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Computer Simulation of the Neural Control of Locomotion in the Cat

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Abstract

Locomotion is one of the most important behaviours and requires interaction between sensors at various levels of the nervous system and the limb muscles of an animal. The basic neural rhythm for locomotion in mammals has been shown to arise from local neural networks residing in the spinal cord and these networks are known as central pattern generators (CPGs). However, during the locomotion, these centres are constantly interacting with the sensory feedback signals coming from muscles, joints and peripheral skin receptors in order to adapt the stepping to varying environmental conditions. Conceptual models of mammalian locomotion have been constructed using mathematical models of locomotor subsystems based on the abundance of neurophysiological evidence obtained primarily in the cat. Several aspects of locomotor control using the cat as an animal model have been investigated employing computer simulations and here we use the same approach to address number of questions or/and hypotheses related to rhythmic locomotion in quadrupeds. Some of the involve questions are, role of mechanical linkage during deafferented walking, finding inherent stabilities/instabilities of muscle-joint interactions during normal walking, estimating phase dependent controllability of muscle action over joints.

This thesis presents the basics of a biologically realistic model of mammalian locomotion and summarises methodological approaches in modelling quadruped locomotor subsystems such as CPGs, limb muscles and sensory pathways. In the first appended article, we extensively discuss the construction details of the three-dimensional computer simulator for the study of the hind leg neuro-musculo-skeletal-control system and its interactions during normal walking of the cat. The simulator with the walking model is programmed in Python scripting language with other supported open source libraries such as Open Dynamics Engine (ODE) for simulating body dynamics and OpenGL for three dimensional graphical representation. We have examined the functionality of the simulator and the walking model by simulating deafferented walking. It was possible to obtain a realistic stepping in the hind legs even without sensory feedback to the two controllers (CPGs) for each leg. We conclude that the mechanical linkages between the legs also play a major role in producing alternating gait.

The use of simulations of walking in the cat for gaining insights into more complex interactions between the environment and the neuro-muscular-skeletal system is important especially for questions where a direct neurophysiological experiment can not be performed on a real walking animal. For instance, it is experimentally hard to isolate individual mechanisms without disrupting the natural walking pattern. In the second article, we introduce a different approach where we use the walking model to identify what control is necessary to maintain stability in the musculo-skeletal system. We show that the actions of most of the hindlimb muscles over the joints have an inherent stability during stepping, even without the involvement of proprioceptive feedback mechanisms. In addition, we observe that muscles generating movements in the ankle joint

of the hind leg must be controlled by neural mechanisms, which may involve supraspinal structures, over the whole step cycle.

Keywords: Locomotion, Computer simulation, Central pattern generator, Muscle activation, Linear transfer functions, Sensory feedback, Neural control

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To my parents

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Abbreviations and Acronyms

AB	anterior biceps
AEP	anterior extreme position
API	Application Programming Interface
CE	contractile element
CNS	central nervous system
CPG	central pattern generator
EMG	electromyographic
EPSP	excitatory post synaptic potential
FRA	flexor reflex afferents
GAS	gastrocnemius
GTO	Golgi tendon organ
HC	Half centre
IP	iliopsoas
L-DOPA	3,4-dihydroxy-L-phenylalanine
LTF	linear transfer function
MIMO	Multiple Input and Multiple Output
MLR	mesencephalic locomotor region
NMSC	neuro-musculo-skeletal-control
ODE	Open Dynamics Engine
PB/ST	posterior biceps and semitendinosus
PEE	passive elastic element
PEP	posterior extreme position
OE	Output-Error
SAT	sartorius
SEE	series elastic element
SISO	Single Input and Single Output
SOL	soleus
TA	tibialis anterior
VL	vastus lateralis

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Chapter 1

INTRODUCTION

Human fascination in mimicking animal behaviours, especially locomotion, through the construction of artificial devices goes back thousands of years. The machine-like control of locomotion in animals and the biologically realistic control of movement in automata (life-like) has fascinated and inspired scientists, engineers and philosophers, since the time of Descartes (Prochazka *et al.*, 2002). Although we have built animal-like machines for hundreds of years, animals have used legs, wings or fins from the early stages of the life on earth and should be able to give us new ideas for designing artificial systems even if they need not be exact replicas.

Locomotion is one of the most important behaviours of an animal and it has been refined through evolution for hundreds of millions of years. Not only for searching food or places to rest but also for escaping predators animal should locomote. The better the animal can walk, swim or fly, the better are its chances of survival. The study of locomotion in legged animals has a long written history too. Based on the behavioural studies, Aristotle in 350 BC presented certain theories related to animal locomotion in his publications “On The Gait Of Animals” and “On The Motion Of Animals”. He discussed the questions such as why animals have an even number of legs or why motion is always initiated on the right side of the body, etc. To understand how far the biological system for locomotion in terrestrial animals has advanced, one can observe the power of moving the limbs quickly and easily by a cat when chasing a prey or how accurately they walk along on top of narrow fences. This thesis concerns on the study of neural control mechanisms behind locomotion in the cat through computer simulations. Moreover, theories learned through this process can be applied in designing artificial systems such as robotic walking emulators (Kimura *et al.*, 2001; Fukuoka *et al.*, 2003; Xiuli *et al.*, 2006) or actuators resembling muscles (Lieber, 1999; Saga *et al.*, 2005).

The design of models of locomotion that incorporate available biomechanical and physiological data provide a common theoretical platform which can benefit both neuroscientists and computer or robot engineers. While robot and computer engineers use more and more features of the biological control systems such as neural networks and fuzzy logic, neuroscientists use more and more concepts and mechanisms of modern control theory. Moreover, due to the advancement of science and technology, study of locomotion in mammals has been divided into several branches of medicine. For instance, physiologists study the functions of large systems such as leg muscles, leg segments, coordination of legs during walking, etc, whereas neurologists study the nervous system controlling the locomotion on a cellular or network level. Another branch study only the kinematics of the legs during stepping. Consequently, vast amount of data related to mammalian locomotion are available as of separate systems for instance, electromyographic (EMG) signals produced during walking (Engberg and Lundberg, 1969; English, 1978), mechanical properties of muscle/tendon and kinetics (Zajac, 1989; Brown *et al.*, 1996), spinal neural circuits and reflex modulation (Grillner and Zangger, 1975; Miller and Scott, 1977; Hultborn, 2006), skeletal kinematics (Shen and Poppele, 1995; Trank *et al.*, 1996) etc. The computer simulations of locomotion can serve as a platform to combine all those separate systems into a complete locomotive system and to study the interactions among the different systems. For this thesis, the neuro-musculo-skeletal-control (NMSC) system of the cat hindlimb is the subject of modelling.

The basic neural rhythm for locomotion in mammals has been shown to arise from local neural networks residing in the spinal cord and these networks are known as CPGs. However, during the locomotion, these centres are constantly interacting with the sensory feedback signals coming from muscle spindles, Golgi tendon organs (GTOs), joint receptors and peripheral skin receptors in order to adapt the stepping to varying environmental conditions. The biological background in relation to the mammalian locomotion will be discussed in more detail in the next chapter. If one wants to investigate a certain interaction from the above mentioned list, it is impossible to do a neurophysiological experiment since we can not isolate a neural mechanism in a living animal. Thus, a more practical solution would be to use a biologically realistic computer simulation of stepping of the animal model that incorporate the NMSC system for locomotion. Hence, a thorough understanding of the neural and mechanical mechanisms that underlie locomotion can be achieved only by using computer simulations in parallel with physiological investigations (Pearson *et al.*, 2006).

1.1. Scope of the Thesis

Our goal is to understand the neural mechanisms behind mammalian locomotion through computational modelling and simulation of stepping. Neural control of locomotion involves all levels of the nervous system in a hierarchical manner (Orlovsky *et al.*, 1999; Kandel *et al.*, 2000) but so far we have mostly concentrated on the lowest level; the peripheral nervous system and the spinal

cord. This Licentiate thesis summarises my work of the past two years. Most of the work presented in this thesis is based on the neural control of mammalian locomotor system, especially the networks responsible for generating rhythmic stepping in the legs and their interactions with limb muscles and proprioceptive feedback. The aim has been to develop a biologically realistic walking model of a quadruped locomotion in a computer simulated environment and to use the model to answer further specific neuro-physiological questions related to rhythmic walking. Involving questions are role of mechanical linkage during deafferented walking, phase dependancies of muscle-joint interactions and their relation to muscle synergies, estimating stability and controlability of muscle action over joints, role of sensory feedback and phase dependent neural control mechanisms. Most of the available neurophysiological data for mammalian locomotion are on stepping in the hind legs of the cat. Therefore, we started with the implementation of a model of the NMSC system for the cat hind leg to be used in a simulated environment.

1.1.1. Structure and Overview

This section follows a brief description of the articles that are included in this thesis and a summary of my contributions to the publications. This concludes the introductory chapter which is followed by a presentation of the relevant biological background on neural control of locomotion focusing on the spinal level. The motor pattern, central pattern generators and limb muscles are revisited as well as their interactions via sensory feedback and reflex pathways. To conclude this chapter a short summary of animal preparations for experimental setups are presented. Subsequently, the modeling approaches are discussed, starting with a brief review of current and past computer models of mammalian locomotion. Questions on the functionality and complexity of the models of locomotor subsystems such as CPGs, limb muscles and sensory pathways are also addressed. Following a short description of the program structure and the system identification methodology involved in **Paper 2**, results from the articles are discussed in a separate chapter. To wind up this thesis we present further directions of our work on which we will be focusing in the future. Then comes the section *Part I* which consists the two publications.

In **Paper 1**, we give the construction details of the three dimensional computer simulator that we developed for investigating the neuro-musculo-skeletal system and its interactions during normal walking of the cat. The implemented model of the cat is based on the previous model developed by Ekeberg and Pearson (2005). We added one more muscle, *sartorius*, to the hind limb musculature and included a central pattern generator (CPG) network for controlling the muscle activations. Moreover, the model is capable of using different control strategies such as CPG driven or finite state controller driven with proprioceptive feedback modulation, for regulating muscle activations by simply adapting the corresponding script file for the controller module. We show the it is possible to obtain rhythmic alternating stepping in the hind legs even without sensory feedback to the two controllers. We conclude that the mechanical linkages be-

tween the legs also play a major role in producing alternating gait.

In **Paper 2**, we measure the muscle–joint interactions, at several postures of the cat hind leg throughout the step cycle, and model them as open-loop linear transfer functions from muscle activations to joint angles. The data for this investigation were obtained from the computer simulator that we developed for studying stepping in the hind legs of the cat. The identification process was done by analysing the response of the joint angles to an impulse in the activation of each muscle, while the leg was in locomotion. We have analyzed the controllability and stability of the each muscle action over the joint angles by using identified system transfer functions and their gain and pole plots. We show that the actions of most of the hindlimb muscles over the joints have an inherent stability during stepping, even without the involvement of proprioceptive feedback mechanisms. Furthermore, we show that the ankle joint requires fine neural control mechanisms throughout the step cycle to generate a smooth walking pattern.

1.2. Summary of Contributions

Paper 1: Building the Simulator

My supervisor Örjan Ekeberg (ÖE) suggested the project and, I constructed the simulator and the cat model using Python scripts and other supported libraries such as Open Dynamics Engine (ODE) for body mechanics and OpenGL for three dimensional graphics. I implemented the muscle model for the hind limb musculature in the simulated environment using existing mathematical models and also implemented the CPG model that generate temporal activation patterns, which resemble the EMG activity (Kandel *et al.*, 2000), for each hind leg muscle. I performed all the simulations and the analyses. I wrote the technical report with feedback from ÖE.

Paper 2: Muscle–Joint Interactions

ÖE and I discussed the feasibility of the project. I did the literature survey and the analytical work, and ÖE contributed with clarifying discussions. I performed all the simulations using the simulator which I implemented to obtain the impulse response data necessary for identifying linear transfer functions (LTFs) for open-loop muscle–joint interactions. The activation levels of the muscles, hind leg joint angles and the time were logged in every $5ms$ throughout the simulation and after the simulation, data were dumped into separate text files which I analysed using system identification tools in Matlab to obtain LTFs for the muscle–joint systems. To cover up the entire step cycle, I selected ten different postures of the hind leg for the system identification. I analysed all the transfer functions in relation to their stability and sensitivity. I wrote most of the paper, with feedback from the co-author.

1.3. List of Publications Included in the Thesis

Paper 1: Nalin Harischandra (2007) Building a computer simulator for the study of stepping of the cat, Technical Report TRITA-CSC-CB 2007:01, Computational Biology and Neurocomputing, School of Computer Science and Communication, Royal Institute of Technology, Stockholm, SWEDEN

Paper 2: Nalin Harischandra, Örjan Ekeberg (Manuscript submitted to Journal of Biological Cybernetics) System identification of muscle-joint interactions of the cat hind limb during locomotion

Chapter 2

BIOLOGICAL BACKGROUND

To understand the computational modelling and construction details of the simulator, first we should get a basic understanding of the mammalian locomotor system we are studying. This chapter introduces the biological background for my research. The first section will begin with a brief review of the history of biological locomotion research and is followed by a closer look at some of the key issues involved in such systems. It describes the rhythmic locomotion with an emphasis on the spinal neural control centres and mechanisms. It also describes what are the sensory feedback to those neural centres and how they are modulated to obtain a stabilized stepping of the legs. The second section gives an overview of the limb muscles and their kinetics and kinematics. Moreover, it describes several spinal reflex mechanisms and the relation to simultaneous (synergistic) activity of limb muscles during walking. The literature on neural control of locomotion can be confusing because different experimental preparations (of the animal) are used in different studies. Hence, some of those experimental preparations will be described in the third section. The reader is assumed to be familiar with basic neuroscience. For a more detailed description, one can look for either one of the many good reviews available (MacKay-Lyons, 2002; Rossignol *et al.*, 2006; Frigon and Rossignol, 2006; Windhorst, 2007) or chapters in several course books available— for instance chapters such as *Locomotion* and *Spinal Reflexes* in the *Principles of Neural Science* book by Kandel *et al.* (2000).

2.1. Locomotion

As mentioned in the previous chapter, the study of locomotion in legged animals dates back to at least to the time of Aristotle (350 BC). During the 17th century, i.e. about two thousand years later, Borelli studied the kinematics and kinetics of different forms of animal locomotion such as walking, jumping, swimming or flying (Borelli, 1989). He described the function of muscles along with a calcu-

lation of the position of the centre of gravity in the human body (Wadden, 1998). His work could be credited as the first biomechanical investigation of the gait or the locomotor pattern. In 1836, Weber and Weber made an effort to understand the mechanisms of human walking and they proposed that the human gait is a result of a pendulum effect with the legs oscillating from the trunk (Weber and Weber, 1836). Later, Braune and Fisher (1895) showed that the swinging of the leg resulted much more from the actions of the muscles than from the gravitational force (see review by Baker (2007)).

Towards the end of the 19th century and the beginning of the 20th century, physiologists began to use more and more invasive techniques to study the locomotor system of mammals like cats, dogs or monkeys. After transection of the lower thoracic region of the spinal cord, an animal (a dog) was able to produce rhythmic extensor and flexor locomotor movements in the hindlimbs and to support itself (Freusberg, 1874; Prochazka and Yakovenko, 2001). These movements could happen spontaneously when the animal was lifted from the ground with the limbs extended and hence could result from various non-rhythmic stimuli. Sherrington (1910) studied reflex walking in cats and dogs. For that, he used various preparations of the animals whose nervous system was transected at different levels. Sherrington (1910) concluded that reflex activity from ipsilateral or contralateral limb proprioceptors were essential for the generation of stepping movements. According to his view, a reflex chain, during which a movement of a limb causes a sensory signal to induce the next movement followed by a further sensory signal triggering the next movement, was responsible for producing the stepping. On the other hand, Brown (1911) carried out similar experiments on animals having removed all inputs from the sensory nerves in the leg and was able to produce the same rhythmic walking movements as Sherrington. This led him to postulate a central mechanism which he described as “*intrinsic factors*”, residing completely inside the spinal cord, for the generation of stepping movements. These spinal neuronal control circuits are now commonly known as central pattern generators (CPGs). CPGs can be found in both vertebrates and invertebrates and are dynamically interacting with afferent feedback and reflex circuitry in order to adapt the locomotor pattern to the environmental and motivational conditions (MacKay-Lyons, 2002; Rossignol and Bouyer, 2004). During late 20th century to present, neurophysiologists have been involved in more investigations on the mammalian locomotor system, especially that of the cat. Those experiments lead to a reasonable understanding of not only the neuronal mechanism such as CPGs, sensory feedback and reflex modulations of the cat locomotor system (Grillner and Zangger, 1975; Duysens and Loeb, 1980; Hiebert *et al.*, 1996; Donelan and Pearson, 2004; Rossignol *et al.*, 2006) but also associated biology such as the mechanical properties of the legs and leg muscles, kinematics of the stepping and patterns of electromyographic activity in leg muscles (Engberg and Lundberg, 1969; Zajac *et al.*, 1981; Shen and Poppele, 1995).

Now we can look into more general and/or more specific details of the neural mechanisms related to spinal control of locomotion. Some of the key issues

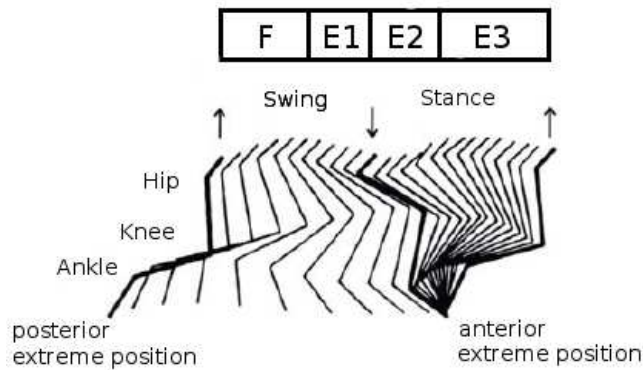


Figure 2.1. The step cycle for locomotion in the cat hindlimb. Limb positions are represented by stick figures. The direction of locomotion is from left to right. The flexion and extension phases are indicated above the stick figures.

such as CPGs and dynamic sensory modulation are briefly described in the theoretical foundation of the **Paper 1**. However those issues, together with some other important issues related to locomotion will be discussed in more detail in the following sub-sections.

2.1.1. Motor Pattern

The rhythmic movements of the legs during stepping are produced by contractions of a large number of muscles. However, the timing and level of activity in different muscles vary widely during the step cycle. The rhythmical pattern and complex sequence of contractions in the muscles during stepping is called the *locomotor pattern* (Kandel *et al.*, 2000). Sometimes the locomotor pattern is referred as *stride cycle*. The pattern has been divided into two main phases, the **stance** and the **swing** (Grillner and Zangger, 1975; Orlovsky *et al.*, 1999). Generally, the extensor muscles (those increasing the joint angles) are active during the stance phase and the flexor muscles (decreasing the joint angle) are active during the swing phase. In addition, some of the muscles contract during both stance and swing. The phases can further be divided into four sub-phases **F**, **E1**, **E2** and **E3** (English, 1978; Orlovsky *et al.*, 1999; Kandel *et al.*, 2000). While F and E1 are sub-phases of the swing phase, E2 and E3 are sub-phases of the stance phase (see Fig. 2.1).

Extension of the hip, knee and ankle joints during the latter part of the stance phase results in the leg being unloaded and lifted off of the ground which initiates the flexion (F) phase. In addition, the flexor muscles in ankle, knee and hip joints become active just before the onset of the swing phase. The swing

phase thus begins with the flexion sub phase (F), where the knee, hip and ankle joints are flexed (Orlovsky *et al.*, 1999; Kandel *et al.*, 2000). While the contractions in the flexors of the hip joint bring the leg forward in relation to the body, the contraction in the knee and ankle flexors shortens the length of the leg, thus raising it from the ground during the first half of the swing phase. As the hip is still being flexed there is an extension of the knee and ankle during the later part of the swing (E1). This is done in anticipation of supporting the body weight later in the stance phase (Kandel *et al.*, 2000). The hip then starts to extend resulting in ground contact terminating the swing phase.

The extensor muscles have a very similar activation pattern. As mentioned earlier, knee and ankle extensors become active towards the end of the swing phase (E1), in anticipation of foot contacting the ground, and stay active throughout the stance phase (E2 and E3). This creates a gross extensor activity, making the limb rigid enough to bear its portion of body weight (Orlovsky *et al.*, 1999). After the ground contact a passive flexion of the knee and ankle joints can be seen (*yielding*, E2). This yielding is essential for an efficient and stable gait since it smoothes out the vertical oscillations. As the cycle continues into the E3 sub-phase, all joints extend providing the propulsive force needed to push the body forward and the antigravitational force to support the body weight (Wadden, 1998; Kandel *et al.*, 2000).

The basic pattern of activity of the stride cycle is preserved over all velocities (Engberg and Lundberg, 1969; Orlovsky *et al.*, 1999). Significant deviations from the general locomotor pattern just described can occur when there is strong phasic drive in descending pathways or strong afferent input (Kandel *et al.*, 2000). Switching between phases of the step cycle depends upon both intraleg and interleg influences or sensory feedbacks, and those will be described in a separate section (see section 2.1.3).

2.1.2. Central Pattern Generators

The localized neuronal circuits or networks responsible for generating stereotypical movements without rhythmic input are commonly referred to as central pattern generators (CPGs) (Ijspeert, 2002). Since we are talking about neural control mechanisms behind locomotion, this section will be concentrated on locomotor CPGs.

It has been shown that animals with varying levels of spinal cord transections (see section 2.3) have the ability to produce a variety of rhythmic movements such as swimming, stepping, scratching and hopping even when isolated from the sensory inputs (Brown, 1914; Grillner and Zangger, 1975; Kandel *et al.*, 2000). The neural rhythm for locomotion in cats, and also in other animals including humans, has been shown to arise from local networks in the spinal cord without the influence from cerebral cortex or brain stem (Baev and Zavadskaya, 1981). A more detailed description of evidences for the existence of CPGs governing locomotion can be found in a review published by MacKay-Lyons (2002).

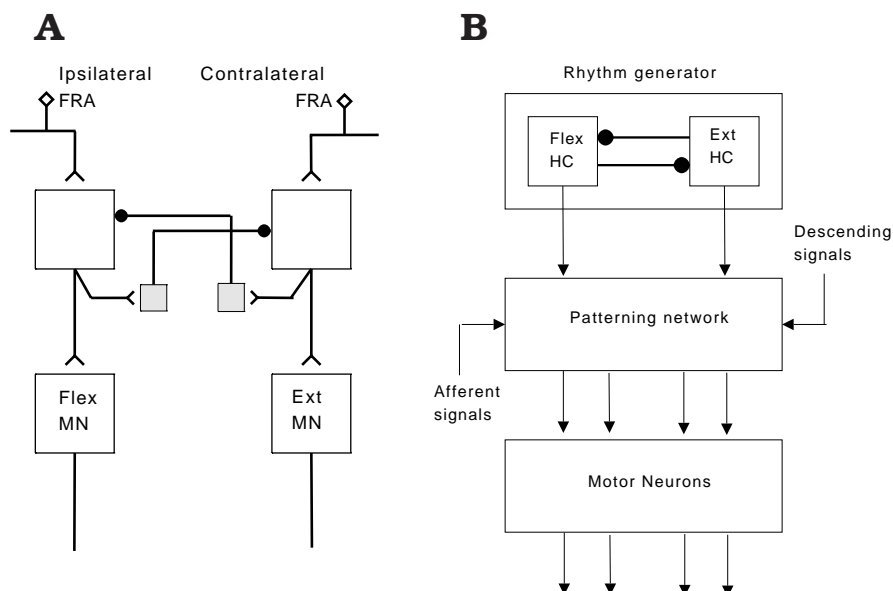


Figure 2.2. **A:** Half-centre (HC) organization of flexor and extensor interneurons: shows reciprocal inhibition between interneurons in pathways mediating long-latency reflexes from FRAs. **B:** Hypothetical locomotor pattern generator: The basic rhythm is produced by mutually inhibiting HCs and establish a general pattern of reciprocity in the activity of flexor and extensor motor neurons, while the details of the temporal pattern are established by an interneuronal network between the HCs and the motor neurons. Descending or afferent signals could modify the temporal motor activity pattern by altering the functioning of interneurons in the patterning network (Kandel *et al.*, 2000).

Due to the greater complexity of the mammalian spinal cord, the exact nature of the pattern generating network has yet to be identified. Although rhythmically active interneurons are widely distributed in the grey matter of lumbar and sacral segments, there is no information on the interconnections between these interneurons or whether any of them are members of the rhythm-generating network (Kandel *et al.*, 2000). However, it has been shown in vertebrates (cat) that there is at least one pattern generator (CPG) for each limb (Grillner and Zangger, 1979; Wadden, 1998). In contrast, we have much more detailed knowledge about the mechanisms of rhythm generation in invertebrates (Bässler and Buschges, 1998) and lower vertebrates (Grillner *et al.*, 1991), which have relatively less complex nervous systems.

Although the general activity of motor-neuron excitation follows the centrally generated pattern (flexion and extension), there are often significant differences. Some motor-neurons have several peaks of activity, and in others the burst of

activation is phase shifted with regard to the general flexor-extensor pattern (Orlovsky *et al.*, 1999). In addition, the basic pattern produced by a CPG is usually modified by sensory feedback from peripheral receptors and signals from higher regions of the central nervous system (CNS) (Rossignol and Bouyer, 2004; MacKay-Lyons, 2002). Therefore the CPG can be viewed as a neuronal network consisting of a phasic rhythm generator and followed by a patterning network (see Fig. 2.2B) converting the bi-phasic signal into a more complex locomotor pattern (Grillner and Zangger, 1975; Kandel *et al.*, 2000). Several hypotheses for rhythm generation in spinal networks have been presented but here, I will briefly describe the bi-phasic rhythm generator hypothesis.

Graham Brown (1910) showed that the isolated spinal cord can generate rhythmic bursts of reciprocal activity in flexor and extensor motor neurons of the hind legs, even in the absence of sensory input. He proposed a bi-phasic arrangement of two groups of neurons which he termed **half-centres** (HCs), that mutually inhibit each other (Grillner and Zangger, 1975; Orlovsky *et al.*, 1999). Later in the 1960s, this hypothesis was supported by studies on cats. In spinal cats treated with L-DOPA, brief trains of stimulation of small-diameter, high-threshold cutaneous and muscle afferents (collectively known as flexor reflex afferents, FRA) evoked long-lasting bursts of activity in either flexor or extensor motor neurons, depending on whether ipsilateral or contralateral nerves were stimulated (see Fig. 2.2A). The interneurons for flexion were found to inhibit the interneurons for extension, and vice versa, thus producing alternating bursts of extension and flexion (Kandel *et al.*, 2000).

2.1.3. Sensory Feedback

Although normal walking is automatic, it is not necessarily stereotyped. Mammals constantly use sensory information from various sensors in the body to adjust their stepping patterns to variations in the terrain and to unexpected events (different environmental conditions). Vestibular inputs from head orientation and anticipatory adjustments from higher visual areas of neocortex are essential for avoiding obstacles and maintaining a stabilised gait. On the spinal level, somatosensory input from the receptors in muscle and skin (proprioception) interact with the CPG to react and compensate for various types of perturbations (Duysens and Crommert Van de, 1998; Windhorst, 2007). Here, we will concentrate on dynamic sensory modulation for the locomotion at the spinal level.

The somatosensory input includes both the afferent information from muscle spindles and Golgi tendon organs (GTOs), and they are generally functioning as a negative feedback mechanism for controlling the muscle length and the muscle force respectively. However, some of these could be changed to positive feedback in a phase dependent manner. For instance, ankle extensor Ib afferents from GTOs contribute to the ankle extensor activity as a positive feedback during the stance phase of a walking cat (Donelan and Pearson, 2004). The proprioception regulates the timing and amplitude of the stepping patterns

(Orlovsky and Feldman, 1972; Frigon and Rossignol, 2006). It is the continuous and dynamic interactions between the CPG and the feedback mechanisms that generate the stable locomotion by modulating transmission in locomotor pathways in a state- and phase-dependent manner (Rossignol *et al.*, 2006). Predominantly these pathways include “spinal reflexes” (see Section 2.2.1) that are mono- or polysynaptic and can affect the ipsilateral or contralateral limb (Duy-sens and Loeb, 1980; Rybak *et al.*, 2002).

One clear evidence for the proprioceptive feedback from limbs regulating the step cycle is that the rate of stepping in spinal and decerebrate cats (see Section 2.3 for different animal preparations) matches the speed of the motorised treadmill on which they are stepping. Specifically, afferent input regulates the duration of the stance phase. As stepping rate increases, stance duration decreases, while the duration of the swing phase remains relatively constant (Wisleder *et al.*, 1990; Kandel *et al.*, 2000). This suggests that some form of sensory input signals the end of stance and thus leads to the initiation of swing.

Several experiments with cats and dogs have indicated that the transition from the stance to swing phase is triggered by the joint receptors in the hip region. This phase transition is dependent upon the geometrical position of the legs at *liftoff* and *touchdown*, termed the posterior extreme position (PEP) and anterior extreme position (AEP) respectively (see Fig. 2.1). In spinal cats walking on a treadmill, flexing the hip causes that limb to stop, and stepping in that limb can then be resumed when the hip is extended to the degree of extension normally reached at the end of the stance (Hiebert *et al.*, 1996; Hiebert and Pearson, 1999; Kandel *et al.*, 2000; McVea *et al.*, 2005). It has been found that the afferents responsible for signalling hip angle for the initiation of the swing phase arise from the muscle spindles in hip flexor muscles (Jiping, 1992; Kandel *et al.*, 2000; Lam and Pearson, 2001). Other important sensory inputs involved in transition from stance to swing arises from the GTOs and muscle spindles in ankle extensor muscles. Electrical stimulation of the afferents from these receptors prolongs the stance phase, often delaying the onset of swing until the stimulus has terminated. This suggests that the leg extensors have to be unloaded to initiate the swing phase (Conway *et al.*, 1987; Whelan *et al.*, 1995; Whelan and Pearson, 1997). Both groups of afferents are active during stance, with the Golgi tendon organs providing the unloading signal to initiate the swing phase (Kandel *et al.*, 2000). The initiation of the flexion phase is also found to be dependent on where in the step cycle the contralateral leg is, which serves to coordinate the limbs for a stable locomotion.

In addition to regulating the transition from stance to swing, proprioceptive feedback from muscle spindles and Golgi tendon organs contributes significantly to the generation of burst activity in extensor motor neurons especially during the stance phase where more activity is necessary in the antigravity muscles for weight bearing. In cats more than 50% of the excitatory input to the extensor muscles during static stance is lost if the Ia- (muscles spindles) and the Ib- (Golgi tendon organs) afferents are removed (Prochazka *et al.*, 1997; Kandel

et al., 2000). The contribution of the GTOs is state-dependent: the excitatory action of the Golgi tendon organs on extensor motor neurons during walking is the opposite of their inhibitory action when locomotor activity is not being generated (see reflex reversal in Section 2.2.1).

Moreover, input from skin receptors can under some circumstances strongly influence the CPG for locomotion (Bouyer and Rossignol, 2003a,b). One important function of these receptors is to detect obstacles and adjust the stepping movements to avoid them. A well-studied example is the *stumbling-corrective reaction* in cats. During the swing phase, a mild mechanical stimulus applied to the dorsal part of the paw elicits a reflex which excites the flexor motor neurons and inhibits the extensor motor neurons, leading to rapid flexion of the paw away from the stimulus. Hence, the result is an over-stepping of the obstacle. Because this reaction is readily observed in spinal cats, it must be produced to a large extent by circuits entirely contained within the spinal cord (Forssberg *et al.*, 1975; Rossignol *et al.*, 2006). As with the Golgi tendon organs, this reflex is phase dependent (Lamont and Zehr, 2006). An identical stimulus applied during the stance phase elicits the opposite response, that is, excitation of extensor muscles that reinforces the ongoing extensor activity. This is an example of a *phase-dependent reflex reversal*: the same stimulus will excite one group of motor neurons during one phase of locomotion and excite the antagonist motor neurons during another phase (Kandel *et al.*, 2000).

2.1.4. Leg Coordination

A proper coordination of movements in different legs is a basic prerequisite to obtain a stable gait in quadrupeds. However, our knowledge of neuronal mechanisms coordinating stepping in walking animals, especially quadrupeds, is limited. Several studies have attempted to gain insight into the neural mechanisms underlying interlimb coordination in walking cats by examining the patterns of stepping especially when pairs of legs step on treadmills running at different speeds (English and Leonard, 1982; Halbertsma, 1983; Cruse and Warnecke, 1992; Akay *et al.*, 2006). This section provides details of some of the postulated hypotheses for the limb coordination of a normal walking cat.

The general view is that each leg is controlled by a separate CPG which can produce the rhythmic movement of a walking leg, and those four CPGs interact with each other to produce the stable stepping in all four legs (Cruse and Warnecke, 1992; Kandel *et al.*, 2000). Furthermore, from split-belt studies it has been found that there exists robust linkages between adjacent pattern-generating networks (Akay *et al.*, 2006). There are both ipsilateral (on the same side of the body) and contralateral coordinating mechanisms in cats. The contralateral influences have been shown to be stronger than that of ipsilateral (Cruse and Warnecke, 1992). If the movements of one limb are perturbed, the restoration of the appropriate coordination appears to be faster for the contralateral pairs than for the ipsilateral pairs (Halbertsma, 1983).

The contralateral influences are symmetrical, which means that the effect from right to left leg or vice-versa (either hind legs or front legs) is the same. Three of the identified contralateral coordination mechanisms are stated as follows; when one leg is in the swing phase it inhibits the contralateral leg from beginning its swing phase, if a leg starts the swing phase it stimulates the contralateral leg to start the stance phase, and the more one leg extends during the stance phase the greater is its effect on the other leg to begin the swing phase (Cruse and Warnecke, 1992; Wadden, 1998). On the other hand, ipsilateral coupling is asymmetric, i.e. the influence from front to hind leg is different from the effect in the reverse direction. In fact, a recent study on the decerebrate cats walking on split treadmills has shown that the ipsilateral pattern generating networks are coupled via descending inhibitory pathways and an ascending excitatory pathway (Akay *et al.*, 2006). From behavioural observation on slow walking cats, Cruse and Warnecke (1992) proposed that “the start for the front leg swing serves as a signal for the hind leg to finish the swing movement”, and this is consistent with the findings of Akay *et al.* (2006). However, neuronal circuitry and mechanisms behind front and hind leg coordination are yet to be discovered. Moreover, the extent to which supraspinal pathways are involved in establishing the pattern of coordination of the fore and hind legs is uncertain. Findings from spinal cats (Miller *et al.*, 1975) and decerebrate cats (English and Leonard, 1982; Akay *et al.*, 2006) suggest that the basic mechanisms for inter-limb coordination are located at the spinal level.

The interleg coordination strategy for running is different from that of the walking. During slow walking, contralateral legs are at 0.5 phase difference, i.e. one leg is in swing while the other is in stance phase (alternating gait). When the speed increases the gait changes from alternating to in-phase (galloping). Therefore the rules governing the switching between phases of each leg may vary with the speed of locomotion as well.

2.2. Limb Muscles

Limb muscles are skeletal muscles that are used to create movements in the leg by applying forces to bones and joints via contraction. Although they are able to contract voluntarily, during locomotion they can contract involuntarily through spinal reflexes. There are several different ways to categorize the type of limb muscle. One method uses the number of joints the muscle is acting on. Using this classification scheme, there are two major types of limb muscles: *uni-functional* (single-joint) muscles and *bi-functional* (two-joint) muscles. Since we are focussing on the hind leg of a cat, I will primarily discuss hindlimb musculature. There are more than twenty muscles identified in the cat hind leg. However, the following muscles or muscle groups are known to be important in generating rhythmic movement during forward locomotion.

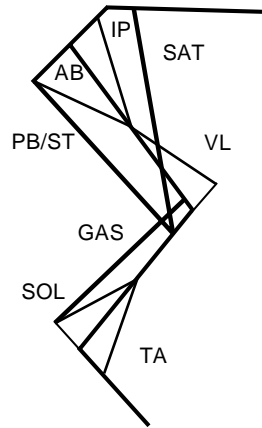


Figure 2.3. A schematic showing some of the muscles in the cat hind leg: AB - Anterior biceps, IP - Iliopsoas, VL - Vastus lateralis, PB/ST - Posterior biceps/Semitendinosus, SAT - Sartorius, GAS - Gastrocnemius, SOL - Soleus, TA - Tibialis anterior

Uni-functional muscles;

- anterior biceps (AB)
- iliopsoas (IP)
- vastus lateralis (VL)
- soleus (SOL)
- tibialis anterior (TA)

Bi-functional muscles;

- sartorius (SAT)
- posterior biceps and semitendinosus (PB/ST)
- gastrocnemius (GAS)

The limb muscles are normally arranged in opposition (antagonistic) so that as one group of muscles contract, another group lengthens (relaxes). Antagonism in the transmission of nerve impulses to the muscles means that it is impossible to generate the contraction of two antagonistic muscles at any one time. However, sometimes it is necessary to activate the antagonistic muscle to 'brake' or slow down the contraction of the agonist muscle in order to smoothen the leg movement, particularly at the end of the motion. This phenomena is known as **co-contraction** (the simultaneous activation of antagonist muscles around a joint) and it provides the nervous system with a way to adapt the mechanical properties of the limb to changing task requirements both in stationary situations and during locomotion. The activities of muscles around a joint are coordinated at the spinal level mostly via reflexes (Kandel *et al.*, 2000).

Now we will deal briefly with the muscle afferents (proprioceptors) that send information about the state of the muscle to the central nervous system (CNS). These include primary (group Ia) and secondary (group II) muscle spindles, Golgi tendon organs (GTOs) and joint receptors. All limb muscles contain all three types of receptors. The spindle receptors sense muscle length and the rate of change of muscle length, whereas the GTO (Ib afferents) senses muscle tension and the rate of change of muscle tension. It is likely that muscle spindle receptor signals provide the information to the CNS to compute the angle of joints. The muscle spindles are made out of *intrafusal muscle fibres* that receive innervation from the fusimotor neurons or γ -**motoneurons**, and the activity of γ -motoneurons modulate the sensitivity of the muscle spindles (Goslow *et al.*, 1973b). On the other hand, *extrafusal or regular muscle fibres* are innervated by skeletomotor neurons or α -**motoneurons**, whose activity produce contraction of the extrafusal fibres that do the work of the muscle. For more detailed description of the receptors, force generation mechanism and morphology of muscles, reader is advised to go through a text book mentioned in the beginning of this chapter.

2.2.1. Spinal Reflexes

Reflexes are “involuntary coordinated patterns of muscle contraction and relaxation elicited by peripheral stimuli” as defined by Kandel *et al.* (2000). It should be noted that here we are talking about reflex circuits that are involved in locomotor control mechanism. The peripheral sensory stimuli for spinal reflexes arise from receptors in muscles, joints and skin and the neuronal circuitry responsible for the generation of rhythmic motor output is mostly contained within the spinal cord. A clear example is walking in the spinalized (see Section 2.3.1) cat. Stepping movements similar to normal stepping can still be generated in such animals (Kandel *et al.*, 2000; Prochazka *et al.*, 2002; Hultborn, 2006).

In early 20th century, Charles Sherrington proposed that simple reflexes, elicited by activation of receptors in skin or muscle, are the basic units for movement. He further proposed that complex sequences of movements can be produced by combining simple reflexes linked together by the brain (Sherrington, 1910, 1913). However, later this view was modified because of the recognition that many coordinated movements can be produced in the absence of sensory information (Brown, 1911; Grillner and Zangger, 1975). Nevertheless, the notion that reflexes play an important role in patterning of motor activity is beyond doubt. The contemporary view is that reflexes are integrated with centrally generated motor commands to produce adaptive movements (Kandel *et al.*, 2000; Rybak *et al.*, 2002; Yakovenko *et al.*, 2004; Rossignol *et al.*, 2006).

Three of the reflexes that are important for control of movement are *flexion-withdrawal*, *crossed-extension* and *stretch* reflex. The flexion-withdrawal reflex and crossed-extension reflex are cutaneous reflexes. Cutaneous reflexes produce coordinated movements that serve protective and postural functions. In the flexion-withdrawal reflex, the limb is quickly withdrawn from a painful stim-

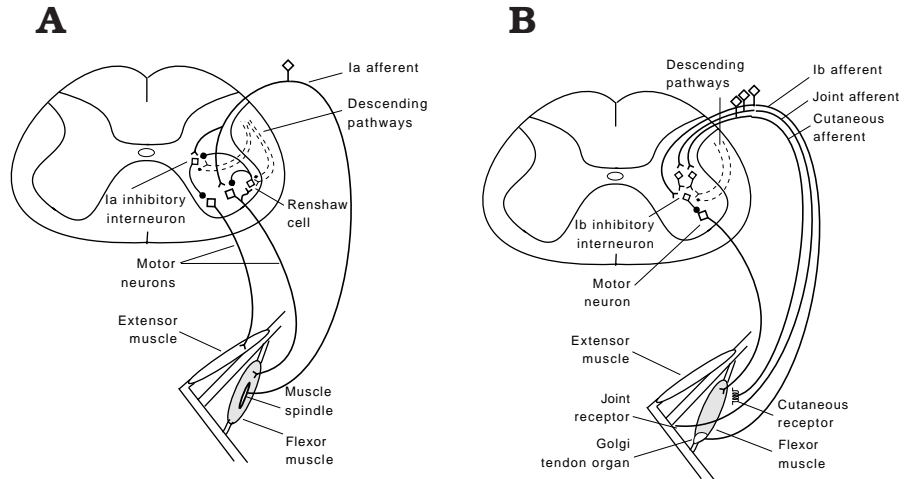


Figure 2.4. **A:** Ia inhibitory interneuron mediates reciprocal innervation in stretch reflex circuits. Renshaw cells produce recurrent inhibition of motor neurons. These spinal interneurons are excited by collaterals from motor neurons and then inhibit those same motor neurons. This negative feedback system regulates motor neuron excitability and stabilises firing rates. **B:** The Ib inhibitory interneurons receive convergent input from tendon organs (Ib afferent), joint and cutaneous receptors and descending inputs. It also receives inputs from muscle spindles (not shown). The descending pathways make excitatory and inhibitory connections to all three interneurons (Kandel *et al.*, 2000).

ulus, usually by simultaneous contraction of all the flexor muscles in the limb. Along with flexion of the stimulated limb, the reflex can produce an opposite effect in the contralateral limb, that is, excitation of extensor muscles and inhibition of flexor muscles. This is the crossed-extension reflex and it serves to enhance postural support during withdrawal of a foot from a painful stimulus. The stretch reflex is a contraction of muscle that occurs when the muscle is lengthened. Spindle afferents make direct (monosynaptic) excitatory connections to motor neurons of the same muscle (see Fig. 2.4A) or muscles having a similar mechanical action (synergism) (Kandel *et al.*, 2000).

Two other important reflexes coordinating muscle actions over a joint are *reciprocal inhibition* and *autogenic inhibition*. Reciprocal inhibition (in some text books, this is known as reciprocal innervation) describes skeletal muscles as existing in antagonistic pairs, where contraction of one muscle results in the simultaneous relaxation of its corresponding antagonist. On the other hand, during autogenic inhibition, stimulation of tendon organ afferent fibres produces disynaptic or trisynaptic inhibition of homonymous motor neurons. Neuronal circuits involved in these reflex mechanisms share several interneurons, a neuron with short processes acting as an intermediate link in a nervous pathway between two neurons with longer processes (Orlovsky *et al.*, 1999; Kandel *et al.*,

2000). Three common interneurons are Ia inhibitory, Ib inhibitory and Renshaw cells (Fig. 2.4). In addition, these neurons provide a pathway for descending inputs from supraspinal centres to modulate the reflex response in state dependent manner (Engberg *et al.*, 1968; Harrison *et al.*, 1983; Nichols, 1985; Serres S.J. *et al.*, 2002). This flexibility allows reflexes to be smoothly incorporated into complex movements initiated by central commands (Duysens and Loeb, 1980; Serres S.J. *et al.*, 2002).

Reflex Reversal and Gating

Most reflexes operate in negative feedback manner. For instance, stretch and autogenic reflex are used to hold length and force of the muscle (respectively) constant in the face of perturbation. Although this is true for stationary postures, during locomotion there may be a switch to positive force feedback from GTO afferents. Positive feedback strengthens the action of the muscle in such a way that it reflexively reinforces the body support when the leg is in stance phase. This has been shown in cats (Forssberg *et al.*, 1975; Duysens *et al.*, 1980; Murphy and Hammond, 1997). Although positive force feedback is associated with instability, it has been shown that the stability is retained due to the length-tension properties of the mammalian muscle (Prochazka *et al.*, 1997).

As mentioned previously, reflex function can be modulated both in gain and sign. During locomotion in the chronic spinal cat a mechanical stimuli applied to the limb has a reversed effect when applied during the swing phase, than during stance phase (Forssberg *et al.*, 1975; Murphy and Hammond, 1997; Rossignol *et al.*, 2006). An object contacting the limb during the swing phase will cause an increased flexion to over step the obstacle whereas the same stimulus during stance phase does not cause flexion reflex since this would cause imbalance.

2.2.2. Muscle Synergies During Locomotion

In general, there is agreement that coordinated movement patterns in any task may be described as synergies (kinematic). During locomotion, these kinematic synergies must be produced, at least in part, by activations of skeletal muscles (Windhorst, 2007). Classical definition of a synergy (muscle) is that a group of muscles that are temporally co-activated and whose period of activity begins and ends synchronously. In general, flexors are active during swing phase while the extensors active during stance phase (see Section 2.1.1). A recent study on cats has been shown that the most of the muscles could be grouped into a number of clusters according to the patterns of EMG onset and offset in both single trials or in averages (Krouchev *et al.*, 2006). They proposed that the base synergies during locomotion are discrete and active during confined sub-intervals of the step cycle and that descending signals act to modulate these synergies to produce different gait patterns.

Muscle synergies in cats have been suggested to be related to foot and limb kinematics in walking and ground reaction forces in stance (Torres-Oviedo *et al.*,

2006). The neuronal systems involved in organizing synergies are complex and include locomotor CPGs, recurrent inhibition, and systems descending from supraspinal structures. Moreover, proprioceptive feedback could adapt the recruitment of centrally organized synergies to behavioural constraints and fine-tune the activation of muscles within a synergy (Dul *et al.*, 1984; Cheung *et al.*, 2005; Windhorst, 2007).

2.3. Experimental Preparations

Much of the information on locomotion has come from studies on the neural control mechanisms of the stepping movements of the cat. Important insights have also come from studies on other animals such as dogs, lamprey, as well as from studying other rhythmic behaviours such as scratching, swimming, etc. On the basis of behavioural studies, intact animal can be used for investigating limb kinematics and electromyographic activity during locomotion. In addition to intact animals, there are two commonly used reduced preparations; **spinal** and **decerebrate** preparations. Furthermore, there are two additional experimental strategies, **deafferentation** and **immobilisation**, that can be used with each of those preparations. In this section, we will briefly explain each of the two preparations and two experimental strategies.

2.3.1. Animal Preparations

Spinal Preparation

The spinal cord can be transected at the lower thoracic level (see Fig. 2.5; transection at **a-a'**), thus isolating the spinal segments that control the hind limb musculature from the rest of the CNS. This allows investigation of the role of spinal circuits in generating rhythmic locomotor patterns. There are two variations in this preparation; **acute** and **chronic**. In **acute** spinal preparations, adrenergic drugs such as L-DOPA (a precursor of the neurotransmitters dopamine and norepinephrine) and nialamide are administered immediately after the transection. These drugs increase the level of norepinephrine in the spinal cord and lead to spontaneous generation of locomotor activity about 30 minutes after administration. On the other hand, in **chronic** spinal preparations, animals are studied for weeks or months after transection. Animals can walk without drug treatment within a few weeks of cord transection. For instance, locomotor activity returns immediately after the transection in kittens but in adult cats daily training sessions are required (Kandel *et al.*, 2000).

Decerebrate Preparation

In this preparation, the brain stem is completely separated at the level of the midbrain (see Fig. 2.5; lesions at **1 and 2**), preventing more rostral centres, especially the motor cortex, from influencing the motor pattern. These preparations allow investigation of the role of the cerebellum and structures in the brain stem in controlling locomotion. Two decerebrate preparations are commonly

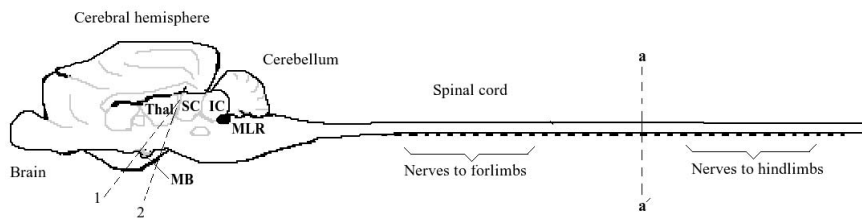


Figure 2.5. A lesion in spinal cord at level $a-a'$ isolates the hind limb segments of the cord but the hind limbs are still able to step on a treadmill. Depending on the exact position of the lesion in the brain stem (cut 1 or cut 2), locomotion either occurs spontaneously (cut 1) or can be initiated by electrical stimulation of the mesencephalic locomotor region (MLR) (cut 2). IC = inferior colliculus; SC = superior colliculus; MB = mammillary body; Thal = thalamus (Kandel et al., 2000).

used. Spontaneous walking occurs in *pre-mammillary* preparations in which the brain stem is transected from the anterior margin of the the superior colliculi to a point immediately rostral to the mammillary bodies (see Fig. 2.5; **cut 1**). When the lesion is situated more caudal to the mammillary bodies (see Fig. 2.5; **cut 2**), spontaneous stepping does not occur, however it is possible to evoke walking by electrical stimulation of the mesencephalic locomotor region (MLR).

2.3.2. Experimental Strategies

Deafferented Preparation

Deafferentation is accomplished by transection of all of the dorsal roots, which carry only sensory axons. Deafferented preparations are rarely used today because the loss of all tonic sensory input drastically reduces the excitability of interneurons and motor neurons in the spinal cord and this complicates the interpretation of the effects of phasic inputs.

Immobilised Preparation

The role of sensory input can be more systematically investigated by preventing the motor neurons from actually causing any movement. This is typically accomplished by paralysing muscles with d-tubocurarine, a competitive inhibitor of acetylcholine that blocks synaptic transmission at the neuromuscular junction (Kandel et al., 2000). Locomotion initiated in such a preparation is known as **fictive locomotion** , the motor nerves to flexor and extensor muscles fire alternately but no actual movement takes place. Thus, the effect of proprioceptive reflexes is removed while tonic sensory input is preserved.

Chapter 3

METHODOLOGY

In this chapter I will briefly discuss the theoretical background for my research. The chapter begins with a brief review of models for quadruped locomotion, from both a current and a historical point of view. As in the previous chapter, the emphasis is on the neural control mechanisms of mammalian locomotion at the spinal level. Then in subsequent sections, methodology of computational modelling of the subsystems for the neuro-musculo-skeletal-control (NMSC) system for stepping in the hind leg of the cat will be discussed in more detail. In addition, a brief description of modelling methods of some of the subsystems can be found in **Paper 1**. The last two sections will be on programming methodology and the system identification technique used in **Paper 2**.

3.1. Review of Models

The interest in using modelling and simulations to study locomotion is driven by the fact that this approach can provide insight into how the nervous system, especially at the spinal level, and the muscles interact to produce coordinated movements of the legs. As mentioned in the previous chapter, during locomotion sensory information from muscle (proprioceptors) and cutaneous receptors is continuously interacting with the locomotor central pattern generator (CPG) to generate adaptive motor output in different environmental conditions. When designing biologically realistic walking models, it is necessary to include relevant models of these subsystems (CPGs, muscles, skeletal dynamics and sensory information) and their interactions. A large number of walking models of vertebrate and invertebrate animals have been developed since the introduction of the field of computational neuroscience. However, it is not possible to give a full detailed review of all the past and present walking models here. Instead reader is advised to go through recently published reviews such as Frigon and Rossignol (2006); Pearson *et al.* (2006) for more detailed description of models of locomotion.

During the last couple of decades, the number and the complexity of different models of mammalian locomotion has increased considerably. However, simulating locomotion in mammals is still in its early stages. Conceptual models of mammalian locomotion have been constructed using mathematical models of subsystems (mentioned above) and based on the abundance of neurophysiological evidence obtained primarily in the cat (Frigon and Rossignol, 2006). Several aspects of locomotor control using the cat as a model have been investigated using computer simulations and some of these will be reviewed here.

Wadden and Ekeberg (1998) developed a neuro-mechanical model of a single leg of a cat to study and evaluate sensorimotor interactions during locomotion. The model includes a CPG (authors termed this as neural phase generator or NPG) that received information from peripheral feedback systems and a “supraspinal” command, resembling the action of MLR, that initiate and select the movements. The model produced stable rhythmic locomotor patterns and stepping velocity could be controlled by modifying the strength of the supraspinal command. Although this model was relatively elementary, it did show that interactions of different modules (distributed control architecture) could effectively control muscle activation and phase transitions in one leg, thus providing a good first step in approximating a CPG for mammalian locomotion.

Ivashko *et al.* (2003) devised a computational model of spinal cord neural circuitry, which includes two coupled CPGs integrated with proprioceptive reflex circuits, that controls locomotor movements of simulated cat hindlimbs. Each hind leg comprised three rigid segments connected to the trunk at the pelvis region and actuated by nine muscles whose activity was driven by a CPG. The spinal circuitry consisted of separate neuronal modules with each module functioning as a minimal neural network necessary for the formation of basic reflex circuits and their integration with the CPG (Rybak *et al.*, 2002). The model was incorporated with several established features such as Ia-mediated reciprocal inhibition and reversal of inhibition to excitation from group Ib afferents during locomotion. Moreover, phase transition was controlled by proprioceptive feedback from both hindlimbs and from touch sensors that signal the ground contact. Simulations showed that the stable locomotion of the hindlimbs is possible with the modeled spinal circuitry and that limb kinematics closely resembled real cat stepping. However, EMG patterns were somewhat differed from the experimental data and the predicted vertical ground reaction forces were much higher than actual forces (Frigon and Rossignol, 2006).

Yakovenko *et al.* (2004) constructed a two legged (hindlimbs) planar locomotor model, with nine segments (eight limb segments with four for each leg and one horizontal torso supported at the front by a frictionless wheel), driven by twelve musculotendon actuators (six for each leg) with Hill-type force-velocity and monotonic force-length properties, to investigate the role of stretch reflexes and the extent to which this sensory input contributes to weight bearing during locomotion. Hindlimb muscles were driven by a CPG and during activity of a given muscle, reflex feedback from group Ia and Ib afferents contributed to the

net EMG profile at a latency of 35 ms, adding 30% to the CPG activation of that muscle during the step cycle. Finite state rules (IF-THEN) were used to govern transitions from stance to swing and from swing to stance (Prochazka, 1993; Prochazka *et al.*, 2002). The authors concluded that when the level of central activity is low, the contribution of stretch reflexes to load compensation can be critical, and on the other hand, when the CPG output provides sufficient load (drive), then the contribution from reflexes is minimal. The main implication of this study is that the intrinsic mechanical properties of leg muscles have a major role in stabilizing leg movements during the stance phase, and that these stabilizing influences can be strengthened by sensory feedback (Pearson *et al.*, 2006).

Ekeberg and Pearson (2005) developed a three dimensional model of a cat consisting of two hind legs controlled by separate finite-state controllers that could be coupled (via mutual inhibition) or uncoupled, and two stiff front legs working as frictionless support. Seven muscles actuated each of the three-segment hindlimbs, and produced a force linearly proportional to the activation level provided by the controller. Each controller had four states (liftoff, swing, touchdown and stance in sequential order) and the transitions were accomplished using sensory signals, which activated different muscle synergies in each state, from the legs. The main objective of this investigation was to evaluate the relative role of the stretch sensitive afferents in hip flexors (joint receptors signalling hip position; hip extension rule), and the force-sensitive afferents in ankle extensors (unloading rule), in initiating the stance-to-swing transition. The authors found that the unloading of the ankle extensor muscles in each leg could, on its own, produce robust walking behaviour and alternating stepping in the hind legs even in the absence of direct coupling between the two hind leg controllers, but a switch to the hip extension rule generated an unstable gait and the model eventually tripped or fell. The general conclusion from their analysis was that a force-feedback signal related to unloading of a leg near the end of the stance phase is probably crucial for initiating the stance-to-swing transition. However, they did not attempt to show how these sensory signals interacted with a locomotor CPG. It should be stated here that the walking model implemented (see **Paper 1**) in this thesis work is based on the above mentioned model.

Rybak *et al.* (2006) designed a two-level locomotor CPG comprising a half-centre rhythm generator and a pattern formation network to simulate the motor neuronal activity recorded during fictive locomotion in decerebrate cats. Their model was able to produce rhythmic locomotor patterns with step cycle periods and phase durations spanning the range observed during fictive locomotion (Yakovenko *et al.*, 2005) and to accommodate the reorganization of reflex circuits during locomotion and realistically reproduce and explain several experimentally observed effects of extensor, flexor and cutaneous afferent stimulation upon locomotor rhythm and motoneuron firing (Quevedo *et al.*, 2000). Rhythmogenic properties of neurons for the rhythm generator have been modeled as for the respiratory CPGs. However, whether such endogenous rhythmogenic properties are present in locomotor CPG neurons is currently unknown (Frigon and Rossignol, 2006).

3.2. Modelling the Body Mechanics

The choice of simulator for the forward dynamics of the body is crucial to the modelling of locomotor systems. This is because the simulation of body dynamics is the most time consuming and mathematically difficult task. There are lots of general purpose simulation tools (SIMM/Dynamic Pipeline, Working Model 2D and SAROS) available nowadays, but most often they lack the desired properties one needs for constructing models with specific requirements. So the trend is to develop the entire program from scratch on ones own. Furthermore, simplifications of body mechanics must be made, and an appropriate level of anatomical complexity must be established. In some cases, a 2D model might be sufficient to address the issue under investigation, whereas other cases might require a 3D model. For this thesis work, we have developed a three dimensional (3D), forward dynamics, computer simulator model of a walking cat. The simulator was programmed using Python scripts and the body dynamics of the cat hindlimbs were simulated using Python wrappers of the Open Dynamics Engine (ODE) ¹ which is an open source, high performance library for simulating rigid body dynamics.

The body and the leg segments (skeleton) were modelled as rigid segments. Centre of mass for each segment was located at the midpoint of each. The masses of the leg segments were taken from Hoy and Zernicke (1985) and the trunk weight was set to a value reasonable for an average cat. In the simulation program, with the help of functions of the ODE library, location and orientation of each segment (body in ODE terminology) in the 3-dimensional space was specified by a set of cartesian coordinates. Additionally, movement of segments in relation to each other was restricted with the help of a set of 'Joints' or 'Constraints' so that they can only have certain positions and orientations relative to each other. The knee and ankle joints were implemented as hinge joints so that they allowed only one degree of freedom while the hip joint allowed two. This was constructed by putting two hinge joints, with their axes perpendicular to eachother, on to a small body part that lies in between the limb thigh and the trunk This allowed the leg to rotate around an axis parallel to the trunk. This movement (rotation of the whole leg) is known as abduction or adduction (see Fig. 3.1), and can be seen in real cats during locomotion. Forelimbs were made stiff and used as support for the trunk and front part of the body.

The mechanical body of the cat was implemented in a 'world' (the world object is a container for rigid bodies and joints) with a gravitational field of relevent strength. The ground was modeled as a horizontal planar surface. Contact between the ground and the hindlimb foot was governed by the coulomb friction with a high friction coefficient and a small restitution parameter. The foots of front legs made frictionless contact with the ground. All these contact parameters were implemented into the model (the cat and the environment) by overriding the built in functions of the ODE library.

¹www.ode.org- Russell Smith is the primary author of ODE

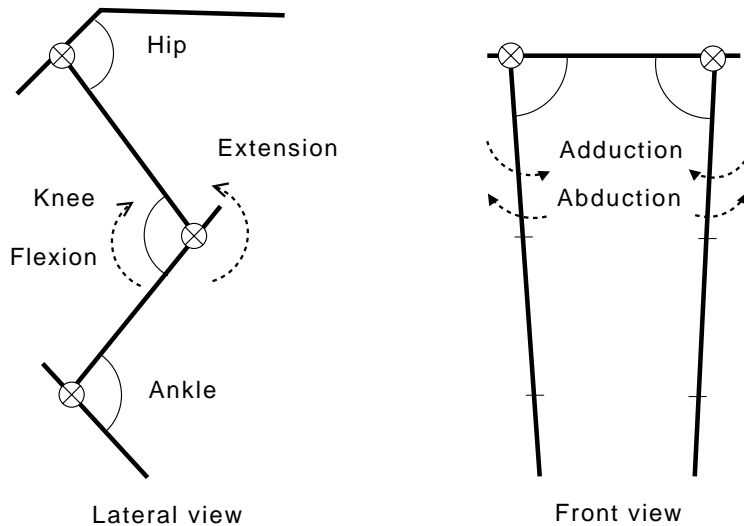


Figure 3.1. A schematic showing limb segments and joints of the cat hindlimb: Each hindlimb consists of three segments, thigh, shank and foot, with four degrees of freedom (DOF). The knee and ankle joints have one DOF, whereas the hip joint has an additional DOF to enable abduction and adduction (see Front view) movements of the limb

The process of simulating the rigid body system through time is called *integration*. In this simulation, each integration step advances the current time by a *time step* of 0.005 ms, adjusting the state of all the rigid bodies for the new time value. In fact, the *time step* can be selected according to the requirements of the investigation; it is a tradeoff between accuracy, stability and the speed of the simulation. The smaller the step, the better the accuracy but slower the simulation. The new positions (of rigid bodies) are calculated by numerically solving equation of motions that are derived by a Lagrange multiplier-velocity based model.

3.3. Modelling the Muscle Dynamics

A general statement of function of skeletal muscle is that the muscle has to produce work to its outside world by exerting force while changing length. Work delivered will be determined by the mechanical and architectural properties of the muscle. Muscular properties can be classified into two categories: *intrinsic* and *contextual* properties. Contextual properties, which are determined by the way the muscle is built, are very important because they determine the specific function of a particular muscle, such as flexor or extensor. Intrinsic properties determine the functional capabilities of muscles to deliver external work (Hui-

jing, 1998). In order to understand and predict the skeletal muscle activities, many of the muscle models are established to assess the importance of parameters for muscular properties (Hill, 1938; Zajac, 1989; Brown and Loeb, 1995; Brown *et al.*, 1996; Shue *et al.*, 1995; Lieber, 1999). However, they generally do not include details about recruitment of different types of motor units, nor do they mimic precisely the detailed properties of individual muscles because, for most muscles, these properties are simply not known (Pearson *et al.*, 2006).

The force produced by a muscle is primarily a function of its length, velocity and level of activation. Although these relationships are more complex, linear models are often sufficient for simulation studies (Ekeberg, 2000). In 1938, Hill developed a phenomenological model of a skeletal muscle, to which he included three linear and independent mechanisms to produce the muscle force. The proposed model was composed of two *elastic* elements, passive elastic element (PEE) and series elastic element (SEE), and one contractile element (CE), which generates the force in accordance with the force-length and force-velocity characteristics of the muscle. All the elastic properties of the muscle are included in both of the 'elastic' elements. As an extension to the Hill-type model, Zajac (1989) introduced tendon and pennation angle into the model. Based on this model and also with experimental data of cat soleus muscle, Brown and Loeb (1995) developed another mathematical muscle model (Scott *et al.*, 1996; Brown *et al.*, 1996) which we adapted to implement the limb muscles for the cat in our simulator.

When implementing a computer simulator, it would be better to use a simplified model. For instance, *activation dynamics* (transformation of neural excitation to activation of the contractile apparatus) of muscles may sometimes be ignored. In that case instantaneous activation levels can be used for force generation. If the CPG model incorporated with a spiking motor neuronal model, then the conversion from spike rate to activation levels must be included in the model. One way of achieving this, as proposed by Zajac (1989) is to use low pass filtering of rectified neural output with a suitable time constant. In this thesis work, the muscle model was implemented with only *contraction dynamics*.

3.3.1. Contraction Dynamics

The muscle contraction dynamics corresponds to the transformation of activation to muscle force and it is primarily described by two relationships; force-length (fl) and force-velocity (fv). In the conceptual Hill-type model, these properties included into the contractile element by a force-length-velocity (flv) relationship controlled by muscle activation. Basically, both the PEE and the CE in parallel are assumed to contribute to generation of muscle force (see Fig. 3.2A). Sometimes muscle elastic element (SEE), different from tendon elasticity, is included in series with the CE. However, in all but short-tendon actuators, the energy stored in cross-bridges is assumed to be very small compared with the total energy stored in the tendon and aponeurosis (Rack and Westbury, 1984; Kandel *et al.*, 2000). Therefore, for many musculotendon actuators, tendon

compliance dominates and SEE can be neglected. In our implementation of the muscle model, tendon and aponeurosis were lumped together and included as one series elastic element. Tendon stiffness for each muscle was taken to match biological data (Rack and Westbury, 1984; Proske and Morgan, 1987; Ekeberg and Pearson, 2005).

Force - Length Relationship

The steady state or static property of muscle fibres is defined by its *isometric force-length (f-l)* curve and the curve is obtained from values of muscle force when both activation and fibre length are constant. Both fully activated and passive (neither neurally nor electrically excited) muscle tissue develop a steady state force when held isometric. The f-l relationship can be described as a *active* force-length curve combine with a exponential *passive* force-length curve (see Fig. 3.2B). The *active f-l* account for the force generated by contractile element, while *passive f-l* account for the force generate by passive elastic element when muscle length over *optimal muscle length* L_o . Optimal muscle length (L_o) is defined as the muscle length at which the maximum muscle force can be generated. The region where active muscle force is generated is usually $0.5L_o < L < 1.5L_o$.

The f-l property of less than fully activated muscle tissues can be considered as scaled version of the fully activated one. However, the passive f-l curve is assumed to be unaffected by activation level (Zajac, 1989).

Force - Velocity Relationship

The force-velocity (f-v) relationship is another contractile property which describes the change of force generation ability of muscle based on the velocity of muscle contraction. When fully activated muscle tissue is subjected to a constant pull (tension), which is larger than contractile force, it initially shortens and then stops (isotonic contraction). Hence, by subjecting muscle to different tensions, sets of different length trajectories can be obtained. From those data sets, an empirical f-v relationship for the muscle can be constructed for any length L , where $0.5L_o < L < 1.5L_o$. At optimal length L_o , a maximum shortening velocity (v_m), above which muscle cannot sustain any tension (even when fully activated), can be defined from the fv relationship (see Fig. 3.2C). Generally, all computer models of muscles used in studies of muscle coordination occupy the same shaped fv curve (Zajac, 1989).

Now we can briefly discuss the implementation details of the muscle model for the hindlimbs of the walking cat model. For more specific details of the model, reader is advised to follow the **Paper 1**. Each hind leg included eight muscles (musculotendons- each has a tendon in series), five of them acting over single joints while the other three (*bi-functional muscles*) acting over two joints (see Section 2.2 and Fig.2.3). As mentioned previously, the simulation of each muscle was based on the mathematical model developed by Brown *et al.* (1996)

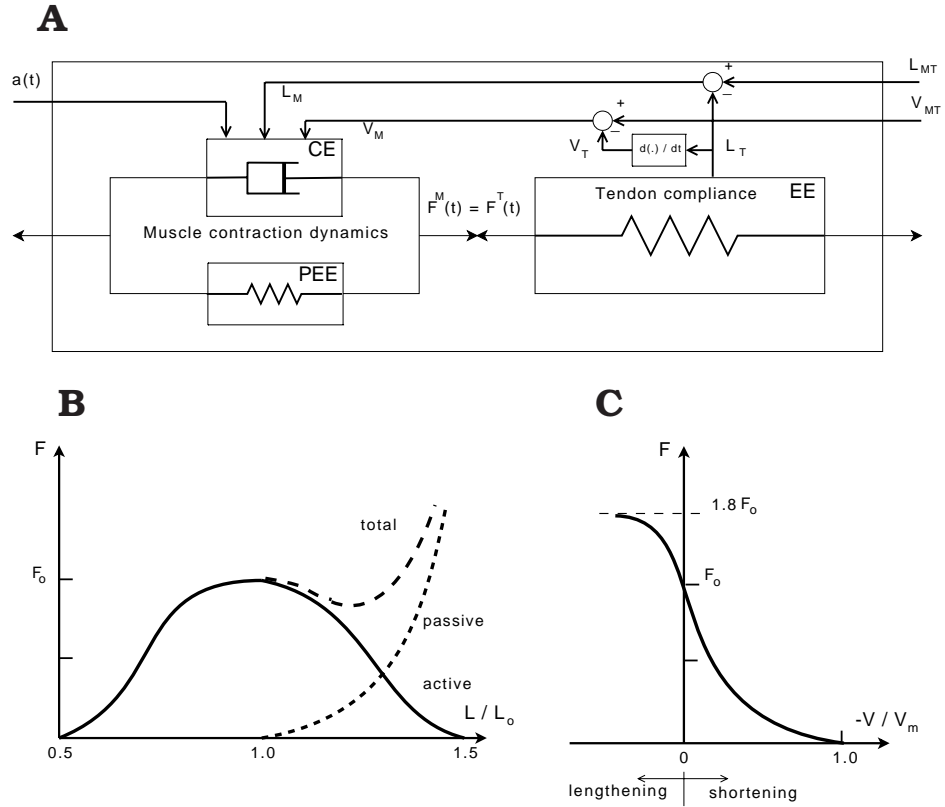


Figure 3.2. **A:** Musculotendon contraction dynamics is given by the interaction between muscle contraction dynamics and tendon compliance. The Hill-type model is used for muscle contraction dynamics. Muscle fibre length L_M and velocity V_M is continuously affected by the tendon because its length changes as force changes. **B:** Isometric force-length relationship of muscle tissue during passive and during fully activated. Peak active force F_0 is developed when fibres are at optimal length L_0 . **C:** The empirical force-velocity relationship when fully activated ($a(t)=1$) fibres are at L_0 . V_m is the maximum muscle shortening velocity (Zajac, 1989).

and the parameters for force, length and velocity relationships were taken from published data (Brown *et al.*, 1996; Burkholder and Lieber, 2001; Ekeberg and Pearson, 2005). The neutral muscle length (muscle lengths at relaxed or neutral posture) for each muscle was set so that they would generally operate at the rising slope region of the f - l curve. Forces generated by each muscle were then converted to joint torques by multiplying by corresponding moment arms that were taken from the work of Goslow *et al.* (1973a). The resultant torque at each joint was the contribution from all muscles acting on that joint. Abduction and adduction movements at the hip joint were controlled by a passive linear

spring with damping. This was similar to a short musculotendon which has high muscular or tendon stiffness.

3.4. Modelling the Neural Control

The heart of sensorimotor interactions is in the spinal cord where the central pattern generator (CPG) for locomotion is located. The CPG provides the basic locomotor rhythm and basic locomotor synergies and, in addition, it continuously interact with the proprioceptive (sensory feedback) inputs in order to regulate the neural activity of limb muscles to produce a stable stepping in the legs. Thus, a model of the neuronal CPG gives an output that represents motoneuron pool activity, which is then transformed via muscle models into forces. The mechanical model including muscles and body dynamics provides the necessary input for models of various sensors such as muscle length, muscle force, and ground reaction force, which can then send feedback signals back into the neuronal model which may include CPG and reflex circuits (Pearson *et al.*, 2006).

3.4.1. Pattern Generating Networks

The lack of physiological data on the organization and properties of interneurons in the central pattern generating networks of walking in mammals has led to simplifications in the modelling of the basic rhythm generating network for locomotion. For simulation studies, depending on the goal of the investigation, the CPG does not always need to include all the complexities such as cellular and synaptic mechanism as long as it reacts to the sensory feedback according to the experimental results. It is reasonable to model the locomotor CPG by a phase dependent component with contributions from sensory feedbacks for adjusting the muscle activity and for switching from one phase to another (Ekeberg and Pearson, 2005; Pearson *et al.*, 2006). In fact there is no pre-defined rules or methods for modelling a CPG in present neuroscience community. Researches have been used models of CPGs developed by themselves as long as they work accordingly (see Section Review of Models).

Basically a CPG model should provide timing (phasic activity) and magnitude information of neural activity for limb muscles. A one way of representing time is as the phase of an oscillator at which sensory signals can directly speed up or slow down the phase (Patla *et al.*, 1985). Alternatively, time can be represented as cyclic transition of explicit neural states corresponding to the extension and flexion of a leg in which sensory signals can trigger transition from one state to the next (Ekeberg and Pearson, 2005). The magnitude of the activation output to each muscle or synergistic muscle group can be regarded as the sum of a phase-dependent part (basic CPG output, and force and length feedback) and a feedback-dependent part (Pearson *et al.*, 2006).

In the model that we have developed for the neuro-musculo-skeletal-control (NMSC) system for the stepping in hind legs, the CPG is a central program which

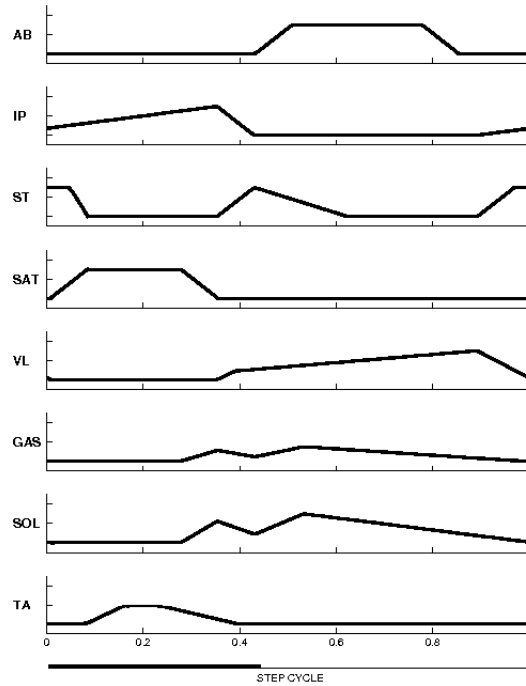


Figure 3.3. Figure shows the activation pattern for each hind limb muscle during a step-cycle. Duration of the swing phase is shown by the black horizontal bar at the bottom of the figure, rest of the cycle is the stance phase

generates a unique activation pattern for each muscle (see Fig. 3.3). These patterns are comparable to electromyographic (EMG) activity of each muscle of the hind limb of the cat during normal walking (Kandel *et al.*, 2000; Ivashko *et al.*, 2003). In both studies (Paper 1 and Paper 2), we did not include known sensory feedback into the controller (reflex pathways), since our aims were to obtain a basic locomotion with only the CPG as a validation for the model dynamics (**Paper 1**) and to obtain the open-loop linear systems for the muscle-joint interactions during stepping (**Paper 2**). However, it is possible to incorporate known sensory pathways by simply modifying the script for the neural controller with feedback mechanisms. Furthermore, the program is capable of switching to a finite state controller which is based on physiological mechanisms for state transitions and activation level control (Ekeberg and Pearson, 2005).

When the simulation is running, the phase in the step cycle of the CPG-activation pattern is specified by an internal clock variable which in turn determined the magnitude of the level of activation to be sent to the corresponding

muscle actuators. Each leg is controlled by a separate CPG having the same pattern but with a fixed phase shift of 50 % from each other and this corresponds to an alternating gait pattern. Additionally, activation pattern (or CPG output) for each muscle can be scaled up or down as required. During the simulation, each leg is progressing sequentially and repeatedly from swing to stance and back to swing. The swing and stance phases are set to about 40 % and 60 % of the step cycle duration respectively, which is an appropriate relationship for medium speed walking (Yakovenko *et al.*, 2004, 2005). Total cycle time was about 650 ms when the cat was moving forward with a speed of about 0.4 m/s on a flat horizontal surface. These parameters can be easily modified by adjusting the corresponding values in the central program.

3.4.2. Sensory Pathways

As discussed in previous chapter (see Sections 2.1.3 and 2.2.1), limb proprioceptors can greatly influence the walking pattern. Hence, accurate physiological models of these receptors which can easily be incorporated into computer simulation of locomotion are required. Even though we did not include sensory feedback into the walking model during these investigations, it is thoroughly discussed when predicting control strategies for limb movements during stepping in **Paper 2**. In fact, sensory feedback will be included in the model during future experiments. A detailed description of modelling sensorimotor interaction during locomotion can also be found in the review of Frigon and Rossignol (2006).

The most important sensory pathways involved in locomotor control are the *Ia* and *Ib* afferent pathways. The properties of the corresponding sensory receptors can be captured by equations or transfer functions that describe their response properties, and these equations have readily been used in computer models of locomotion (Prochazka and Gorassini, 1998; Yakovenko *et al.*, 2004). Furthermore, models of muscle spindles should include appropriate dynamic fusimotor ($\alpha - \gamma$ coactivation) activity in order to regulate the spindle's sensitivity (Taylor *et al.*, 2000). A recently developed mathematical model, to mimic the structure and physiology of primary and secondary muscle spindles, has incorporated gamma-innervations into the model (Mileusnic *et al.*, 2006). In addition, a complex mathematical model of GTOs has recently been developed (Mileusnic and Loeb, 2006). However, due to the complexity of these models incorporating them into a walking model in a computer simulated environment would be a difficult task since they require longer computational time. Generally, in many cases it can be sufficient to detect discrete events or to assume a linear relationship between the sensed value and the sensory signal (Pearson *et al.*, 2006).

Another important sensory receptors for the control of locomotion are cutaneous or skin receptors. Although, these inputs are important in correcting limb trajectory and foot positioning, most locomotor models incorporate them simply as a foot contact sensor (Wadden and Ekeberg, 1998; Ivashko *et al.*, 2003; Ekeberg and Pearson, 2005) or as a force transducer.

3.5. Program Structure

So far, we have been discussing the modelling methods of the subsystems of the neuro-musculo-skeletal-control (NMSC) model for locomotion in the hind legs of the cat. Let us now discuss how these systems or modules and their interactions are implemented into one main programme to obtain the walking cat model in the simulated environment. As mentioned previously, the simulator is programmed using the *Python* scripting language (python 2.4.4 ²) and it is developed as a collection of modules and submodules in an object oriented manner. This object oriented programming technique allows easy access to various parameters such as muscle forces, muscle lengths, ground contact, and joint angles, which could be used for monitoring and for assessment of each simulation trail. As shown in the schematic diagram (see Fig. 3.4), numerical solver for *rigid body dynamics* (mechanical part), *neural control system* and *3D graphical engine* are the main modules of the program.

The mechanical part of the simulation, i.e. to numerically simulate the leg and body dynamics of the cat, is done using the rigid body simulator library Open Dynamics Engine (ODE 0.5, see Section 3.2). To be exact, we used PyODE ³, which is a set of open source python bindings for the ODE, since the programming was done in Python. In addition, this module includes the simulation of the surface properties of the ground and the gravitational acceleration of the world in which the cat resides. Next important module is the neural control system which is developed as a separate system which included three main sub modules: joints, muscles and controllers (CPGs). The joints module is functioning as a communicating medium between the ODE driven mechanical system and the muscle module by taking the joint angles and angular velocity information into the module and then calculating muscles velocities and lengths. Length and velocity information together with the activation level for each muscle from the neural controller are then fed to the muscle model which in turn produce the forces in each muscle using the mathematical muscle model (see Section 3.3). These forces are multiplied by corresponding lever arms to calculate the torques that are directly applied to the corresponding leg joints of the mechanical model. The controller is a separate python script and it could be designed as a CPG network (Ivashko *et al.*, 2003) as we did in this thesis work (see Section 3.4.1) or could be a finite-state controller (Ekeberg and Pearson, 2005). It is possible to incorporate sensory feedback into the control algorithm by plugging sensory information while the simulation running. These can be force and length feedback or ground contact that mimics the action of Golgi tendon organs, muscle spindles and cutaneous receptors of the foot respectively. The 3-dimensional representation of the cat and the environment on the computer screen is done by a separate module, graphical engine, which is implemented using PyOpenGL 2.0 ⁴, which is the cross platform Python binding to OpenGL and related Application Programming Interfaces (APIs).

²www.python.org

³<http://pyode.sourceforge.net>

⁴<http://pyopengl.sourceforge.net>

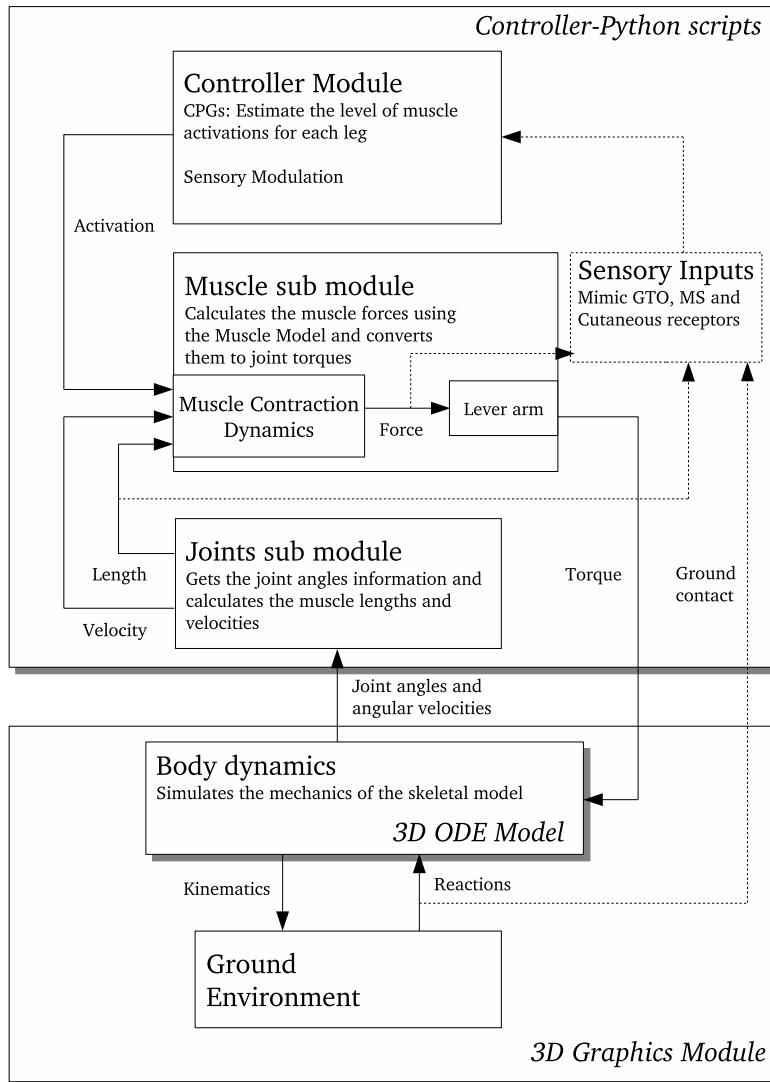


Figure 3.4. Schematic diagram of the simulation program. Control system, rigid body mechanics with Open Dynamic Engine (ODE) and graphic module are the main components of the program. Blocks and paths showed in dashed lines are not included in this work. GTO: Golgi Tendon Organ, MS: Muscle Spindles.

Time varying data such as individual muscle forces and their lengths, joint angles, angular velocities, ground contact, etc can be sampled and logged onto a *text* file that can be accessed after the simulation for analysis purposes. For instances, in the experiment that was set up to model the open-loop linear transfer functions for muscle–joint interactions in the hindlimb during locomotion, the perturbed activation levels of the muscles and the affected hind leg joint angles were sampled and logged in every 5 ms throughout the simulation (see **Paper 2**). When running on a 2.00 GHz processor, the rate of simulation was approximately 15% of real time. This high rate gave the opportunity to perturb and asses the quality of the simulation efficiently.

Each simulation follows a sequence of steps (procedures) which are as follows (a flowchart for the simulation programme can be found in **Paper 1**):

1. Start;
2. Create model $T = 0, T_{end}, Timestep$;
3. Initialization, *Muscles, Joints*;
4. Graphics, *Pre – draw, Draw and Post – draw*;
5. Body dynamics and Control system;
Update Joints, Update Muscles
Collision detection
Neural controller
Log data
world.step, Contacts empty
6. $T = T + Timestep$;
7. If $T \leq T_{end}$ Then Goto step 4;
8. Write logged data in to Files;
9. End;

3.6. System Approximation for Muscle–Joint Interactions

In this section we will go through somewhat different topics than those we discussed earlier. In **Paper 2**, we modeled linear transfer functions for the interactions between muscle activations and joint angles. So let us discuss some of the theoretical background, especially how linearization was possible, what simplification that we made on approximating total Multiple Input and Multiple Output (MIMO) system, and which model structure that was used. Indeed, this is necessary to understand the system identification process that we adapted in **Paper 2**. At the end of this section, we will see some examples of continuous linear transfer functions that describe the muscle–joint interaction at a certain point in the step cycle. As mentioned previously, the data (muscle activations, joint angles and timing information) necessary for this investigation were logged during the simulation and then (after the simulation) written into text files for

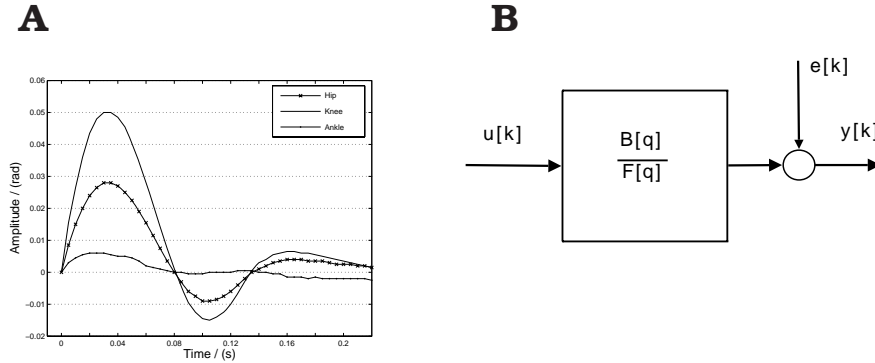


Figure 3.5. A: Responses of hind leg joint angles to a positive impulse in activation level of VL muscle (knee extensor) during mid stance. The impulse amplitude is set at 10% of normalized activation and its duration is about 5 ms (not shown). **B:** The Output-Error (OE) model structure; y , u and e are output, input and noise sequences respectively.

the analyses. The transfer function modelling was done using the *system identification* tools in Matlab 7.0.4 (R14)⁵.

The muscle force is dependent on activation, length and velocity (see Section 3.3). In fact, these dependencies are both dynamic and non-linear. Additionally, there are bifunctional muscles that are acting over two joints. Therefore, non-linearities in the muscle-joint interactions are unavoidable. However, it is possible to use a local linear approximation for a muscle-joint interaction within a short duration around a leg position in the step cycle. The linear transfer functions can be identified by analysing the response of each joint (see Fig. 3.5A for an example) for a positive impulse of activation of a muscle. It should be mentioned that the amplitude and the duration of the impulse must be kept relatively small to minimize non-linearities.

For one leg posture within the step cycle, the total system matrix is 8×3 since we included eight muscles and three joints (*Hip*, *Knee* and *Ankle*) in each hind leg of the simulated walking model of the cat. In reality this would be a Multiple Input and Multiple Output (MIMO) control system. However, in the present investigation we did not include any sensory feedback to the muscles or CPGs (here, our aim is to identify open-loop linear transfer function between muscle activation and joint angle; see Paper 2) and hence there will be no interactions among the muscles. In fact, the lower the strength of interactions, the more a system behaves like a set of independent systems that can be analyzed separately. Therefore, we can simplify the total system by identifying individual systems from each muscle to each joint as a Single Input and Single

⁵www.mathworks.com

Output (SISO) system.

It is now time to take a look at some of the possible model structures. The auto-regressive with exogeneous input (ARX), autoregressive moving average with exogeneous input (ARMAX), output error (OE) and Box Jenkins (BJ) are some of the well defined model structures. Here, we are not going to describe each and every model, instead we will briefly discuss the adapted model structure, i.e. *Output-Error (OE)* which is especially useful for those cases where we want to minimise the error $e[k]$ (see Fig. 3.5B). The error $e[k]$ term in all above mentioned model structures except OE has a dominant role in representing noise characteristics. In OE, $e[k]$ represents the difference between the actual and predicted outputs and may include possible non-linearities. Therefore the *OE* model structure is suitable for our simulation study since there were no measurement noise that should be modelled as for a real experiment. We selected the same model structure and model orders for all the muscle–joint interactions (24 systems). This simplified the identification process and gave us a better foundation to compare individual systems.

In a real animal, action of the muscle over a joint (or joints) is continuous. Therefore any approximation to describe the muscle–joint interactions must be a *continuous system*. However, in an experiment we can only measure the input–output data at certain time intervals with a suitable sampling frequency. Therefore the transfer functions can be first identified as *discrete systems* with the corresponding sample period (in our case 5 ms) and then can be converted to the continuous domain. The discrete system for the OE model can be described using an equation of the following form,

$$y(t) = \frac{B(q)}{F(q)}u(t - n_k) + e(t) \quad (3.1)$$

where y and u are the output and input sequences, respectively, and e is the error term. The polynomials B and F are defined in terms of the backward shift operator q :

$$B(q) = b_1 + b_2q^{-1} + \dots + b_{nb}q^{-nb+1} \quad (3.2)$$

$$F(q) = 1 + f_1q^{-1} + \dots + f_{nf}q^{-nf} \quad (3.3)$$

The model orders nb , nf and input delay parameter n_k can be selected according to the modelling requirements or to have a better fit. In this study, nb , nf and n_k are set to 1, 2 and 1 respectively and the motivation behind the selection of those parameter values can be found in the next chapter when we discuss the results in more detail.

Finally, we will show some examples of identified linear transfer functions between muscle activation and joint angles. The continuous systems modeled for the interaction between VL muscle and the corresponding limb joint (at the middle of the stance phase) are as follows;

$$Hip(s) = \frac{s + 410.7}{s^2 + 35.81s + 1853} \quad (3.4)$$

$$Knee(s) = \frac{1.807s + 742.8}{s^2 + 36.91s + 1826} \quad (3.5)$$

$$Ankle(s) = \frac{0.2959s + 124.2}{s^2 + 61.31s + 2243} \quad (3.6)$$

Chapter 4

RESULTS AND DISCUSSION

This chapter will summarise the results from this thesis work. With the biological and theoretical background from previous chapters, below we discuss the constructed neuro-mechanical simulator for the study of the locomotion in the hind legs of the cat and some of the results from experimental investigations using the neuro-musculo-skeletal model that we developed.

4.1. Neuro-mechanical Simulator

The first step was to assess the basic functionality of the simulation, especially the musculo-skeletal system. Due to the lack of biological information and computational complexities, it is impossible to capture all the features of the locomotor system when building a computer simulator for the stepping in the cat. The body was modelled using ODE and composed of thirteen segments, three for each leg and the trunk. Mass of each segment was assumed to be uniformly distributed (see Section 3.2). Movements in each hind leg was generated by eight muscles which is undoubtedly a subset of all leg muscles and all the muscles were simulated using the same model with a different set of parameters for each (see Section 3.3 and **Paper 1** Appendix). Figure 4.1B shows the normalised total force-length relationship of the simulated *soleus* muscle. During the locomotion, all the muscles were operating at the rising slope region (linear) of the force-length curve. The vertical line in the figure corresponds to the active length of the soleus muscle at neutral posture. Length of the soleus was either increased or decreased around the neutral point when the ankle joint flexed or extended respectively. Furthermore, force generated by a muscle was varied with the shortening or lengthening velocity of that muscle. Force-velocity relationship for the maximally activated soleus muscle at maximum length is shown in the Figure 4.1C and shortening of the muscle corresponds to a negative velocity.

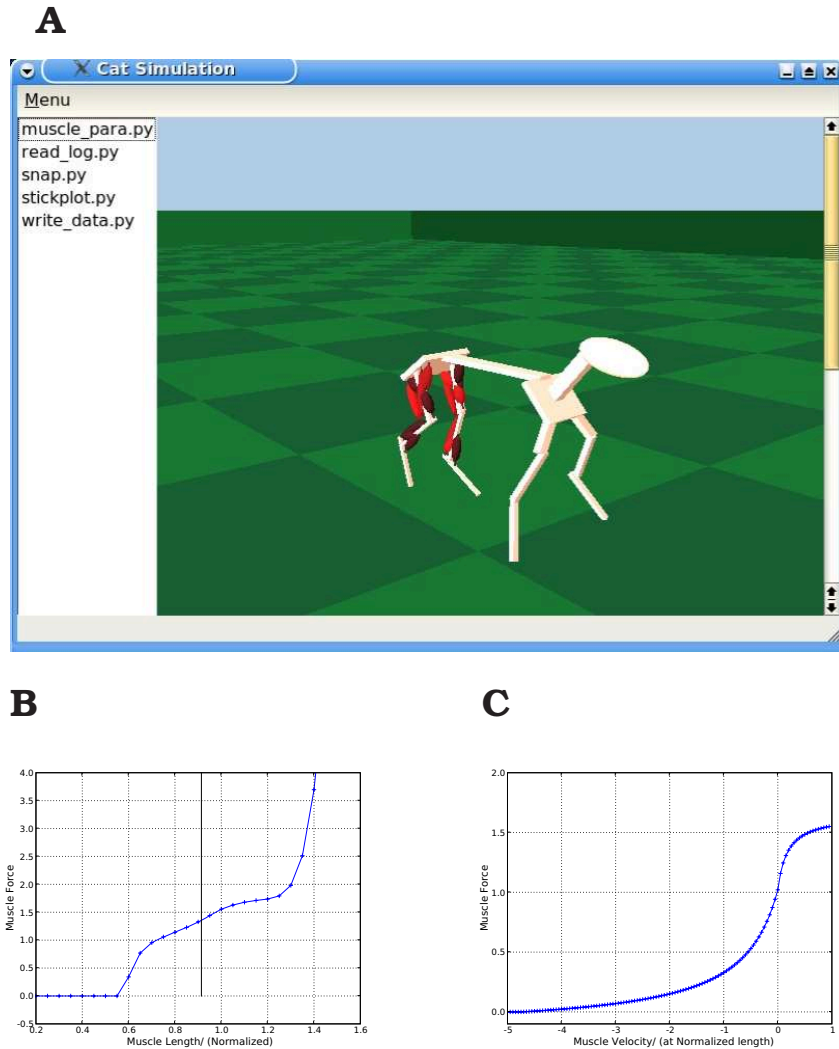


Figure 4.1. **A:** This figure shows a snapshot of the 3-dimensional cat model in the simulated environment. Hind limbs are controlled by the muscles but the fore legs are stiff and support the trunk. **B:** Force-length (Normalised) relationship for the simulated soleus (SOL) muscle at maximum excitation. **C:** Force-velocity curve for the maximally activated soleus muscle. Muscle length is at maximum length

The second step was to assess the stepping function. The spinal neural controller was modelled on a system level, that is, we did not attempt to include neuronal activities or circuits into the model. For instance, the CPG directly output the activity pattern for each muscle of a leg. In addition, the simulation

was simplified by excluding activation dynamics of the muscles i.e. muscles were directly activated by the output from CPG. It was possible to obtain stable stepping in the hind legs, after systematically adjusting the maximum activation level for each muscle. This adjustment only scaled (up or down) the level of activation but did not affect the temporal pattern.

We have constructed a three-dimensional dynamic simulation model of a four legged animal (cat) in order to assess the functional characteristics of neuronal mechanisms that control the leg muscles during the stepping behaviour (**Paper 1**). As described in previous chapters, the neural control of quadruped locomotion is a highly complex task that involves a number of parallel control mechanisms out of which some are not known. Furthermore, considerable amount of knowledge is available on the system level rather than in neuronal circuitry level (Ekeberg, 2000). Therefore the neuro-mechanical model was implemented on a system or functional level and we did not attempt to include all the known bio-physical properties into the model specially for the neural control system as long as it produces a stable realistic walking pattern. The simulation described in this thesis work include only the hind legs of the cat and fore legs are not controlled by the muscles, instead they are made stiff (see Fig. 4.1A). The model is capable of incorporating known sensory feedback to the controller by simply modifying the Python script for the control module (see Section 3.5). Furthermore, it is possible to include neuro-mechanical controllers for the front legs as well. This would be one of the future improvements to the simulator and it is promising since the neurophysiological experimental data on the coordination of fore and hind legs of walking cats were published recently (Akay *et al.*, 2006).

4.2. Deafferented Walking

One of the first experiments carried out with the implemented model in the simulated environment was to simulate the deafferented walking. The neural control module for that (basically CPG) was designed by excluding the modulation of sensory feedback from peripheral receptors. In fact, this investigation was done to test the functionality of the muscle model and the skeletal dynamics. It was possible to obtain a stable and alternating stepping in the model (see Fig. 4.2), even though there were no sensory feedbacks to either controllers (CPGs) or muscles. In fact, physiological studies on the spinal cats with a lesion in the Dorsal Root Ganglions (DRG) have shown the possibility of generating locomotor-like rhythmic motor output in the absence of peripheral sensory feedback (Brown, 1911; Grillner and Zangger, 1975). However, it showed some deviations from the typical locomotion pattern of the hindlimb of an intact cat. During the *early swing* phase, the foot was dragged a little and the model showed some discrepancy of foot placement towards the end of the swing (touch down). In fact, neurophysiological studies on decerebrate cats have shown that the unloading signals from the ankle extensor muscles are important for initiating the swing phase (Kandel *et al.*, 2000; Donelan and Pearson, 2004). Moreover, cutaneous inputs from the foot pads in the cat play a major role in precision walking

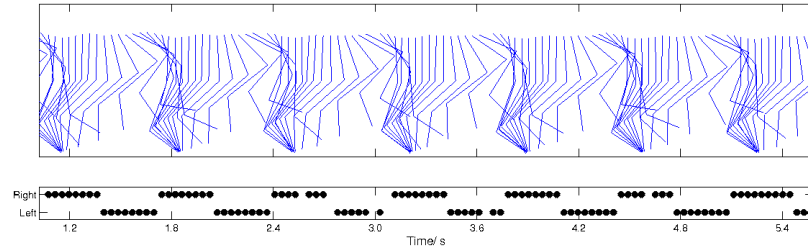


Figure 4.2. Top diagram shows the stepping of the right hind leg where the model was walking over a flat ground with no sensory feedback to the muscles or central pattern generators. The time interval between each snapshot is 20ms. Bottom diagram shows the timing of the ground contact for the two legs (black marks).

for intact cats and in foot placement for spinalized cats (see Section 2.1.3 and **Paper 2**).

4.3. Muscle–Joint Interactions

In this section, we will discuss the results of another investigation that we carried out with the simulator and the model of locomotion. As described in **Paper 2**, we have identified open-loop linear transfer functions from each limb muscle activation to each joint angle, at ten different postures of the leg covering the whole step cycle. In the paper, we have introduced a novel method to quantitatively describe the musculo-skeletal system that is isolated from the neural control and sensory feedback mechanisms while the system is engaged in ongoing locomotion. In fact, for this experiment we used the *deafferented* walking situation discussed in the previous section. In order to create a clear picture of the results and their significance, we will describe them under two sub-topics; controllability and stability.

4.3.1. Controllability

What is meant by *controllability*? Here in this investigation, controllability refers to the ability of the muscle activation in changing (affecting) the corresponding joint angle. The higher the controllability the quicker the response and the larger the effect on the joint. This definition should not be mixed up with the ‘controllability’ defined in modern control theory. From this analysis, it is possible to identify phase dependancy of muscle activity over joints, synergistic muscle groups and importance of spindle sensitivity control during each phase of the step cycle.

In order to investigate the controllability or sensitivity of each joint of the hind leg by each muscle, we plot the 'gain' of all muscle-joint transfer functions for one step cycle (see Fig. 4.3). As seen from the gain plots, *Anterior biceps* (AB) showed more sensitivity over the control of joint angles during the swing phase than that of stance. Similar pattern could be seen in the *Soleus* (SOL) muscle as well. On the other hand, the effect of activation level of *Iliopsoas* (IP) on the joint angles was dominant during the stance phase. If we look at those three gain plots more carefully, we see that the high sensitivity of the muscle occurred when it had been suppressed or received no regular activation from the CPG. Therefore, this pattern could be due to the fact that the corresponding muscle was in a stretched state when the joint was at either extended or flexed position. In fact, neurophysiological experiments have shown that the stretched muscle of an antagonist pair is more excitable than the other (Rossignol *et al.*, 2006). However, the electromyographic (EMG) activity of those muscles are more pronounced during the unstretched phase (see Fig.4.3). Hence, there should be a mechanism to increase the sensitivity of the muscle spindles during shortening in order to produce proper EMG activity that is necessary for generating limb trajectory for stepping. Thus, dynamic and phase dependent control of the CPG on muscle spindles sensitivity through alpha-gamma co-activation is very important for stabilization of the gait (Murphy and Hammond, 1997; Taylor *et al.*, 2000; Windhorst, 2007). In fact, alpha-gamma co-activation, which is a good example of dynamic sensorimotor interactions, varies with the task as well (Prochazka, 1989; Rossignol *et al.*, 2006).

On the other hand, some muscles could not generate any response on the joint angles in certain positions of the leg within the step cycle. For instance, change in activation of *Gastrocnemius* (GAS) and PB/ST muscle showed no response on any joint angles during early or middle stage of the swing phase respectively. The SOL muscle did not affect any joint angle during mid stance. Even, if we were to include fusimotor drive (gamma activation), we can not expect much improvement of the gains of the muscle-joint systems for SOL. In contrast, the GAS muscle did affect all the three joints during stance phase. Therefore, neuronal circuits that activate synergistically these two muscles should play a major role in force generation in SOL with changing movement conditions. Moreover, we can see that the sensitivity of the GAS muscle on the joint angles follows the pattern of the EMG activity, even though the muscles did not include any proprioceptive modulation, and this suggest that the GAS forces are associated with the activation coming from the CPG. In fact, in real cats, peak forces of *Medial Gastrocnemius* (MG) are found to be well correlated with the EMG activities (Kaya and Herzog, 2003). One other observation is that the bifunctional muscles (ST, SAT and GAS) showed increased sensitivity during the transition from swing to stance. This is indeed the case in real animals. Quevedo *et al.* (2000) has found that in motoneurons of bifunctional muscles, excitatory post synaptic potentials (EPSPs) were often largest at the transition between flexion and extension phases (Rossignol *et al.*, 2006).

Another observation from the *Gain* plots is the sign reversal of the gain of VL-

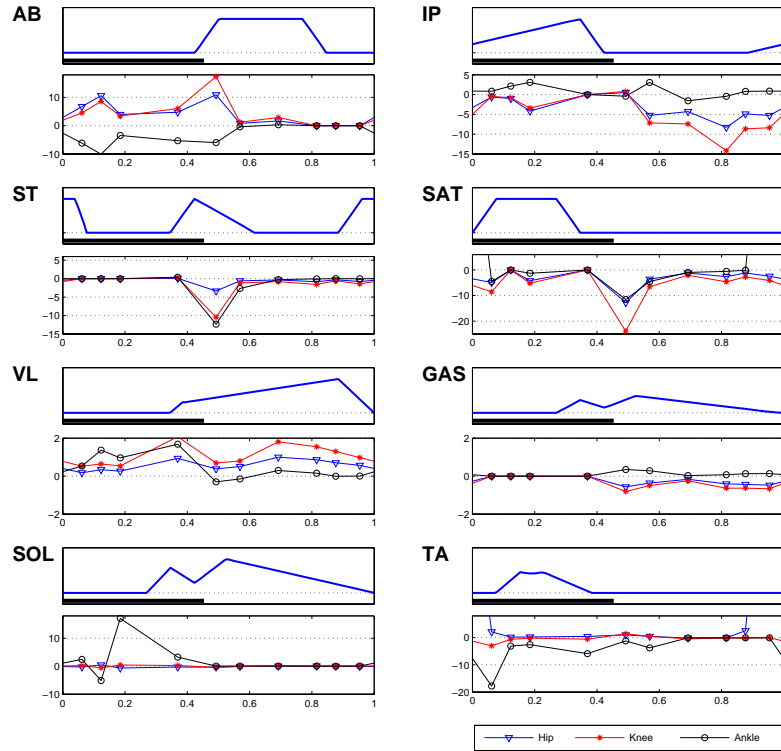


Figure 4.3. Variation of activation and the gain of the identified transfer functions during a step cycle of the walking cat model. Each block of two panels, top- Activation and bottom- Gain, corresponds to one of the muscles of the cat hindlimb (see Fig. 2.3). In each activation panel, the horizontal black bar shows the duration of the **Swing** phase. Gain values of the systems between the muscle activation and the three joints are shown in each panel and the legend is shown at the bottom of the figure.

ankle system when the leg was moving from *swing* to *stance*. Similar pattern could be seen in the transfer functions between IP and all three joint angles; ankle, knee and hip, when the leg transits from swing to stance. Furthermore, gain of the system between ankle-flexor or TA and the knee angle showed the same effect. However, the sign of the above mentioned systems' gains changes back during the middle or late stance phase. Since, we did not include any sensory feedback from muscles or joint receptors to CPGs or muscle itself, this *phase dependent* sign reversal of the gain coefficient of some of the systems could be due to either reaction to ground contact of the foot and its mechanical linkage with the other limb segments or varying activity of the other muscles acting on the same joint. The significance of this result is that it mandates

different control strategies or reflex modulation depending on the position of the leg within the step cycle.

4.3.2. Stability

To investigate the stability properties of the identified continuous systems, we have plotted the location of their *poles* in the s -plane with respect to the leg position in the step cycle (see Fig. 4.4). Here, we demonstrate pole diagrams only for four muscle-joint systems and for the other four muscles the reader should consult **Paper 2**. For the comparison, the order of the denominator of all the transfer functions was set to two. Therefore, in most of the cases, poles are complex conjugate pairs. We have tested to increase the order of the denominator and did not find any qualitative improvement of the systems impulse response over the measured simulated impulse response for any muscle-joint interaction. In fact, by including a second order *denominator* to the Output Error (OE) model, we were able to capture the length and velocity dependencies of the muscle force since the joint angle and the change in joint angle (angular velocity) is directly related to the muscle length and velocity.

It is possible to identify several clusters of poles from different leg positions, meaning that it should be possible to use similar strategies for controlling leg movements with small changes. In general, poles of the muscle-joint systems within one phase, stance or swing, belonged to one cluster. The muscle-joint systems between the VL, GAS, ST, SAT and IP muscles and the hip and knee joints clearly show the grouping according to the *phase* of the moving leg. Hence, the existence of phase dependent neural control mechanisms for locomotion is a necessary condition. Transition from one control strategy to the next would involve locomotor CPG, sensory feedback, synergistic activity of muscles and other neuronal circuits that involve phase dependent reflex modulation (Forssberg *et al.*, 1975; Krouchev *et al.*, 2006; Rossignol *et al.*, 2006). Muscle synergies in cats have been suggested to be related to foot and limb kinematics in walking and ground reaction forces in stance (Torres-Oviedo *et al.*, 2006). Moreover, proprioceptive feedback could adapt the recruitment of centrally organized synergies to behavioural constraints and fine-tune the activation of muscles within a synergy (Cheung *et al.*, 2005; Windhorst, 2007).

In contrary to the previous result, it is hard to find clear separation of pole distribution in SOL (see Fig. 4.4) or TA muscle-joint systems. By looking at the figure, we see that there is no clear grouping in pole positions of the systems related to the *ankle* joint as well. This could be due to the fact that the ankle joint is situated more distally to the body and is subjected to more perturbations from the ground reaction forces and hence require more fine neural control, which may involve additional supra-spinal structures, over the whole step cycle. Another observation from the pole plots is the similarity in the pole spreading pattern of the systems on the s -plane for a same muscle between hip and knee joints.

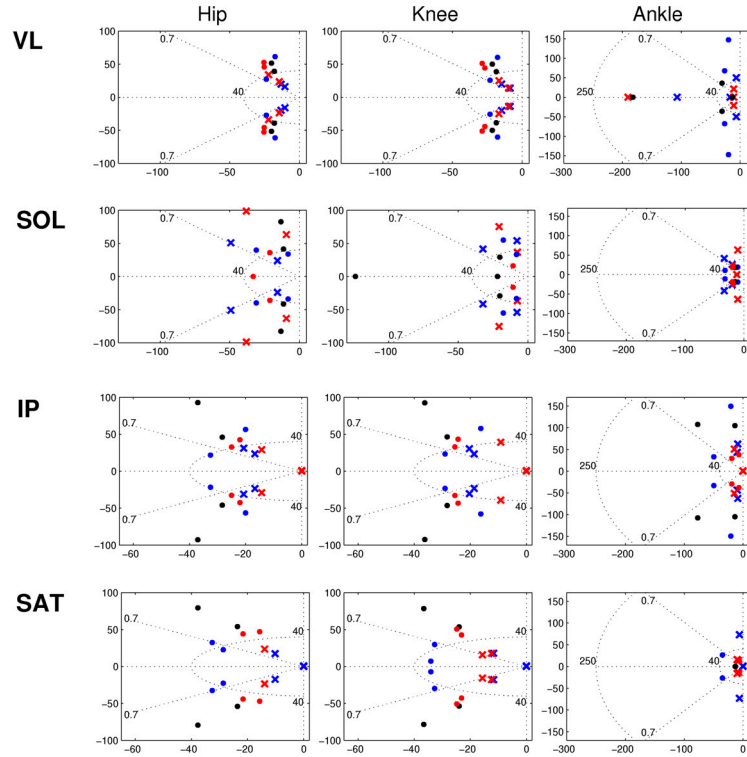


Figure 4.4. Location of the poles of the identified transfer functions during a step cycle of the walking cat model. Each row corresponds to one of the muscles (top two-distal and bottom two-proximal) of the cat hind leg. Hip, Knee and Ankle panels show the location of the poles of the system between the muscle and the corresponding joint. Note that the IP and SAT has a different horizontal scale for the Hip and Knee panels. Legend: '•' - during **Stance** phase, 'x' - during **Swing** phase; color scheme: 'blue' and 'red' for early and late in each phase respectively, 'black' is for middle stance.

Sometimes change in activation level of a muscle can cause oscillations in the joint (angle) on which muscle is acting. In addition, these oscillations can propagate to other joints since limb segments are connected to each other. From control theory, we know that how rapidly a system responds is determined by how far into the left half plane the poles of the system are. On the pole diagrams (see Fig. 4.4), the dotted radial line represents systems with a damping coefficient of 0.7, which is a reasonable margin for critically damped systems (damping coefficient increases in counter-clockwise direction in the upper half of the left half plane). Most of the stable muscle-joint systems show sufficiently damped (but still under-damped) conditions. This may be due to the fact that biological systems are evolved to adapt the most efficient or least energy consuming mech-

anisms. However, there were systems that generate oscillations before settling. This implies that neural feedback control mechanisms are essential for stabilizing the inherent instabilities (oscillations) of these muscle–joint systems. In fact, neurophysiological studies have identified several proprioceptive pathways such as the monosynaptic stretch reflex, reciprocal inhibition and recurrent inhibition via *Renshaw* cells (see Section 2.2.1), which give more stiffness to the muscle and more damping action to the joint (Kandel *et al.*, 2000; Hultborn, 2006; Windhorst, 2007).

Another observation from these plots is the effect of the limb muscle on distant joints (joints on which muscle is acting indirectly). If a pole is near the imaginary axis and far away from the origin, the muscle–joint system with that pole generates oscillations, which could last for a long time even though they damped out, in the output joint angle. However, several muscles acting over a same joint in this manner could easily cause instabilities in that joint. We found that, for instance, SOL and TA (ankle extensor and ankle flexor) can generate more oscillations in the hip joint during both *late stance* and *late swing*, while AB and IP (hip extensor and hip flexor respectively) can create oscillations in the ankle joint. Moreover, VL could affect the ankle joint in the same manner during *early stance* phase.

4.4. Concluding Remarks

4.4.1. Neuro-mechanical Simulation

The use of computer simulations to examine the locomotor system of the cat has been a prominent technique in recent past. They provide a powerful tool for combining large amount of data on the neuronal, muscular and mechanical components involved in walking (Ekeberg and Pearson, 2005). Simulations can be used for assessing neuronal mechanisms that govern the walking behaviour, the function of the individual muscles or muscle synergies, the role of sensory feed back in controlling the magnitude and timing of motor activity and the interactions between mechanical components (Pearson *et al.*, 2006). Furthermore, simulations enable direct monitoring of individual components of the locomotor system and the functional effects of modifying or removing one of those individual components. However, it is impossible or inappropriate to include all the neuro-physiological properties of the neuro-musculo-skeletal-control system for locomotion into the simulation since it may introduce unwanted complexities to the model that would increase the computational cost and time. Level of complexity of the simulation model should be a compromise between the type of investigation and the available computational infrastructure. Nevertheless, the use of simulations of walking in the cat for gaining insights into more complex interactions between the environment and the neuro-muscular-skeletal system will undoubtedly become important especially for questions where a direct neurophysiological experiment can not be performed on a real walking animal.

4.4.2. Muscle–Joint Interactions

Let us state the major conclusions that we made from the system identification experiment (**Paper 2**). In this investigation, we have demonstrated that simulation of neuro-musculo-skeletal (NMS) elements of the cat hind legs can be used to identify open-loop linear transfer functions, from each limb muscle activation to each joint angle, throughout the whole step cycle. Here, we introduce a novel method to identify the musculo-skeletal system, that is isolated from the neural control and sensory feedback mechanisms, while the system is engaged in ongoing locomotion. We found that the actions of most of the hindlimb muscles over the joints display inherent stability during stepping, even without the involvement of any proprioceptive feedback mechanisms. However, action of the VL, TA and SAT muscles during the *late stance* phase cause all three joints to be unstable. A similar effect could be seen in the action of the PB/ST muscle during the *late swing* phase. Hence we conclude that additional neuronal control circuitry is required in activity regulation of those muscles, in order to establish stable stepping of the hind legs especially during phase transitions. Moreover, we could see a clear distinction in the pole distribution (along the step cycle) for the systems related to the *ankle joint* from that of the other two joints, *hip* or *knee*. A similar pattern, in which the poles were scattered over the s -plane with no clear clustering according to the phase of the leg position, could be seen in the systems related to SOL and TA muscles and hence we conclude that these muscles should be controlled by a neural mechanism, which may involve supraspinal structures, over the whole step cycle. Furthermore, the linear transfer functions identified in this approach will be useful in designing electro-mechanical actuators for robotic walking emulators that resemble muscle action on joints.

Chapter 5

FUTURE WORK

Our main objective is to understand better the neural mechanisms behind control of locomotion and sensory feedback on stabilizing the gait in quadrupeds. Here, we introduce a computer simulator to study the neuro-musculo-skeletal-control (NMSC) system for locomotion in the hind legs of a quadruped animal, especially the cat, and also a novel method to identify the musculo-skeletal system, that is isolated from the neural control and sensory feedback mechanisms, while the system is engaged in ongoing locomotion. Additionally, in both investigations, the neural controller module (CPG) did not include sensory feedback coming from muscles (proprioceptors) or skin receptors (cutaneous). The future goals are to increase the adaptation capabilities of the neural controller by including dynamic sensorimotor interactions and to include NMSC for the front legs.

Since we already have a neuro-mechanical simulator which is constructed in a *modular architecture*, any modification to a module or submodule can be performed easily without interfering others. In fact, object oriented programming technique allowed easy access to parameters (measurable quantities) such as muscle force, muscle length, and joint angles which are required for modelling sensory feedback and reflex pathways (see Section 3.4.2). After incorporating sensory feedback into the controller, fine tuning of control parameters will be done in order to obtain a robust stepping, on horizontal ground, in the hind legs. In our present model, front legs are made stiff and included only as supports for the trunk. However, their segment lengths and weights are chosen to match available physiological data. Therefore, the only thing needed to make them *active* is to include leg musculature and CPGs to regulate the activation of each muscle. The CPG for each forelimb will be modeled at the system level as we did it for the hindlimbs. For this, available EMG data on front leg muscles during locomotion will be adapted (English, 1978; Akay *et al.*, 2006). Furthermore, synergetic activity of front leg muscle groups, during locomotion, has been

studied recently (Krouchev *et al.*, 2006) and those data undoubtedly will be useful in modelling the CPGs.

As we discussed in section 2.1.4, our knowledge of neuronal mechanisms coordinating stepping in quadruped animals is very poor. A few studies have attempted to gain insight into the neural mechanisms underlying *interlimb coordination* in walking cats by examining the patterns of stepping especially when pairs of legs step on different treadmills (English and Leonard, 1982; Halbertsma, 1983; Cruse and Warnecke, 1992). Recently, Akay *et al.* (2006) introduced several hypotheses for the front and hind leg coordination of a normal walking cat. We aim to use the completed walking model (with four legs), in the simulated environment, to test the hypotheses related to limb coordination. Perhaps, we will be able to develop new control strategies for the ipsilateral and contralateral coordination of legs. In fact, finding a control algorithm (to regulate and combine four controllers, CPGs) which gives robust, adaptive, efficient and realistic stepping in each leg would be advantages since it can be implemented on a controller of a quadruped-robotic device.

With the fully equipped walking model, we will be able to define new experimental investigations in order to understand the neural control of locomotion. For instance, changes in limb kinetics and kinematics during slope (up or down) or crouch walking can be easily investigated. In fact, there are neurophysiological data, on such behaviours of cats, available for comparison or to use in modelling (Trank *et al.*, 1996; Gregor *et al.*, 2006). Other possible use of the simulator involve further investigations on perturbation analysis of the walking model. The model can be subjected to external forces while walking or can be set to walk in different terrains or slippery surface to identify changes in limb kinematics. From those results, we will be able to predict control requirements and what needs to be included in NMSC system to maintain stability in such situations.

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Part I.

Papers

Paper I

Building a Computer Simulator for the Study of Stepping of the Cat

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Abstract

We have developed a three-dimensional (3-D) computer simulator for investigating the neuro-musculo-skeletal system and its interactions during normal walking of the cat. Main components of the cat model are the simulation of skeletal dynamics and the control system that includes a mathematical muscle model and a central pattern generator (CPG) network. The simulator is programmed in Python scripting language with other supported open source libraries such as Open Dynamics Engine (ODE) for body dynamics and OpenGL for 3-D graphical representation. Modular structure and the object oriented programming technique allows easy access to the model parameters and the modules can be easily modified without altering the entire program. To test the model's functionality, a simple experiment, during which the cat was set to walk on a flat surface with only the hind legs' muscles were controlled by two separate CPGs with no sensory feed back, was carried out. It was possible to obtain a realistic stepping in the hind legs even without sensory feedback to the two controllers for each leg. We conclude that the mechanical linkages between the legs also play a major role in producing alternating gait.

Keywords: Computer simulation; Locomotion; Central pattern generator; Body dynamics; Sensory feedback; Muscle model

1 Introduction

Locomotion is one of the neuronal mechanisms that has been evolved from early stages of the life on earth. The study of locomotion in legged animals has a long written history too. Based on the behavioural studies, Aristotle in 350 BC presented certain theories related to animal locomotion in one of his publications, “*On The Gait Of Animals*”. During the beginning of the 20th century, Brown (1911) discovered in his experiments with decerebrate cats that the possibility of generating rhythmic pattern for walking without descending signals from the brain and feedback signals from the sensory pathways of the leg. These *intrinsic factors* (name given by the Brown) located at the spinal level are currently known as Central Pattern Generators (Grillner and Zangger, 1975). Towards the latter part of the 20th century, researches either from physiological or neurological background were involved in more investigations on the mammalian locomotor system, especially that of the cat. Those experiments lead to a reasonable understanding of the neuronal mechanism of the cat locomotor system and associated biology such as the mechanical properties of the legs and leg muscles, kinematics of the stepping and patterns of electromyographic activity in leg muscles (Ekeberg and Pearson, 2005). Furthermore, the neural controller and the musculo-skeletal apparatus of the cat limb locomotion is believed to be one of the most efficient and evolved control systems (Jiping et al, 1988) and the stepping of the cat is a behaviour well suited for modeling and simulation studies.

Over the past fifteen years, the knowledge about the neuronal mechanisms that control the mammalian walking has increased. Identification of central pattern generating networks that are involved in regulating the walking behaviour (Brown, 1911; Baev and Zavadskaya, 1981; Kandel et al, 2000), identification of contributions from peripheral sensory receptors that are modulating the centrally generated rhythmic activity (Hiebert et al, 1996; Donelan and Pearson, 2004; Frigon and Rossignol, 2006) and the development of mathematical models for cat limb muscles (see the next section) lead to the development of reasonably realistic computer simulations of the locomotor system for the cat. When using a computer simulator, it is possible to isolate some of the individual mechanism in functional context and run the simulation to investigate the possible outcomes. This is a huge advantage, since it is impossible to isolate individual neuronal mechanisms or set of mechanisms in intact or behaving animals for experiments in neurophysiological studies. Another possibility is to use some of the control strategies used in the simulation study to construct biologically inspired robotic systems (Lieber, 1999; Prochazka, 2002; Kimura et al, 2001; Fukuoka et al, 2003).

Three recent studies demonstrated the use of realistic simulations for the stepping in the hind leg of the cat (Ivashko et al, 2003; Yakovenko et al, 2004; Ekeberg and Pearson, 2005). Ivashko et al (2003) used a two-dimensional simulation to propose a neuronal architecture for the pattern generating networks in the spinal cord and their interactions with the reflex circuits. In another study, two-dimensional simulation of the hind legs was used to investigate the importance of stretch reflex

circuits in stabilising the gait by controlling the level of activity in load bearing muscles (Yakovenko et al, 2004). Ekeberg and Pearson (2005) developed a three-dimensional simulation model of the hind legs to examine the sensory mechanism that are considered important in controlling the transition from stance to swing during stepping in the cat. After considering the above examples, it is evident that the use of realistic computer simulations in the study of the locomotion is a potential, reliable and emerging technique for researches in this field.

This led us to develop a three-dimensional (3D) cat legs model that incorporate known properties of neuronal mechanisms, muscles and body mechanics for stepping in a computer simulated environment. The cat model that we developed and described in this report is based on the model developed by Ekeberg and Pearson (2005).

The simulator is constructed in a modular manner and the three main modules are numerical solver for body dynamics, control system and graphic engine. The control system includes separate sub modules for simulating leg muscles, joint interactions and central pattern generators (CPGs). Body dynamics and graphic engine are modeled using the Open Dynamics Engine (ODE) and the OpenGL respectively. The main program or the software is developed using *Python* scripts and other related open source libraries. We will discuss the construction methodology in detail in the Methods section of this report. Next section will give you some physiological and neurological background information which is necessary for understanding the walking model and the simulator. A basic experiment was performed to test the simulator's functionality. During the experiment, only the two hind legs' muscles were controlled by two separate CPGs without sensory feedback modulation while the fore legs were kept stiff. It was possible to simulate stable stepping in the hind legs of the cat, similar to simulations done by Ekeberg and Pearson (2005).

2 Theoretical Foundation

When assembling a biological realistic model for neuro-mechanical simulation in the stepping of the cat, it needs to be included with models for body and muscle dynamics, central pattern generators and further more for proprioceptive receptors. In this section we will briefly go through some of the biological models or concepts to provide the necessary background to understand the neuro-musculo-skeletal system.

2.1 Central Pattern Generator

Central pattern generators are neuronal circuits which can generate rhythmic activity without rhythmic input (Ijspeert, 2002). In relation to vertebrate locomotion, including cats and humans, it has been shown that the rhythm arises from local neural networks reside in the spinal cord (Kandel et al, 2000). In fact these local networks are Central Pattern Generators or CPGs, as first proposed by Brown

(1914), which create the motor pattern for locomotion. Studies of spinal preparations of cats on treadmills show the existence of a CPG at the spinal level which generates the rhythmic locomotor patterns without the influence from cerebral cortex or brain stem (Baev and Zavadskaya, 1981; Kandel et al, 2000; MacKay-Lyons, 2002). In addition, the CPG is capable of generating basic rhythmic motor output in the absence of peripheral feedback (Brown, 1911; Grillner and Zangger, 1975). But in intact animals, CPGs are dynamically interacting not only with each other but also with supraspinal inputs and sensory feedbacks in order to adapt the locomotor pattern to the environmental and motivational conditions (MacKay-Lyons, 2002; Rossignol and Bouyer, 2004; Rossignol et al, 2006).

For simulation studies, depending on the goal of the investigation, the CPG does not always need to include all the complexities such as cellular and synaptic mechanism unless it reacts to the sensory feedback according to the experimental results. It is reasonable to model the locomotor CPG by a phase dependent component with contributions from sensory feedbacks for adjusting the muscle activity and for switching from one phase to another (Ekeberg and Pearson, 2005; Pearson et al, 2006).

2.2 Sensorimotor Interactions During Locomotion

Sensory information from various sensors in the mammalian body plays a major role in adapting the basic locomotor pattern to the environmental conditions. Vestibular inputs from head orientation and anticipatory adjustments from higher visual areas of neocortex are essential for avoiding obstacles and maintaining a stabilized gait. In the spinal level, proprioceptive inputs from muscle spindles, Golgi tendon organs and joint receptors interact with the CPG to react and compensate for various types of perturbations. In this report, we will focus on the spinal networks regulating locomotion.

A locomotor step cycle can be divided into two main phases; “stance”, where extensor muscles get activated for load bearing and “swing”, where flexor muscles get activated. Although the CPG can produce the basic locomotor pattern, feedback inputs from proprioceptors play a major role in smooth transition from swing to stance and vice versa. Further more they can affect the timing and amplitude of the locomotor activity (Frigon and Rossignol, 2006). Recent studies of decerebrate cats walking on treadmills show the evidence for influence of sensory feedback on locomotion (Hiebert et al, 1996; Hiebert and Pearson, 1999; Donelan and Pearson, 2004). For instance, initiation of swing is governed by unloading of the ankle extensor muscles. This hypothesis is supported by the observations of Conway et al (1987); Whelan et al (1995); Whelan and Pearson (1997). Another sensory mechanism involved in transition from stance to swing is the activation of flexor muscles by the afferents from the hip region (Hiebert et al, 1996; McVea et al, 2005). Thus, when constructing a biologically realistic simulator for stepping in the cat, it is essential to include the sensory signals and their interactions with the CPGs.

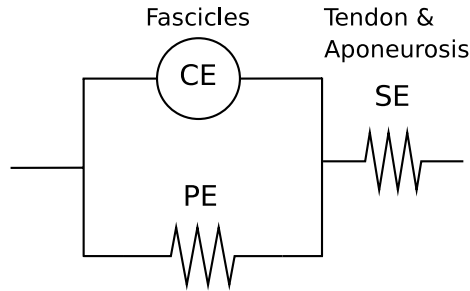


Figure 2.1: Schematic of the three element model: a series elastic element (SE) for the connective tissues and a passive elastic element (PE) in parallel with an active contractile element (CE) for the fascicles (Brown and Loeb, 1995).

It is the continual and dynamic interactions between the central program and the feedback mechanism that generate the stable locomotion by modulating transmission in locomotor pathways in a state- and phase-dependent manner (Rossignol et al, 2006). Predominantly these pathways include “spinal reflexes” that are mono- or polysynaptic and can affect the ipsilateral or contralateral limb (Duysens and Loeb, 1980). Both afferents from the muscle spindles and Golgi tendon organs are involved in these reflexes and they are generally functioning as a negative feedback mechanism for controlling the muscle length and the muscle force respectively. However, some of these could be changed to positive feedback in a phase dependent manner, for instance ankle extensor Ib afferents from Golgi tendon organs contribute to the ankle extensor activity as a positive feedback during the stance phase of a walking cat (Donelan and Pearson, 2004).

2.3 Mathematical Muscle Model

Muscles generate the force and hence torque to move the limbs in a certain trajectory. The mathematical models of muscles are necessary to understand and implement strategies for limb control in a simulator environment. The force produced by a muscle is primarily a function of its length, velocity and level of activation. Although these relationships are more complex, linear models are often sufficient for simulation studies (Ekeberg, 2000). In 1938, Hill used those relationships as three linear and independent mechanisms to produce the muscle force. He assumed the muscle to be composed of two *elastic* elements and one parallel *contractile* element, which generates the force in accordance with the force-length and force-velocity characteristics of the muscle. Those two ‘elastic’ elements represent dynamic and static elastic properties of the muscle.

As an extension, Zajac (1989) introduced tendon and pennation angle into the Hill-type muscle model. Furthermore, based on this model and also with experimental data of cat soleus muscle, Brown and Loeb (1995) developed another math-

ematical muscle model (Scott et al, 1996; Brown et al, 1996) which we adapted to implement the limb muscles for the cat in our simulator. As shown in the Figure 2.1, tendon and aponeurosis were lumped together and included as one series elastic element.

When implementing a computer simulator, it would be better to use a simplified model. For instance, activation dynamics of muscles may sometimes be ignored. In that case instantaneous activation levels can be used for force generation. If the simulator incorporate with a spiking motor neuronal model, then the conversion from spike rate to activation levels must be included in the model. One way of achieving this, as proposed by Zajac (1989) is to use low pass filtering of rectified neural output with a suitable time constant. In this study, the model was implemented with only muscle contraction dynamics.

3 Methods

Building a simulator for a neuro-musculo-skeletal (NMS) system would be difficult, if we model the whole system as a single module. One of the promising choices is to use different modules for different subsystems, for instances modules for neural control, muscle mechanics and body dynamics of the NMS system and combining them with proper interactions. Each subsystem can be considered as a mathematical entity that has to be parameterised or modeled and implemented in the simulation environment. In this section, we will look in more detail how the each subsystem implemented in the three-dimensional simulator for the stepping in the cat. However, in this report, we will focus on implementation of the hind legs and their locomotion on a flat ground when they attached to a trunk and stiff fore legs that form frictionless contacts with the ground.

This simulation is based on the 3-dimensional forward dynamic simulation model of the hind legs of the cat developed by Ekeberg and Pearson (2005). Each limb has three segments: thigh, shank and foot with four degrees of freedom. While the movements at hip and knee joints are controlled by torques produced by four muscles, movement at ankle is controlled by three muscles arranged to resemble actual muscles in the cat hind limb (Figure 3.1). In addition, the hip joint is also subjected to abduction-adduction movements which give it an additional degree of freedom and those movements are controlled by a passive spring (musculo-tendon with high stiffness). Activity pattern for each muscle of a leg is generated by a central program (mimicking CPG) and the magnitude of the activation level could be automatically adjusted by a controller based on known physiological mechanisms.

3.1 Simulation of body dynamics

The skeleton of the cat (the body and the leg segments) were modeled as rigid segments with the use of ODE (Open Dynamics Engine ¹) which is an open source, high performance library for simulating rigid body dynamics. Centre of mass for each segment is located at the midpoint of each. The masses of the leg segments were taken from Hoy and Zernicke (1985) and the trunk weight was set to 2 kg which is reasonable for an average cat. In the simulation program, with the help of functions of the ODE library, location and orientation of each segment (body in ODE terminology) in the 3-dimensional space was specified by a set of cartesian coordinates. Additionally, movement of segments in relation to each other is restricted with the help of a set of ‘Joints’ or ‘Constraints’ so that they can only have certain positions and orientations relative to each other. The *knee* and *ankle* joints are implemented with *hinge joints* so that they allow only one degree of freedom while the *hip* joint allows two. This functionality is obtained by putting two hinge joints, with their axes perpendicular to each other, on to a small body part that lies in between the thigh (limb) and the trunk. This mechanism allows the leg to rotate around an axis parallel to the trunk and supports abduction-adduction movements that can be seen in real cats.

The mechanical body of the cat was implemented in a “world” with a gravitational field strength of 9.81 m/s^2 . The ground is modeled as a horizontal surface and the *contact* between the ground and the hindlimb foot is governed by the coulomb friction with a high friction coefficient and a restitution parameter of 0.01. This was implemented with overriding the built in *collision detection* function of the ODE library.

The process of simulating the rigid body system through time is called *integration*. In this simulation, each integration step advances the current time by a time step of 0.005 ms, adjusting the state of all the rigid bodies for the new time value. These new locations are calculated by numerically solving equation of motions that are derived by a Lagrange multiplier velocity based model. The adapted method was the standard “Big matrix” method that takes time on the order of m^3 and memory on the order of m^2 , where m is the total number of constraints (www.ode.org).

3.2 Simulation of leg muscles

Each modeled hind leg included eight muscles; five of them acting over single joints- hip flexion (*iliopsoas* - IP), hip extension (*anterior biceps* - AB), knee extension (*vastus lateralis* - VL), ankle extension (*soleus* - Sol), and ankle flexion (*tibialis anterior* - TA) and three bifunctional muscles acting on two joints- hip extension and knee flexion (*posterior biceps and semitendinosus* - PB/ST), hip flexion and knee flexion (*sartorius* - SAT), and knee flexion and ankle extension (*gastrocnemius* - Gas, see Figure 3.1). The simulation of all the muscles was based on the mathemat-

¹www.ode.org

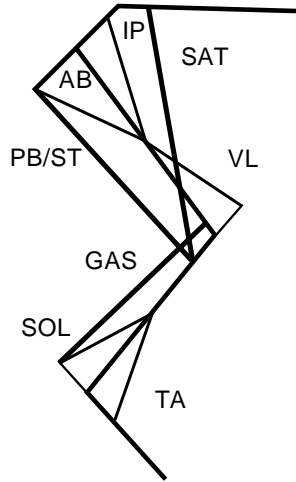


Figure 3.1: Included muscles in the cat limb model.

ical model introduced by Brown et al (1996). The parameters used for calculating the force-length and force-velocity relationships were taken from published papers (Brown et al, 1996; Ekeberg and Pearson, 2005). As described in the mathematical muscle model section, each muscle also included a series elastic tendon and the tendon stiffness for each was set to match biological data (Rack and Westbury, 1984; Proske and Morgan, 1987; Ekeberg and Pearson, 2005).

The generated muscle force was then converted to joint torques by multiplying with the corresponding moment arm. The moment arms for each muscle were taken from the published experimental data (Goslow et al, 1973). Furthermore, moment arm was scaled by a factor (≤ 1) to resemble the effect of shortening of perpendicular distance to the muscle axial force from the joint centre, when the joint is more flexed or extended. At neutral posture, the muscle lengths were set about 75-85 % of the maximum length (see Appendix) so that they would generally operate at the rising slope region (partially linear) of the force-length curve. When the simulation is running, during each time step, lengths and velocities of the muscles were calculated from the geometry of the limb segments, moment arms and the actual angular velocities (obtained from ODE) of joint movements and fed them together with activation level from the controller to each muscle model, which in turn calculate the torque to be applied on each joint. The force and hence torque was scaled linearly with the activation level. Maximum level of activation for each muscle were adjusted (different scaling factor for each muscle) manually, in order to produce a reasonable realistic movements of the legs. The resultant torque at each joint is the algebraic summation of contributions from all the muscles acting on that joint.

Abduction and adduction movements at the hip joint were controlled by a passive

linear spring with damping. This is similar to a muscle with a tendon which has high stiffness. The neutral angle of the spring was set to two degrees of adduction which caused the hind leg to lean slightly inward.

3.3 Simulation of the neural activity: EMG Pattern

The activity level of each muscle in each leg was controlled by a central program which generates a unique pattern for each muscle. These patterns are comparable to electromyographic (EMG) activity of each muscle of the hind limb of the cat during normal walking (Kandel et al, 2000; Ivashko et al, 2003). In this study, we did not include known sensory feedback (reflex pathways) into the controller, since our aim was to obtain a basic locomotion with only the CPG as a validation for the model dynamics. However, it is possible to incorporate known sensory pathways by simply modifying the controller with feedback mechanisms for future use. Furthermore, the program is capable of switching to a finite state controller which is based on physiological mechanisms for state transitions and activation level control (Ekeberg and Pearson, 2005).

Figure 3.2 shows the normalised activation levels for each muscle during a one step cycle. Each leg was controlled by a separate CPG having the same pattern but with a fixed phase shift of 50 % from each other and this corresponds to an alternating gait pattern. During the simulation, each leg was progressing sequentially and repeatedly from swing to stance and back to swing. The swing and stance phases were set to about 40 % and 60 % of the step cycle duration respectively, which is an appropriate relationship for medium speed walking (Yakovenko et al, 2004, 2005). Total cycle time was about 650 *ms* and cat was moving forward with a speed of about 0.4 *m/s* on a flat horizontal surface.

When the simulated cat was walking, the phase in the step cycle of the CPG-activation pattern was specified by an internal clock variable which in turn determined the magnitude of the level of activation to be sent to the corresponding muscle actuators. During the early part of the swing phase, the hip flexor (IP), bifunctional hip flexor and knee flexor (SAT), bifunctional knee flexor and hip extensor (PB/ST), and ankle flexor (TA) muscles were activated simultaneously to initiate the swing by lifting the foot from the ground. Then the increased activity of the hip and ankle flexors (see Figure 3.2) moved the limb forward in the air. Towards the end of the swing phase, decreased activity in flexor muscles and increased activity in extensors, particularly bifunctional hip extensor and knee flexor (PB/ST), and ankle extensor and knee flexor (Gas) muscles, caused the termination of the swing. Finally, the stance phase was initiated when the foot contacted the ground.

During the stance, hip extensor (AB), knee extensor (VL), bifunctional ankle extensor and knee flexor (Gas), and ankle extensor (SOL) muscles were activated in order to bear the trunk weight and to move the body in forward direction. Activity of extensor muscles first increased and then decreased as the stance progressed.

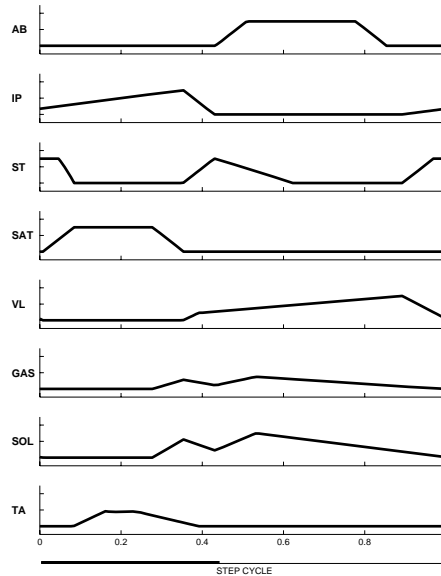


Figure 3.2: EMG activity: Figure shows the activation pattern for each hind limb muscle during a step-cycle. Duration of the swing phase is shown by the black horizontal bar at the bottom of the figure, rest of the cycle is the stance phase.

During the end part of the stance, the hip flexor and bifunctional knee flexor/hip extensor muscles were activated in order to facilitate the swing initiation.

3.4 Programming and running the simulation

The simulation program was developed as a collection of modules that are interacting with each other. This object oriented programming technique allowed easy access to various parameters which could be used for monitoring and for assessment of each simulation trail. The mechanical dynamics solver which is the Open Dynamics Engine (ODE 0.5), the control system (CPG) and the graphical engine are the main modules of the simulation program. These modules were combined into one main program written in the scripting language Python (python 2.4.4¹). Additionally, the numerical simulation of leg muscles and the model of the neural control system were also written in the Python language. PyODE², which is a set of open

¹www.python.org

²<http://pyode.sourceforge.net>

source python bindings for the ODE, was used to numerically simulate the leg and body dynamics of the cat. Presenting the 3-dimensional graphical environment on the screen was done with the PyOpenGL 2.0³, which is the cross platform Python binding to OpenGL and related APIs. Figure 3.3 shows the sequence of steps followed when the simulation running.

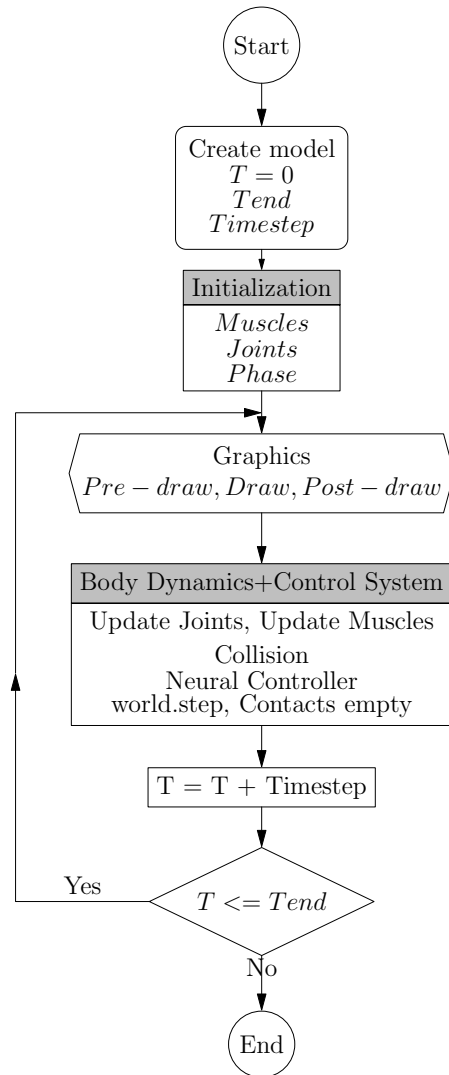


Figure 3.3: Flow chart of the simulation program.

³<http://pyopengl.sourceforge.net>

The simulator was developed and executed within the Debian GNU/Linux operating system. The time step for the mechanical rigid body simulator (ODE) was 5 *ms* and the muscle model, controller and the graphics engine were also updated at the same rate. When running on a computer with a 2.00 GHz processor (Intel Pentium- Mobile centrino), the rate of the simulation was approximately 15% real time; for instance, a 3 *s* experiment took about 20 *s* to simulate.

4 Results

The main objective of this report was to discuss the implementation techniques and methods of the walking model in detail. However some of the results obtained in the experiment discussed in early sections (CPG driven basic locomotion) will be given in this part as a validation to the simulation model.

In the cat model, hind limb segments were controlled by eight muscles (Figure 3.1) that have different characteristics (see Appendix). Figure 4.1A shows the normalised total force–length relationship of the simulated soleus muscle. During the locomotion, all the muscles were operating at the rising slope region (partially linear) of the force–length curve. Vertical line in the figure corresponds to the active length of the soleus muscle at neutral posture. Length of the soleus was either increased or decreased around the neutral point when the ankle joint flexed or extended respectively. Furthermore, force generated by a muscle was varied with the shortening or lengthening velocity of that muscle. Force–velocity relationship for the maximally activated soleus muscle at optimal length is shown in the Figure 4.1B and shortening of the muscle corresponds to a negative velocity.

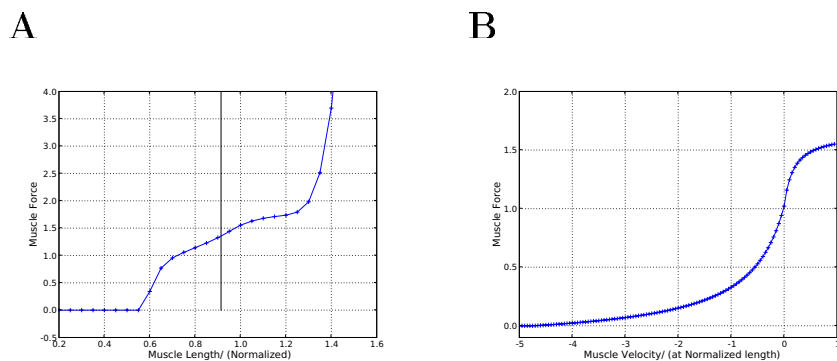


Figure 4.1: **A**: Force–length (Normalised) relationship for the simulated soleus (SOL) muscle at maximum excitation. **B**: Force–velocity curve for the maximally activated soleus muscle. Muscle length is at optimal length.

The simulation developed at this stage was of minimal complexity. Activation levels of the hind limb muscles were controlled by two separate central pattern generators. The two CPGs started with a phase shift of 50% from each other and this relationship was kept fixed. Sensory feedback from proprioceptors for phase transition (Ekeberg and Pearson, 2005) or reflex pathways, especially Ia and Ib afferents, which modulate the CPG activity (Rybak et al, 2002; Ivashko et al, 2003) were not included in this simulation. The parameters used for the muscles, tendons and body segments were set to match the available biological data (see Appendix) and were

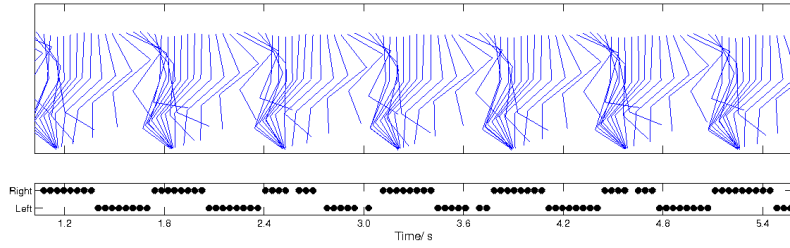
fixed throughout the experiment. The simulation was capable of producing stepping in the hind leg, after systematically adjusting the maximum activation level for each muscle. This adjustment only changed or scaled (up or down) the level of activation but did not affect the temporal pattern of activation.

The pattern of the simulated steps were qualitatively similar to those in normal walking cats. Flexion and extension of the joints can be seen during *swing* and *stance* phases respectively (Figure 4.2A). Nevertheless, the pattern of the steps slightly changed from one step cycle to the next. This could be clearly seen when comparing the angle profiles of each joint for several cycles (see Figure 4.2B). On average, angle profiles of each leg resembled those occurring in normal walking cats. Furthermore, strong reciprocal coordination between right and left hind legs was found to exist (see Figures 4.2A and 4.2C). Since there were fixed phase shift of 0.5 between the two CPGs that control the muscle activity in each leg, this coordination must be entirely due to this coupling.

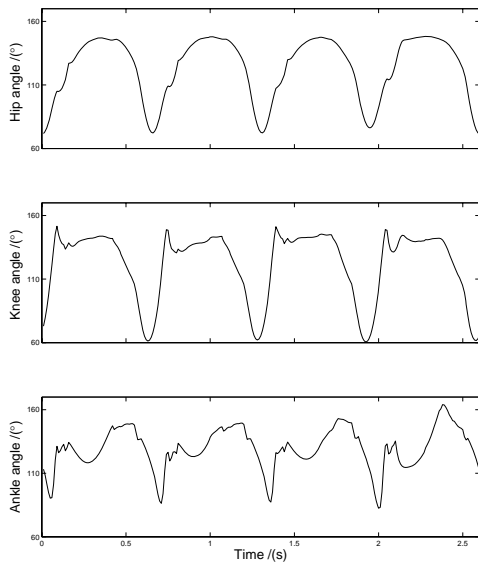
During the early swing phase, the knee and ankle flexed simultaneously to lift the foot from the ground. Then the hip joint started to flex in order to move the leg forward (Figure 4.3C). The amount of knee flexion during the swing phase was less compared to that of normal walking cat. During the late part of the swing, knee and ankle extended to facilitate the termination of the swing phase by touching the ground (Figure 4.3D). However, this caused the leg to extend unnecessarily. This could be due to the fact that the controller did not have the sensory information and reflex modulation (see Discussion). Figures 4.3B to 4.3E shows the four distinct phases F, E1, E2 and E3 (Engberg and Lundberg, 1969; Kandel et al, 2000; Ekeberg and Pearson, 2005) that characterise the joint movements in the step cycle of each leg.

The Figure 4.3A shows the mechanical structure of the model in the simulated three-dimensional environment. In this investigation, the fore legs were made stiff as a support for the front end of the body. Hind limbs were controlled by musculo-tendon actuators (shown in the 3D model) and made friction contacts with the ground surface whereas contacts between forelimbs and ground were frictionless.

A



B



C

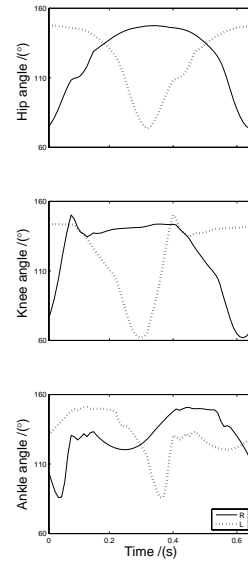
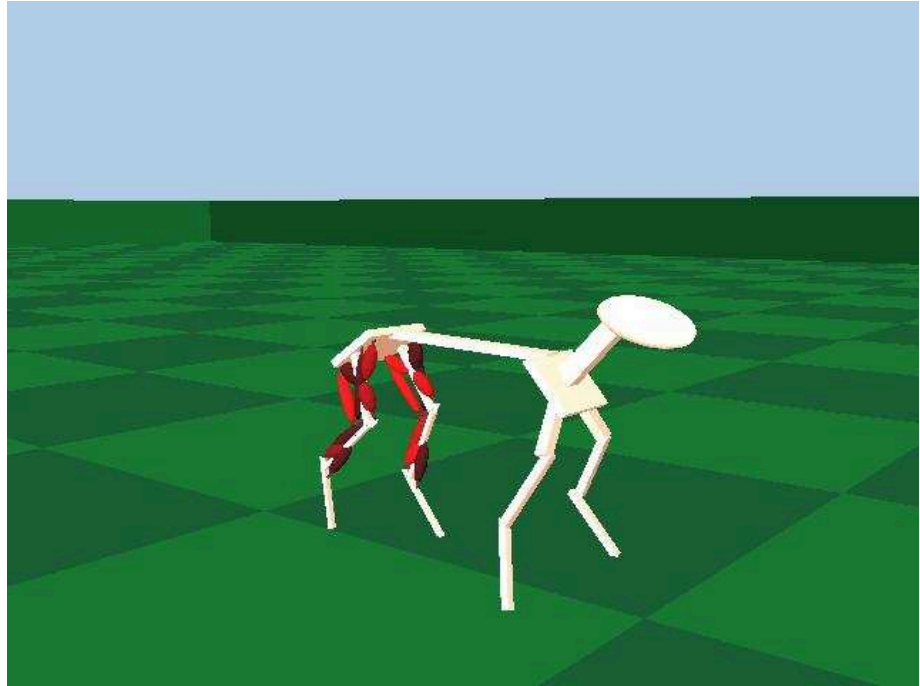


Figure 4.2: **A:** Stick diagram for the right hindlimb locomotion. Bottom strip chart shows timing of the stance and swing phases for both legs; black strip stands for stance. **B:** This figure shows the variation of the simulated hind limb joint angles during normal walking on a flat surface. **C:** Patterns of the joint angles, averaged over seven cycles.

A



B



C



D



E



Figure 4.3: **A**: This figure shows a snapshot of the 3-dimensional cat model while the simulation running. Hind limbs are controlled by the muscles but the fore legs are stiff and support the trunk. Figures from **B** to **E** show screenshots of the right hind leg at different time points in the step-cycle (for clarity muscles are not shown). **B**: Lift off. **C**: Swing. **D**: Late swing- Touch down. **E**: Stance.

5 Discussion

A three-dimensional dynamic simulation model of a four legged animal (cat) has been constructed in order to assess the functional characteristics of neuronal mechanisms that control the leg muscles during the stepping behaviour. The neuronal control of quadruped locomotion is a complex task that involves a number of parallel operating mechanisms out of which some are not known. Furthermore, considerable amount of knowledge is available on the system level rather than in neuronal circuitry level (Ekeberg, 2000). Hence the neuro-mechanical model was implemented on a system level and we did not attempt to include all the known biological properties into the model specially for the control system as long as it produces stable realistic walking pattern. Additionally large amount of available neurophysiological data on the subject of mammalian locomotion is confined to the control of stepping in the hind legs of the cat. This led to develop neuro-mechanical computer simulations for the stepping in the hind legs of the cat (Ivashko et al, 2003; Yakovenko et al, 2004; Ekeberg and Pearson, 2005). The simulation described in this investigation included only the hind legs of the cat and we further simplified the problem by excluding the modulation of sensory feedback from peripheral proprioceptors with the leg controller. This is due to the fact that our objective was to introduce the simulator model and its construction details with some functionality. Nevertheless, the model is capable of incorporating known sensory feedback to the controller by simply modifying the script (program) for the control module. Furthermore, it is possible to include neuro-mechanical controllers for fore legs as well. This would be one of the future improvements to the simulator and it is promising since the neurophysiological experimental data on the coordination of fore and hind legs of walking cats were published recently (Akay et al, 2006).

When building a computer simulator for the stepping in the cat, it is impossible to capture all the features of the locomotor system of the cat due to the fact that the lack of biological information and computational complexities. The body was modeled using ODE and composed of thirteen segments, three for each leg and the trunk. Mass of each segment was assumed to be uniformly distributed. Each hind leg was controlled by eight muscles which is undoubtedly a subset of all leg muscles and all the muscles were simulated using the same model with a different set of parameters for each. In this investigation, fore legs were not controlled by muscles instead made stiff. The spinal neural controller was modeled on a system level, that is, we did not attempt to include neuronal activities or circuits into the model. For instance, the CPG directly output the activity pattern for each and every muscle of a leg. Furthermore, simulation was simplified by excluding activation dynamics of the muscles i.e. muscles were directly activated by the output from CPG. Although the model was simplified as described above, it is sufficiently complex to realistically reproduce stepping in the cat. For instance, Figure 4.2 shows the characteristics of the simulated stepping, with no sensory modulation, in the hind legs of the cat on a flat surface which mimic the normal rhythmic pattern of the walking behaviour.

The simulator was constructed by combining several modules and sub modules into one main program. Programming was done with the *Python* scripting language in an object oriented manner. A schematic diagram of some of the main interconnections among the modules within the simulation program is depicted on the Figure A.2 in the Appendix. The mechanical part of the simulation was done using the rigid body simulator Open Dynamics Engine. This included the skeletal model of the cat, the surface properties of the ground and the simulation of the gravitational acceleration of the world in which the cat resides. Neuronal control module was developed as a separate system which included three main sub modules: joints, muscles and controllers (CPGs). The joints module was functioning as a communicating medium between the ODE driven mechanical system and the muscle module by taking the joint angles and angular velocity information into the module and then calculating muscles velocities and lengths. Length and velocity information together with the activation level for each muscle from the neural controller were fed to the muscle model which in turn produced the forces in each muscle using the mathematical muscle model. These forces were multiplied by corresponding lever arms to calculate the torques that were directly applied to the corresponding leg joints of the mechanical cat model. The controller is a separate python script and it can be designed as a CPG network (Ivashko et al, 2003) as we did in this experiment or can be a finite-state controller (Ekeberg and Pearson, 2005). It is possible to incorporate sensory feedback to the control algorithm by plugging sensory information while the simulation running. These can be force, length feedback or ground contact that mimics the action of Golgi tendon organs, muscle spindles and cutaneous receptors of the foot respectively. The 3-dimensional representation of the cat and the environment on the computer screen is done by a separate module, graphic engine which was created using OpenGL graphics libraries. Model data such as individual muscle forces and their lengths, joint angles, angular velocities, ground contact, etc in each timestep could be logged onto a file that can be accessed after the simulation for analysis purposes. When running on a 2.00 GHz processor, the rate of simulation was approximately 15% of real time. This high rate gave the opportunity to perturb and assess the quality of the simulation efficiently.

The use of computer simulations to examine the locomotor system of the cat has been a prominent technique in recent past. They provide a powerful tool for combining large amount of data on the neuronal, muscular and mechanical components involved in walking (Ekeberg and Pearson, 2005). Simulations can be used for assessing neuronal mechanisms that govern the walking behaviour, the function of the individual muscles or muscle synergists, the role of sensory feedback in controlling the magnitude and timing of motor activity and the interactions between mechanical components (Pearson et al, 2006). Furthermore, simulations enable direct monitoring of individual components of the locomotor system and the functional effects of modifying or removing one of those individual components. However, it is impossible or inappropriate to include all the neuro-physiological properties of the neuro-musculo-skeletal system for locomotion into the simulation since it may introduce unwanted complexities to the model that would increase the computational cost

and time. Level of complexity of the simulation (model) should be a compromise between the type of investigation and the available computational infrastructure.

6 Future Work

In this report, we have discussed the construction details of the computer simulator for the stepping in the cat and the performance in a simple experiment that involved two separate controllers for the two hind legs with no sensory feedback. Possible use of this software involve further investigations and perturbation analysis of the walking model. Currently, the simulator being used in a system level analysis of the muscle–joint interactions in the hind leg of the cat during locomotion. Incorporating sensory modulation into the neural controllers of the legs and investigation of the coordination among all four legs during normal walking of the cat are some other experiments we are planing to do with this software in future.

Acknowledgement

I would like to express my deep sense of gratitude to Docent **Örjan Ekeberg**, for his invaluable help, guidance, supervision and encouraging comments during the course of the project and drafting the report. I am grateful to Swedish International Development Cooperation Agency (SIDA) for financial support.

Appendix A

A.1 Muscle model equations

The simulation of the muscle force is based on the mathematical model of Brown et al (1996). The total force F is estimated by combining the length F_L , velocity F_V dependencies and the passive stretch component F_P according to the equation

$$F = F_{max} \cdot (a \cdot F_L \cdot F_V + F_P)$$

where a is the neural activation and F_{max} is the maximal isotonic force. All lengths are normalized with respect to L_{max} (the length where $F_L = 1$).

The force-length dependence is

$$F_L(x) = e^{-|\frac{x^\beta - 1}{\omega}|^\rho}$$

with parameters $\beta = 2.3$, $\omega = 1.26$ and $\rho = 1.62$.

The force-velocity dependence is calculated as

$$F_V(x, v) = \frac{b_1 - a_1 v}{v + b_1}; \text{ when } (v \leq 0)$$
$$F_V(x, v) = \frac{b_2 - a_2(x)v}{v + b_2}; \text{ when } (v > 0)$$

with parameters $a_1 = 0.17$, $b_1 = -0.69$, $a_2(x) = -5.34x^2 + 8.41x - 4.7$ and $b_2 = 0.18$. Negative velocities correspond to shortening of the muscles.

The passive force is given by

$$F_P(x) = 3.50 \cdot \ln(e^{\frac{x-1.4}{0.05}} + 1.0) - 0.02 \cdot (e^{-18.7 \cdot (x-0.79)} - 1.0)$$

A.2 Musculo-tendon parameters

All muscles were connected to the skeletal model via a series tendon which represent the series elasticity in the muscle model. In order to reduce the complexity, the pennation angle for each muscle was set to be zero. The muscle parameters include the L_{max} , F_{max} and the lever arm (s) which take care of the conversion between the muscle force and torque. Bifunctional muscles had two different lever arms at their two ends. The maximum muscle lengths and lever arms were set to match the available biological data (Goslow et al, 1973). Tendon stiffness was set as a constant value for each muscle and some of the values were taken from the experimental data (Rack and Westbury, 1984; Proske and Morgan, 1987).

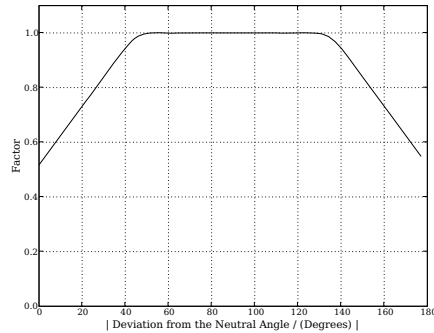


Figure A.1: Scaling factor for lever arms: depend on the current joint angle and the neutral angle for that joint.

At a neutral posture with the hip at 65° , the knee at 100° and the ankle at 105° , all single joint (unifunctional) muscles were set to have a length of 85% of L_{max} and the length of all bifunctional muscles were at 75%. This was adapted from the model developed by Ekeberg and Pearson (2005). When estimating the muscle torques, lever arms are multiplied by a scaling factor to mimic the shortening of the effective perpendicular distance from the centre of rotating axis (see Figure A.1).

Following table summarizes the Musculo-tendon parameters for the hind limb muscles.

Muscle	L_{max} (mm)	F_{max} (N)	T. Stiffness (N/mm)	Lever arm (mm)	Action
Anterior Biceps	70	80	50	30	Hip extension
Pliopsoas	70	80	50	44	Hip flexion
Vastus Lateralis	50	60	30	09	Knee extension
Soleus	50	30	20	15	Ankle extension
Tibialis Anterior	50	30	20	15	Ankle flexion
Sartorius	80	40	30	16 38	Hip flexion Knee flexion
Semitendinosus	70	40	30	30 38	Hip extension Knee flexion
Gastrocnemius	60	55	40	15 05	Ankle extension Knee flexion

A.3 Segment parameters

All the limb segments and the trunk are modeled as rectangular blocks with the centre of mass at the middle along the length. Cross section of the limb segments are square in shape.

	Mass (g)	Length (mm)	Height (mm)	Width (mm)
Trunk	2000	230	80	70
Hind leg				
Thigh	200	90	30	30
Shank	100	100	20	20
Foot	60	70	10	10
Fore leg				
Scapula	50	50	40	40
Thigh	200	70	30	30
Shank	100	80	20	20

A.4 Hip joint abduction/adduction

A passive torque-spring with linear elasticity and damping is used to control the abduction and adduction movements at the hip joint. The neutral position for the hip joint is set to 2 degrees of adduction. The spring parameters are:

Stiffness	0.2 Nm/rad
Damping	0.3 Nms/rad

A.5 Simulation Program

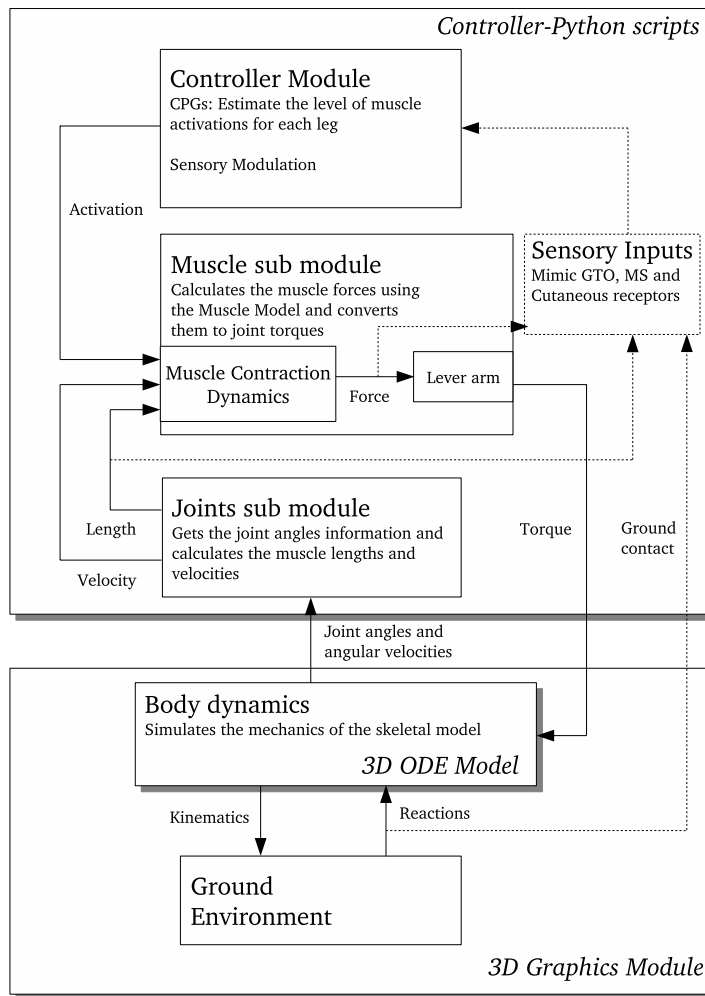


Figure A.2: Schematic diagram of the simulation program. Control system, rigid body mechanics with Open Dynamic Engine (ODE) and graphic module are the main components of the program. Blocks and paths showed in dashed lines were not included in this investigation. GTO: Golgi Tendon Organ, MS: Muscle Spindles.

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Paper II

Biological Cybernetics manuscript No.
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System identification of muscle–joint interactions of the cat hind limb during locomotion

Received: date / Revised: date

Abstract Neurophysiological experiments in walking cats have shown that a number of neural control mechanisms are involved in regulating the movements of the hind legs during locomotion. It is experimentally hard to isolate individual mechanisms without disrupting the natural walking pattern and we therefore introduce a different approach where we use a model to identify what control is necessary to maintain stability in the musculo-skeletal system. We developed a computer simulation model of the cat hind legs in which the movements of the each leg are controlled by eight limb muscles whose activations follow a centrally generated pattern with no proprioceptive feedback. All linear transfer functions, from each muscle activation to each joint angle, were identified using the responses of the joint angles to an impulse in the muscle activation at several postures of the leg covering the entire step cycle. We analyze the controllability and stability of the each muscle action over the joint angles by using identified system transfer functions and their gain and pole plots. We found that during the *late swing*, activity of *Posterior biceps /Semitendinosus* (PB/ST) muscle causes the joints to be unstable. In addition, *Vastus lateralis* (VL), *Tibialis anterior* (TA) and *Sartorius* (SAT)

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muscle–joint systems were found to be unstable during the *late stance* phase and we conclude that those muscles depend on neuronal feedback in order to maintain the stable stepping in the hind legs especially during *late swing* and *late stance* phases. Moreover, we could see clear distinction in the pole distribution (along the step cycle) for the systems related to the ankle joint from that of the other two joints, hip or knee. A similar pattern, in which the poles were scattered over the s-plane with no clear clustering according to the phase of the leg position, could be seen in the systems related to *Soleus* (SOL) and TA muscles and hence we conclude that these muscles should be controlled by neural mechanisms, which may involve supraspinal structures, over the whole step cycle.

1 Introduction

Mammalian locomotion requires interactions between sensors at various levels of the nervous system and the limb muscles. If one is to devise biologically realistic walking artifacts, either computer simulations or robots emulating walking, it is necessary that these sensorimotor interactions, specially at the spinal level, are incorporated into the neural control system (Frigon and Rossignol 2006). Moreover, in recent past, computer simulations have been used to simulate different aspects of locomotor control in cats, for instance central rhythm generation, role of spinal reflexes, and stance-to-swing transition (Yakovenko et al 2004; Ivashko et al 2003; Rybak et al 2006; Ekeberg and Pearson 2005). It has been argued that a thorough understanding of the neural and mechanical mechanisms that underlie locomotion can be achieved only by using computer simulations in parallel with physiological investigations (Pearson et al 2006). All these models have included sensorimotor interactions into the neural controller for the locomotion. However, a firm understanding of the neural mechanism (sensorimotor), behind the movement control of the cat hindlimb during walking, requires an understanding of the muscle–joint interactions (feed forward or open-loop system) as well. According to the modern control theory, open loop control cannot become unstable as long as the controlled system or plant is stable. Hence, finding the open-loop muscle–joint interactions is a proper choice to identify inherent instabilities of the muscle action over joints. For neurophysiologists, knowledge of the systems between muscles and the leg joints during walking will give means of identifying control requirements and assessing them with the available neurophysiological data regarding spinal control of locomotion, such as reflex modulation controlling muscle activation, muscle synergies (Krouchev et al 2006) etc. As far as robot engineers

are concerned, the identified systems can be used in designing electromechanical actuators which resemble actual muscles for biologically realistic walking emulators (Lieber 1999; Kimura et al 2001; Fukuoka et al 2003). This investigation will focus on parametric identification of the muscle–joint system of the cat hind leg and the analysis of the stability from a control point of view. In physiological experiments, it is impossible to identify pure muscle–joint interactions during normal walking since there is no way to isolate the above mentioned interaction from sensory feedbacks and other neuronal mechanisms. Therefore, for this investigation, we have developed a 3-dimensional, forward dynamic, computer simulation of the cat hind legs in which the leg movements are generated by eight simulated limb muscles per leg, three of which are spanning two joints. The implemented model was based on the model developed by Ekeberg and Pearson (2005).

In all mammals, the basic rhythmic locomotor pattern and the synergetic activity of muscles are produced by central pattern generators (CPGs) located in the spinal cord (Brown 1911; Ijspeert 2002) and this is the place where sensorimotor interactions related to locomotion are taking place (Grillner and Zangger 1975; Duysens and Van de Crommert 1998; MacKay-Lyons 2002). Limb muscles generate forces, which are graded according to the activity level in motoneurons controlled by the CPG, and acting upon corresponding joints in order to generate torques required to maintain stability and propel the body forward. The other factors that are affecting the magnitude of the muscle force are muscle length and its velocity (Zajac 1989; Herzog et al 1992; Brown et al 1996). Therefore, depending on the leg position within the step cycle, generated muscle force (hence torque) will vary accordingly. Hence proper adaptation of the muscle activity level coming from the CPG taking into account the muscle state is necessary for stable stepping. The muscles acting over a joint will directly cause either flexion or extension of that joint, but in addition, a muscle will indirectly affect the other joints. For instance, during real locomotion, perturbation of hip joints affect the distal joints, i.e. knee and ankle joints (Orlovsky and Feldman 1972).

Depending on the phase, it is obvious that the leg kinetics and kinematics should be different since the foot-tip is constrained not to move and is supported by the ground during stance whereas it is free to move in the air during swing. Moreover, electromyographic (EMG) patterns for the limb muscles show that flexors are active during swing while extensors are active during stance and some of the extensors active during late swing as well (Engberg and Lundberg 1969; Kandel et al 2000). This synergetic activity of the muscle groups, together with the kinematics of the limb, suggest that the action of the muscles over a joint will vary

according to the leg position along the step cycle. This fact is supported by the results of the neurophysiological studies that have shown evidence for phase dependent neural control mechanisms in the leg (Rossignol et al 2006). Duenas et al (1990) showed clear evidence for a phase dependency of the monosynaptic reflex during locomotion in the cat. The action of some of the reflex mechanisms, for instance fusimotor drive for the ankle extensor of the cat hindlimb (Murphy and Hammond 1997), could get reversed depending on the phase of the walking leg. Therefore, the system level analysis of the muscle–joint interactions at several positions throughout the step cycle will give more insight to the understanding of the controllability and the stability of the locomotion. Additionally, we may be able to identify the functional role of the sensory feedback in terms of the control requirements for the muscle–joint systems to be stable. Detailed reviews of dynamic sensorimotor interactions were recently published (Rossignol et al 2006; Windhorst 2007) and some of those will be related, when discussing the results.

The kinetics and kinematics of the cat hindlimb during stepping has been studied extensively (Shen and Poppele 1995; Trank et al 1996). However, we have not been able to find any previous system level perturbation analysis of the hindlimb muscle–joint interactions of a *walking* cat. In one study, feedback regulation of *standing posture* has been analysed using a dynamical model of the neuro-musculo-skeletal (NMS) mechanics of a cat hindlimb (Jiping et al 1991). A somewhat similar investigation has been done on a real cat hind leg to measure how force generation of the *soleus* muscle produces ankle extension (Shue et al 1995). However in that experiment, the leg was being kept fixed by clamping at the knee joint and strapping the paw to a cantilever beam that rotated on a servo-motor shaft that controlled the mean ankle angle. The nerve to the *soleus* muscle had been attached to a cuff electrode through which the stimulation pulses were sent. This cumbersome procedure can not be used for a similar analysis of a walking animal. We here introduce an alternate approach using a biologically realistic computer simulation of stepping in an animal model that incorporates the full neuro-musculo-skeletal system for locomotion. This has the additional advantage of getting rid of measurement noise which can not be eliminated during physiological experiments. Naturally, the accuracy and reliability of such a method depends on how realistic the model is, and to some extent the accuracy of the numerical computations.

The linear transfer function between the activation of a limb muscle and the corresponding change in joint angle was identified by analysing the response of the joint angle to a small perturbation (impulse) in the mus-

cle activation level. The identification process will be described in detail in the next section. The perturbation was done while the simulated cat hind legs were in locomotion and several postures of the leg throughout the step cycle were selected. In this way, we were able to capture the transitions (changes) of the system when the leg was moving from one phase to another. Next, we examine the sensitivity and controllability of the joints by each limb muscle and the stability of the each muscle–joint system. Furthermore, in the discussion section, we compare some of the known neurophysiological mechanisms related to stepping in the cat hindlimb with the results obtained from the simulation experiments.

2 Methods

Data for the system identification and analysis were obtained using a three dimensional (3D), forward dynamics, computer simulation model which incorporated two hindlimbs of a walking cat, each controlled by eight simulated muscles. The simulator was programmed using the Python language and the activation levels of the muscles and the hind leg joint angles were sampled every 5 ms throughout the simulation. The systems between the muscle activity and the joint angles were approximated as linear systems around the point of interest (position of the leg) and ten such points were selected throughout the step cycle, four during the swing phase and six during stance.

2.1 Simulation model

The body dynamics of the cat hindlimbs were simulated using Python wrappers of the Open Dynamics Engine (ODE, www.ode.org) which is an open source, high performance library for simulating rigid body dynamics. Each hindlimb was modelled with three segments: thigh, shank and foot with four degrees of freedom. While knee and ankle joints had one degree of freedom (DOF), the hip joint had an additional DOF to enable abduction and adduction movements of the limb. The masses of the leg segments were taken from data published by Hoy and Zernicke (1985) and the trunk weight was set to 2 kg. Forelimbs were made stiff and used as support for the trunk and front part of the body. When the simulation was running, the cat was walking forward with an average velocity of 0.4 m/s and the duration of a step cycle was about 650 ms. Graphical representation of the 3D cat model was done by a separate module that we programmed in Python using Python wrappers of the OpenGL libraries.

2.1.1 Simulating Muscles

Each hind leg included eight muscles, five of them acting over single joints while the other three (*bifunctional muscles*) acting over two joints (see Fig. 1). The simulation of each muscle was based on the mathematical model introduced by Zajac (1989) and the parameters for force, length and velocity relationships were taken from published data (Brown et al 1996; Ekeberg and Pearson 2005). Furthermore, each muscle incorporated a series elastic tendon (Zajac 1989) and the tendon stiffness was set to match biological data (Rack and Westbury 1984; Proske and Morgan 1987). Forces generated by each muscle were then converted to joint torques by multiplying by corresponding moment arms that were taken from the work of Goslow et al (1973).

2.1.2 Simulating Central Pattern Generators (CPGs)

The activation level of each hind leg muscle was controlled by a central program, generating a unique temporal pattern for each muscle (see the Activation panels of Fig. 4 and Fig. 5). These activity patterns resemble the electromyographic (EMG) activity of corresponding muscles of the hind limb of the cat during normal walking (Kandel et al 2000; Ivashko et al 2003). The flexor muscles were predominantly active during the *swing* phase while the extensors were active during the *stance* phase. The main objective of this investigation was to identify the open-loop transfer functions between the leg muscle activations and the joint angles of a cat during locomotion. Therefore, it was important to study the system without any sensory feedback. Fortunately, it was possible to obtain a stable and alternating stepping in the model (see Fig. 2), even though there were no sensory feedbacks to either controllers (CPGs) or muscles. In fact, physiological studies on the spinal cats with a lesion in the Dorsal Root Ganglions (DRG) have shown the possibility of generating locomotor-like rhythmic motor output in the absence of peripheral sensory feed back (Brown 1911; Grillner and Zangger 1975).

2.2 System Identification

The muscle force dependance on activation, lengthening and velocity are both dynamic and non-linear. Additionally, some of the muscles are acting over two joints. Therefore, non-linearities in the muscle-joint interactions are unavoidable. However, it is possible to use a local linear approximation for a muscle-joint interaction

within a short duration around a point (leg position) in the step cycle. This could be verified by applying positive and negative impulses for a muscle activation and observing the responses in the joint angles (see Fig. 3). Although the magnitude of the input impulse was relatively high (10 % of maximum activation), the duration of the pulse was set to a small value (less than 0.01 s) and hence it was possible to obtain a linearized model. The transfer functions were identified by analysing the response of each joint for a positive impulse of activation of a muscle. After the simulation, logged data were written into text files and the analyses were done using the system identification tools in Matlab 7.0.4 (R14).

2.2.1 System Approximation

The total system matrix was 8×3 as we included eight muscles (see sect. 2.1.1) and three joints (*Hip*, *Knee* and *Ankle*) in each hind leg of the simulated walking model of the cat. In reality this would be a Multiple Input and Multiple Output (MIMO) control system. However, in this investigation we did not include any sensory feedback to the muscles or CPGs and hence there will be no interactions among the muscles. Therefore, we can simplify the total system by identifying individual systems from each muscle to each joint as a Single Input and Single Output (SISO) system.

We selected the same model structure and model orders for all the muscle–joint interactions (24 systems). This simplified the identification process and gave us a better foundation to compare individual systems. The adapted structure was the *Output-Error (OE)* model and it was suitable for our simulation study since there were no measurement noise that should be modelled as for a real experiment. Systems were first identified as discrete systems with a sample period of 5 ms and then converted to the continuous domain using Matlab built-in function ‘d2c’. The discrete system is described using an equation,

$$y(t) = \frac{B(q)}{F(q)}u(t - n_k) + e(t) \quad (1)$$

where y and u are the output and input sequences, respectively, and e is the error term. The polynomials B and F are defined in terms of the backward shift operator q :

$$B(q) = b_1 + b_2q^{-1} + \dots + b_{nb}q^{-nb+1} \quad (2)$$

$$F(q) = 1 + f_1q^{-1} + \dots + f_{nf}q^{-nf} \quad (3)$$

The selected model orders nb and nf were 1 and 2 respectively (see sect. 4 for motivation). Input delay parameter n_k was set to 1.

3 Results

The continuous linear systems from each muscle activation to joint angle of the hind leg were identified at ten different postures of the leg covering the entire step cycle. Out of the 240 ($8 \times 3 \times 10$) transfer functions only 16 had their poles in the right half plane (RHP). This means that the response of those systems will be oscillatory and growing exponentially (unstable). These instabilities occurred in some muscle–joint interactions with the leg moving at *late swing* or *late stance* phase. During the *late swing*, only *Posterior biceps /Semitendinosus* (PB/ST) muscle–joint systems showed instability. However, *Vastus lateralis* (VL), *Tibialis anterior* (TA) and *Sartorius* (SAT) muscle–joint systems were identified as unstable during the *late stance* phase. These instabilities indicate that active sensory feedback is required to control the activation of those muscles when the leg is loaded or unloaded (see sect. 4). Furthermore, almost all the stable systems showed a characteristic property of having poles closer to the unit circle on the pole-zero plot for the discrete version of the systems (not shown).

In order to investigate the sensitivity or controllability of each joint of the hind leg by each muscle, we plot the gain of all muscle–joint systems during one step cycle (see Gain panels of Fig. 4 and Fig. 5). According to the gain plot, *Anterior biceps* (AB) showed more sensitivity over the control of joint angles during the swing phase than that of stance. Similar pattern was seen in the *Soleus* (SOL) muscle. On the other hand, the effect of activation level of *Iliopsoas* (IP) on the joint angles was dominant during stance phase. In each of the above cases, when the muscle showed high sensitivity, it had been suppressed or received no regular activation from the CPG. Therefore, this pattern could be due to the fact that the corresponding muscle was in a stretched state when the joint was at either extended or flexed position. In fact, some muscles could not generate any response on the joint angles in certain positions of the leg within the step cycle. For instances, activating *Gastrocnemius* (GAS) and PB/ST muscle showed no response on any joint angles during early or middle stage of the swing phase respectively. Additionally, during the middle of the stance phase, SOL had no controllability of any of the three joint angles. One other observation is that the bifunctional muscles (ST, SAT and GAS) showed increased sensitivity during the transition from swing to stance.

Another observation from the *Gain* plots (Fig. 4 and 5) is the sign reversal of the gain of the *VL-ankle angle* system when the leg was moving from *swing* to *stance*. Similar pattern could be seen in the transfer functions between IP and all three joint angles; ankle, knee and hip, when the leg transits from swing to stance. Furthermore, gain of the system between ankle-flexor or TA and the Knee angle showed the same effect. However, the sign of the above mentioned systems' gains changes back during the middle or late stance phase. Since, we did not include any sensory feedback from muscles or joint receptors to CPGs or muscle itself, this *phase dependent* sign reversal of the gain coefficient of some of the systems could be due to either reaction to ground contact of the foot and its mechanical linkage with the other limb segments or varying activity of the other muscles acting on the same joint. The significance of this result is that it mandates different control strategies or reflex modulation depending on the position of the leg within the step cycle. We will discuss this in more detail in the next section.

We further investigated the properties of the identified continuous systems by analysing the change of position of their *poles* in the *s*-plane with respect to the leg position in the step cycle (see Hip, Knee and Ankle panels of the figures Fig. 4 and Fig. 5). As mentioned in the section 2.2.1, the order of the denominator of the transfer functions was set to two. Therefore, in most of the cases, poles were complex conjugate pairs. We have tested to increase the order of the denominator and did not find any qualitative improvement of the systems impulse response over the measured simulated impulse response for any muscle-joint interaction. It was possible to identify several clusters of poles from different leg positions, meaning that it should be possible to use similar strategies for controlling leg movements with small changes. In general, poles of the muscle-joint systems within one phase, stance or swing, belonged to one cluster. The muscle-joint systems between the VL, GAS, ST, SAT and IP muscles and the hip and knee joints clearly show the grouping according to the *phase* of the moving leg. However, it was hard to find this separation in SOL or TA muscle-joint systems. Furthermore, there were no clear separation in pole positions of the systems related to *ankle* joint. Another observation from the pole plots is the similarity in the pole spreading pattern of the systems on the *s*-plane for a same muscle between hip and knee joints.

How rapidly a system responds is determined by how far into the left half plane the poles of the system are. On the pole diagrams, the dotted radial line represents systems with a damping coefficient of 0.7, which is a reasonable margin for critically damped systems (damping coefficient increases in counter-clockwise di-

rection in the upper half of the left half plane). The effect of the limb muscle on distant joints could be seen on the pole plot diagrams. If a pole is near to the imaginary axis and far away from the origin, the muscle–joint system with that pole generates oscillations, which could last for a long time even though they damped out, in the output joint angle. However, several muscles acting over a same joint in this manner could easily cause instabilities in that joint. For instance, SOL and TA (ankle extensor and ankle flexor) can create more oscillations in the hip joint during both *late stance* and *late swing*, while AB and IP (hip extensor and hip flexor respectively) can generate oscillations in the ankle joint. Additionally, VL could affect the ankle joint in the same manner during *early stance* phase.

4 Discussion

The amount of movement of a limb joint is caused by the resultant torque exerted upon that joint in combination with the effects of gravitational and ground reaction forces. The resultant torque is the algebraic sum of the total torques generated by muscles acting over the joint, which in turn is dependent on the muscles length, velocity, activation and passive elastic properties (Zajac 1989; Loeb 1995; Scott et al 1996; Brown et al 1996). By including a second order *denominator* to the OE model (see sect. 2.2.1), we were able to capture the length and velocity dependencies of the muscle force since the joint angle and the change in joint angle (angular velocity) is directly related to the muscle length and velocity. A first order approximation was sufficient for the *numerator* of the model since the activation effect on force was linear in the neighbourhood of the perturbation or impulse.

Our experimental approach was dependent on having ongoing walking without actual sensory feedback. Although it was possible to obtain a stable alternating stepping in the hind leg of the cat model with no sensory feed back, it showed some deviations from the typical locomotion pattern of the hindlimb of an intact cat. During the *early swing* phase, the foot was dragged a little and the model showed some discrepancy of foot placement towards the end of the swing (touch down). In fact, neurophysiological studies on decerebrated cats have shown that the unloading signals from the ankle extensor muscles are necessary for initiating the swing phase (Kandel et al 2000; Donelan and Pearson 2004). Moreover, cutaneous inputs from the foot pads in the cat play a major role in precision walking for intact cats and in foot placement for spinalized cats (Bouyer and Rossignol 2003a,b).

Most of the stable muscle–joint systems show sufficiently damped (but still under-damped) conditions (see sect. 3). This may be due to the fact that biological systems are evolved to adapt the most efficient or least energy consuming mechanisms. However, there were systems that generate oscillations before settling. This implies that neural feedback control mechanisms are required for stabilizing the inherent instabilities of these muscle–joint systems. In fact, neurophysiological studies have identified several proprioceptive pathways such as the monosynaptic stretch reflex, reciprocal inhibition and recurrent inhibition via *Renshaw* cells, which give more stiffness to the muscle and more damping action to the joint (Kandel et al 2000; Hultborn 2006; Windhorst 2007).

As mentioned in the results section, the poles of some of the muscle–joint systems were clustered according to the phase of the leg position (see Fig. 4 and 5). Hence, the existence of phase dependent neural control mechanisms for locomotion is a necessary condition. Transition from one control strategy to the next would involve locomotor CPG, sensory feedback, synergistic activity of muscles and other neuronal circuits that involve phase dependent reflex modulation (Forssberg et al 1975; Krouchev et al 2006; Rossignol et al 2006). Muscle synergies in cats have been suggested to be related to foot and limb kinematics in walking and ground reaction forces in stance (Torres-Oviedo et al 2006). Moreover, proprioceptive feedback could adapt the recruitment of centrally organized synergies to behavioural constraints and fine-tune the activation of muscles within a synergy (Cheung et al 2005; Windhorst 2007). However, in our experiments systems related to SOL and TA muscles (ankle extensor and ankle flexor respectively) and to the ankle joint did not show clear separation in the pole placement for the two phases (Fig. 5). This could be due to the fact that the ankle joint is situated more distally to the body and is subjected to more perturbations from the ground reaction forces and hence require more fine neural control, which may involve additional supra-spinal structures, over the whole step cycle.

The stretched muscle of an antagonist pair is more excitable than the other (Rossignol et al 2006). This is clearly visible on the gain plots for AB, IP and SOL muscles (see Fig. 4 and 5). However, the activity (EMG) of those muscles are more pronounced during the unstretched phase. Therefore, dynamic and phase dependent control of the CPG on muscle spindle sensitivity through alpha-gamma co-activation is very important for stabilization of the gait (Murphy and Hammond 1997; Taylor et al 2000; Windhorst 2007). In addition, alpha-gamma co-activation varies with the task as well (Prochazka 1989; Rossignol et al 2006). The

SOL muscle did not affect any joint angle during mid stance. Even if we were to include fusimotor drive we can not expect much improvement of the gains of the muscle–joint systems for SOL. On the other hand, the GAS muscle did affect the all three joints during stance phase. Therefore, neuronal circuits that activate synergistically these two muscles should play a major role in force generation in SOL with changing movement conditions. Moreover, sensitivity of the GAS muscle on the joint angles follows the pattern of the EMG activity (see gain plot for GAS, Fig. 5), even though the muscles did not include any proprioceptive modulation, and this suggest that the GAS forces are associated with the activation coming from the CPG. In fact, in real cats, peak forces of *Medial Gastrocnemius* (MG) are well correlated with the EMG activities (Kaya and Herzog 2003).

5 Conclusions

Our present investigation have clearly demonstrated that simulation of neuro-musculo-skeletal (NMS) elements of the cat hind legs can be used to identify open-loop linear transfer functions, from each limb muscle activation to each joint angle, throughout the whole step cycle. Here, we introduce a novel method to identify the musculo-skeletal system, that is isolated from the neural control and sensory feedback mechanisms, while the system is engaged in ongoing locomotion. We found that the actions of most of the hindlimb muscles over the joints display inherent stability during stepping, even without the involvement of any proprioceptive feedback mechanisms. However, action of the VL, TA and SAT muscles during the *late stance* phase cause all three joints to be unstable. Similar effect could be seen in the action of the PB/ST muscle during the *late swing* phase. Hence we conclude that additional neuronal control circuitry is required in activity regulation of those muscles, in order to establish stable stepping of the hind legs especially during phase transitions. Furthermore, the linear transfer functions identified in this approach will be useful in designing electro-mechanical actuators, that resemble muscle action on joints, for robotic walking emulators. Finally, the use of simulations of walking in the cat for gaining insights into more complex interactions between the environment and the neuro-muscular-skeletal system will undoubtedly become important especially when a direct neurophysiological experiments can not be performed on a real walking animal.

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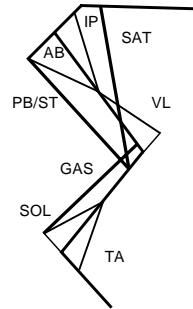


Fig. 1 Movements of each model leg were generated by eight actuators mimicking the actions of muscles in the cat hind legs: AB - Anterior biceps, IP - Iliopsoas, VL - Vastus lateralis, PB/ST - Posterior biceps/Semitendinosus, SAT - Sartorius, GAS - Gastrocnemius, SOL - Soleus, TA - Tibialis anterior

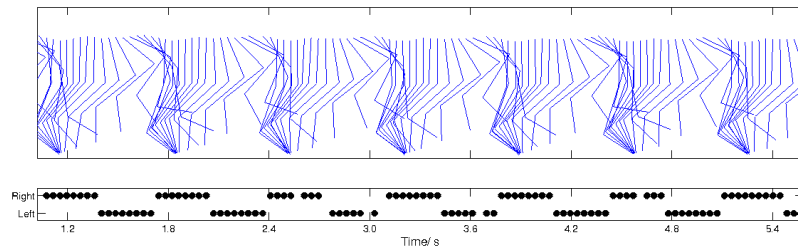


Fig. 2 Top diagram shows the stepping of the right hind leg where the model was walking over a flat ground with no sensory feedback to the muscles or central pattern generators. The time interval between each snapshot is 20ms. Bottom diagram shows the timing of the ground contact for the two legs (black marks).

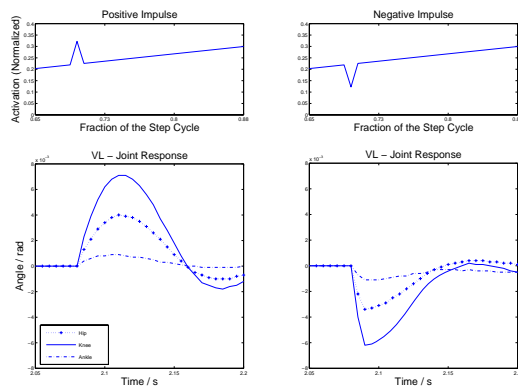


Fig. 3 Responses of the hind leg joint angles for a positive and negative impulse of the VL muscle (see Fig. 1) activation. Magnitude of the impulse was set to 0.1 of the normalized activation and the duration was about 5ms. These diagrams show the responses at a time where the leg was in the middle of the **Stance** phase.

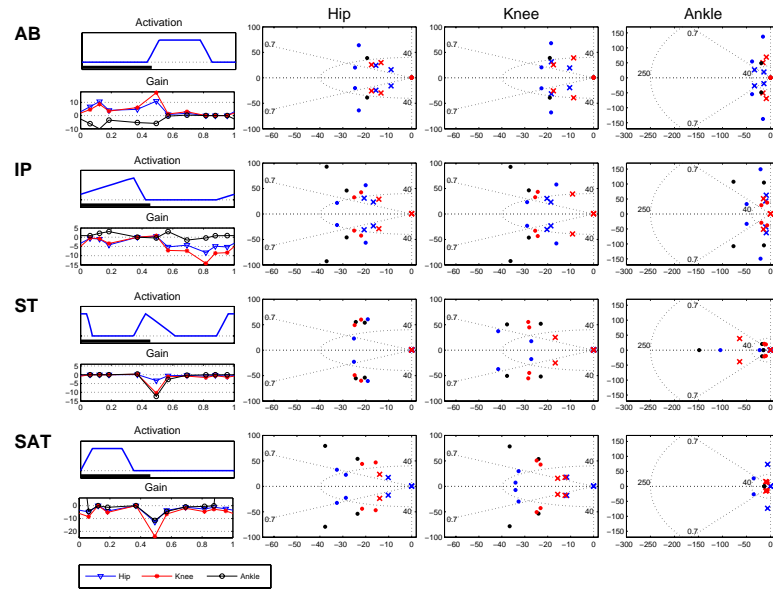


Fig. 4 Variation of activation and the gain and poles of the identified systems during a step cycle of the walking cat model. Each row corresponds to one of the proximal muscles of the cat hind leg (see Fig. 1). In each *Activation* panel, the horizontal black bar shows the duration of the **Swing** phase. Gain values of the identified systems between the muscle and the three joints is shown in each *Gain* panel and the legend is shown at the bottom of the figure. *Hip*, *Knee* and *Ankle* panels show the location of the poles of the system between the muscle and the corresponding joint; '•' - during **Stance** phase, 'x' - during **Swing** phase; legend for color scheme: 'blue' and 'red' for *early* and *late* in each phase respectively, 'black' is for *middle* stance.

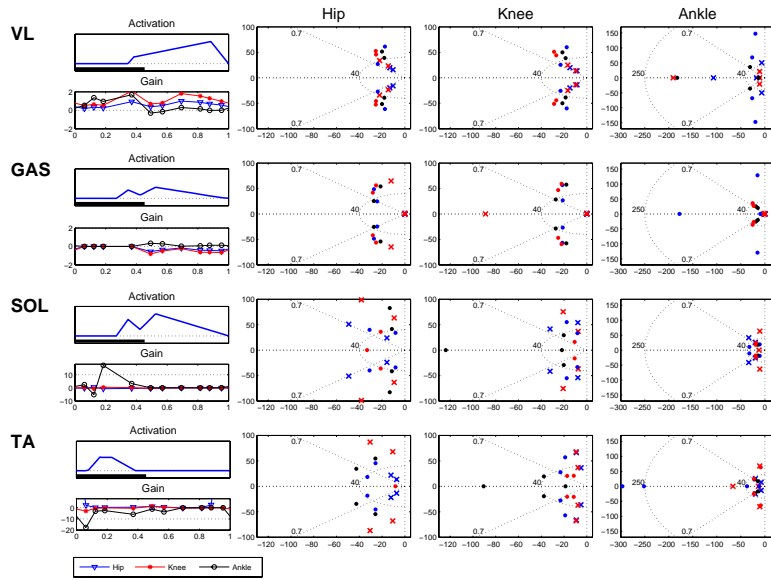


Fig. 5 Variation of activation and the gain and poles of the identified systems during a step cycle of the walking cat model. Each row belongs to one of the distal muscles of the cat hind leg (see Fig. 1). Figure legends are same as in the Fig. 4 except the horizontal scales of the *Hip* and *Knee* panels.



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