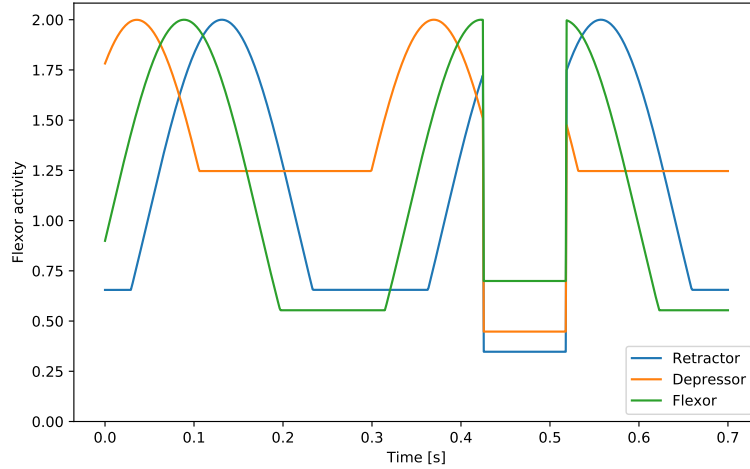


Figure 14: Flexor activity of the LM leg with rule 1 active for approximately 0.1s at $t = 0.42$. The LM leg is locked in stance until the posterior leg (LH) reaches the end of its swing, signaling the end of rule 1 activation.

Rule 2 and rule 3 both increase the oscillation frequency for the duration of their activation. The resulting effects on the muscle activity is plotted on Figure 15. We observe continuity in the oscillations during and after the activation of both rules, meaning that the rule offsets effectively manage to avoid the jumps in the oscillation curves. The activation of both rules is followed by a shortening of the remaining stance phase, and they stop once the target leg initiates its swing phase.

For efficient use of these rules that modulate the frequency of oscillation on the front legs, an additional manipulation was made necessary. The variations in oscillation frequency are not directly transferred to the motion of the leg, e.g. if we double the master oscillator frequency at half stance, the remaining stance will not be the exact same motion but twice faster. Indeed, an increased frequency means that the torque, although increasing/decreasing faster, will have less time to act on the dynamics of the leg. Due to the very high clipping of the front legs, the true amplitude of their oscillations is made very narrow if we leave the clipping as it is. That combined with an increased frequency results in a reduced range of motion, in particular of the front legs, to the extent that the legs do not display a complete range of motion and reach a significantly lower height in swing. That could cause problems as a leg could not be reaching a threshold needed for the activation of some intra-leg feedbacks. To deal with that, the clipping on the front legs was reduced. The amplitude of the oscillations is therefore increased and the effects of any potential frequency change are working properly.

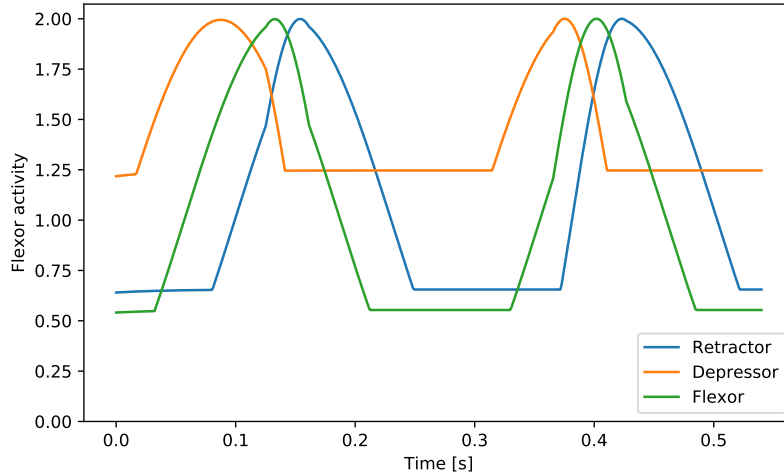


Figure 15: Flexor activity of the LM leg with the activation of rule 3 and rule 2. Rule 3 is activated by the anterior (LF) leg from $t = 0.125$ to $t = 0.160$ and rule 2 is activated by the contralateral leg (RM) from $t = 0.365$ to $t = 0.415$. Here, the activation of both rule 2 and 3 triggers the doubling of $\nu_{interleg}$ for the duration of the rule.

5 Discussion

In this contribution, we present the implementation of the sensory feedback in a neuromechanical model of a *Drosophila melanogaster* on two different levels : the intra-leg coordination ruling the coordination of the activity between the joints of a leg, and the inter-leg coordination, providing a set of rules that modulate the inter-leg phase shifts. Using the available theoretical knowledge in the field, we try to observe to what extent the previous network of the simulation can be modified and adapted to take sensory feedback into account, and how the current model can benefit from the implementation of the gathered knowledge in the field.

On a single-leg coordination level, the major contribution of the work by (Bidaye et al., 2018) has shown to be very useful. Although not all the sensory signals are implemented in the current simulation, as some of them either do not occur at the expected time, or others were not bringing any improvement to the intra-leg coordination pattern (e.g. the fCO extension feedback on the hind legs). The implementation of some particular sensory events selectively triggering certain muscle activation as described in the review by (Bidaye et al., 2018) ends up being a positive addition to the model. It becomes especially interesting when considering the simultaneous implementation of inter-leg feedback in the simulation. An important condition to reduce the complexity of the inter-leg coordination is to try to even up the stance and swing respective duration among the legs, and the feedbacks can be modulated to bring a leg down or lift it up earlier in the rhythmic oscillation. The intra-leg feedback therefore seems to be an interesting addition in regard of the inter-leg coordination, as it provides a tool to ensure the good functioning of coordination rules. The intra-leg feedback also improves the overall stability and the amount of pull that can be generated through retraction (mainly performed by the middle legs' retraction). However, the activation of some feedbacks can fail in certain occurrences, as their activation is mainly relying on some thresholds and added conditions to minimise the chances for it to become active at a different stage of the gait cycle. The interaction of the inter-leg feedback and its ability to modulate the oscillation frequency can, in

very specific and rare circumstances cause a reduced range of motion, for instance in the front legs, if not enough time is available to produce the extensor amplitude necessary to reach the fCO threshold. Using very specific conditions and adding extra constraints on the leg angles and other attributes wishes to prevent these unexpected situations from happening, but it does not always manage to do so.

The starting focus of the project was to add the contribution of the single-leg feedback, but the interaction of the two levels of feedback eventually showed to be more interesting, as the improvement of the gait really seems to be relying on the simultaneous use of both intra- and inter-leg feedbacks. The inter-leg feedback is able to act on the inter-leg frequency and on the inter-leg phase shifts to modulate the coordination between the legs with the ultimate aim to converge to tripod gait. The three implemented rules are aiming towards a tripod locomotion pattern, and they tend to do so after 3-4 gait cycles. Rule 1 seems to work especially well and is a very efficient mean to act on the coordination between two adjacent legs. The frequency modifications applied by rule 2 and 3, however can have a more negative impact on the stability of the fly. Their effects seem to be optimal on the hind and middle legs, but the front legs are a lot more sensitive to frequency changes. Even a slight increase in the frequency of the front legs results in a significantly stronger retraction impulse, and this can sometimes cause the legs to lift off the ground for a few time steps, which can reduce the amount of time that can be saved in stance in these specific legs.

If the semester were to restart, less resources and time would be spent in physiologically understanding the mechanisms of intra-leg sensory feedback. Indeed, dealing with the adaptability of the network and of the inter-leg coordination felt more interesting and was only started in the last third of the semester. Intra-leg feedback is still an essential tool necessary for the good functioning of the project, but spending more time thinking about other gait patterns that could be expressed with the current simulation, or considering other alternatives to deal with the complexity of the network would have been an exciting work. The complexity of the network is now down to reading the output of the Coxa master oscillators and inferring the activity of each leg from it. That question could be studied with more depth, as there seems to be a way to have all the remaining Coxa joint oscillators reading the output of a central master oscillator. Generating one oscillation and having all the Coxa oscillators copying it incorporating the inter-leg frequency and phase shifts might offer a reliable way to express the same gait pattern with a unique oscillator.

Overall, the current simulation provides a way to express a tripod gait with a simple network. Further work could be done on first considering the addition of extra rules or modification of the current interleg rules to improve the number of gait cycles needed for the simulation to recover from some unexpected phase perturbations. A fast transition from a disturbed gait to an optimised gait would obviously be preferred and more optimal, as the simulation could be subject to a high frequency of unexpected events, and the faster it finishes dealing with a perturbation, the faster it can deal with another one, making the model more robust to them.

In addition, tripod gait is aimed here, but the implementation of other inter-leg coordination rules should be a way to express different types of gait, without having to modify the mechanisms of intra-leg coordination. The sensory feedback implemented should provide a template for the expression of different gait patterns if wanted. Indeed, other patterns such as trotting or some forms of quadruped gait could be more adapted to a certain simulation depending on the walking pace, and implementing the adapted coordination rules could offer a solution to that issue. Finally, it paves the way to the implementation of more complex and essential adaptive

mechanisms such as reflexes. For example, the elevator reflex could be one interesting addition to the present simulation. The ultimate goal of such simulation would be to be able to model walking on varying environments, such as walking on uneven terrain, containing holes, or on inclined ground. The adaptive nature of locomotion quickly becomes essential in order to deal with more unpredictable conditions of walking or to deal with unexpected perturbations and get back to an efficient gait as fast as possible.

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7 Gantt Chart

Week		
1	Expectations	<ul style="list-style-type: none"> - Meet up with lab director and supervisor - Visit the lab - Introduction to the project and guidelines
	Comment	A meeting with both the lab director and supervisor permitted to get familiar with the aim of the project
2	Expectations	<ul style="list-style-type: none"> - Dive into literature and read the provided articles - Strengthen knowledge around the subject of locomotion behavior of insects and of the fly in particular
	Comment	Many articles on intra-leg sensory feedback were read. Looking back the focus might have been too directed towards intra-leg feedback when inter-leg feedback felt more interesting and useful to implement. All knowledge gathered around the subject was not always useful to the project but in the end it is part of the research work
3	Expectations	<ul style="list-style-type: none"> - Identify most important modulators of sensory feedback, which sensors to implement - Find out what they are capturing - Where to model them on the already developed fly model
	Comment	The location, function and functioning of the chosen sensors correctly identified. Some time spent on learning about their distribution and their functioning when only what they sense and what they cause really matters to the current project. It delayed the start of the following week's work
4	Expectations	<ul style="list-style-type: none"> - Set up environment - Familiarise with code and model - Design architecture of network and connections incorporating the sensors in the model
	Comment	The project was first started using a virtual box but it quickly showed up as being inefficient and not able to display the simulation at a decent rate. The setting up of a dual boot and other issues with reproducing the work environment again delayed the start of the coding part of the project
5	Expectations	<ul style="list-style-type: none"> - Adapt the network and the CPGs to take the sensory feedback into account in the model (at the code level) - Run an optimization with the implemented architecture to check if everything runs correctly
	Comment	Modification of the torque equation and some primary insights on how to reproduce the effects of the sensory feedback, but more work needed to have all the three sensors in action
6	Expectations	<ul style="list-style-type: none"> - Midterm presentation on 22/10/2020 - Catch-up with planning if necessary
	Comment	More time spent on working on what sensory events to implement and what muscles they activate or inhibit

7	Expectations	- Start optimisation process - Analyse behavior of the model with newly implemented network
	Comment	As acknowledged in the midterm presentation, acting on the torque ended up not providing an efficient way to act on the motion of the fly. Rethinking of the problem.
8	Expectations	- Further optimisation - Debugging
	Comment	Adaptation of the implementation of the feedback on the output of the oscillators rather than on the torque. Intra-leg sensors starting to work, but less time than expected to improve their performance
9	Expectations	- Adding effect of sensory feedback on interleg coordination and stance/swing transitions
	Comment	More time spent on intra-leg sensory feedback as it is not point. Review of the literature on inter-leg feedback discovered during the first stage of literature review
10	Expectations	- Removal of sensors that might disturb the model - Simplify the sensory feedback component of the network getting rid of the connections that are not significant for the model
	Comment	Inter-leg coordination ended up being the main interest of the implementation so the focus was directed towards making the inter-leg feedback work to improve the stability of the fly
11	Expectations	- Testing sensory feedback with more degrees of freedom - Complexify the network if necessary
	Comment	Still working on the inter-leg feedback. Unfortunately not much time left to think back on a working complete implementation and to consider adding/removing things.
12	Expectations	- More optimization - Consider implementation of exteroceptors, justifying which ones and why these particular ones
	Comment	Discovery of issues in very rare situations when some rules are activated on back to back, and realisation of the offset jumping issue with a combination of rules. Week spent figuring out how to deal with that issue
13	Expectations	- Document the code/comment, detail how/where to run the code - Draft of final report to get some feedback
	Comment	Documentation of the code done all along the semester. Dealing with the front legs high clipping issue and with another problem involving different boundaries used for the left and right side of the simulation body
End	Expectations	- Final report, material and code submission - Final presentation on the 14th of January
	Comment	Time spent on completing the report

Table 1: Gantt chart comparing the expectations before the semester with their fulfilment after completion of the project.