UNIVERSITÉ DU QUÉBEC À MONTRÉAL

LES RÉPONSES DES MEMBRES INFÉRIEURS À DES TRANSLATIONS MÉDIO-LATÉRALES IMPRÉVUES PENDANT LE MOUVEMENT DE PÉDALAGE

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RESPONSES OF LOWER LIMBS TO UNEXPECTED MEDIO-LATERAL TRANSLATIONS DURING PEDALLING MOVEMENT

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Résumé

Les perturbations vers la gauche ou vers la droite sont des occurrences quasi-quotidiennes pour un bon nombre de gens. Se faire bousculer en marchant dans la foule ou subir les effets inertiels d'un véhicule de transport en commun tournant ou s'arrêtant soudainement ne sont que deux exemples communs de telles situations. De plus, les perturbations dues aux glissements latéraux sont fréquemment observées chez les personnes âgées. Les articulations des membres inférieurs et du tronc ont moins de latitude de mouvement dans le plan frontal que dans le plan sagittal. En conséquence, lors d'une translation médio-latérale inattendue le système nerveux central (SNC) utilise probablement des stratégies compensatoires différentes du cas de la direction antéro-postérieure. Le but de cette étude était d'évaluer les stratégies compensatoires utilisées lors de perturbations perpendiculaires au plan du mouvement. Un vélo ergométrique modifié fut utilisé comme modèle de mouvements rythmiques ; dans une telle situation, les effets de l'équilibre sont de beaucoup amoindris et les réactions compensatoires peuvent être attribuées à la perturbation du mouvement rythmique.

Pour les fins de cette étude les sujets eurent à pédaler sous quatre conditions expérimentales différentes : dynamique active (DA), au cours de laquelle les sujets pédalaient à une fréquence de 1 Hz maintenue à l'aide d'un métronome et d'information présentée sur un écran d'ordinateur ; dynamique passive (DP), au cours de laquelle les mouvements enregistrés sous la condition DA étaient reproduits à l'aide d'un moteur dynamométrique tandis que les sujets devaient simplement relaxer; statique active (SA), au cours de laquelle chaque sujet devait essayer de reproduire l'activité musculaire produite par leur soléaire sous la condition DA; statique passive (SP), au cours de laquelle les sujets devaient simplement maintenir chacune des positions du cycle de pédalage tout en relaxant. Des mouvements vers la gauche et vers la droite d'à peu près 1 *g* ($9.8\ ms^{-2}$) d'accélération furent appliqués aléatoirement à l'aide d'un cylindre électrique pendant une des quatre phases du cycle de pédalage : propulsion (P), récupération (R), transition PR, et transition RP. L'activité électromyographique (EMG) du soléaire (SOL), du médial du gastrocnémien (MG), du tibial antérieur (TA), du vaste latéral (VL), du biceps fémoral [chef court] (BF), et du tenseur du fascia lata (TFL) furent enregistrés et analysés. Les réponses EMG furent divisées en deux époques (E) selon la latence de la réponse : E_1 (80-250ms) et E_2 (250-400ms).

Autant pour E_1 que pour E_2 les perturbations vers la gauche et vers la droite provoquèrent des réactions condition-dépendantes dans le TFL, le BF, le MG et le SOL, des réactions phase-dépendantes dans le TFL, le BF et le VL, et des réactions direction- dépendantes dans le BF et le TA. Les réactions durant E_1 furent notablement atténuées par la répétition de la perturbation alors que les réactions durant E_2, déjà moins prononcées, eurent tendance à demeurer relativement constantes au fil des répétitions successives. Ces résultats permettent de conclure que, même dans des situations où l'équilibre n'est pas un facteur important, les mouvements soudains vers la gauche ou vers la droite provoquent des réactions musculaires spécifiques et complexes dépendantes de la condition, de la phase, et de la direction lors du pédalage sur vélo ergométrique. De plus, les résultats de l'étude suggèrent que le feedback sensoriel, causé soit par le mouvement actif ou passif, joue un rôle important dans le déclenchement des réponses musculaires.

Mots clés: Mouvement rythmique, perturbation, EMG, phase-dépendance, tâche-dépendance

Abstract

Left- and right-ward perturbations are common in everyday life. For instance, being bumped into while walking in a crowd or walking inside a mass transit vehicle as it makes a sudden turn are frequent occurrences. Also, perturbations due to sideways slipping are commonly observed in the elderly. The ranges of joints motion in the lower limbs and trunk are much smaller in the frontal plane than those in the sagittal plane. As a result, during an unexpected medio-lateral translation, the CNS is likely to employ different strategies compared to those used in the antero-posterior direction. The goal of this study was to assess the compensatory strategies to perturbations perpendicular to the plane of progression. A modified stationary cycle ergometer has been used as a model of rhythmic movements; in this model the effects of balance are greatly diminished and the observed compensatory results can be attributed to the perturbed rhythmic movement.

In this study, subjects were asked to pedal under 4 different conditions: dynamic active (DA) whereby they pedaled at 1 Hz frequency with the help of a metronome and a visual display; dynamic passive (DP) in which the recorded pedal motions from the DA condition were replayed through a torque motor and subjects were told to relax; static active (SA) in which each subject was asked to match the Soleus activity to that of the DA condition; static passive (SP) whereby subjects just oriented the lower limbs in different pedaling positions and were told to relax. Left- and right-ward translations with approximately 1 *g* (9.8 ms^{-2}) acceleration were randomly applied with an electrical cylinder during one of the 4 phases of the pedaling cycle: propulsion (P), recovery (R), transition PR, and transition RP. EMGs of the Soleus (SOL), Medial Gastronemius (MG), Tibialis Anterior (TA), Vastus Lateralis (VL), Biceps Femoris [Brevis] (BF), and Tensor Fascia Latae (TFL) were recorded and analyzed. The EMG responses were divided into 2 epochs (E) based on the latency: E_1 (80-250ms) and E_2 (250-400ms).

In both E_1 and E_2, left- and right-ward translations evoked condition-dependent responses in TFL, BF, MG and SOL, phase dependent responses in TFL, BF and VL, and direction dependent responses in BF, TA. On the other hand, the E_1 responses were attenuated after several trials whereas the E_2 responses, which tended to be much smaller, remained relatively constant as the number of trials increased. In conclusion, despite situations in which the balance was relatively well controlled, left- and right-ward translations evoked complex and specific condition-, phase-, and direction-dependent muscle responses during cycle ergometry. Also, the results of the study suggest that the sensory feedback, either created by active or passive movement, plays an important role on the gating of the reflex pathways.

Keywords: Rhythmic Movement, Perturbation, EMG, Phase-dependency, Task-dependency

1 Introduction

Patterns of muscular activations in response to different kinds of perturbations during diverse tasks and conditions have received considerable attention. In most of those studies, postural responses for balance control during stance (Nashner, 1977; Moore et al., 1988; Henry et al., 1998a, 1998b) and locomotion (Nashner, 1980; Tang et al., 1998; Misiaszek et al., 2000), particularly walking and running, have been investigated. In perturbed walking or running condition, the reactions consist of corrective responses to maintain and control postural equilibrium and keep up the ongoing movement. To break down these complex corrective responses into their components, it is desirable to design an experiment which can purely study rhythmic movement in response to a perturbation without the confounding influence of balance (Ting et al., 1998; Raasch and Zajac, 1999; Ting et al., 2000). According to this concept, the complexity of the task control will be greatly simplified and the observed results can be attributed only to the corrective responses due to the perturbation of the rhythmic movement and not to the balance control as a confounding factor.

In this study, muscular responses of lower limbs to unexpected linear right- and left-ward translations during pedaling were investigated using a modified cycle ergometer. The main reason for choosing cycle ergometry in this study is that it has the benefit of isolation of rhythmic movement from consideration of postural equilibrium control and body weight support (Raasch and Zajac, 1999; Ting et al., 2000) and permits the study of a pure rhythmic action. In addition, alterations of the task are limited since the joint trajectories and orientations of the lower limbs are restricted in cycle ergometry. As a result, mechanical degrees of freedom are limited and variations in the kinematics of cycling are highly reduced due to the constrained environment of the ergocycle (Raasch and Zajac, 1999). Another advantage of this experimental model is that the conditions, task mechanics and load and speed of cycling can be well controlled (Brooke et al., 1981; Ting et al., 1998; Ting et al., 2000). Moreover, data collection is easier as the subject is moving the limbs but staying in one place.

The pedalling task is a bipedal locomotor action with many similarities to walking, e.g. phasing and frequency of leg movements, alternation in flexion and extension, and the major part of power generation occurring in the extension phase (Raasch and Zajac, 1999; Ting et al., 2000). The optimal frequency of the rhythmic movement in both walking and pedaling is approximately 1 Hz (Winter, 1983; Coast and Welch, 1985). In both tasks, modulation of reflexes is phase dependent and the pattern is similar (Capaday and Stein, 1987; Yang and Stein, 1990; Brooke et al., 1992; Brown and Kukulka, 1993). Therefore, it is likely that the neuronal components involved in the control of pedaling are employed in the gait control as well (Ting et al., 2000).

Perturbation due to horizontal sliding is commonly observed in the elderly, but it can also be seen in adults and children. During an antero-posterior fall, the anatomy and biomechanics of the lower limbs allow one to have a wider range of balance control. That is not the case in the medio-lateral sliding. It has been demonstrated that the falling prediction factor in elderly is much better quantified by the amount of variability in the control of lateral stability than antero-posterior stability (Maki et al., 1994).

During walking or running, pushing from the sides may happen. This type of disturbance, which is perpendicular to the plane of progression, is common in crowded places such as subway stations, or shopping malls, where people are orienting in different directions. Patla et al. (1999) studied what happens when somebody is pushed to the side when walking forward. However, as mentioned earlier, the compensatory responses during perturbed walking contain the balance correction responses and the recovery responses for continuing the task after a disturbance. Therefore, balance, as a confounding factor, does not allow us to isolate the various components of compensatory responses of the nervous system. By taking advantage of cycling as a rhythmic movement, the observed responses can only be attributed to the recovery responses for the progression of the rhythmic movement after perturbation.

1.1 Objectives

This experiment is conducted in order to assess the underlying mechanism of the central nervous system (CNS) in response to a disturbance perpendicular to the plane of locomotor task. In other words, this study tries to understand how lateral perturbations reshape the locomotor output. More specifically, this study applies unexpected medio-lateral translations to seated subjects during cycling. To better understand the response mechanism for continuation of pedaling after perturbation, the responses are compared with pedaling without perturbation and with static pedal positions (no locomotor task).

To achieve this goal, the relationship between medio-lateral translation and phase-dependent changes in the EMG activities of the selected lower leg muscles were quantified to demonstrate the EMG adjustments by the central nervous system in maintaining the ongoing rhythmic movement.

1.2 Hypothesis

In this study, we hypothesize that applying medio-lateral translation evokes responses that are phase, task, and direction dependent.

1.3 Importance

By using a modified cycle ergometry approach, this study provides a unique insight into how the CNS controls and maintains an ongoing rhythmic movement after a medio-lateral disturbance with minimal balance consideration. Limited numbers of studies have investigated how the CNS responds to medio-lateral translation during locomotion and none of them has used cycling as a locomotion paradigm for this kind of perturbation.

1.4 Limitations

There are some limitations in this study:

1- The pedalling task used in this study differs from conventional cycling whereby the person is sitting over the pedals. The ergocycle, used in this experiment, has a 90° shift from common bikes as the seat is positioned behind the pedals. This limits the interpretations of the results with respect to conventional cycling.

2- As the study is on pedaling, the results can not be applied directly to the other types of rhythmic movement like walking.

3- Passive conditions in this study do not represent the complete absence of higher level controls over the lower limbs. Moreover, since the limbs were not attached except at the foot level, the subjects had to prevent the hip from going into an abduction and external rotation, thereby stopping the limbs from flopping around. For this reason, there was often a small level of activity in the lower limb muscles during passive conditions.

4- It is possible that the subjects used their upper limbs to attenuate the effects of the lateral perturbations.

2 Background

During the interaction of the body with its surrounding environment (Mergner et al., 1997), e.g. when quiet stance is perturbed (Runge et al., 1998) or during locomotion, three main types of sensory inputs –visual, vestibular and somatosensory inputs from receptors of muscles, skin, and joints– are used and processed by the central nervous system to maintain balance or regulate locomotion. In this particular study, the vision input will not be blocked since Zedka et al. (1998) reported that visual feedback does not have any significant effect on the EMG patterns in seated subjects. Therefore the focus is on the other two main source of sensory information.

As this study deals with both rhythmic movement and perturbation, this background review will first examine how locomotion is controlled by the nervous system. Then, the roles of vestibular and somatosensory inputs during locomotion are reviewed. Finally, this review will present studies about perturbations during static and dynamic situations.

2.1 Neural Control of Locomotion

Even though locomotion, a simple stereotyped movement, is a mentally effortless rhythmic task which is subconsciously performed, it is not easily controlled. It needs to be flexible, dynamic and adapted to the goal and to the internal and external environment. Moreover, it involves the control of balance, the anticipatory control, and the compensation for unexpected perturbations (Grillner and Wallen, 1985; Forssberg et al., 1980). Animal studies have revealed that locomotion results from continuous interactions between neural networks in the spinal cord –groups of neurons capable of generating the rhythm which is termed the central pattern generator (CPG)–, descending inputs from supraspinal levels and sensory afferent inputs. In the following, the role of the CPG, supraspinal control, and somatosensory inputs during locomotion are briefly reviewed.

2.1.1 Central Pattern Generators (CPGs)

The CPG concept is based on animal studies, such as cats, which show that the spinal cord, if properly stimulated, is able to produce the rhythmic pattern without any input from the sensory afferents or supraspinal centers (Grillner, 1981). For instance, Brown (1911) showed that even after transection of the spinal cord in deafferented cats, the rhythmic activity in the hindlimb muscles continues for a short period of time. Grillner and Zangger (1974) repeated Brown's experiment with some adjustments and got similar results. By repetitive stimulation of the Mesencephalic Locomotor Region (MLR), Shik et al. (1966) demonstrated that decerebrate cats can pace and if the stimulation intensity increases, the speed of locomotion augments and the movements go from walking to trotting and then to galloping. By injection of DOPA in low spinal cats, Grillner and Zangger (1974) observed rhythmic activity in the hindlimb muscles. A so-called "fictive locomotion", which completely removes any movement-related sensory inputs by paralyzing the muscles, typically by means of neuromuscular relaxant injection, is the most persuasive evidence of the existence of CPGs in cats. In paralyzed spinal and decerebrate cats, the rhythmic activity can be recorded in the ventral roots or motoneurons after injection of L-DOPA or Clonidine (Chandler et al., 1984; Pearson and Rossignol, 1991; Jordan et al., 1979) which demonstrates that spinal interneuron circuits are able to generate a coordinated and stereotyped pattern when isolated from all possible descending and sensory feedback inputs. Even though, in these prepared animals, the generated locomotor patterns resemble those of the intact animals, none of these findings imply that supraspinal and sensory signals are not important for locomotion during normal conditions. In fact, they play significant roles in goal-directed, proper, and adjustable locomotion.

Although the CPG concept in quadrupeds is well established, there is still no clear answer whether CPGs exist in humans and non-human primates (MacKay-Lyons, 2002). The results of studies on primates suggest that one of the main differences is an increased importance of the corticospinal tract in primates during locomotion comparing to cats (Duysens and Van de Crommert, 1998). That is, the supraspinal has greater control and influence over the spinal neuronal circuits in order for the human body to be in an upright position while maintaining equilibrium during locomotion (Dietz, 2002). However, there is supportive evidence for human CPGs founded on the studies of complete and incomplete Spinal Cord Injury (SCI) patients. Studies on SCI patients of World War I (Holmes, 1915) and World War II (Kuhn, 1950) revealed some functional capacities of the isolated human spinal cord. In 1994, Calancie et al. presented supportive evidence for CPGs in human; an incomplete SCI patient showed stepping like movement in response to the hip extension when lying supine. However, as afferent sensory inputs and partial descending signals were available in this incomplete SCI patient, it is possible these inputs may have contributed to the observed phenomenon (MacKay-Lyons, 2002). In another type of study, Dimitrijevic et al. (1998) applied non-patterned electrical stimulation to the lumbar spinal cord of complete SCI patients and, as a result, observed rhythmic locomotor-like EMG activity and stepping in the lower limbs. Based on the results, they concluded that a train of stimuli probably initiates the movement by activation of spinal interneuron circuits of CPG and after that the additional peripheral input induces the activation. They also found that lack of inputs from brain stem's noradrenergic descending pathway leads to the duration of this locomotion to be limited to a few minutes and the EMG amplitudes to quickly decay (Dimitrijevic et al., 1998).

Training a spinal cat over a treadmill activates the sensory inputs and consequently central neuronal circuits and develops recovery of walking in the animal (Barbeau and Rossignol, 1987; Edgerton et al., 1991; Bélanger et al., 1996). This neural circuit plasticity does not imply that the same CPG has been recovered; it might be that the spinal circuits are retrained and new neural circuitry are shaped (Van de Crommert et al., 1998). Extension of these findings to persons with SCI has led to partial recovery of gait and improvements in EMG activity in these patients after assisted locomotor training over treadmills with body weight support and upholding of upright posture (Barbeau et al., 1987; Dietz et al., 1995; Wernig et al., 1995). Even though these findings are in line with the existence of CPGs in humans, the most convincing evidence for CPGs, fictive locomotion, has no direct equivalent in humans and has not yet been established to confirm that all the neural circuitry needed for locomotion in humans are placed in the spinal cord (Dietz, 2003; MacKay-Lyons, 2002; Dimitrijevic et al., 1998). The observation that complete SCI patients, at different levels of the spinal cord, were not able to perform unassisted locomotion after training, confirms that, in bipedal gait, supraspinal inputs play a key role during locomotion (Van de Crommert et al., 1998).

2.1.2 Supraspinal Control of Locomotion

Neural control of the motor system and locomotion is believed to be hierarchically organized (Pearson, 1993). The motor control areas of the cerebral cortex, which issue simple and general commands, are at the highest level of this organization. After that, the structures placed in the brainstem region consider other factors, such as equilibrium, and integrate those factors into the descending command, then relay this information to the next level of the hierarchy, the spinal cord (Pearson, 1993; Drew et al., 2002; Poppele and Bosco, 2003). The CPGs embedded in the spinal cord produce the coordinated patterns of the neural activations of the muscles, involved in the locomotion, and relay them to the muscles through the α motor neurons, the lowest level of this system which was termed "final common path" by Sherrington in 1910, to produce the desired locomotor movements. Parameters that vary less are at higher levels of control, while parameters that vary more are at the lower levels of this hierarchical organization (Grasso et al., 2004). Owing to this multilevel control system, the control of locomotion by the brain centers is simplified (Shik and Orlovsky, 1976).

The descending inputs from supraspinal levels not only control the initiation and termination of the CPG activity for the locomotion, but also provide the required parameters for the CPG to produce the demanded motor program; these parameters, such as speed and type of locomotion, are modified based on the goal and the higher level processed sensory information and feedbacks. The cerebral cortex is involved in detail control of a rhythmic movement only in limited circumstances like overcoming an obstacle in the locomotion path (Drew et al., 2002); the supraspinal levels control the leg movements directly for locomotion and intervene or bypass the CPG (Buford, 2005). The sensory inputs, mainly from the somatic sensation, vision, and vestibular sensory systems, have direct modulatory effects through short and mid latency responses on the CPG to adjust the locomotion based on the internal and external environmental factors (Nashner, 1980; Dietz et al., 1984; Dietz, 1992; Schubert et al., 1997; Cathers et al., 2004; Bent et al., 2005). These responses are phase and task dependent, so they can have a regulatory control on the locomotion (Nashner, 1980; Bélanger and Patla, 1987; Patla and Bélanger, 1987; Bent et al., 2005).

The supraspinal control consists of the motor cortex, at the top of the hierarchy, the cerebellum, and the brainstem regions. The structures in the brainstem, that influence the locomotor activities, comprise the Subthalamic Locomotor Region (SLR) (Shik and Orlovsky, 1976), the MLR (Shik and Orlovsky, 1976), the red nucleus (Orlovsky, 1972b; Lavoie and Drew, 1997), the reticular formation (Drew and Rossignol, 1984), and the vestibular nuclei (Orlovsky 1972a,b). The vestibular system is of interest to us because, through the vestibulospinal tract, information regarding linear and angular accelerations of the head will be relayed to the lower levels of the hierarchy.

2.1.2.1 Vestibular Contribution to Locomotion

The vestibular apparatus includes two main structures: three orthogonal semicircular canals and the otolith organs (Wilson and Jones, 1979). Semicircular canals sense angular acceleration and are dynamic receptors. The otoliths consist of utricle and saccule which detect linear accelerations and are dynamic as well as static position receptors (Brooks, 1986). The vestibular system is sensitive to linear and angular acceleration as small as 0.06 ms^{-2} and 0.1 $°s^{-2}$, respectively (Benson et al., 1986). It has been known that the vestibular system, through the vestibulospinal tract, one of the descending pathways in mammals, has modulatory effects on lower limbs (Grillner et al., 1970). Wilson and Yoshida (1969) directly applied stimulation to the lateral vestibular (Deiters') nucleus of cats and recorded the effects of this stimulus on ipsilateral hindlimb extensor cells. They found that Deiters' nucleus evokes monosynaptic excitatory post-synaptic potentials (EPSPs) in some of those muscles, mainly in soleus and gastrocnemius motoneurons, and polysynaptic EPSPs in most hindlimb extensor motoneurons. At the same time, Grillner et al. (1970) also found that the stimulation of Deiters' nucleus evokes mono- and polysynaptic excitatory effects in ipsilateral alpha- and gamma-motoneurons.

Orlovsky (1972a, 1972b), in a series of experiments on cats, studied the role of different descending systems during locomotion. He observed that, in cats with intact cerebellum, vestibulospinal neurons have increased activity during locomotion which is in phase with locomotor cycle; they have maximum activation at the end of swing phase and during stance phase. Any damage to the Deiters' nucleus diminishes or decreases activity of the ipsilateral extensors. These results suggest that phased activity of vestibulospinal neurons is an important factor for excitation in the stance phase (Orlovsky, 1972a, 1972b). Applying a weak stimulus in the appropriate phase of the stepping cycle can considerably increase muscular activity; such a stimulation of Deiters' nucleus during stance phase causes enhanced muscular activity of the ipsilateral extensors, while it does not have any influence on the ipsilateral extensors during swing phase. Also, weak stimulation of Deiters' nucleus does not have any influence on timing and rhythm of stepping (Orlovsky, 1972b).

In another interesting study, Orlovsky and Pavlova (1972) evoked vestibular responses of Deiters' neurons by inclining a cat in a frontal plane during static condition and locomotion. As expected, in the static condition, vestibulospinal neurons showed increased activity during the tilting and for a short time afterwards. However, these responses were strongly inhibited during locomotion, proportional to the locomotion speed. Therefore, they suggested that this inhibition prevents the signals of the vestibular system, due to the irregular and accidental head and body movements during locomotion, to falsely disturb the locomotor cycle. In other words, if not inhibited, the responses of vestibular receptors to a perturbation during rapid running could upset the periodic activity of Deiters' neurons and as a result, stop the locomotor cycle.

Galvanic Vestibular Stimulation (GVS) is a useful technique that allows researchers to manipulate the human vestibular system. In quiet stance studies, the GVS technique has been used to change the firing rate of vestibular afferents in order to produce body sway in standing subjects (Nashner and Wolfson, 1974; Goldberg et al., 1984; Britton et al., 1993) which resulted in the observation of two responses in the soleus muscle, discriminated by their latencies and amplitudes. Manipulation of GVS revealed that vestibular signals largely affect the long latency responses; however, the appearance of these responses after GVS depends on two conditions: the muscles should be involved in postural equilibrium and the vestibular system should be the dominant source of information used for postural control (Britton et al., 1993). Accordingly, the responses in the soleus muscle will be eliminated when subjects are seated, when they open their eyes, or when they lightly touch a fixed support surface during the GVS (Britton et al., 1993).

Furthermore, the vestibular signals produced during tilt or translation can be disrupted or enhanced by GVS (Inglis et al., 1995), which has revealed that the vestibular system has small effects on the short latency response but large effects on the long latency response, suggesting that the vestibular system plays a key role in the control of the magnitude of postural movement and establishment of final postural equilibrium (Britton et al., 1993; Inglis et al., 1995) if the acceleration of body movement surpasses a threshold (Nashner et al., 1989).

During slow locomotion, subjects followed an arched trajectory after GVS stimulus was applied (Fitzpatrick et al., 1999; Jahn et al., 2000). Based on GVS studies, Bent et al. (2005) proposed that the vestibular information is phase- and task-dependently weighted. They observed that in transition between states, e.g. from stance to walking or from walking to stop, the vestibular information has an enhanced influence. Also, the vestibular control of the upper body is different from that of the lower body (Bent et al., 2005).

Consistent with Orlovsky and Pavlova's (1972) findings, Brandt et al. (1999) and Jahn et al. (2000) observed that while a dog with profound unilateral vestibular loss had a severe postural imbalance toward the affected side when standing, it was able to run without any problem. Also, patients with acute unilateral vestibulopathy and healthy subjects with a post-rotation transient vestibular tone imbalance or GVS stimulated had significantly smaller deviation from their path and maintained their balance during running compared to walking (Brandt et al., 1999; Jahn et al., 2000). They proposed that the CNS inhibits the descending vestibular signals during fast locomotion –i.e. the influence of vestibulospinal signals are decreased so it can not interfere with the highly automated locomotor pattern– and uses other reliable afferent sensory systems such as somatosensory and vision for the adjustment of locomotor pattern. In parallel with that, it has been observed that complete loss of vestibular system has little effect on the performance of gait (Dietz et al., 2001).

Functional magnetic resonance imaging (fMRI) studies on brain activation patterns during imagined locomotion is consistent with the mentioned findings and has shown that during highly automatic locomotion, such as running, the vestibular area of the brain is inhibited, so the vestibular signals do not interfere or disturb the locomotor pattern (Jahn et al., 2004). Also, during normal cycling on an ergometer, GVS does not have any significant influence on EMG activities of leg muscles because balance control is not involved (Iles et al., 2007).

2.1.3 Somatosensory Contribution to Locomotion

Sensory afferent signals not only let humans receive information about internal and external environments, but also may have direct excitatory or inhibitory effects on muscles through reflex pathways, either monosynaptically or polysynapitcally, during normal conditions (Darton et al., 1985; Mathews, 1991; Zehr and Stein, 1999). But what role do they play in locomotion? Even though the spinal pattern generator is capable of rhythm generation without sensory afferent feedbacks, the details of the produced rhythm are abnormal and lacks precise and adjustable pattern (Pearson, 1993; Van de Crommert et al., 1998). Abnormalities consist of inconsistency in cycle duration and interlimb coordination, having irregular contact pattern (Wetzel et al., 1976), and apparent variability in the activity pattern of flexor and extensor muscles (Grillner and Zangger, 1975). Modification of the generated pattern based on the external conditions is only possible by inputs from sensory system. A good example of the regulatory influence of afferent feedback in locomotion can be seen in a spinal cat walking on a treadmill; the speed of locomotion is adapted to any changes in the speed of the treadmill similar to what seen in intact animals (Forssberg et al., 1980).

Afferent feedback not only provides information for the CNS to regulate the locomotor cycle duration, but also to adjust the amplitude of muscle activities, based on environmental demands (Rossignol et al., 2006). According to Pearson (1993), there are three important roles for sensory afferent feedbacks during locomotion in order to adapt the locomotion to the environment. The first one is the organization of "temporal ordering" of the rhythm, whereby the sensory feedback supplies information to the CPG to guarantee that the motor pattern is properly timed for position, direction of movement, and force in moving body structures. The second role is "regulation of phase transition", likely to ensure that there is a limited range for the extent of body parts movements and a certain phase of the movement does not start until a defined biomechanical state, appropriate for initiation of that phase, has been achieved. The last role is "reinforcement of ongoing motor activity", mostly those involved in power stroke and load bearing such as the extensor activity associated with stance. These regulatory roles by afferent feedbacks are achievable because descending pathways and spinal reflex pathways converge on spinal interneuron circuits (CPG), and as a result, it allows the CPG to integrate all the inputs and commands in the spinal level in order to shape the final motor output (Schomburg, 1990). By recruiting reflex pathways, the CPG controls their gain during locomotion and presynaptically or postsynaptically modulates reflexes.

The regulatory role of sensory afferents during locomotion can be achieved by those afferent inputs that have direct access to the CPG, i.e. stimulation of their receptors or their sensory fibres results in rhythm entrainment or resetting (Hultborn et al., 1998; Van de Crommert et al., 1998). During walking, three essential sources from proprioceptive and exteroceptive afferents have direct access to the CPG (Van de Crommert et al., 1998). There are two load-related afferent inputs and one hip joint position-related afferent input which make essential contributions to CPG activation during human locomotion (Dietz, 2002); the load-related afferents are group Ib afferents of Golgi tendon organs from extensors and cutaneous afferents in the skin of the foot.

Duysens and Pearson (1980) observed that during locomotor activity, isometric contraction of triceps surae, either induced by ventral root stimulation or gradual increment of stretch applied to the Achilles tendon in the fixed hindlimb of pre-mammillary cats, prolongs the ankle extensor muscle activity and suppresses ankle flexor activity. As the electrical stimulation or the applied stretch to the Achilles tendon could have resulted in activation of both Ia and Ib fibres, it was unclear which group I fibres were involved in this resetting effect. Later, in 1987, Conway et al. demonstrated that during fictive locomotion in a cat, electrical stimulation of the plantaris nerve could prolong extensor activation during stance phase and delay initiation of flexor activation. If the stimulation was applied during the swing phase, it could suppress the ongoing motor activity and reset the rhythm to extensor activity. However no such behaviour could be observed after high frequency low amplitude vibration of the extensor muscle which recruits Ia afferent fibres. As weak electrical stimulation of the plantaris nerve strongly activates Ib afferents, this study clearly revealed that Ib afferents from force-sensitive Golgi tendon organs are involved in this phenomenon. While during static conditions Ib afferents have autogenic inhibitory effects, in active locomotion the group Ib afferents undergo a phase dependent reflex reversal and evoke excitation of extensor motoneurons. This reflex reversal has been confirmed by Gossard et al. (1994) at the intracellular level. As a result of this reflex reversal, the positive feedback reinforces the extensor activity and prolongs the stance phase due to the loading and it inhibits the initiation of the swing phase until the load on the stance limb decreases (Duysens and Pearson, 1980).

The activity of the cutaneous afferents in the skin of the foot is also used by the CNS to monitor loading. Electrical train stimuli of the sural nerve, which innervates the lateral border of the foot, had similar effects as Ib afferents stimulation, in which they prolonged the extensor activity during stance phase and delayed initiation of the swing phase (Duysens and Pearson, 1976). Tactile stimulation of the dorsum of the foot during swing phase generates an increase in the flexor activity and during stance phase results in an increase in the extensor activity (Forssberg et al., 1977). These results suggest phase-dependent reversal of cutaneous reflex during locomotion of spinal cats. Similar reversal of cutaneous reflexes is also obtained in human studies (Yang and Stein, 1990; Duysens et al., 1990). The functional importance of this reflex reversal is that the increased extensor activity during stance would protect the limb from possible displacement and the increased flexor activity during swing would carry the limb over an imminent obstacle.

Hip joint position related afferent inputs play a regulatory role in the control of locomotion and have direct access to the CPG. Grillner and Rossignol (1978) showed that the onset of swing phase is dependent on the hip joint angle. This is also demonstrated during fictive locomotion in spinal and decerebrate cats in which the rhythmic hip movement entrains the locomotor rhythm (Andersson and Grillner, 1983; Pearson and Rossignol, 1991; Kriellaars et al., 1994). It is believed that mainly the muscles around the hip are responsible for signalling the hip joint position information (Dietz et al., 1995); stretching of hip flexors due to the hip extension activates the Ia afferents from flexor muscle spindles and results in the initiation of flexor muscle activity, through monosynaptic stretch reflex, near the end of stance phase (Van de Crommert et al., 1998). Brooke et al. (1992) have also shown that the knee and ankle angles are important in reflex phase modulation during cycling.

2.2 Perturbation

A common method used to address questions of motor control is to apply a form of perturbation and characterize the strategies employed by the neuromuscular system in response to that particular perturbation. For instance, in the case of locomotion, the responses are characterized by the deviations from the stereotypical pattern and depict how the CNS adjusts the pattern for recovery or adaptation. Based on the goal of the study, different kinds of perturbations can be applied. Linear translation is the form of perturbation used in this study. While most studies of this kind have been focused on translation in the direction of ongoing movement, this study examines translations perpendicular to the plane of the ongoing locomotor activity; seated subjects pedal in the sagittal plane while the applied translations are in the frontal and transverse planes – left- and right-ward. We are interested in quantifying the CNS response to this kind of perturbation and determining the underlying mechanism. To reach this goal, the study design includes translation during static and dynamic (cycling) conditions. In the following, findings of other related studies are reviewed.

2.2.1 Perturbation during Static Situations

Upright stance seems to be a simple task for humans while it is achieved by complicated work of the nervous system; it incorporates multiple sensory information regarding position, velocity, and acceleration of the body parts with respect to the internal and external environment and then provides anticipatory motor actions in order to achieve equilibrium (Massion, 1992; Horak and MacPherson, 1996; Peterka, 2002). If the equilibrium is lost, the corrective motor reactions compensate this loss.

Horak and Nashner (1986) observed two strategies or combination of them in response to antero-posterior translation during upright stance, which they called the *ankle* and *hip strategies*. The ankle strategy restores the equilibrium by rotating the body around the ankle joint. The response starts from the ankle and emits distal to proximal, to the thigh and then the trunk muscles. However, in the hip strategy, horizontal shear forces generated by the hip joints produce the compensatory response. Contrary to the ankle strategy, the response emits proximal to distal with no ankle response. But when are these strategies used? Nashner (1982) suggested that the CNS recognizes the joint closest to the perturbation site and starts stabilization from that joint. Horak and Macpherson (1996) suggested that if the perturbation is slow, the ankle strategy is used by the CNS, whereas for large and rapid translations, the hip strategy is able to stabilize the body. In the case of a very large or fast translation, none of the ankle or hip strategies are able to produce enough compensatory reactions and the *stepping strategy* will be employed by the CNS (Horak and Macpherson, 1996). However, Maki and McIlroy (1997) revealed that contrary to the orderly manner of strategy selection proposed by Horak and Macpherson (1996), the strategies can be initiated in parallel.

Compared to antero-posterior translation, the number of studies on the effects of translation in the frontal plane are limited. Moore et al. (1988) studied the responses to horizontal translation of stance in multiple directions. They concluded that the response characteristics are highly dependent on the perturbation direction: The onset latency, temporal relationships between muscles, and amplitude of muscle activities vary based on the direction of the translation. Henry et al. (1998a) suggested that depending on the translation direction, muscles are recruited at different times, which allows them to play various roles as part of the selected muscle synergies. For instance, some muscles that were not anatomic synergists took part in a synergy in response to specific translation direction. They proposed that a complex central organization, rather than a simple reflex or fixed muscle synergy, is responsible for this process and the magnitude of response is determined by the peripheral input.

Henry et al. (1998b) compared the responses of sagittal translation with those of frontal translation. They revealed that a similar EMG activation pattern occurs in both planes to recover equilibrium; first, an early proximal muscle activation occurs, followed by the distal to proximal muscle activation pattern. For instance, in lateral translation, the tensor fascia latae is the first muscle which is activated and plays an important role in moving the body centre of mass. After that, the distal muscles stabilize the loaded leg and finally the other thigh and trunk muscles are recruited.

Based on these findings, they proposed that the CNS mechanism for controlling the body centre of mass after translation is the same in both directions; however, the responses are adapted to the biomechanical and anatomical constraints (Henry et al., 1998b).

These relatively stereotyped responses during stance tend to have rather long latency; in the case of lateral translation, the first response commences at 103 ms following the perturbation and in the case of antero-posterior translation, the first muscle activation is in the range of 105-116 ms (Henry et al., 1998b) or in the range of 73-110 ms (Horak and Nashner, 1986). This suggests that the CNS is able to recover equilibrium in different conditions with remarkable flexibility (Rietdyk et al., 1999).

Determining the triggering source for balance control of perturbed standing subjects has been of interest for researchers. Based on the latency of responses, Nashner (1977) proposed that the information coming from the ankle, as the body pivot overtop of it, is the trigger source. However, proprioceptive inputs from other muscles such as trunk and neck had a response time similar to the response time of gastrocnemius (Keshner et al., 1988). Also, the role of vestibular as a triggering source should be considered. By exposing patients with somatosensory loss, due to the diabetic peripheral neuropathy but with intact vestibular and visual sensory information, to rearward translation, Inglis et al. (1994) observed that the onset of EMG activities at all segments were delayed 20-30 ms. Horak et al. (1994) concluded that vestibular signals trigger postural responses to support surface translations in a standing human if proprioceptive signals occur at the same time. Also, they did not observe any differences in latencies and muscle activation patterns of leg and trunk between patients with acute bilateral vestibular loss and healthy subjects. By applying GVS, Inglis et al. (1995) proposed that vestibulospinal information plays a significant role in fast postural movements to shape the final equilibrium position, but not as the primary triggering source. Similarly, the findings of Hlavacka et al. (1998) suggest that the vestibular system has a great influence during the dynamic phase of the postural response, and during later components of balance correction. Horak et al. (1990) proposed that vestibular signals are necessary for balance correction using hip strategy. In contrast, Runge et al. (1998) suggested that this in not the case and the vestibular signals are not necessary for hip strategy.

To elucidate the interaction between vestibular and proprioceptive signals and answer these controversies, Allum and Honneger (1998) ran a study using normal subjects and those with vestibular loss during backward support surface translation. They designed a moving platform which allowed them not only apply horizontal translation on subjects, but also apply rotation around the ankle joint of subjects synchronized with translation. In this way, they could nullify the ankle rotation, enhance the ankle rotation, or have a normal ankle rotation while the support surface is suddenly displaced backward. They observed that muscle stretch due to the ankle or knee rotation does not trigger balance-correcting responses. Based on the observation that the amplitude and the latency of balance-correcting responses in both normal subjects and those with vestibular loss were almost the same, even with null ankle condition, they suggested that rotation of the trunk is the primary triggering source during stance as it can reliably detect the onset of perturbation. After the primary signal occurs, a central mechanism uses the vestibular and knee signals, as the second triggers, and ankle and neck signals, as the third triggers, to shape the final pattern of muscle activations based on prior knowledge of the body posture and the environment; these are all in the stabilizing period where the CNS has more flexibility to choose appropriate signals from these sensory systems.

But what is the triggering source of postural response during sitting following translation? Forssberg and Hirschfeld (1994) performed an experiment to study whether vestibular, somatosensory, or interaction between both inputs trigger and modulate the postural responses in sitting humans. They designed an apparatus which allowed them to apply antero-posterior translation as well as rotation in the sagittal plane on subjects while they sat erect with almost straight legs. By this design, they were able to investigate the trigger source of postural adjustment in sitting subjects after perturbation. They observed that both legs-up rotation and forward translation induced and initiated "a backward rotation of the pelvis", "a backward sway of the lower trunk", and "a backward displacement of the head". The basic structure of muscular responses was fairly similar in both conditions with some condition-dependent differences. To elucidate the role of the vestibular system in these responses, they placed the subjects behind and in front of the centre of rotation to change the head acceleration. In this way, the rest of the body was perturbed similarly to when subjects were placed in the centre of rotation of the apparatus, while the vestibular system was under different acceleration. The results showed that the hip and trunk muscle activation patterns were similar in all three conditions. The authors concluded that there is strong evidence that "the otoliths, sensitive to linear acceleration, do not trigger the postural adjustments during sitting" and the semicircular canals, sensitive to angular rotation of the head, could not be triggered on time to trigger the postural adjustments in this experiment. They suggested that somatosensory signals raised from pelvis rotation, such as alteration in pressure distribution under buttock sensed by cutaneous receptors, may play a role as the triggering source. This is in line with the findings of Allum and Honneger (1998) about the role of trunk rotation as the primary triggering source for balance correction during stance.

2.2.2 Perturbation during Dynamic Situations

During human locomotion, the CNS employs two balance control mechanisms for maintaining dynamic equilibrium: proactive and reactive balance control strategies

(Patla, 1993). The proactive mechanism uses a feed-forward strategy and activates automatic postural adjustments prior to any phase of voluntary movement that has a potential threat to stability. This mechanism is integrated into walking and prevents loss of balance during locomotion. On the other hand, the reactive mechanism is a feedback strategy and activates automatic postural adjustments after a threat to stability, due to external factors, is sensed and detected. The proactive strategy mainly uses somatosensory and vestibular signals for the detection of disturbance and generating the automatic responses for regaining balance after a disturbance (Patla, 1993). Our interest is focused on the studies of the reactive control process.

Nashner (1980) was one of the pioneers in applying perturbation on walking human subjects and study the reactive balance control responses. The perturbation consisted of antero-posterior translation, upward and downward translation, and plantar- and dorsi-flexion of the ankle joint of the stance leg. The responses were movement specific, fast, stereotypically organized into the rhythmic pattern, and had a large magnitude compared to the background EMG level even when facing a relatively small perturbation. In addition, the adjustments varied based on the phase of the cycle (i.e., phase-dependent) and also on the expectation of the subjects. As the adjustments were similar to those seen in quiet stance studies with the same type of perturbation, Nashner (1980) suggested that the CPG used the same postural synergies employed during perturbation of stance. The timing of reactive responses began at 95-110 ms after the onset of perturbation and lasted for about 100-400 ms. Nashner (1980) proposed that the difference between the trajectory anticipated by the CNS and the performed trajectory is the main source for triggering the coordinated EMG adjustments.

During walking, leg and thigh muscles play very important roles in recovering balance after a slip type perturbation, due to the movement of the gait platform (Nashner, 1980; Dietz et al., 1984). Dietz et al. (1984) suggested that distal leg muscles alone can recover the postural equilibrium after this type of perturbation during locomotion. Tang et al. (1998) studied the role of proximal muscles (i.e., hip and trunk) in responses to slip perturbation during gait and confirmed that they do not contribute significantly in regaining postural balance after perturbation. However, consistent with Nashner's (1980) study, the responses in leg and thigh muscles were rapid (e.g., 90-140 ms after onset of perturbation) and had a large magnitude and a relatively long duration of 70-200 ms. Tang et al. (1998) suggested that leg and thigh muscles absorb the energy transferred to the body due to this type of perturbation and as a result the disturbance of the upper body would be minimized. The interlimb coordination between two legs is also crucial for continuing the forward progression of the locomotor task and achieving a dynamic equilibrium (Dietz et al., 1994; Tang et al., 1998).

Slow or fast perturbations have different effects on the onset latency, magnitude, and duration of the responses (Dietz et al., 1987). For instance, responses in the gastrocnemius muscle start at 90 ms during slow perturbation (2.5 ms^{-2}) and at 70 ms in fast perturbations (14 ms^{-2}) (Dietz et al., 1987). Also, Dietz et al. (1987) showed that faster perturbation increases the magnitude and duration of responses.

Other studies have performed different kinds of perturbation rather than horizontal translation during locomotion. Using electrical stimuli, the results have shown that compensatory responses are task dependent (Patla and Bélanger, 1987) and phase dependent (Bélanger and Patla, 1987). Reflex reversal has also been observed during walking (Yang and Stein, 1990). Misiaszek et al. (2000) applied load on the leg at the end of stance phase and observed enhancement of ongoing extensor muscle activity. They also proposed that during walking, if perturbation is applied, then ongoing movement continues once the centre of mass is sufficiently stable. Otherwise, the task of locomotion will be paused.

The issue of perturbation during locomotion, without balance consideration, has not been adequately addressed in the neural control literature. Also, the number of publications about medio-lateral translation is significantly lower, quasi-inexistent, compared with those in the antero-posterior direction. In this study, we examine the corrective EMG responses, with minimal balance component, for progression of the locomotor task after a medio-lateral translation is applied.

3 Materials and Methods

3.1 Subjects

Similar studies used diverse number of subjects [e.g., from ten (Brown and Kukulka, 1993), to eleven (Sakamoto et al., 2006), and even to eighteen (Ting et al., 2000) subjects]. Based on the result of our pilot study and using the SigmaStat software, 10 subjects were needed for power of 80% with α=5%. In this study, ten subjects in good physical condition and without a history (self-reported) of neuromuscular, vestibular, orthopaedic or metabolic disease were recruited without remuneration for their time. The subject pool was primarily from the university student population. Subjects' ages were between 22 and 30 years old (4 females and 6 males).

3.2 Pedalling

To achieve the goals of this study, four pedalling conditions were designed: Dynamic Active (DA), Dynamic Passive (DP), Static Active (SA), and Static Passive (SP). The two dynamic conditions are representative of the rhythmic movement. During the dynamic active movement, subjects were required to pedal at a 1 Hz frequency since humans normally walk with this frequency (Winter, 1983). The term of active in the DA condition means that the subject is pedalling voluntarily, employing the hierarchical organization of locomotion. The pedalling trajectory of the subject was recorded and used for the dynamic passive movement. In other words, throughout the DP condition, subjects were not to voluntarily exert any force to move the pedals. Rather, a torque motor mimicked the same trajectory produced in the DA condition, and subjects relaxed while their lower limbs followed the passive pedaling movements. While the two dynamic conditions have similar kinematic patterns, the CNS plays different roles. In the DP movement, only sensory information is relayed to the CNS and minimal motor signals for the locomotor movement are generated by the CNS or the Spinal Pattern Generator.

In this experiment, the static conditions allow us to perform a comparative study of the responses of the CNS to the perturbation while it is not involved in the control of the rhythmic movement. For this aim, in both static conditions, the lower limbs of subjects were adjusted and firmly stabilized to one of the four pedalling positions (phases - explained below). Hence no muscular effort was needed to retain a static configuration. During the static active condition, subjects were asked to match their contraction level of the soleus muscle to the same level observed during DA condition for the corresponding crank arm position in pedalling. For this purpose, an oscilloscope, placed in front of the subject, provided information about the contraction level of the soleus muscle and allowed the subject to adjust and maintain the desired muscle activity. In the static passive condition, subjects were required to relax. The condition was similar to the SA condition, except that subjects did not contract any lower limb muscles or exert any force.

In all four conditions, the subjects' feet were attached and secured to the pedals by a custom-made foot plate and Velcro. The custom-made foot plate made the foot behave as one segment by preventing the metatarsal joint rotation (Brooke et al., 1992) and assuming the foot and the pedal were one rigid body (Hull and Jorge, 1985). Moreover, it ensured that the placement of the feet on the pedals was constant.

Based on the action of the lower extremity during pedalling, the "power" and "recovery" phases of the cycle are defined as the positions of the cycle where the lower limb is propelling the crank and recovering its position in order to get ready for replication of the power phase, respectively (Brown and Kukulka, 1993). In this experiment, the cycle is divided into four equal intervals, or phases. Based on the modified ergocycle, the crank at the top-dead centre (0°) corresponds nearly to the middle of the propulsion (P) or power phase (Jorge and Hull, 1986) whereas 180° corresponds almost to the middle of the recovery (R) phase (Brooke et al., 1992). The transition phases are represented at 90° (PR [propulsion-recovery] transition) and 270° (RP [recovery-propulsion] transition). Figure 3-1 illustrates the four pedalling phases in this study.

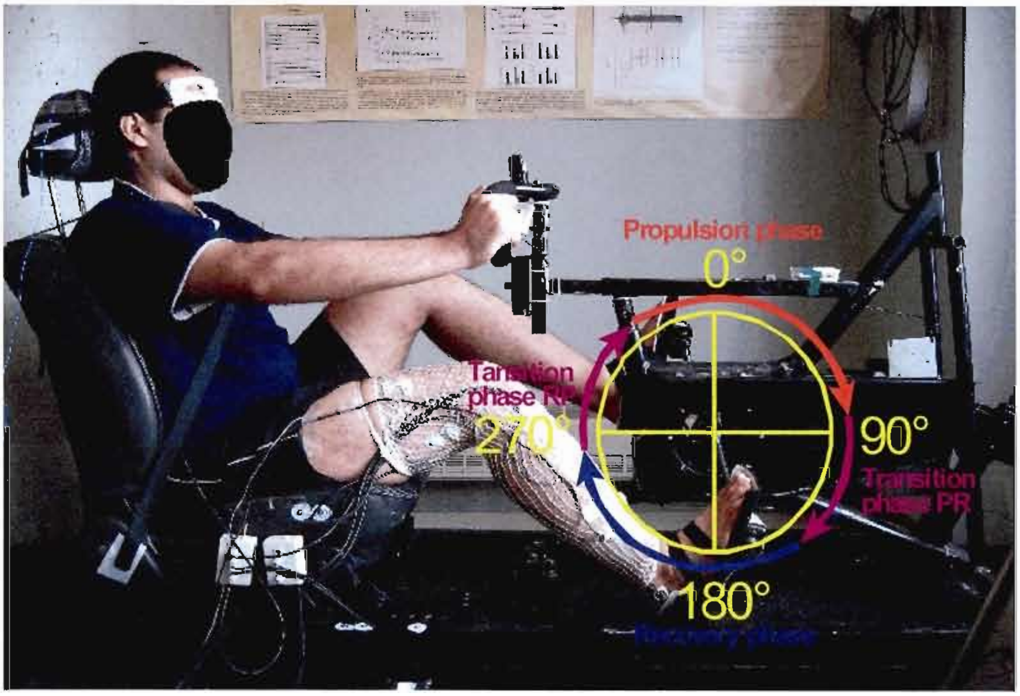

Figure 3-1: Four pedalling phases: the propulsion (P), the PR transition, the recovery (R) and the RP transition phases

3.3 Order of the Pedalling Conditions

In repeated measure designs, incidental influences can happen for a variety of reasons such as fatigue, boredom, or practice, and can affect later observations. As this study was a repeated measures design, the incidental influences due to the order of the study conditions were controlled or minimized by systematic counterbalancing. However, because the DP and SA conditions respectively needed the trajectory and level of muscle activities information from the DA condition, the subject could start experimental conditions either with SP or DA condition. If the subject began with SP condition, there were two possible combinations of conditions whereas with the DA condition, there were six possible combinations. Therefore, the experimental conditions could be systematically counterbalanced in every eight subjects.

3.4 Linear Rightward-Leftward Translation

Linear rightward (RT - left to right) and leftward (LT - right to left) translations with the peak acceleration of 9.8 ms^{-2} (1g) and 2.54 cm displacement were applied pseudo-randomly to the table (see description below) of the cycle ergometer in each phase of the pedalling cycle. Pseudo-random translations prevented participants from anticipating the direction of the translation.

3.5 Measurements

In order to quantify the effects of the translation, EMG activities of selected muscles, applied force to the pedal by the subject, the ankle angle, the crank arm position, and the acceleration of the head during translation were recorded during the experiment. Records of EMGs were made by utilizing bipolar silver/silver chloride pre-gelled surface electrodes fixed over six muscles: three leg muscles [Soleus (SOL), Tibialis Anterior (TA), and Medial Gastrocnemius (MG)], two thigh muscles [Biceps Femoris (BF) short head, Vastus Lateralis (VL)], and one hip muscle [Tensor Fascia Latae (TFL)]. BF and TA were selected as representative of the flexor muscle groups of knee and ankle, respectively. VL, MG, and SOL were chosen from the extensor muscle groups of the lower limb. TFL has been shown to be the first muscle activated during medio-lateral translation of standing subjects (Henry et al., 1998b). The radius of the electrodes (model MEDITRACE 133) was 15 mm and the centre to centre distance of each electrode pair was 30 mm. The EMG signals were amplified using a GRASS QP511 system with a bandpass 10-300 Hz.

The applied force on the pedal was quantified using force sensitive resistors (model FlexiForce^{TM} 1*lb*), which were positioned on the first metatarsal head, and amplified by a custom-built amplifier. A custom-made electrogoniometer (variable resistor with two armatures) with its amplifier was used to transduce the ankle joint kinematics. By using an electrical sensor (*Hall Effect* Sensor), for zero degree detection, and a 10 bits optical encoder, the angular position of the crank arm was transduced to digital signals with an accuracy of 0.35°. The angular position of the crank arm was needed to determine the phase of the cycle for applying the translation, and was used for playback during DP condition where the torque motor mimicked the trajectory of DA condition. In addition, it was used for analysis of the cycle duration and trajectory.

To measure the linear acceleration of the head in the direction of the translation, a miniature unidirectional ceramic accelerometer (PCB PIEZOTRONICS: ICP® Accelerometer model 352C22) was attached over the right mastoid process of the subject with the axis of its maximal sensitivity aligned perpendicular to the sagittal plane and stabilized by an elastic headband. The sensitivity of the accelerometer was 1 mV/ms^{-2} (9.8 mV/g). The accelerometer was then connected to an amplifier (PCB PIEZOTRONICS: Signal Conditioner model 480B21).

All the measurement devices were calibrated before each experiment.

3.6 Experimental Setup

Figure 3-2 shows a general view of the apparatus used in this study. The modified cycle ergometer and the seat were placed on a translational sliding table. Also, the sliding table was placed on minimal friction rollers over the stabilization platform. By using the electrical cylinder and the motor, placed between the table and the stationary platform (base), the desired translation could be applied.

Two computers were used in this setup. One of them recorded the pedaling trajectory of the subject during the dynamic active condition. Then, the recorded data was sent back to the controller, which activated the torque motor for the reproduction of the pedaling trajectory during the dynamic passive condition. The computer also used the pulses to trigger the translations in the appropriate phases.

The second computer was used for data (i.e., EMG, head acceleration, ankle position, pedal force, and pedal crank position) recording. The signals were transmitted to a Digidata 1200/Axoscope, an analog to digital (A/D) converter hardware/software system, and stored on the computer. All signals were sampled at a rate of 2 kHz per channel.

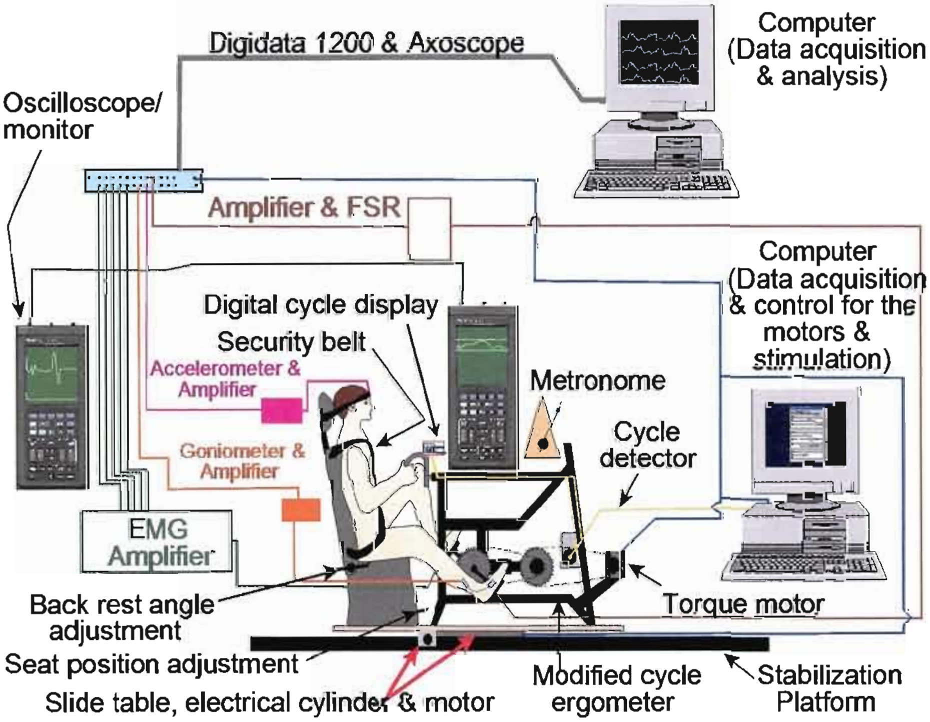

Figure 3-2: A general view of the experimental setup

3.7 Experimental Procedures and Recordings

Following a clear description of the study and detailed experimental protocol, and after all the questions regarding the experiment were answered, the subject was asked to sign the written consent form to participate in this experiment (see Section 0, Appendix A). This study has been approved by *Le Comité d'éthique du Département de Kinanthropologie (CÉKIN), un sous-comité du Comité institutionnel d'éthique de la recherche chez l'humain (CIÉR) de l'Université du Québec à Montréal (UQAM.* (UQÀM – Kinanthropologie ethics committee).

Afterwards, the experiment began with proper skin preparation, by using abrasive gel and alcohol until the skin got a light red color, to remove the dead skin layer. Then the electrode positioning over the bellies of the six selected muscles was carried out. Proper skin preparation plays a major role on the quality of the EMG measurements by providing a stable electrode contact and low skin impedance. To ensure that the impedance levels between pairs of electrodes at the recording sites were less than 10 kΩ, they were measured and verified using an impedance-meter (GRASS EZM 5). To minimize the effect of neighbouring muscle activities on EMG signals (cross-talk effect), care was taken to locate the recording electrode pair over the central position of the muscle belly (Konrad, 2005).

After preparing the subject, she/he was instructed to sit in a comfortable position with the arms holding the handles of the cycle ergometer, and the trunk and the head were fixed to the seat by using non-elastic Velcro straps. The accelerometer, force sensitive resistors, and electrogoniometer were positioned as mentioned above. Also, the feet were placed in the foot plate and firmly attached to the pedal. The baseline noise of the raw signals from all measurement devices was visually inspected. For the numerical inspection of noise, the average noise level of rectified EMG signals for every muscle during rest condition should be less than 3.5 μV for a 5 second duration (Konrad, 2005).

All subjects were allowed to familiarize themselves with cycling on the modified ergometer. In order to pedal smoothly and consistently, they were instructed to maintain a 60 rpm cadence by following the audible beat of a metronome and a monitor that indicated the speed of pedaling. The experiment followed the order of the pedalling conditions assigned to each subject. To minimize the effect of fatigue during the experiment, adequate rest periods were allowed between the pedalling conditions based on the subject's wishes. In each pedalling condition, the experimenter collected at least ten trials in each translation direction for each phase, with 6-9 s inter-translation intervals. The translation was pseudo-randomly applied to the ergometer table in such a way that every four consecutive translations include all four pedalling phases. In the DA condition, the subjects pedaled for 20 non-perturbed cycles before the first translation.

3.8 Data Analysis

The recorded EMG data were further processed after acquisition. In all EMG signals, the gain of the amplifier, utilized during data collection, was taken into consideration during calculations. Visual inspection of EMG signals revealed that in some subjects the EMG recordings of the TFL muscle were contaminated with wire movement artefacts. In order to remove these artefacts from the EMG data, all EMG signals were high-pass filtered with the cut-off frequency of 40 Hz using a second order zero lag Butterworth high-pass filter (Redfern et al., 1993). The cut-off frequency was determined by visual inspection in order to remove heart rate artefacts. Then the EMG data were rectified and linear envelopes were created using a second order zero lag Butterworth low-pass filter with the cut-off frequency of 10 Hz. Following this, based on the condition, whether static or dynamic, different processing steps were used for each subject.

3.8.1 Dynamic Conditions Analysis

In Dynamic Active and Passive conditions, those cycles which were faster or slower than the requested 1 second with the threshold of 100 ms, were removed. This criterion caused mostly removal of some of the first and last cycles, where subjects either started or wanted to stop the pedalling task. Then, the perturbed cycles in the four phases and two directions were selected. The rest of the cycles were considered to be the control cycles except those ones after 270° perturbations as the perturbation effects on muscle activities might continue to the start of the next cycle. The DA data was used for calculating the normalization factors; first, the duration of all control cycles was normalized to a 1 second duration and a 99% confidence interval (CI) of EMG amplitude data of each muscle was calculated. For each subject, the maximum of 99% CI of the duration-normalized control cycles of each muscle in the DA condition was used for amplitude normalization of EMG data of that muscle in each condition, i.e. DA, DP, SA, and SP.

Following the calculation of the normalization factors, the amplitudes of the filtered EMG data were normalized. The analysis window was set to 400 ms from the onset of the translation and the corresponding data from the control and perturbed cycles for each phase were selected. The integrated EMG (IEMG) was calculated in two epochs of 80-250 ms and 250-400 ms. The first one (E_1) considers medium and long latency responses while the second (E_2) window includes some of the voluntary component of the responses due to the translation. Afterward, mean, standard deviation, and 95% CI of the IEMGs for the perturbed cycles and control ones were calculated.

To investigate the effects of the translation on the kinematics of the movement, the cycle duration of the perturbed cycles versus the control ones was analysed in the DA condition. The DP condition was not analysed since the servomotor mimicked the DA movement and trajectory of the cycling and the pedalling was not controlled by the subject. Two different sets of calculations over the pedalling movement were performed. In the first analysis, the perturbed trials of a specific phase and direction were selected and the cycle durations in four consecutive cycles were used: the durations of the immediate cycle before (C_b), the cycle during (C_d), the first cycle after (C_1), and the second cycle after (C_2) the translation. The coefficient of variation (COV – the standard deviation divided by the mean) and its 95% CI for each group of trials of these four cycles was calculated. Also, the duration itself was investigated in such a way that in each trial the durations of C_d, C_1, and C_2 were normalized based on the duration of C_b. In this way, the variations in cycle duration during the DA condition could be reduced. Then mean, standard deviation, and 95% CI for the trials C_b, C_1, and C_2 were estimated. Obviously, due to the normalization, the duration of C_d was 100% in each trial and the mean would be the same. This analysis is called *full cycle duration analysis*.

In the second analysis, the analysis was focused within the perturbed cycles as there may be a very brief adjustments. Each perturbed cycle was broken into quarter cycles and the analysis is called *quarter cycle duration analysis*. To this end, the quarter cycle duration of the first quarter before (qC_b), first quarter after (qC_1), and second quarter after (qC_2) the selected translated quarter as well as the selected translated quarter (qC_d) itself were extracted. In order to better understand this analysis, assume that the trials of the RT translation at 180° are selected. Then for each trial, the quarter cycles are formed for the qC_b (90°-180°), the qC_d (180°-270°), the qC_1 (270°-360°), and the qC_2 (0°-90°, which takes place in the next cycle). The durations of these quarters were also extracted for the control trials. In order to consider the variations of cycle duration during the course of DA condition, the quarters were normalized to their qC_d duration. Then the mean, standard deviation, and 95% CI for perturbed and control trials were estimated. Due to the duration normalization, the duration of qC_b was 100% for all trials and as a result the mean and upper and lower CIs would be 100%.

3.8.2 Static Conditions Analysis

In both static conditions, the amplitudes of the filtered EMG data of each muscle were normalized based on the corresponding normalization factor estimated in the DA condition. Similarly to the dynamic conditions, the analysis window was set to 400 ms from the onset of the translation and the corresponding data from the perturbed trials for each phase and direction was selected. The 100 ms EMG data before the onset of the translation (background muscle activity) was used as control data. The ensemble-average of 100 ms background EMG activity was estimated for each trial and was subtracted from the corresponding perturbed data The IEMG was calculated for the same two epochs, E_1 (80-250ms) and E_2 (250-400ms). Then, for each subject, mean, standard deviation, and 95% CI of the IEMGs for the perturbed cycles were calculated.

The EMG onset latency of each muscle for each subject was manually measured using the AxoScope software (Axon Instruments Inc.). The latencies were not measured in dynamic conditions because it was difficult to differentiate them from the varying levels of background EMG activities. It was observed that the responses adapt rapidly in the static conditions. Therefore, only the onset latencies of the first two or three trials of the static passive conditions, if a response was present, in each subject were measured. The criterion was that if the EMG activity after perturbation rose more than 2 standard deviations above the background activity and continued for at least 20 ms, that point is considered to be the onset of the response. In order to investigate the habituation behaviour in the observed responses, *adaptation plots* for each subject in each specific direction and phase were created. The plots display the IEMG value versus the trial number. If any adaptive attenuation happens, with increment of the trial numbers, decrement in the IEMGs will be observed.

3.8.3 Statistical Analysis

The experiment design is a partial three-way repeated measure design. There are three factors (independent variables). The first factor is the pedalling *Condition* which has four levels of DA, DP, SA, and SP. The second factor is the *Phase* of the pedalling in which translation has been applied. It consists of four levels of 0°, 90°, 180°, and 270°. The third factor is the translation *Direction* which has two levels of Left and Right. However, the SA factor is only measured at 0°, in which the Soleus muscle is active, and makes the experiment a partial three-way design. Table 3-1 illustrates the factors and their levels in this experimental design.

Table 3-1: The experimental design of the study (L=Leftward and R=Rightward translation).

Conditions:	**DA**								**DP**								**SA**		**SP**							
Phases:	**0°**		**90°**		**180°**		**270°**		**0°**		**90°**		**180°**		**270°**		**0°**		**0°**		**90°**		**180°**		**270°**	
Directions:	**L**	**R**	**L**	**R**	**L**	**R**	**L**	**R**	**L**	**R**	**L**	**R**	**L**	**R**	**L**	**R**	**L**	**R**	**L**	**R**	**L**	**R**	**L**	**R**	**L**	**R**
Subject 1																										
Subject 2																										
...																										
Subject n																										

The cells in Table 3-1 are filled with the calculated IEMGs (the dependent variable) for each subject. The *Mixed Model*, one of the generalized methods of analysis of variance (ANOVA), has been used for statistical analysis of this experiment. The mixed model provides the flexibility to handle not only the mean of a response variable, but also its variability as well. It models the repeated measurements and considers both fixed and random effects.

The statistical analyses were performed for each of the six muscles under study – TFL, BF, VL, MG, SOL, TA– in the two IEMG epochs of E_1 and E_2. In total, 12 statistical analyses were performed. In all of them, the IEMG was modeled to be the function of the three factors and their interactions (full factorial design). Therefore, the analyses tested the significance of *Condition*, *Phase*, *Direction*, *Condition*Phase*, *Condition*Direction*, *Phase*Direction*, and *Condition*Phase*Direction* treatments.

If significant, a Bonferroni t test post-hoc analysis was performed after by using pair-wise comparisons of the selected levels of the main effects. The Bonferroni method adjusts the observed significance level ($\alpha = 5\%$) for the fact that multiple comparisons are made when several Student's t statistic are used. All the reported effects in the following sections are based on $P<0.05$ and the corresponding adjusted value for the number of comparisons in post-hoc analysis.

4 Results

In the following, the results are categorized based on the experimental condition, i.e. DA, DP, SA, and SP, and then followed by general results. It should be noted that, *LT* translations refer to right to left translations whereas the movement in *RT* translations are from left to right. Initial analysis of the data showed no gender differences in the results and therefore all data were pooled together. Also, the ankle angle data did not provide any additional information due to the translations and therefore were excluded from the results. As the force data was highly contaminated with noise, it was not used in the results analysis. The accelerometer data were used for determination of translation direction. Because further analysis of accelerometer data was beyond the scope of this project, it was also left out of the results.

4.1 Results of the Dynamic Active Condition

4.1.1 Muscle Activity Patterns in Unperturbed Cycles

During the analysis of the DA condition, it became obvious that the muscle activity pattern during cycling is subject-dependent and inter-subject variations in the muscle activity patterns exist. However, the general pattern for all subjects has been the same. To better illustrate this, the mean and 95% CI of non-perturbed cycles, which are normalized in duration and amplitude, for two of the participants are shown in Figure 4-1. The general pattern of muscle activation during cycling is described in the following.

The uniarticular Soleus muscle, an ankle extensor, and biarticular Gastrocnemius, a knee flexor and ankle extensor, are greatly active during the power generation phase in which their activity commences in the midway of 270° to 0° and continues to the 90° (in some subjects slightly after that). Another lower leg muscle, the uniarticular

Tibialis Anterior, an ankle dorsiflexor which is antagonistic to the triceps surae muscle group (SOL and MG), is activated in the recovery phase from around 180° to 270°. From the upper leg muscles, Biceps Femoris (short head), as an unarticular knee flexor, is activated midway between 0° and 90° and its activity extends to the end of the propulsion-recovery (PR) transient phase. It turns off in the recovery phase and starts slight activity in the recovery-propulsion (RP) transition phase. Vastus Lateralis, another thigh muscle which is a uniarticular knee extensor, initiates its activity in the RP transition phase and terminates slightly before the midway of 0° to 90°. Tensor Fascia Latae, the only muscle chosen from the hip muscle groups, acts as a hip flexor and thigh abductor. The activity of the TFL muscle is between 90° and 270°, which comprise the PR transient and recovery phases.

4.1.2 Effects of Translation on Muscle Activation Patterns in the DA Condition

Figure 4-2 and Figure 4-3 displays the ensemble-average of the perturbed trials following RT and LT translations, respectively, in all four phases of the pedalling. Each one of the panels shows 400 ms EMG activity following the onset of perturbation. The displayed control cycles in the figures are slightly different from those shown in Figure 4-1 in such a way that their duration is the original duration and is not scaled like the normalized ones in Figure 4-1.

Each row is representative of one of the six muscles, while each column is the phase of the pedaling cycle where the translation was applied. The translation instant is exactly displayed at the zero ms time in each panel. In both figures, the thin black line and its two surrounding black dashed lines are the mean and the 95% CI of the control cycles, respectively. In the following figures, the thick red line and its two surrounding thinner lines are the mean and the 95% CI of the RT perturbed cycles, while the green ones are those of the LT perturbed cycles.

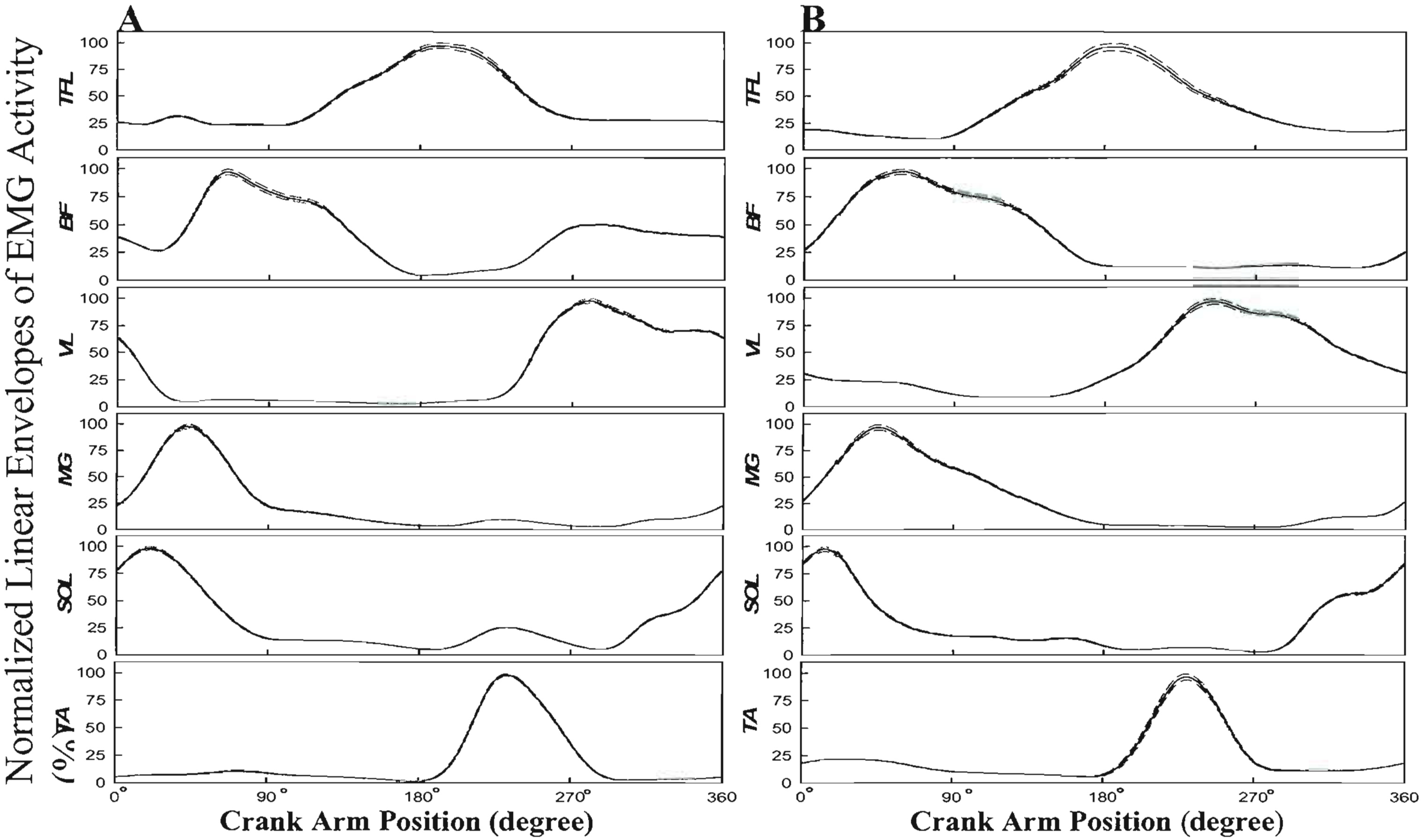

Figure 4-1: Dynamic Active Condition: the ensemble-average of linear envelopes of EMG data of the six muscles for the unperturbed (control) cycles in subject #11 (A) and subject #4 (B). Inter-subject variation in the EMG activation patterns is clear. The 95% CIs are shown by the dashed lines. The muscles from top to bottom are Tensor Fascia Latae (TFL), Biceps Femoris (BF) short head, Vastus Lateralis (VL), Medial Gastrocnemius (MG), Soleus (SOL), and Tibialis Anterior (TA). The EMG data are normalized in duration (0-360°) and in amplitude (maximum value of 95%CI).

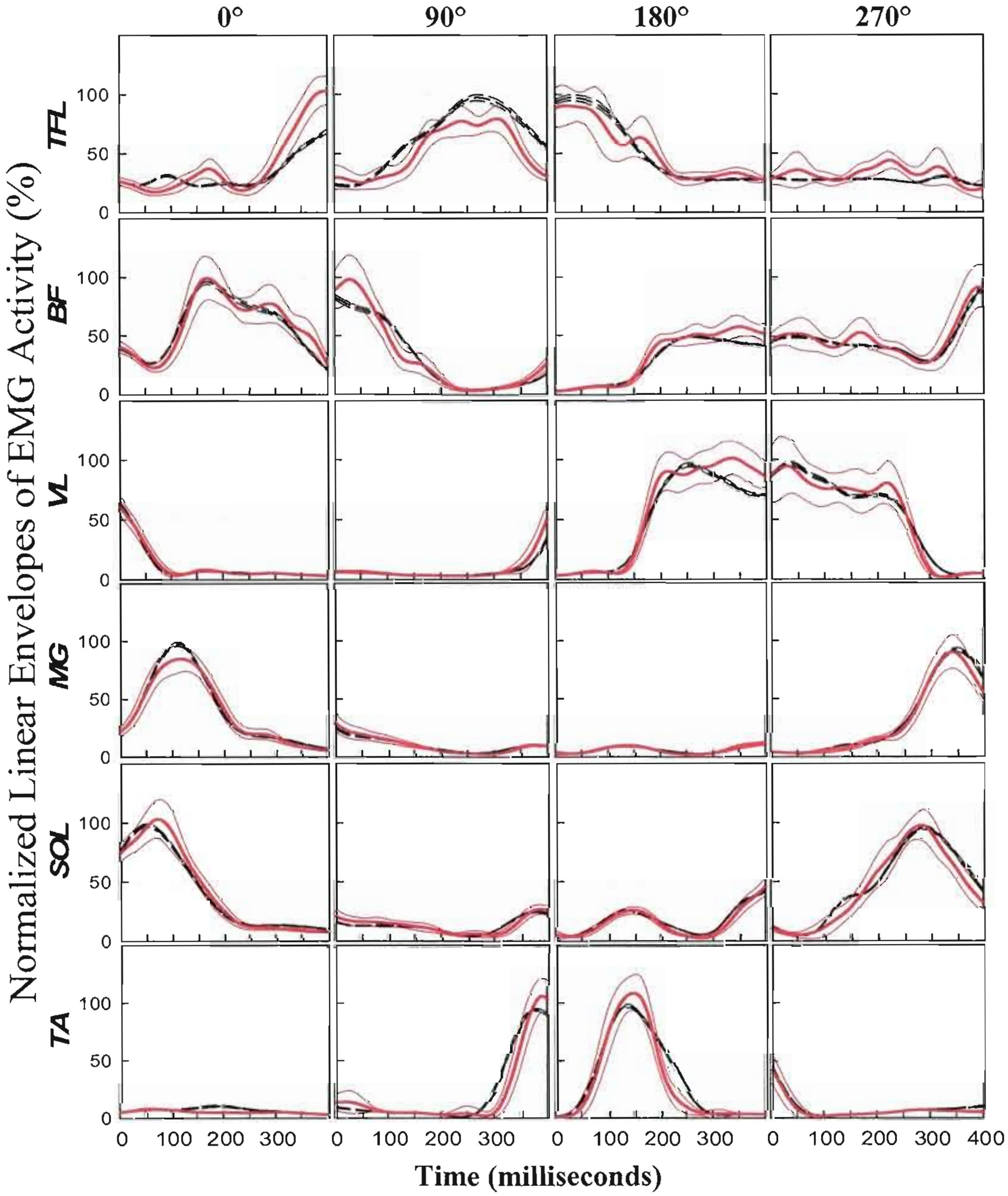

Figure 4-2: Changes in the muscle activation patterns of the six muscles under study after *RT* translations in the DA condition in subject #11. The 400 ms window time was used for the analysis. Each row is representative of one of the six muscles. The phase of the pedaling, in which the translation has been applied, is written on top of each column and corresponds to the zero ms in each panel. The mean and the 95% CI of the control cycles are shown by dashed lines while those of the RT perturbed cycles are shown by thicker solid lines.

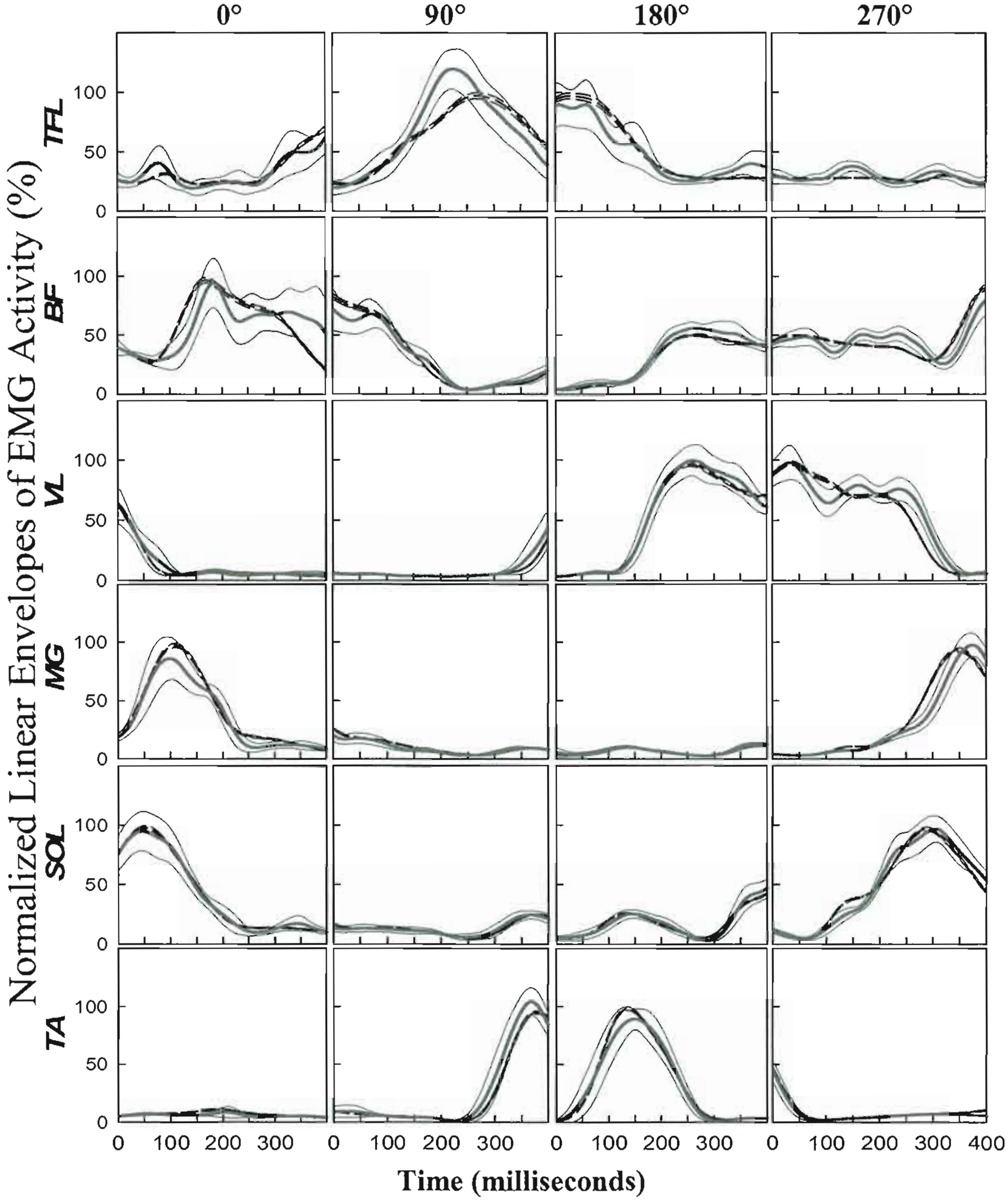

Figure 4-3: Changes in the muscle activation patterns of the six muscles under study after *LT* translations in the DA condition in subject #11. The 400 ms window time was used for the analysis. Each row is representative of one of the six muscles. The phase of the pedaling, in which the translation has been applied, is written on top of each column and corresponds to the zero ms in each panel. The mean and the 95% CI of the control cycles are shown by dashed lines while those of the LT perturbed cycles are shown by thicker solid lines.

Similar to the inter-subject variability observed in the control trials (e.g. Figure 4-1 *A* and *B*), the responses due to the translations have shown inter-subject variability as well. To reduce theses variabilities, the calculated integrated EMG (IEMG) data of the perturbed cycles were subtracted from those of the control cycles for each subject. The calculated *response IEMGs* of the subjects were then pooled together. Figure 4-4 displays the quantification of the EMG adjustments elicited by the linear medio-lateral translations during the dynamic active condition for the group of subjects. The left panels are the response IEMGs of the E_1 (80-250 ms after the onset of translation) and the right panels are those of the E_2 (250-400 ms after the onset of translation).

During the DA condition, the results evidently suggest that the TFL muscle shows strong modulation to the translation. The responses in the E_1 (medium and long-latency responses), are only significantly[1] elicited in the 90° phase of pedalling. The LT translation had excitatory effects on the TFL activity while the RT caused inhibition of the TFL activity. One should keep in mind that as the movement is in progress, the 90° phase of translation means that the responses are not solely observed at that 90° position. In the case of translations at 90°, the E_1 responses, which have a latency of 80-250 ms after the translation, occur when the crank arm position is somewhere between 120°-180° phase of the pedalling cycle.

The responses in E_2 (i.e. 250-400 ms after the onset of the translation) have similar effects; E_2 in the case of 90° translation phase corresponds approximately to the crank arm position at 180°-235°.

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[1] The results of the statistical analysis are shown in Appendix B: Statistical Analysis Results.

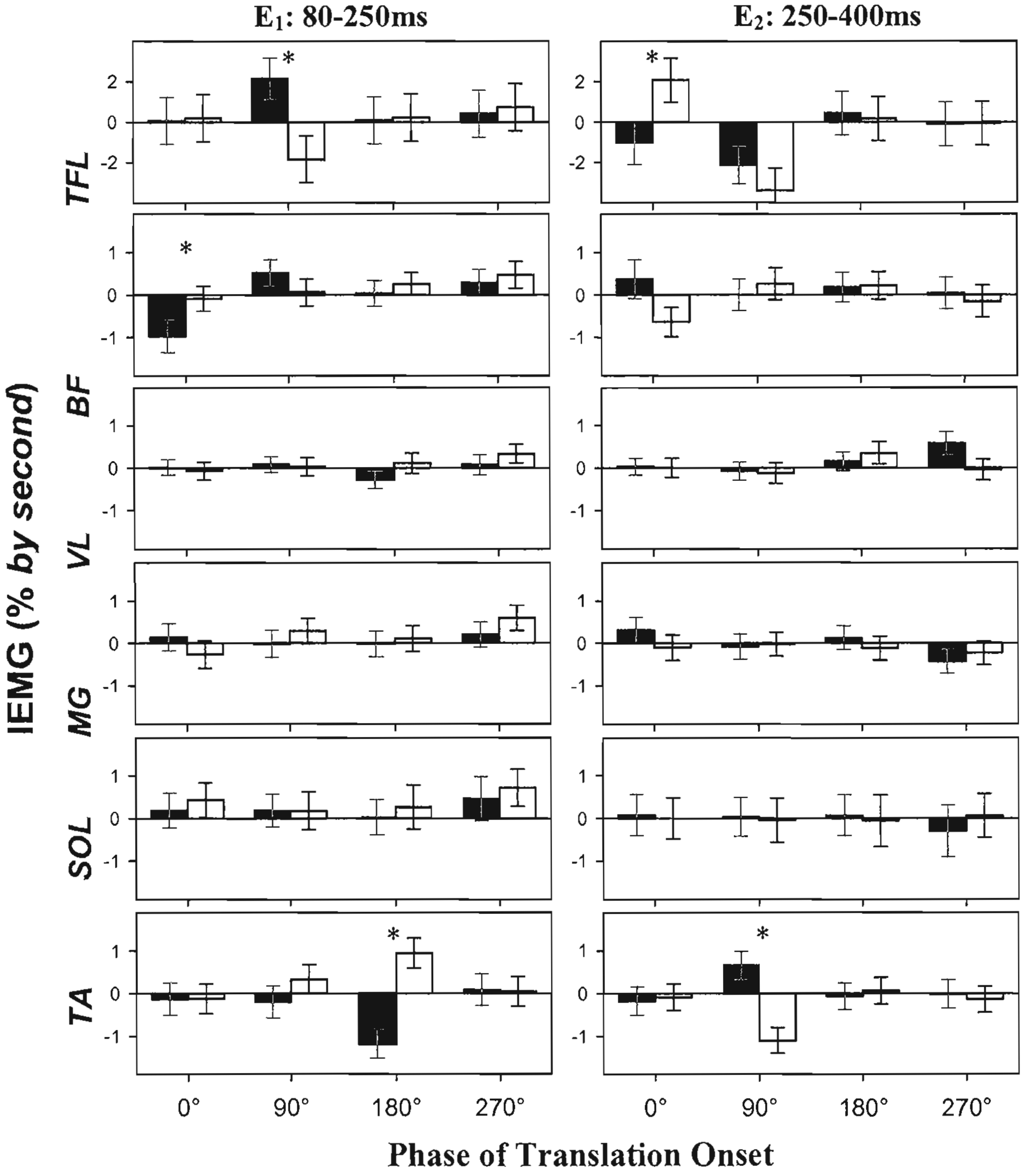


Figure 4-4: Response IEMGs during the Dynamic Active condition in the four phases of the pedaling task. The left panels are the measurements of the EMG modulations using 80-250 ms IEMGs (E_1) and the right panels are those of 250-400 ms IEMGs (E_2). The mean of response IEMGs of the LT translations are shown by filled black bars while those of the RT translations are displayed by white bars. The 95% CIs are displayed by crossed lines. Significant differences between responses of LT and RT translations are marked by asterisks.

In the E_2, which includes a voluntary component, strong modulations are also present. The modulations due to the translation at 90° phase of pedaling continued into the voluntary response region. The excitatory effects at the E_1 due to the left translation changed to inhibitory ones in the E_2. However, the inhibitory effects of the RT translation over TFL activity at the E_1 continued to the E_2 and were in fact reinforced. The RT translation at 0° phase of pedaling has increased the TFL muscle activity in the second epoch, while the LT translation did not impose any significant effects over the TFL.

The BF, VL, MG, and SOL muscles all showed excitatory modulations during RT translations at 270° phase of pedaling in its first epoch. However, the differences were not significant for the second epoch. Other significant responses are seen in the TA muscle. During the 180° phase of pedalling, left- and right-ward translations caused inhibitory and excitatory responses on the TA in the E_1, respectively. However, this pattern is reversed in the 90° phase of pedalling in the E_2 of the TA. In the BF muscle, the LT translation at 0° inhibited the activity in the E_1, while it excited the activity in the E_2. Also, the VL muscle was more excited during the second epoch after LT translation at 270°.

The muscles have either not shown any significant modulations or have shown only minor changes in response to the translations in the rest of direction-phase combinations.

4.1.3 Effects of Translation on Cycle Duration

To investigate the effects of translation on the kinematics of the movement, two different analyses were performed over the cycle duration: analysis of the cycle durations before and after the translations and their coefficient of variations, and analysis of the quarter cycle durations before and after the translations. They are called *full cycle duration analysis* and *quarter cycle duration analysis*, respectively.

4.1.3.1 Full Cycle Duration Analysis

Cycle durations in four consecutive cycles were used in this analysis: the durations of the first cycle before (C_b), the cycle during (C_d), the first cycle after (C_1) and the second cycle after (C_2) the selected translated. The durations of C_d, C_1, and C_2 were normalized to the duration of C_b. In this way, the variations in cycle duration during the DA condition would be reduced. The mean, standard deviation, and 95% CI for the trials were then calculated. Obviously, due to the normalization, the duration of C_b was 100% in each trial and the mean would be the same. Figure 4-5 displays the results of pooling all subjects' cycle duration data together.

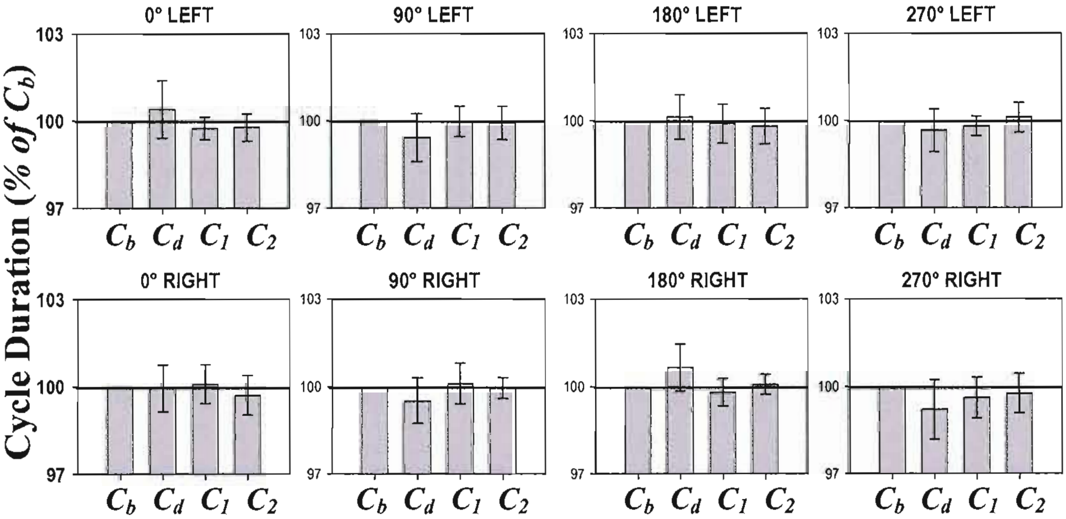


Figure 4-5: Full Cycle Duration Analysis of all subjects. C_d is the perturbed cycle. The phase and direction of the perturbation is written at the top of each panel. C_b, C_1, and C_2 are the cycle before, the first cycle after, and the second cycle after the translation, respectively. In each panel, the durations are normalized based on the C_b, which is considered to be the control trial. The vertical bars are the means and the error bars are the 95% CI. The total number of the translated cycles of all subjects that are used is equal to 1068 translations.

Figure 4-5 strongly suggests that the medio-lateral translations do not have any significant influence over the full cycle durations. In other words, the linear left- and right-ward translations do not alter the speed of the cycling. The cycle duration analysis in each subject also confirmed that; none of the subjects' cycle duration was significantly altered. Furthermore, the coefficient of variation analysis of each subject revealed that there is no significant difference between the COV of the perturbed cycles and their adjacent cycles. The COV analysis plots of the two subjects with the lowest and highest COVs are displayed in Figure 4-6 and Figure 4-7.

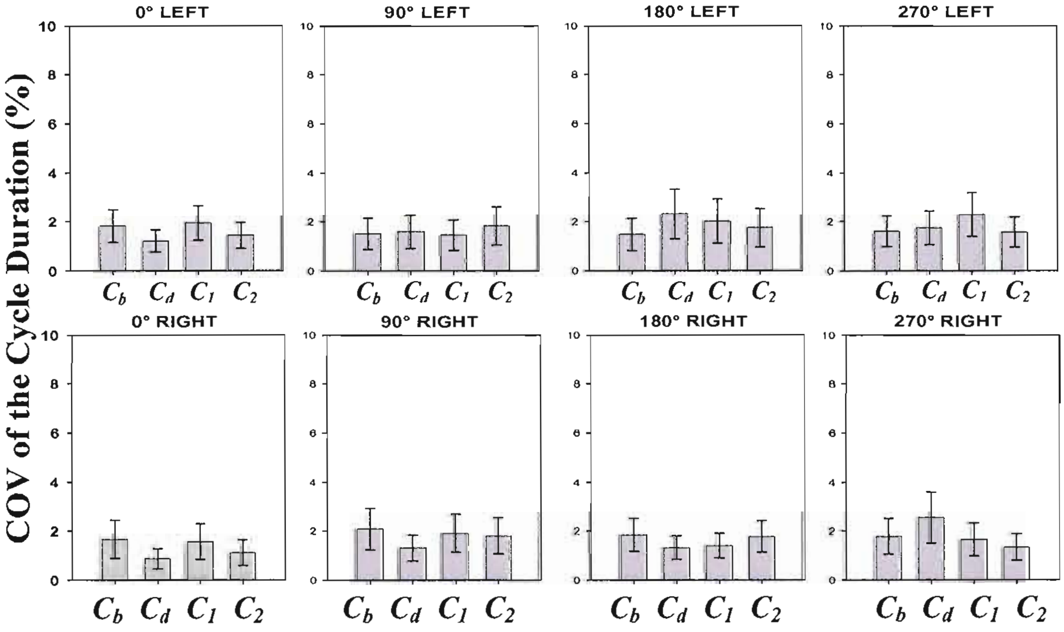


Figure 4-6: The lowest coefficient of variation of the cycle durations among the subjects was observed in subject #10. Refer to Figure 4-5 for the labels.

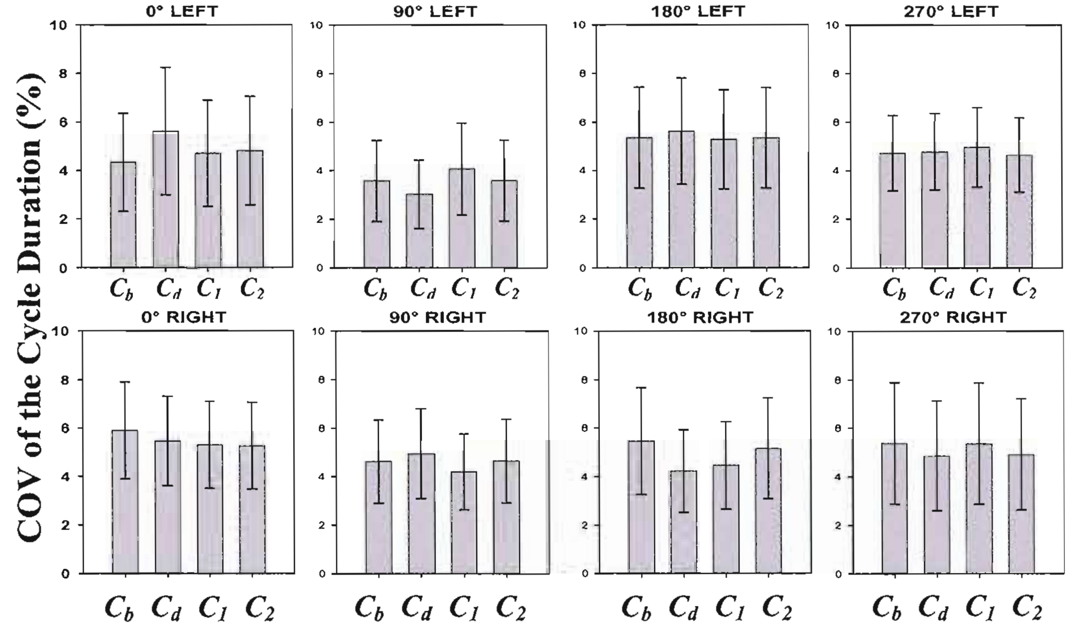


Figure 4-7: The highest coefficient of variation of the cycle durations among the subjects was observed in subject #12. Refer to Figure 4-5 for the labels.

4.1.3.1.1 Full Cycle Duration Analysis of the First Translated Trials

The analysis of the static conditions, explained in further details in section 4.4.2, revealed that the EMG adjustments were attenuated as the number of trials increased. Therefore, in the DA condition, the cycle durations of the early trials of the subjects were studied; it allows to investigate whether DA responses also experienced response attenuation. This can be inferred if the early trials show different cycle duration modulations than the pooled data of all cycles, which is presented in section 4.1.3.1. The full cycle duration analysis of all trials revealed that no difference can be observed in the perturbed trials. However, the cycle duration analysis of the first disturbed trials revealed that this is not the case. Except for two subjects that had started with two static passive translation tests before the start of the DA condition test, the duration of the translated cycles was less than the two neighbouring cycles in all subjects. Figure 4-8 presents the mean and 95% CI of the difference between cycle duration of the two early translated trials with their preceding and following unperturbed cycles. The graph implies that the cycle durations of the early translated trials (C_d) are lower than their first cycle before (C_b), first cycle after (C_1) and second cycle after (C_2). In other words, in the early translated trials, subjects sped up (cycle duration was reduced by 36 ms on average) when the translation was applied, but recovered in the cycle following the translation.

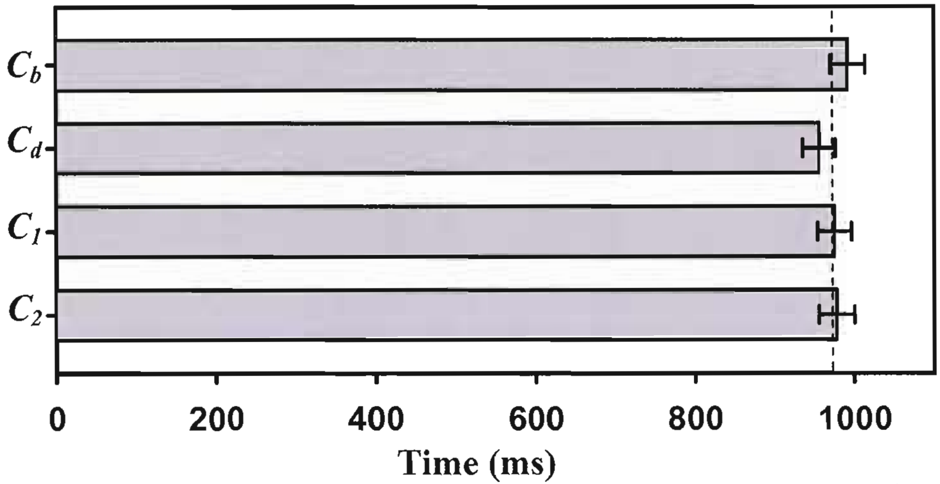


Figure 4-8: The difference in the cycle duration of the (two) early translated trials with the preceding and following cycles. The mean (shown by bars) and 95% CI (shown by lines crossing the bars) of the pooled data from the subjects are shown. The dashed line represents the mean of the first cycle before (C_b) and can be used for the comparison.

4.1.3.2 Quarter Cycle Duration Analysis

Since there was little change in the full cycle durations it was felt that perhaps the changes occurred within the translated cycle itself. Thus, in this part, the analysis focused on within the perturbed cycle in such a way that each perturbed cycle was broken into quarter cycles. Refer to section 3.8.1 for more information regarding the analysis steps performed in this task. Figure 4-9 displays the results of this analysis.

An important point that can be extracted from the results is that there are couplings between left- and right-ward translations in different phases. In the LT translation at 0° (called 0° left) situation, the first quarter instantly after the translation (0°-90°) has not shown any significant difference with the corresponding control quarters. The next quarter (90°-180°) also has been the same. However, the 180°-270° shows significant reduction in cycle duration compared to the control quarters. This pattern can be seen at 180° right and therefore there is a pattern coupling between 0° left and 180° right. The rest of the panels follow this coupling property. In the 90° left, the durations of the translation quarter and the one after were significantly reduced, while the duration of the third quarter has increased. This pattern is the same as the 270° right. In the 180° left and the 0° right coupling, no significant changes in quarter cycles duration are observed. In the 270° left and 90° right coupling, only the second quarter after the translation has shown significant reduction in duration.

4.2 Results of the Dynamic Passive Condition

4.2.1 Muscle Activity Patterns in Unperturbed Cycles

There were technical problems during the course of the dynamic passive condition, therefore the data could be collected on only four subjects. The main reason was that the servomotor was programmed to mimic the exact trajectory of the DA condition. Therefore, if small involuntary resistances caused a lag in the phase of the planned trajectory, the feedback controller of the servomotor tried to reach the original trajectory. This caused an irregular and broken trajectory, which further caused involuntary resistance or pushing by subjects. In the four subjects who performed the DP condition well, either they were able to completely relax their muscles or they followed the trajectory but with approximately half of the muscle activity needed during dynamic active condition. To some extent, the muscle activity pattern during cycling was subject-dependent. Figure 4-10 displays, for one the subjects who performed the DP successfully, the mean and 95% CI of non-perturbed cycles, which are normalized in duration and amplitude.

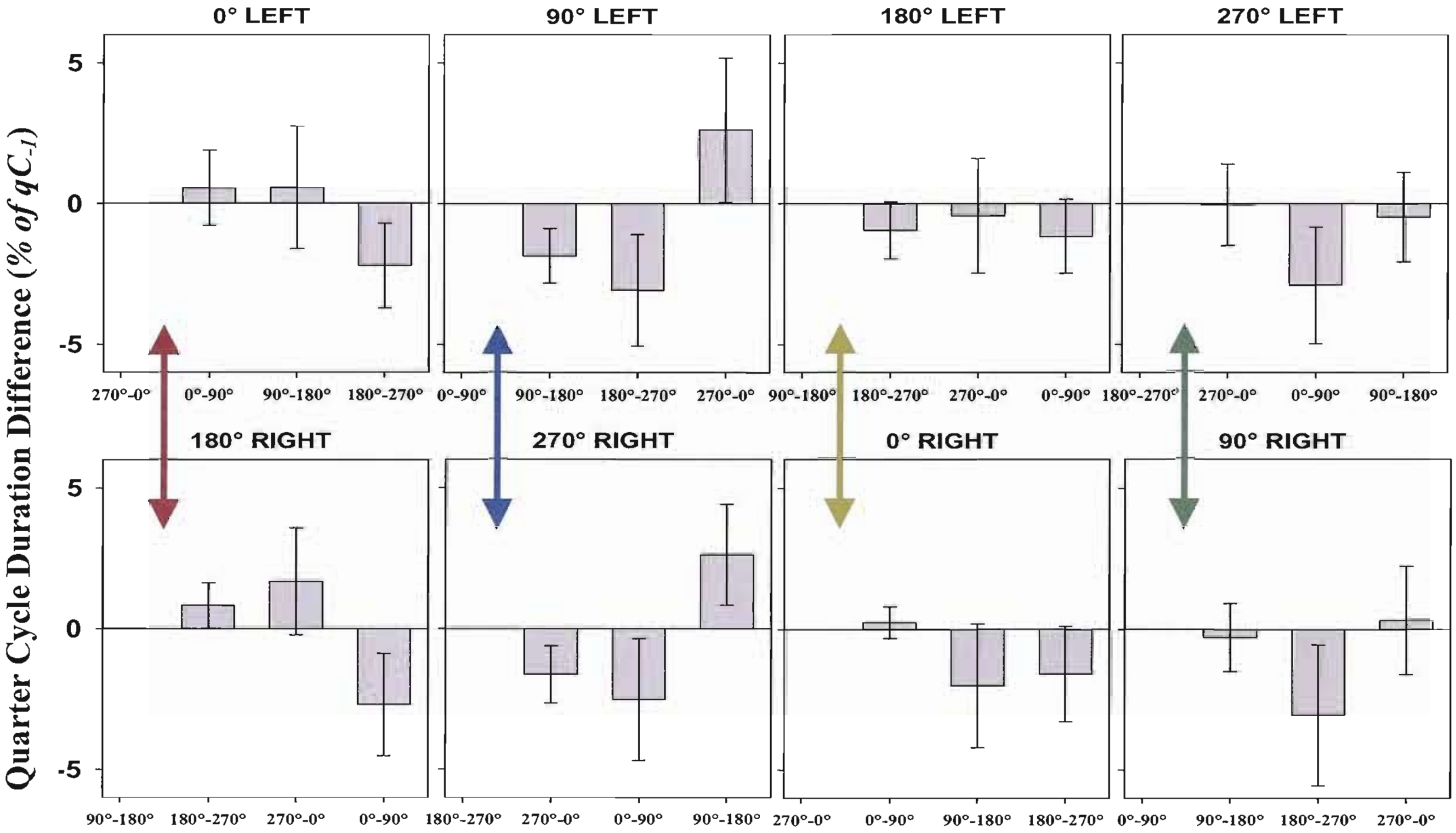


Figure 4-9: Quarter Cycle Duration Analysis. The phase and direction of the perturbation is written at the top of each panel. Note that the patterns are coupled (shown by arrows): 0° left-180° right, 90° left-270° right, 180° left-0° right, and 270° left-90° right.

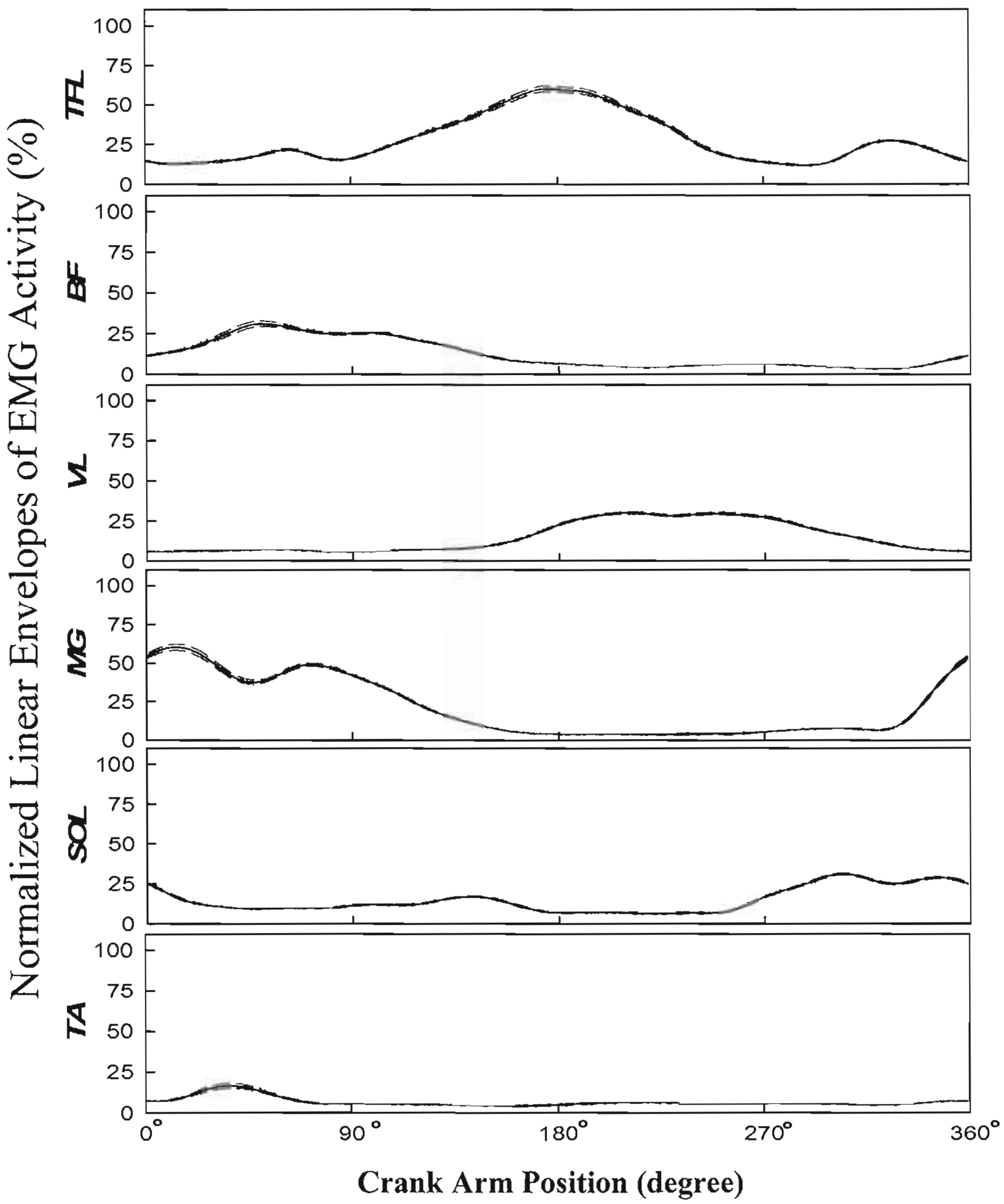


Figure 4-10: Dynamic Passive Condition: the ensemble-average of linear envelopes of EMG data of the six muscles for the unperturbed (control) cycles in subject #4. The 95% CIs are shown by the dashed lines. The subject was able to reduce the muscle activity of BF, VL, SOL, and TA in DP condition to less than 30% of the DA condition, while this amount for TFL and MG was less than 60%.

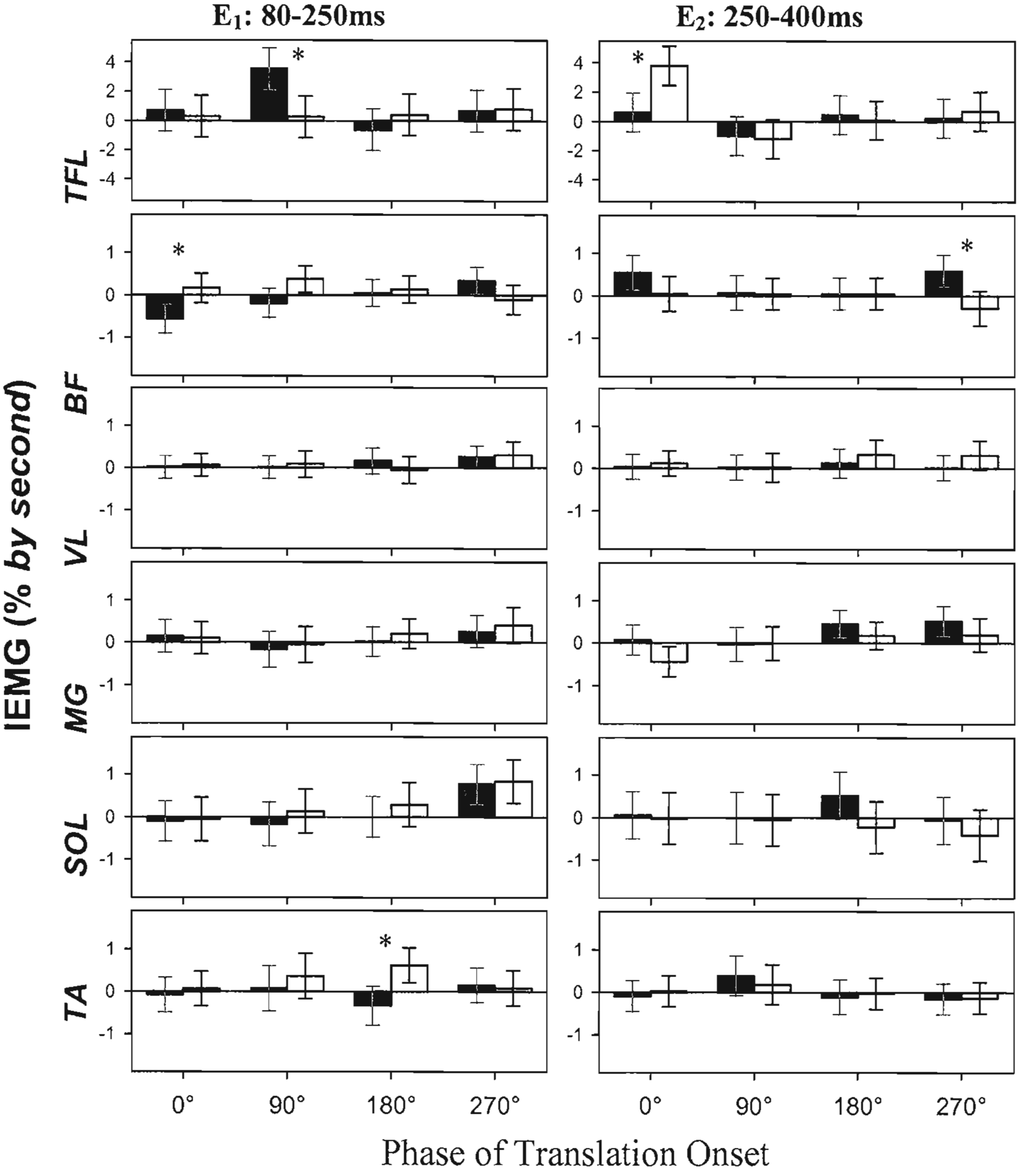
4.2.2 Effects of Translation on Muscle Activation Patterns in the DP Condition

Similarly to the procedure performed for the DA condition, the IEMGs of perturbed cycles were subtracted from those of control cycles for each subject. Then, the *response IEMGs* for the subjects were pooled together. The results are shown in Figure 4-11. The left panels are the response IEMGs of the E_1 and the right panels are those of the E_2. As mentioned previously, all data of each muscle are normalized to the normalization factor obtained in the DA condition.

As can be seen in Figure 4-11, the TFL muscle shows strong modulation to the translation during the DP condition. The elicited responses in the E_1 were only significant in the 90° phase of pedalling when LT translation was applied. It had excitatory effects on the TFL activity while the RT translation did not elicit any significant TFL response in this phase. In the E_2, strong excitatory modulations of the TFL due to the RT translation at the 0° phase of pedalling were observed.

The VL, MG, and SOL muscles have shown excitatory modulations during RT translations at the 270° phase of pedaling in the E_1. The SOL muscle was also excited by the LT translation at this phase in the E_1. Other significant responses are seen in the TA and BF muscles. During the 180° phase of pedalling, RT translation caused excitatory responses on the TA in the E_1. In the BF muscle, the LT translation at 0° resulted in an inhibition in the E_1, while an excitation in the E_2.

The muscles have either not shown any significant modulations or have shown only minor changes in response to the translations in the rest of direction-phase combinations.



E_1: 80-250ms

E_2: 250-400ms

Figure 4-11: Response IEMGs during the Dynamic Passive condition in the four phases of the pedaling task. The left panels are the measurements of the EMG modulations using 80-250 ms IEMGs (E_1) and the right panels are those of 250-400 ms IEMGs (E_2). The mean of response IEMGs of the LT translations are shown by filled black bars while those of the RT translations are displayed by white bars. The 95% CIs are displayed by crossed lines. Significant differences between responses of LT and RT translations are marked by asterisks.

4.3 Results of the Static Active Condition

4.3.1 Effects of Translation on Muscle Activation Patterns in the SA Condition

In the static active condition, the activity of the soleus muscle was supposed to be matched with its corresponding muscle activity level in the dynamic active condition. However, as the soleus muscle of all subjects was active only at the 0° phase of pedalling, the SA condition has been tested in this phase for all subjects. In the rest of the phases, i.e. 90°, 180°, and 270°, the activity level of the soleus was low and the condition was the same as static passive. The activity level of the soleus muscle in the four phases of the experiment can be seen in Figure 4-1.

The EMG of each muscle after perturbation was subtracted from the background EMG. Then the IEMG of this difference was calculated. Afterward, the *response IEMGs* of the subjects were pooled together for each muscle. Figure 4-12 displays the quantification of the EMG adjustments elicited by medio-lateral linear translations in terms of response IEMGs during static active condition for the group of subjects.

Similarly to the dynamic conditions, the TFL muscle has shown strong modulation in response to the translation. The RT translation has shown significant excitatory effect on the TFL activity in the first epoch, while the LT translation caused excitatory effect in the second epoch. The BF muscle was excited by both left- and right-ward translations in the E_2. The MG and SOL muscles showed excitatory responses to the LT translation in the E_1. In addition, the SOL muscle has shown excitatory response to the RT translation in the first epoch. No other significant results were observed in the SA condition following the translation.

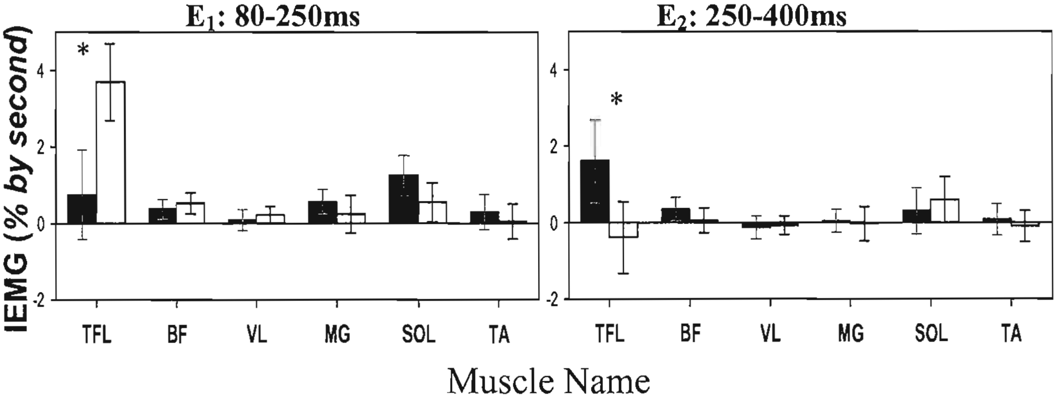


Figure 4-12: Response IEMGs of the six muscles used in the study during the Static Active condition in the 0° crank arm position. The level of the activity has been matched with the dynamic active condition at the 0° phase. The activity of the soleus muscle in other phases has been low, so they were not measured during SA condition. The left panels are the measurements of the EMG modulations using 80-250 ms IEMGs (E_1) and the right panels are those of 250-400 ms IEMGs (E_2). The mean of response IEMGs of the LT translations are shown by filled black bars while those of the RT translations are displayed by white bars. The 95% CIs are displayed by crossed lines. Significant differences between responses of LT and RT translations are marked by asterisks.

4.4 Results of the Static Passive Condition

4.4.1 Effects of Translation on Muscle Activation Patterns in SP Condition

In the static passive condition, the lower limbs of subjects were adjusted and firmly stabilized to one of the four pedalling positions, i.e. 0°, 90°, 180°, and 270°. Hence, no muscular effort was needed to retain a static configuration and subjects were asked to relax. However, in practice, some muscles were slightly active to hold the lower limbs in the static configuration. Similarly to the static active condition, the EMG of each muscle after translation was subtracted from its corresponding background EMG and the IEMG of this difference was calculated. Figure 4-13 displays the pooled *response IEMGs* of the subjects for each muscle after medio-lateral linear translations.

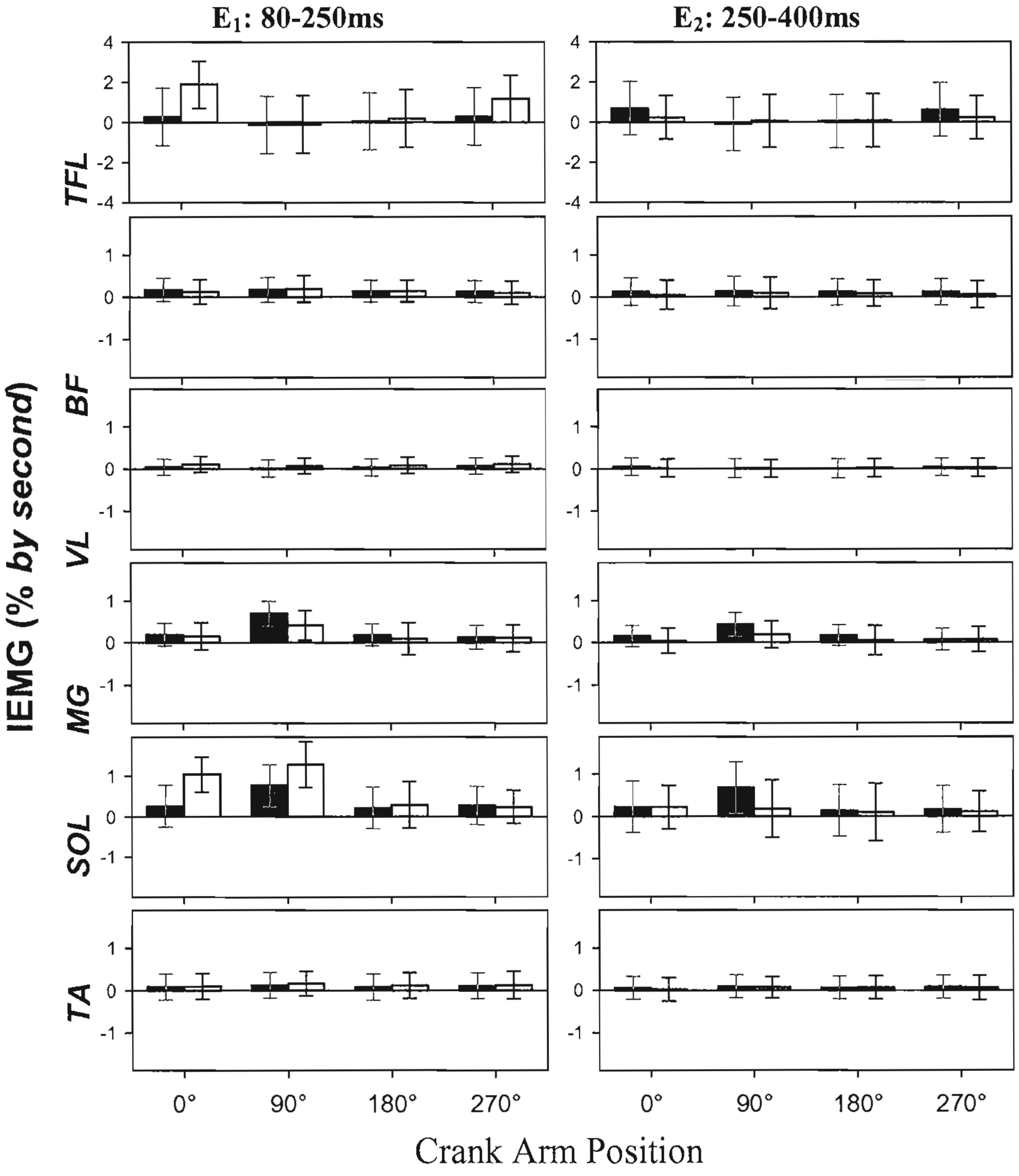


Figure 4-13: Response IEMGs during Static Passive condition in the four phases of the pedaling task. The left panels are the measurements of the EMG modulations using 80-250 ms IEMGs (E_1) and the right panels are those of 250-400 ms IEMGs (E_2). The mean of response IEMGs of the LT translations are shown by filled black bars while those of the RT translations are displayed by white bars. The 95% CIs are displayed by crossed lines.

At the 0° crank arm position, the RT translation in the static passive condition caused excitatory responses in the TFL and SOL muscles during 80-250 ms after the onset of translation. In SOL and MG muscle, at the 90° crank arm position, both LT and RT translations excited these muscles during E_1. The excitatory effect of LT translation at this phase continued to the second epoch for MG and SOL. The rest of muscle-phase combinations did not show any significant response to the translation.

4.4.2 Adaptation of EMG Adjustment Patterns in Static Conditions

As this study is a repeated measures design, in order to control and minimize the incidental influences due to the order of the study conditions, systematic counterbalancing have been used during the experiment. This has been described in details in section 3.3. In those situations where the subject started with a static passive condition or the static condition was in the second order, and the CNS responded to the translation (generally at SP-0° and SP-90°), we observed that with increasing the number of trials, the adjustment responses get more attenuated. Figure 4-14 displays the adaptive decrease of EMG modulations after repeated left- and right-ward translations in one of the subjects who started the experiment with static passive at 0°. In the figure, the abscissa represents the trial number and the ordinate represents the IEMG measure. The red filled triangles are the RT translations, while the green cross marks are the LT ones. The fast adaptation of the CNS in response to the translation during the E_1 is evident.

We were not able to quantify this in dynamic conditions, as the translations were applied pseudo-randomly at different phases (unlike the static conditions that the phase is constant in each stage of the experiment).

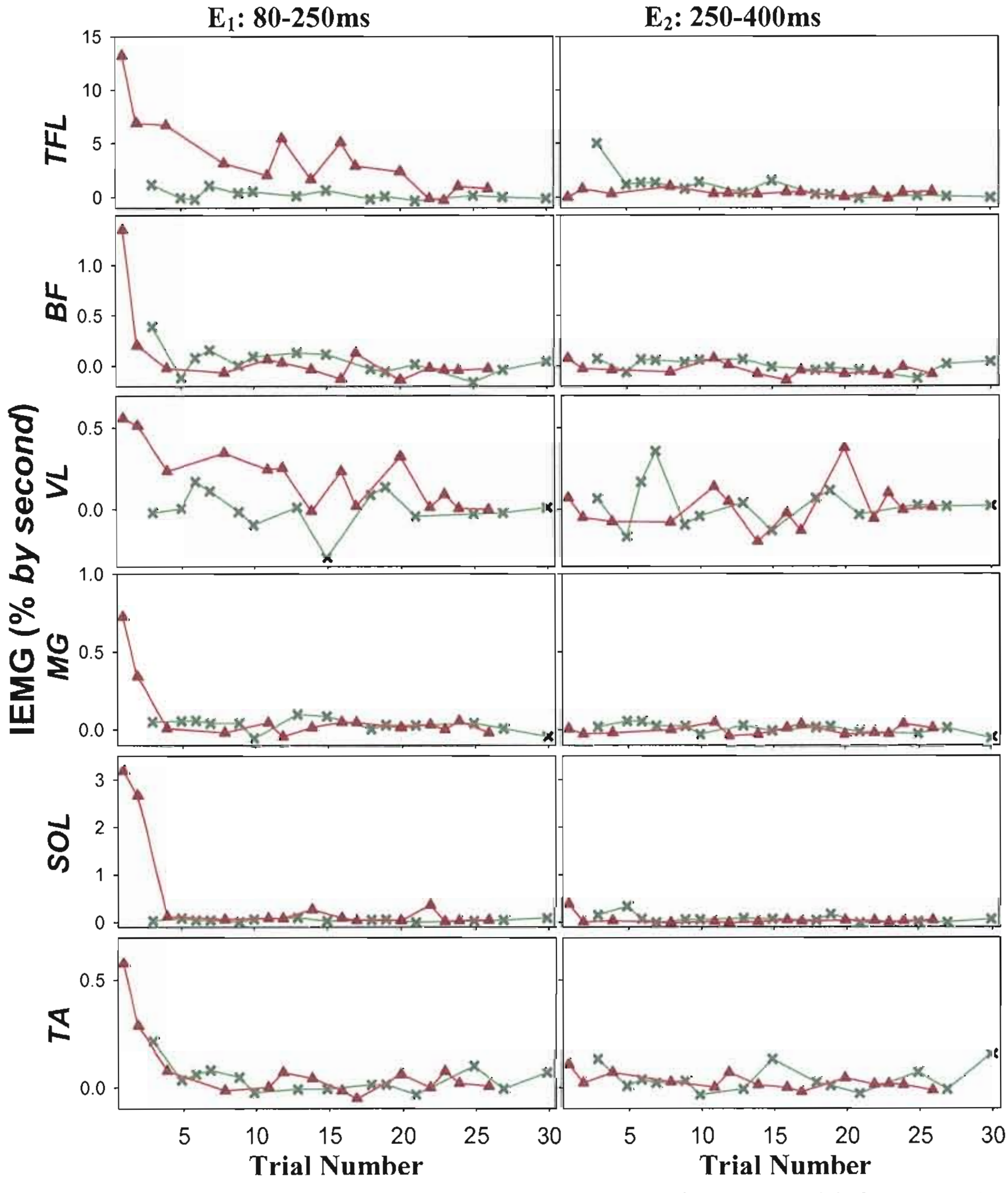


Figure 4-14: Adaptive attenuation of response IEMGs after repeated left- and right-ward translations in subject #11 during SP at 0°. The abscissa represents the trial orders and the ordinate represents the IEMG value of each muscle in the right leg in each trial. The left panels are the IEMGs at the E_1 and the right panels are the ones at the E_2. The RT trials are shown by lines with triangles while the LT ones are shown by lines with cross marks. The rapid habituation during the first epoch is evident in the plots.

4.4.3 Muscle Response Latencies

Since the responses were clearly distinguishable from the background EMG activity in the static passive condition, the latencies of the EMG adjustments could be measured. However, due to the fast adaptive attenuation of the responses, only the first two or three trials were used. Generally, in reaction to the applied translations, the evoked medium-latency responses were observed around 90-130 ms, whenever they were present. The long-latency responses were evoked around 160-200 ms after the onset of the translation. The temporal pattern of activation was variable between the subjects. While most of the time, the response delay time of the TA, SOL, MG were close to each other, the responses of the TFL, BF, and VL muscles sometimes started sooner, and other times later than the TA, SOL, MG muscles, without any specific pattern. Figure 4-15 displays the raw EMG data of the first responses of one of the subjects, recorded after applying RT translation while his right leg was positioned and fixed at the 0° crank arm position. The first six rows are the responses of the six muscles from the right leg to the RT translation. The seventh row is the accelerometer, sensitive to medio-lateral translations. The last row is the translation pulse, which indicates the onset of translation.

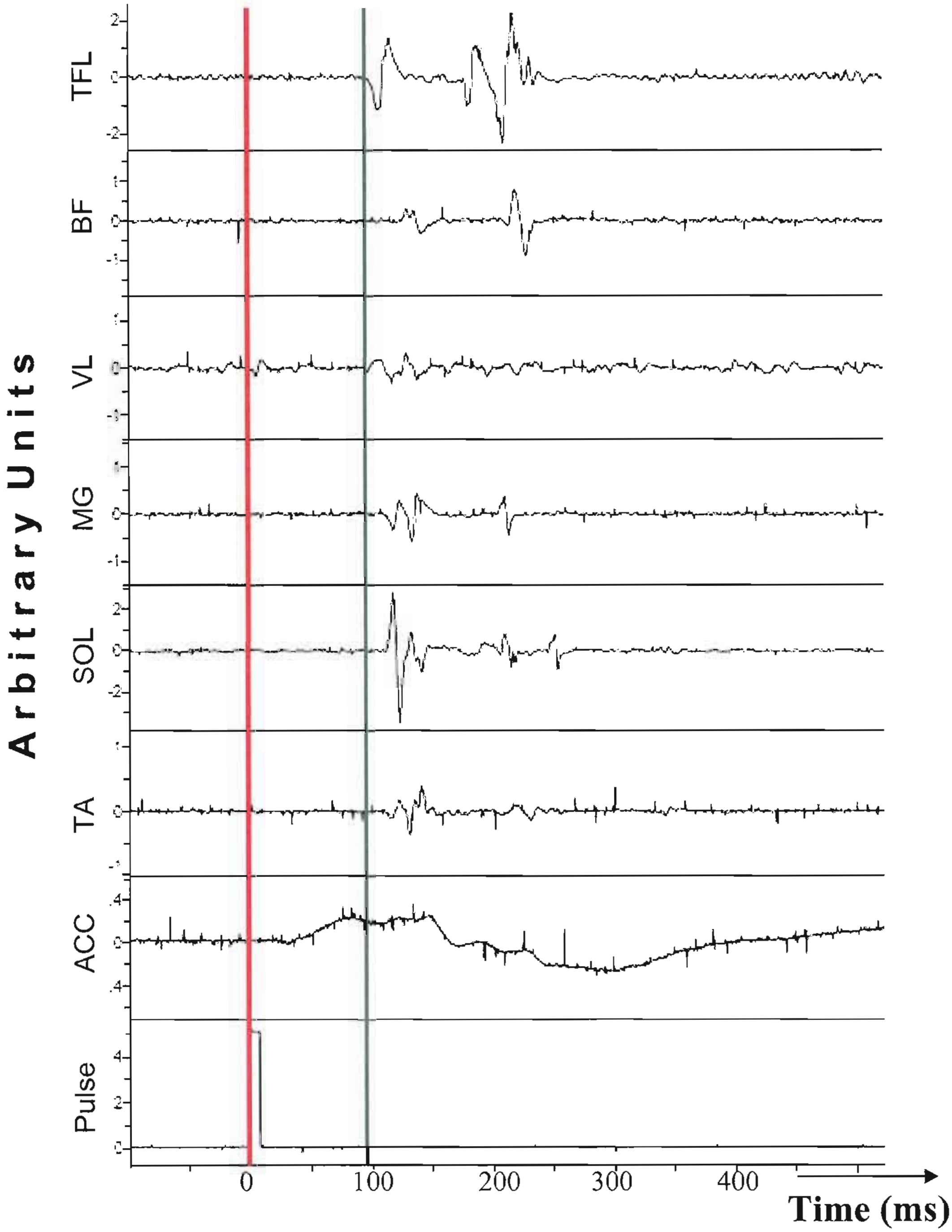


Figure 4-15: Raw EMG data of the first responses of participant #11 during RT translation at static passive 0°. The two distinct responses of the medium and long latency are evident. The left vertical line shows the onset of the translation, which is marked by 0 ms. The right vertical line shows the time when the first response is observed. The Y axes are in arbitrary unit.

4.5 Summary of Muscle Activity Modulation Patterns in response to Left- and Right-ward Translations

By summarizing the results, the adjustments of muscle activity patterns after the linear medio-lateral translations in different condition-direction-phase combinations can be investigated together. Table 4-1 summarizes the responses observed during this experiment, mentioned previously in sections 4.1.2, 4.2.2, 4.3.1, and 4.4.1.

Comparison of the TFL responses in different conditions reveals that during the DP condition, the excitatory responses are the same as those of the DA condition, while the inhibitory responses are absent. The maximum background EMG level of the TFL, situated at around the 180° phase of pedalling, was about half of its level during the DA (Figure 4-1 *B*, Figure 4-10), while the excitatory responses were slightly higher in the DP condition, although they were not statistically significant (Figure 4-4, Figure 4-11). In the BF muscle, the adjustment pattern has been the same in the DA and the DP, except at the Right-270° translation. VL, MG, and SOL followed the same excitation patterns after the RT translation at 270° in both the DP and the DA condition with almost the same response amplitude while their maximum background EMG was at least reduced to half in the DP condition. In the TA muscle, the RT translation at 180° had the same excitatory response amplitude.

Static conditions do not have any adjustment patterns similar to dynamic conditions. Also, the only common pattern between the SA and SP conditions is during the RT translation at the 0° phase in the SOL muscle, with the level of response two times higher in the SA condition than the SP condition.

Table 4-1: Summary of the EMG adjustments after the applied translations. The "E_1" and "E_2" are the abbreviations for Epoch-1 and Epoch-2, respectively. The letter "E" with dark shading stands for Excitation and "I" with light shading represents Inhibition. The empty cells are the situations where no significant modulatory effects have been observed after the translation.

Condition	Direction	Phase	Muscle											
			TFL		BF		VL		MG		SOL		TA	
			E_1	E_2	E_1	E_2	E_1	E_2	E_1	E_2	E_1	E_2	E_1	E_2
DA	Left	0°			I	E								
		90°	E	I										E
		180°											I	
		270°						E						
	Right	0°		E										
		90°	I	I										I
		180°											E	
		270°			E		E		E		E			
DP	Left	0°			I	E								
		90°	E											
		180°												
		270°									E			
	Right	0°		E										
		90°												
		180°											E	
		270°					E		E		E			
SA	Left	0°		E	E				E		E			
		90°	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
		180°	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
		270°	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
	Right	0°	E		E						E			
		90°	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
		180°	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
		270°	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
SP	Left	0°												
		90°							E	E	E	E		
		180°												
		270°												
	Right	0°	E								E			
		90°							E		E			
		180°												
		270°												

5 Discussion

5.1 Task-, Phase-, and Direction- dependency of the Responses

The intent of this study was to analyze and investigate the responses of the CNS during dynamic (rhythmic movement) and static conditions while the need for the balance control by the CNS is greatly minimized. The general hypothesis of this experiment was that applying medio-lateral translation evokes responses that are phase-, task-, and direction-dependent. Based on the results, summarized in Table B-1 of Appendix B: Statistical Analysis Results, this statement could be restated separately for each muscle. Our results suggest that after applying linear left- and right-ward translations during modified stationary cycling, the medium and long latency responses of the TFL, BF, and SOL are task-dependent (*condition*-dependent), those of the BF and VL are phase-dependent, and those of the TA are direction-dependent. However, the responses, due to the applied translations, of the TFL and MG are task-dependent, those of the TFL and VL are phase-dependent, and those of the BF and TA are direction-dependent.

If both E_1 and E_2 responses are considered together, then the results imply that applying linear left- and right-ward translations during modified stationary cycling evokes task- and phase-dependent responses in the TFL, task-, phase-, and direction-dependent responses in the BF, phase-dependent responses in the VL, task-dependent responses in the MG and SOL, and direction-dependent responses in the TA. These findings are in line with the findings of other researchers that states the EMG compensatory responses are phase-dependent (Capaday and Stein, 1986; Patla and Bélanger, 1987;) and task-dependent (Bélanger and Patla, 1987; Capaday and Stein, 1987).

However, this cannot be generalized as these results are only based on the main effects while significant interactions are present. The interactions suggest more complicated level of task-, phase-, and direction-dependency of the results. Though, as the simple effects –all combinations of the condition, phase, and direction for a translation– have been analyzed in the results section, all situations in the finest level of factorial combinations have been investigated.

5.2 Triggering Source of the Corrective Responses

Based on the results, we propose that during the static conditions in this specific experiment, the vestibular system plays a key role in generating adaptive responses. This seems to be in contrast to the findings of Forssberg and Hirschfeld (1994) that stated somatosensory signals are the triggering source in seated subjects. The reason for our claim regarding the triggering source is based on the medium latency response attenuation, observed in the static conditions. In the early trials, i.e. 1, 2, or 3, of the static passive condition, the responses in the E_1 consisted of the two distinctive responses; the first one is attributed to the medium latency (around 90-130 ms) and the second one to the long latency (around 160-200 ms) responses. The medium latency response diminishes very fast after the second or third trial; however the long latency responses, which are included in E_1, still exist (not shown separately). Except for the SOL and MG muscles, the long latency responses of the other muscles get attenuated with increasing number of trials. Based on the studies of Inglis et al. (1994), regarding the onset of EMG activities when somatosensory information are present or not, and Inglis et al. (1995), which revealed the vestibular system has a small effect on the short latency response while it has a large effect on the long latency response, it seems that in the early trials, the somatosensory information and vestibular information are used in generation of the responses. However, the CNS quickly adapts to the translations, because in contrast to the balance studies (Nahsner, 1977; Henry et al., 1998a, 1998b), where the EMG adjustments are essential for preventing the fall and recovering the balance, there is no threat to the stability of the body after the translation due to the experiment design.

In addition, Forssberg and Hirschfeld (1994) identified the origin of the somatosensory signals in their experiment and stated that somatosensory signals raised from pelvis rotation are the triggering source. Allum and Honneger (1998) came up with a similar conclusion in standing subjects in which they emphasized about the role of trunk rotation as the primary triggering source for balance correction during stance. In this experiment, the subjects are well attached to the modified ergocycle and the translation is applied to the whole platform. Therefore, the amount of rotation by pelvis is much lower than in the experiments by Forssberg and Hirschfeld (1994). As a result, our findings regarding the role of the vestibular system in the observed responses in Table 4-1 do not contrast others. Also, in the static passive condition, the excitation of the extensors is in line with the findings that stimulation of Deiters' nucleus evokes monosynaptic EPSPs mainly in soleus and gastrocnemius motoneurons, and polysynaptic EPSPs in most hindlimb extensor motoneurons (Wilson and Yoshida, 1969; Grillner et al., 1970). In addition, the CNS needs to regulate head stability in order to use the vestibular information for postural adjustments of the trunk and body (Allum et al., 1997). However, in this study the head is stabilized with strap and therefore the vestibular information can be faithfully used by the CNS.

During the dynamic conditions, based on the design of this experiment, we were not able to clearly distinguish which one of the sensory systems triggered and influenced the generation of the observed corrective responses.

5.3 Effects of Right and Left Leg Coupling during Cycling on Cycle Duration after Translation

During cycling, the right and left leg are coupled together with 180° phase lag. Although all the EMG measurements were from the right leg in this study, the coupling results observed in Figure 4-9 can be illustrated based on Table 4-1. During the LT translation at propulsion phase, while the right leg is at the 0° crank arm position, the left leg is situated at the 180° crank arm position. The LT translation at propulsion phase of the right leg is an ipsilateral translation at recovery phase of the left leg. Therefore, when analysing the muscle activity pattern of the right leg during propulsion phase with LT translation (0°-left), one can look at the muscle activity pattern at recovery phase with RT translation (180°-right) to investigate how the muscles of the left leg are responding to the translation. Hence, the results are coupled and seem similar in Figure 4-9.

During 0°-left and 180°-right, the first two quarters do not show any significant changes in the cycle duration. In Table 4-1, one can observe that this has happened because at the 0°-left, the BF inhibition-excitation patterns cancel each other out and the excitation of the TA at 180°-right does not have any influence on the power generation for speeding the cycling. The third quarter cycle, even though it has a significantly reduced cycle duration, can not be described by the EMG activity patterns in Table 4-1 as it is out of range of the E_1 and E_2 of the study. The significant reduction in the quarter cycle durations of the 90°-left may be due to non-significant excitation of the VL, MG, and SOL of the left leg (as can be seen at 270°-R in Table 4-1). During the 180°-left, inhibition in the TA of the right leg and excitation in the TFL of the left leg, and during the 0°-right excitation in the TFL of the right leg and inhibition in the TA of the left leg has happened, which did not have any effect on the cycle duration. The last couplings are 270°-left and 90°-right in which the second quarter after the translation has shown significant reduction. During 270°-left translation, the excitation of the VL of the right leg in the second epoch is the main reason for the significant reduction of the second quarter cycle duration. The inhibition of the TFL and TA in the left leg does not contribute to this process. The same process happens during 90°-right translation; however the VL of the left leg was excited and the TFL and TA of the right leg were inhibited.

5.4 Temporal Pattern and Magnitude of Muscles Recruitment

As mentioned in section 4.4.3, no specific recruiting patterns based on the response latencies have been observed in the static conditions. The latencies are roughly in the same range as those reported by Henry et al. (1998b) during lateral translation in the standing subjects. However, Henry et al. (1998b) found that the EMG pattern activation occurs with early proximal muscle activation, the TFL in this case, followed by the distal to proximal muscle activation pattern. This contrasting result can be explained by the fact that there are no threats to the stability as a subject is well secured in this study. The current experiment also restricts the number of degrees of freedom that the CNS has to control.

Nashner (1982) proposed that after perturbation, at first, the CNS stabilizes the joint closest to the perturbation site. In the studies on the standing subjects (Horak and Nashner, 1986; Henry et al., 1998a, 1998b) or the seated subjects (Forssberg and Hirschfeld, 1994), this is meaningful, as the joints are perturbed in different orders based on the experimental setup. However in this study, the whole body with the modified ergocycle together have been translated left- and right-ward. As a result, no specific joint has been disturbed prior to the other joints. Hence, this can partly explain why no specific temporal pattern of the muscles reaction exists in this study.

The responses of the TFL to the translations, whenever significant, are 2 to 4 times higher than those in the other five muscles (Figure 4-4, Figure 4-11, Figure 4-12, Figure 4-13). This is due to the characteristics of the TFL muscle. The TFL muscle plays a role as a hip flexor, an internal rotator, and a thigh abductor (Kapandji, 1987).

Preuss and Fung (in press) have shown that the activation of the TFL muscle is more concurrent with the responses of the lower limb than the movements of the trunk. Therefore, during medio-lateral translation, between the six muscles under study, the TFL is the most prominent muscle in responding to the lateral translation. The activation of the TFL is in line with other lateral translation studies (Henry et al., 1998b).

Comparing the magnitudes of the EMG adjustments, in response to the translations, with other studies that applied perturbation during walking (Nashner, 1980; Tang et al.; 1998) and quiet stance (Moore et al., 1988; Henry et al., 1998b;) shows that the responses are generally much smaller than the other studies. This can be explained by the fact that in those studies balance is a critical factor. The CNS "must" respond to the perturbation, otherwise loss of balance and fall would happen. As mentioned before, in this experiment, participants are seated and the confounding influence of balance is greatly reduced.

5.5 Adaptive Attenuation of Responses

The adaptive attenuation of the EMG responses in the static conditions is most evident in Figure 4-14 (section 4.4.2). In the dynamic active condition, this adaptive attenuation can be inferred from the cycle duration analysis results (section 4.1.3.1.1) where the first perturbed trials, irrespective of the phase or direction of the translation, showed significant reduction in their cycle durations. This can only be explained by relatively large EMG adjustments in response to the translation. However, the responses get attenuated rapidly. The attenuation of the responses has also been observed in a standing experiment (Nashner, 1976). Nashner showed that if the ankle dorsiflexion is not a threat to the postural stability, adaptive attenuation of the functional stretch reflex will appear; however, if it threatens the balance, adaptive facilitation in the functional stretch reflex will appear. In this study, in the early perturbed trials, the CNS generates large magnitude corrective responses. These responses may have been inappropriate for the task and hence the CNS attenuated the responses after each trial. As suggested by Nashner (1976), this can be explained from the perspective of the motor control theory by Welford (1974). Welford proposed that the motor system continuously adjusts its "model" while executing a task under unpredicted varying condition by a reduction in the exceptional errors in the following trials.

5.6 Neural Control Aspects of the Experiment

Comparing the DA condition (the task of active pedalling) with the DP condition (the task of passive pedalling) in Table 4-1 demonstrates some evident characteristics. During the DP condition, the muscle activities were reduced to around 5%-50% of the corresponding DA condition. However, the excitatory muscle activation pattern was almost identical to the DA condition. In addition, the amplitude of the EMG adjustments in the DP condition is almost the same as the DA condition regardless of the fact that the descending drives to the muscles have been cut tremendously. On the other hand, all the inhibitory adjustments, except the one of the BF muscle at propulsion phase with LT translation (0°-left) during the E_l, were absent. One common feature of these two movements is that during the passive pedalling, sensory afferent feedbacks similar to those found in the active pedalling are sent to the CNS. It is probable that the passive cycling activates the same neural circuits, which are active during the DA condition, and the gains of afferent pathways are modulated based on the sensory afferent inputs. This confirms the suggestions by Ting et al. (1998) regarding the gain modulation of the afferent pathways during the locomotor task: they are modulated in such a way that to be strongly effective during the power phase -limb extension- and ineffective during the recovery phase –limb flexion.

Moreover, this finding fits well with the results from the experiments regarding training spinal cats over a treadmill. They have shown that this training activates the sensory inputs and consequently the central neuronal circuits (CPG) and develops recovery of walking in the animal (Barbeau and Rossignol, 1987; Edgerton et al., 1991; Bélanger et al., 1996).

Based on Table 4-1, no common pattern has been observed between the responses observed in the static and dynamic conditions. However, as mentioned in section 4.1.2, one should keep in mind that during dynamic conditions as the movement is in progress, the phase in which the translation has been applied does not imply that the responses are solely attributed to that phase. The E_1 is the area of 80-250 ms after the translation, which implies that the crank arm position has moved ahead approximately 30°-90° from the onset of the translation at the specific phase. The responses in the E_2 (i.e. 250-400 ms after the onset of the translation) correspond approximately to the responses from 90° to 145° after the translation. Even when considering this factor, only the responses of the SOL muscle during RT translations at the 0° of the static conditions are matched with the 270° of the dynamic conditions. The static active condition represents the voluntary control of the CNS over the lower limb and the level of the activity of the soleus muscle in this condition has been matched with its activity during dynamic active condition. In other words, the efferent drives to the muscles have been the same in DA and SA. If the same spinal circuits were recruited for the control of the efferent drives in DA and SA, perturbation would have resulted in similar compensatory responses. However, the EMG adjustments due to the translation have been different. This suggests that different spinal circuits, rather than those involved during static conditions, organize the task of rhythmic movement. In other words, a controller, such as the CPG, controls the locomotor task. These neural circuits are responsible for generating appropriate reactive responses in the case of perturbation as well. In contrast, it should be noted that in this study, the confounding influence of balance has been removed and the CNS probably requires minimal intervention to control balance. This is in line with the results of studies on primates suggesting an increased importance of the corticospinal tract in primates during locomotion comparing to cats (Duysens and Van de Crommert, 1998). That is, the supraspinal has greater control and influence over the spinal neuronal circuits in order for the human body to be in an upright position while maintaining equilibrium during locomotion (Dietz, 2002).

6 Recommendations for Future Studies

In this study, except TFL, the other recorded muscles were in the plane progression. In future studies, we recommend that other muscles which are in the plane of translations such as Adductors and Peroneus muscles should be recorded and analyzed. Also, by using more sensitive foot pressure sensors, cycle duration changes could be better explained. In order to better eliminate habituation, experiment setup should be modified in such a way that longer breaks between conditions be given to subjects. This removes the effect of order of conditions and the results from each condition will be similar to first trials.

To better determine the triggering sources of the responses in this experiment, we recommend recruiting subjects with impaired somatosensory (such as diabetic patients) and impaired vestibular systems and comparing their results with the results of this study.

7 Conclusions

This study has clearly shown that the medio-lateral translations evoke muscle–specific task–, phase–, and direction–dependent responses during modified cycle ergometry. However, the interactions are significant and the dependency should be considered in the finest level of factorial combination. The result implies that when the whole body of seated subjects is translated left- or right-ward, the vestibular system plays an important role in the late components of the corrective responses if the subjects are in static condition. The complex EMG pattern in response to the translation in the different conditions, seen in the results, suggests that even when the CNS does not deal with the control of balance, it still exhibits complicated neural control in response to perturbation. However, the CNS is less constrained in choosing the temporal pattern of muscle recruitment. Finally, the results of the study suggest that the sensory feedback, either created by active or passive movement, plays an important role on the gating of the reflex pathways. Further work is required to better determine the triggering sources of the responses after a medio-lateral disturbance during an ongoing rhythmic movement with minimal balance consideration.

Appendix A: Consent Form

Université du Québec à Montréal
Formule de consentement

J'accepte d'apporter **volontairement** ma collaboration au projet de recherche intitulé, **Responses of Lower Limbs to Unexpected Medio-Lateral Translation during Pedalling Movement**, mené sous la direction de professeur Marc Bélanger, PhD à l'Université du Québec à Montréal. Je suis au courant de la nature de cette recherche, qui m'a été présentée oralement, dont le but poursuivi est de façon générale l'avancement de la science et plus particulièrement: d'examiner la modification de mouvements de pédalage suite à des perturbations de l'équilibre. Ces perturbations pourraient être comparées à des virages rapides ou des accélérations du corps et de la tête lorsqu'une personne est debout dans un autobus ou un train de métro.

Ma participation à titre de sujet impliquera:
Que je m'assoie sur un ergocycle modifié (bicyclette stationnaire avec siège derrière les pédales) et que je pédale à une vitesse de 60 tours par minute. J'aurai des électrodes d'enregistrement fixées à la surface de la peau au-dessus de certains muscles du membre inférieur afin de mesurer leur activité durant les mouvements. Je serrai soumis à des translations (mouvements linéaires) vers la gauche ou vers la droite de la plate-forme sur laquelle se situe l'ergocycle (similaire à un arrêt ou un départ rapide d'un train de métro ou d'un autobus). Dans une autre partie de l'expérience, je relaxerai pendant qu'un moteur dynamométrique déplacera mes membres en mouvements de pédalage alors que je recevrai les translations. Dans une troisième partie de l'expérience, mes membres inférieurs seront placés en positions de pédalage et j'aurai à contracter mes muscles comme si je pédalais, et je recevrai les mêmes types de translations. Dans une dernière phase du projet, mes membres inférieurs seront placés en positions de pédalage, j'aurai à relaxer et je recevrai les translations ci-haut mentionnées.

Conséquemment, toutes les précautions sont prises pour minimiser au maximum les inconvénients et les risques pour ma personne. J'accepte de participer à cette recherche étant cependant entendu que je pourrai me retirer, en tout temps, sans préjudice et pour des motifs dont je serai le seul juge.

Il est entendu que, si après le début de ma collaboration à cette recherche, les responsables prévoient que sa poursuite présente des risques pour mon bien-être, ils devront m'en informer et m'inviter à me retirer.

Je reconnais également que les responsables pourront mettre fin à ma collaboration en tout temps quand ils le jugeront nécessaire.

Il est convenu que les renseignements recueillis à mon sujet dans le cadre de cette étude pourront être utilisés par les responsables aux seules fins énoncées dans la présente recherche et, à la condition que les éléments qui pourraient être de nature confidentielle ne soient pas divulgués dans le public d'une façon telle que l'on puisse m'identifier.

Cette recherche a reçu l'approbation du Comité institutionnel d'éthique de la recherche chez l'humain (CIÉR) de l'UQAM (secrétariat du Comité : service de la recherche et de la création, Université du Québec à Montréal, C.P. 8888, succursale Centre-ville, Montréal, QC, H3C 3P8 – Téléphone : 514-987-3000 poste 7753). Toute question sur le projet, plainte ou commentaire peut être adressé au chercheur. Pour toute question sur les responsabilités des chercheurs ou, dans l'éventualité où la plainte ne peut leur être adressé directement, vous pouvez faire valoir votre situation auprès du CIÉR.

Signé à Montréal en duplicata, ce ______________________________
(Date)

____
(Participant)

____
(Responsable)

Nahid Norouzi Gheidari,
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Appendix B: Statistical Analysis Results

As mentioned in section 3.8.3, the mixed model analysis of variance was used to study each muscle separately. Table B-1 has summarized the twelve statistical analyses (6 muscles by 2 epochs) performed in this study. Only the significant situations have been filled with the corresponding Fischer's statistics value. The degrees of freedom in each significant situation have been placed in the parentheses and the asterisk emphasizes that the value has been significant at $\alpha=0.05$. Table B-1 is useful for testing the hypotheses of the experiment regarding the task– (condition), direction–, and phase–dependency of the responses after applying medio-lateral translations.

In the previous sections, all the significant results were stated based on the Bonferroni t test post-hoc analysis. Therefore, Table B-1 only provides the general view over the problem and experiment question, while the details have been reported in the previous sections. In order not to elongate the text, in the discussion (section 5), whenever appropriate, the details regarding the main effects and marginal means have been added to the text.

Table B-1: The Results of the Mixed Model Analysis of Variance Statistical tests. The asterisk represents the statistically significant conditions with the corresponding Fischer's test value and its degrees of freedom. The E_1 and E_2 are the abbreviations for Epoch-1 and Epoch-2, respectively.

	Factors	**Muscle Name**					
		TFL	**BF**	**VL**	**MG**	**SOL**	**TA**
E_1	**Condition**	F(3,40) = 5.24 *	F(3,148) = 10.79 *			F(3,128) = 5.36 *	
	Direction						F(1,142) = 10.65 *
	Phase		F(3,148) = 7.97 *	F(3,127) = 2.75 *			
	Condition * Direction	F(3,40) = 4.58 *					F(3,142) = 4.79 *
	Condition * Phase		F(6,148) = 3.58 *		F(6,146) = 2.87 *	F(6,128) = 4.40 *	
	Direction * Phase	F(3,40) = 7.06 *	F(3,148) = 4.15 *				F(3,142) = 10.24 *
	Condition * Direction * Phase		F(6,148) = 3.61 *				F(6,142) = 4.50 *
E_2	**Condition**	F(3,40) = 4.38 *			F(3,146) = 3.39 *		
	Direction		F(1,148) = 6.29 *				F(1,142) = 4.94 *
	Phase	F(3,40) = 15.73 *		F(3,127) = 2.77 *			
	Condition * Direction	F(3,40) = 7.59 *					F(3,142) = 3.01 *
	Condition * Phase	F(6,40) = 3.66 *			F(6,146) = 3.71 *		
	Direction * Phase	F(3,40) = 4.84 *	F(3,148) = 3.51 *				F(3,142) = 5.79 *
	Condition * Direction * Phase						F(6,142) = 4.78 *

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