DEPARTAMENT DE EDUCACIÓ FÍSICA I ESPORTIVA

THE IMPLICATION OF SUBCORTICAL MOTOR CENTERS IN VOLUNTARY HUMAN ACTIVITIES.

ANA QUERALT BLASCO

UNIVERSITAT DE VALÈNCIA
Servei de Publicacions
2009

Aquesta Tesi Doctoral va ser presentada a València el dia 20 de juliol de 2009 davant un tribunal format per:

- Dr. Jacques Duysens
- Dr. Antonio Oliviero
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Dipòsit legal: V-4180-2010
I.S.B.N.: 978-84-370-7703-1
Edita: Universitat de València
Servei de Publicacions
C/ Arts Gràfiques, 13 baix
46010 València
Spain
Telèfon:(0034)963864115

UNIVERSITAT DE VALÈNCIA
Facultat de Ciències de l’Activitat Física i l’Esport
Departament d’Educació Física i Esportiva

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TESIS DOCTORAL
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Valencia (Spain), 2009

To the people who make life easier

ACKNOWLEDGEMENTS

There are always many people to whom we have to thank what we do or what we achieve in our life. Thanks…

… To Juan M Castellote and Josep Valls-Sole for their wise advices, wishing that these investigations would only be the beginning. Thanks for your stimulus to continue growing intellectually.

… To Carlos Pablos for his accessibility and kindness, being always willing to help.

… To the friends I have met in Nijmegen, specially the staff of the Deparment of Rehabilitation, because you make me feel at home with your kindness and dedication.

… To my parents, who injected me the needed severity and constancy at work. And to my sister, for trusting on me.

… To my family in law for their niceness and welcome since the first time we met.

… To all my friends who direct or indirectly have supported me in doing this thesis, understanding my full-time dedication in last years.

… And finally to Javi, with whom I share my life, for all his support, comprehensiveness and patience, with the desire to be always with him.

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ABBREVIATIONS

ANOVA	analysis of variance
APAs	anticipatory postural adjustments
BF	biceps femoris
EMG	electromyographic
RF	rectus femoris
SAS	startling auditory stimulus
SD	standard deviation
SOL	soleus
TA	tibialis anterior

Note: abbreviations that have been only used in figures and tables are explained in the corresponding legends.

CHAPTER 1

GENERAL INTRODUCTION AND OBJECTIVES

1.1 Introduction

Sciences have been historically developed in order to elucidate and explain natural phenomena. For this general purpose science branches have analyzed deeply on their own field having later the duty of synthesize back to approach nature. Within the area of physiology, movement research has been historically focused on studying limited parts of the organism in order to ascertain basic rules of muscular and joint governance. At some level, conclusions from these studies give clues about the human motor functioning. However, some parts of motor behaviour are not completely understood yet. The human body contains a high number of muscles and joints, all of which must be controlled during the execution of coordinated, functional movement. Human tasks fulfilment, or human movement in general, arises from the interaction of multiple processes, including those that are related to perception, cognition and action.

Development of techniques in the last decades, such as functional magnetic resonance imaging and high speed cameras, has fostered a deep understanding of basic concepts and has offered a lot of literature. Main advances have been made in the comprehension of goal-oriented tasks such as lower limb support and trunk stability during standing (e.g. Crenna et al. 1987; Keshner et al. 1988; Mouchnino et al. 1992; Allum et al. 2001; Gill et al. 2001), gait (e.g. Perry 1992; Harris and Wertsch 1994; Ounpuu 1994), sitting (e.g. Brogren et al. 1998; Genthon et al. 2007; van Geffen et al. 2008) and their transitions (e.g. Goulart and Valls-Sole 1999; Janssen et al. 2002; Roy et al. 2007; Nadeau et al. 2008), skilled upper limb functions such as reaching and grasping (e.g. Paulignan et al. 1991a; 1991b; Castiello and Begliomini 2008) and manipulation (e.g. Johansson and Cole 1992; Johansson et al. 2001; Valero-Cuevas 2005; Flanagan et al. 2006) and visual control in perception and action (e.g. Goodale and Milner 1992; Bardy and Warren 1997).

Concerning brain governance, different approaches about motor control have been carried out and fundamental concepts have been explored such as differences in position and movement (Brooks 1983; Henatsch and Langer 1985); levels of volition and consciousness devoted to the task (Posner and Rothbart 1998; Wegner and Erskine 2003); differentiation of self-triggered and externally demanded tasks in which cognitive processes have a central role (Jahanshahi et al. 1995; Jenkins et al. 2000); the complexity of the response -having the possibility of choosing between responses or just performing a predetermined action- (Goodrich et al. 1990; Henderson and Dittrich 1998). These approaches have facilitated the study and differentiation of levels of automatized, learned tasks having high influence in the areas of human training for better physical performance.

Then, motor control research, usually studied in relation to specific activities, provides insight into principles for the ways movements are controlled. Understanding the control of action implies understanding the motor output from the nervous system to the muscles (Shummway-Cook and Woollacott 2001).

1.2 Motor control of voluntary human activities

Analysis of voluntary movements is a way of trying to understand how the subject makes decisions and how the peripheral apparatus executes them (Latash 1998). In everyday life we perform a huge variety of functional tasks that require voluntary movements. The type of movement needed is determined in part by the nature of the task being performed. Understanding the control of movement requires an awareness of how tasks regulate, or constrain, movement (Shummway-Cook and Woollacott 2001).

These movements are usually the consequence of the reaction to an internal or external stimulus. In daily life people are used to react to diverse stimuli, visual, auditory, mechanical and others. Some of them are expected (for instance, when we are waiting for the traffic light to change colour to cross the street) but they can also be unexpected (a glass bottle accidentally falling to the floor behind someone). In both cases, movement will be executed as a reaction to an external stimulus, visual in the first case and auditory in the second. Apart from the mental state in which expectation plays a role, movement is also influenced by what the person was doing at the moment of stimulus presentation (whether being static or dynamic).

In general, voluntary movements are accompanied by postural adjustments which show three main characteristics (Massion 1984): they are “anticipatory” with respect to movement, “adaptable” to the conditions in which the movement is executed and “influenced” by the instructions given to the subject concerning the task to be performed. Therefore, these postural adjustments, known as anticipatory postural adjustments (APAs), preceed planned postural perturbations and minimize them with anticipatory corrections. Since the first study of Belenkii et al (1967) which showed changes in the electromyographic (EMG) activity of postural muscles, many studies concerning APAs have been performed. Taking into account the results of APAs studies, Aruin (2002) suggest that there are three major components that influenced APAs: motor action, perturbation and postural task. As any voluntary movement, especially a fast one, induces postural perturbations (Aruin 2002), APAs should be considered in studying the preparation and execution of voluntary movements.

Voluntary movements may be not only unique but also repetitive. A separate remark should be done for rhythmic muscle activities. Cyclical patterns needed for walking, running, respiration or other rhythmical activities are generated by neural networks, which are specialized in repeating particular actions over and over again (Duysens and Van de Crommert 1998). The term central pattern generator is generally used when refering to such neural network for locomotion. There are abundant studies in animals that lead to the assumption of a central pattern generator underlying the central control of locomotion (reviews of Duysens and Van de Crommert 1998; Grillner et al. 2008). However, it has not been until the last decades when the presence in humans of a central pattern generator for locomotor activity has been considered (Calancie et al. 1994; Dimitrijevic et al. 1998; Gerasimenko et al. 2002). Evidences of the existence of that neural network in humans are delivered, for instance, by studies with spinal cord injury patients or experiments in which specific sites of the spinal cord are electrically stimulated.

1.2.1 Differential movement task attributes

Movement tasks can be classified taking into account specific attributes that are inherent in the task. Shummway-Cook and Woollacott (2001) dealt with the following task attributes: discrete versus continuous tasks, stability versus mobility tasks, attention continuum, and open versus closed tasks. These previous task attributes are explained in the following paragraphs. Concerning the upper limb, they also mentioned the manipulation continuum task attribute although it is not pertinent to be explained here.

A task can be classified as discrete or continuous. Moving from sitting to standing or lying down in bed are examples of discrete movement tasks in which the beginning and the end of the tasks are recognizable. In contrast, in continuous tasks such as walking or running the end point is decided arbitrarily by the performer.

Stability tasks such as sitting or standing are performed with a nonmoving base of support. In contrast, in mobility tasks such as walking or running there is a moving base of support.

Movements are also classified using the attribute of attentional demand. Static postural tasks have primarily the lowest attentional demand while in mobility tasks such as walking or obstacle avoidance attentional demands are increased.

Closed movement tasks are characterized by fixed patterns of movement that are performed in relatively constant environments. However, open movements tasks are performed in a changing environment, making the ability to plan a movement difficult. The terms *open* task and *closed* task are also used in other contexts related to movement. The terms *open-loop* and *closed-loop* are used to describe two modes of movement control. Open-loop movements are not sensitive to environmental feedback and in closed-loop control a movement is sensitive to the environment. Moreover, the terms *open chain* and *closed chain* have been also used to characterized movements. An open chain movement is one in which the distal joint is free to move while in a closed chain movement the distal segment encounters resistance within the environment.

Furthermore, in the context of reaction time tasks, where preparedness can be studied, an important distinction should be done regarding response complexity (Klapp 1996). In simple reaction time experiments the required response is identified first and then an imperative signal indicates that the response should be produced. By contrast, in choice reaction time experiments any informative precue is not included. Only the imperative signal informs about which response should be performed. Therefore, in choice reaction time tasks the preprogramming of a response may not be fully possible and the reaction time is longer than in simple reaction time tasks.

1.2.2 Subcortical stimulation studies

It is commonly accepted that when people react to a stimulus, the premotor and supplementary motor areas of the cerebral cortex play an important role in the motor preparation and execution of voluntary movements. However, if a rapid movement execution is needed, subcortical motor centers may be involved to speed up voluntary motor activities (Valls-Sole et al. 2008). In such a situation, an unexpected and abrupt sensory input may trigger the motor response by a direct activation of the prepared subcortical structures, a phenomenon termed ‘StartReact’ (Valls-Sole et al. 1995; 1999; Carlsen et al. 2004a; 2004b). The unexpected and abrupt stimulus is known as the startle stimulus. The consequence of a startle reaction is an involuntary motor response which consists of a generalized muscle contraction (Landis and Hunt 1939). Within that series of involuntary muscle movements, the eyeblink reaction is the fastest, most reliable, and most resistant to habituation component of the human startle reflex (Landis and Hunt 1939). In general, this startle reaction is considered as one of the fastest motor reactions of humans and animals.

Therefore, in order to ascertain the subcortical implications in the preparation and execution of voluntary movements, subcortical stimulation studies have been performed. Startle stimulation has been used in such studies since the startle reaction occurs via a subcortical reflex mechanism and sensory inputs activate the reticular formation and the descending reticulo-spinal tract to the spinal cord (Davis et al. 1982). Usually, in humans, the startle reaction is induced by auditory stimuli, although there are other methods such as visual or cutaneous stimuli (Berg and Balaban 1999).

In a context of simple reaction time task experiment subjects are able to prepare sufficiently in advance their motor programme for rapid execution at the imperative signal perception (Valls-Sole et al. 1995; 1999; Siegmund et al. 2001; Carlsen et al. 2004a; 2004b). Then, a fast voluntary human reaction can be observed. However, when a startling auditory stimulus (SAS) is applied at the same time as the imperative signal, subjects execute the required and prepared task even faster while maintaining the basic motor program undisturbed (Valls-Sole et al. 1995; 1999; Siegmund et al. 2001; Carlsen et al. 2004a; 2004b). This StartReact effect is convincingly present in the simple reaction time tasks. In choice reaction time tasks, in which the preprogramming of the response may not be possible, the StartReact effect is also present with some reservations as it was observed in some forms of choice reaction time tasks and not in others (Valls-Sole 2004; Kumru et al. 2006; Oude Nijhuis et al. 2007; Reynolds and Day 2007). Valls-Sole et al. (2008) suggests that there is some degree of subcortical preparation in choice reaction time tasks paradigms.

Consequently, preprogramming of voluntary responses can be analyzed with the 'StartReact' effect. It has been fully investigated in relatively simple actions, such as ballistic movements (e.g. Valls-Sole et al. 1999), neck movements (e.g. Siegmund et al. 2001; Oude Nijhuis et al. 2007), or movements of a single finger (e.g. Carlsen et al. 2004a; 2004b). Only a few experiments have been reported on relatively complex movements such as tip-toeing (Valls-Sole et al. 1999) or the recent stepping experiments of MacKinnon et al (2007) and Reynolds and Day (2007). Therefore, to our knowledge, this is the first time that the StartReact effect is studied in some more complex voluntary movements such as sit-to-stand, gait-pattern and obstacle avoidance during walking. It is not known whether such motor programmes are prepared and executed in the same way as the previous 'StartReact' models and, of more interest, the preprogramming at the level of the coordination of APAs, subsequent motor patterns (as gait-pattern following gait initiation) and obstacle avoidance strategies.

Nowadays, two options in relation to the underlying physiological mechanisms of the ‘StartReact’ effect are considered (Valls-Sole et al. 2008). One suggests that motor programmes are represented in subcortical motor structures, where they are accessible to activation by the startling stimulus (Valls-Sole et al. 1999; Carlsen et al. 2004a; Sanegre et al. 2004). The second possibility is that the energy of stimulus used as imperative signal increases with the presence of the startle. This is exemplified by intersensory facilitation (Nickerson 1973; Gielen et al. 1983) and the responses are attributed to the joint stimulation of multiple sensory modalities.

1.3 Outline of the thesis

The current investigation is focused on human activities that are performed voluntarily. We have selected on purpose three different tasks to deeply study the preparedness and the execution of voluntary human movements. They all are everyday activities which although functionally related have differential characteristics.

In order to cover the differential task attributes presented previously, three movement tasks were selected to be part of the thesis. A separate experiment was done for each task in which specific objectives were considered.

The first task is the **sit-to-stand** manoeuvre, a discrete task in which subjects change from a sitting to a standing position. Both initial and end positions are static and stable, and the task does not have high attentional demands. It is a closed movement as it was performed in a fixed environment. The experiment was performed in a context of a simple reaction time task and special attention was paid to APAs versus prime movers.

The second task is **gait initiation** followed by **gait-pattern**. Subjects initiated gait from a standing still position and performed at least three steps at their own pace. The initial position was also static and stable but the end position was decided by the performer. Therefore, it shares aspects of a discrete and a continuous movement task. As in the sit-to-stand task, subjects do not have high attentional demands. It is also a closed movement and it was performed in a context of a simple reaction time task. Special attention was paid to the establishment of the gait-pattern after an external manipulation of the timing of gait initiation and to the concept of central pattern generator.

Obstacle avoidance during walking is the third task. Subjects walked on a treadmill and they were instructed to avoid unexpected obstacles presented on the subject’s path. In contrast to the previous tasks, obstacle avoidance during walking is a clear continuous and dynamic task performed in a moving base of support.

Moreover, the attentional demands are increased and it is an open movement as the environment is changeable. As subjects could avoid obstacles using two strategies (short step strategy or long step strategy), the experiment could be considered as a choice reaction time task.

The general objective of the current dissertation is to **analyse the subcortical implications in the preparation and execution of complex voluntary movements**. Three studies will be presented: sit-to-stand as a simple reaction time activity to analyse APAs and muscle coordination; gait initiation and gait-pattern as a complex activity to add the analysis of a subsequent motor pattern; and obstacle avoidance strategies to add the analysis of choice responses in a dynamic situation. Each one of the following three chapters corresponds to a complete separate experiment with specific introduction, objectives, methods, results, discussion and conclusion. Next a summary of each chapter is presented.

Chapter 2 is entitled **“The effects of a startle on the sit-to-stand manoeuvre”**. Simple ballistic movements are executed faster in reaction time task paradigms when the imperative signal is accompanied by a SAS. We examined whether this effect also occurs in complex movements such as the sit-to-stand manoeuvre, taking into account both anticipatory postural adjustments and prime movers. Nine healthy volunteers performed sit-to-stand to visual imperative signal either presented alone (control trials) or together with SAS (test trials). Reaction time, measured as the time between the imperative signal and take-off was significantly shortened in test trials when SAS was applied at an interval of 0 ms with respect to the imperative signal. The onset latency of EMG bursts recorded from tibialis anterior, lumbar paraspinal, quadriceps and biceps femoris muscles reduced proportionally to the shortening of take-off. However, these effects were not observed if SAS was delivered 150 ms after the imperative signal, when the manoeuvre had already started. Our results suggest that stimuli acting on subcortical motor structures speed-up but do not otherwise interfere with the execution of the motor programs underlying the sit-to-stand manoeuvre.

Chapter 3 is entitled **“Speeding up gait initiation and gait-pattern with a startling stimulus”**. Human gait involves a repetitive leg motor pattern that emerges after gait initiation. While the automatic maintenance of the gait-pattern may be under the control of subcortical motor centres, gait initiation requires the voluntary launching of a different motor program. In this study, we sought to examine how the two motor programmes respond to an experimental manipulation of the timing of gait initiation. Subjects were instructed to start walking as soon as possible at the perception of an imperative signal that, in some interspersed trials, was accompanied by a SAS. This method is known to shorten the latency for execution of the motor task under preparation. We reasoned that, if the two motor programmes were launched together, the gait-pattern sequence would respond to SAS in the same way as gait initiation. We recorded the gait phases and the EMG activity of four muscles from the leg that initiates gait. In trials with SAS, latency of all gait initiation-related events showed a significant shortening and the bursts of EMG activity had higher amplitude and shorter duration than in trials without SAS. The events related to gait-pattern were also advanced but otherwise unchanged. The fact that all the effects of SAS were limited to gait initiation suggests that startle selectively can affect the neural structures involved in gait initiation. Additionally, the proportional advancement of the gait-pattern sequence to the end of gait initiation supports the view that gait initiation may actually trigger the inputs necessary for generating the gait-pattern sequence.

Chapter 4 is entitled **"The effects of an auditory startle on obstacle avoidance during walking".** Movement execution is speeded up when a startle auditory stimulus is applied with an imperative signal in a simple reaction time task experiment, a phenomenon described as StartReact. The effect has been recently observed in a step adjustment task requiring fast selection of specific movements in a choice reaction time task. Therefore, we hypothesized that inducing a StartReact effect may be beneficial in obstacle avoidance under time pressure, when subjects have to perform fast gait adjustments. Twelve healthy young adults walked on a treadmill and obstacles were released in specific moments of the step cycle. On average the EMG onset latency in the biceps femoris shortened by 20 % while amplitude increased by 50 %, in trials in which an auditory startle accompanied obstacle avoidance. The presentation of a startle increased the probability of using a long step strategy, enlarged stride length modifications and resulted in higher success rates, to avoid the obstacle. We also examined the effects of the startle in a condition in which the obstacle was not present in comparison to a condition in which the obstacle was visibly present but it did not fall. In the latter condition, the obstacle avoidance reaction occurred with a similar latency but smaller amplitude as in trials in which the obstacle was actually released. Our results suggest that the motor programmes used for obstacle avoidance are likely stored at subcortical structures. The release of these motor programmes by a

SAS may combine intersensory facilitation and the StartReact effect.

Finally, in Chapter 5 the main conclusions of the thesis and some final remarks are presented.

CHAPTER 2

THE EFFECTS OF A STARTLE ON THE SIT-TO-STAND MANOEUVRE

2.1 Introduction

The sit-to-stand manoeuvre is a complex voluntary movement requiring the coordinated activation of many muscles, some of them performing associated APAs and others acting as prime movers (Gahery and Massion 1981; Massion 1984; Gahery 1987; Goulart and Valls-Sole 1999; Hirschfeld et al. 1999). One of the first muscles to be activated is the tibialis anterior, which is thought to be an important APA muscle for the displacement of the body center of gravity to the appropriate position for the sit-to-stand manoeuvre (Gollhofer et al. 1989; Kasai and Kawai 1994). According to Goulart and Valls-Sole (1999), the lumbar paraspinal, quadriceps, and hamstrings are the muscles most consistently activated in a patterned sequence around the moment of take-off from the seat. These muscles, activated at onset latencies between 500 and 600 ms after an imperative signal when the manoeuvre was performed in the context of a simple reaction time task paradigm, were considered representative prime movers for the sit-to-stand manoeuvre.

In simple reaction time task paradigms, subjects have the possibility to fully prepare the motor programs for the fastest possible execution after perception of the sensory cue used as imperative signal (Henderson and Dittrich 1998). Consequently, the latencies of bursts of EMG activity recorded from prime movers or the accelerometric signal recorded from the moving segment in simple reaction time task paradigms are consistently the shortest possible ones throughout a number of trials. However, if a SAS is delivered together with the imperative signal, the whole reaction is significantly speeded up to values similar to those of the startle reaction (Valls-Sole et al. 1995; 1999; Siegmund et al. 2001; Carlsen et al. 2004a; 2004b). In spite of its effects on reaction time, SAS does not modify the typical triphasic pattern of a ballistic movement (Hallett et al. 1975), which suggests that the whole motor program is represented in the subcortical motor structures activated by the SAS, i.e. the brainstem reticular formation and the reticulospinal tract (Davis et al. 1982; Lingenhöhl and Friauf 1994).

This so-called StartReact effect has been fully investigated in relatively simple actions, such as ballistic wrist movements (Valls-Sole et al. 1999), neck movements (Siegmund et al. 2001), or movements of a single finger (Carlsen et al. 2004a; 2004b), with only a few experiments on complex movements such as tip-toeing (Valls-Sole et al. 1999) or step initiation (MacKinnon et al. 2007). In this study, we wanted to determine whether the StartReact effect occurs in sit-to-stand, a complex learned movement that involves both prime movers and postural adjustment muscle activity. We reasoned that knowing the effects of SAS on sit-to-stand at different time intervals after the imperative signal would bring information on human programming of learned complex motor actions. We expected to answer questions such as whether the StartReact effect involves APA muscles, whether it can affect prime movers activated at a relatively long latency after the imperative signal, and whether SAS can interfere with the temporal link between APA muscles and prime movers.

2.2 Methods

2.2.1 Participants

Nine healthy subjects (six males and three females) participated in the study. The age of the participants was between 25 and 50 years (mean 33.6 years), the mean height was 173.6 cm (SD 12.5 cm), and the mean weight was 70.8 kg (SD 14.8 kg). The experiments were conducted in accordance with the Declaration of Helsinki. All subjects gave their informed consent for the study, which was approved by the Ethical Committee of the Hospital Clínic of Barcelona.

2.2.2 Recording and stimulation

Pairs of surface silver/silver chloride electrodes (0.7 cm diameter) were used to record the EMG activity of the tibialis anterior, lumbar paraspinal, quadriceps, and biceps femoris. A piezoelectric accelerometer attached to the subject's forehead was used to record head and body movements. We also recorded the time of take-off as the artefact caused by the separation of a pair of conventional electrodes, one of them attached to the subject's shorts, and the other attached to the surface of the chair, covered with aluminium foil. In this way, a clear artefact was generated in the oscilloscope when the two electrodes became separated. All recordings were done with an electromyography Mystro5Plus (Vickers Medical, Surrey; London). The band-pass frequency filter was set at 50-1,000 Hz for the EMG activity and at 0.1-10 Hz for the accelerometer. A gain of 500 μV per division and an analysis time window of 2 s were used in most recordings but they were adjusted conveniently in specific cases. The signal was fed into a personal computer provided with an analysis program (Acknowledge, MP100; Biopac Systems, Bionic, Barcelona). Sample rate was 1,000 Hz.

The imperative signal was a white 5 cm^2 square appearing on a black computer screen situated at eye level. It was preceded by a verbal warning and a forewarning mark that appeared with a fixed foreperiod of 5 s. The oscilloscopic sweep was triggered 500 ms before the imperative signal. A SAS was obtained by discharging the coil of a MagStim 200 magnetic stimulator on top of a metallic platform (Valls-Sole et al. 1999). The sound produced in this way, measured at a distance of 1 m from the source with a Brüel and Kjaer Impulse Precision Sound Level Type 2204, was of an intensity of 130 dB sound pressure level.

2.2.3 Procedure

Subjects were sitting comfortably on a stool, whose height was conveniently adjusted for each subject. Subject’s position was carefully set, with feet flat on the floor, ankle joint laying in a plane slightly posterior to the knee joint, arms folded over the chest, trunk relaxed, and face looking forward. They were instructed to stand up as fast as possible for the detection of the imperative signal. They were asked to do so in the most conventional way with the only request of not displacing their feet from the initial position. In control trials, only the imperative signal was delivered. In test trials, a SAS was delivered together with the imperative signal, or at the following predetermined intervals: 0, 50, 100, 150, and 200 ms. We collected a total of 60 trials per subject, 45 control trials and 15 test trials (3 for each interval). Such a relatively small number of test trials per interval was intended to avoid fatigue and lack of attention. Short breaks between consecutive trials were also introduced on demand. Subjects were warned that there could be an auditory stimulus at the same time as the presentation of the imperative signal, and were instructed to disregard that stimulus and concentrate in responding to the imperative signal as fast as possible. Subjects performed the manoeuvre a few times before beginning with the experiments, and they also received a few SAS with no instruction to move, for them to be aware of the type of interfering stimuli.

2.2.4 Data analysis

Trials in which subjects made an erroneous or partial movement were excluded from the analysis and repeated on-line. All data were grouped according to the conditions and intervals of the study. The mean and the standard deviation were calculated for each group of data. The primary outcome measure was reaction time, calculated between imperative signal and take-off. Onset of EMG activity in recorded muscles, and of movement recorded with the accelerometer, was considered at the first deviation from the baseline larger than 50 µVs. The amount of EMG activity was measured in the rectified EMG, as the area of a predefined segment of 100 ms beginning at onset latency for each particular muscle as well as for the signal recorded by the accelerometer. The analysis of the effects of SAS on latencies of individual muscles EMG activity was carried out on values expressed as percentages of take-off, in order to account for interindividual differences. We compared data of control and test trials over time using repeated measures ANOVA for group comparisons, with a level of significance at $P = 0.05$.

2.3 Results

Subjects performed the task with no difficulties. The percentage of trials repeated on-line was less than 5%. No reactions were observed in the recorded muscles in any subject when SAS was presented without previous instruction to prepare the task. As expected, the general pattern of muscle activation in control condition (Figure 2.1A) included an early activation of the tibialis anterior followed, after a clear delay, by the patterned activation of the three prime movers, in a consistent order (lumbar paraspinal, quadriceps and biceps femoris). Onset of movement occurred between tibialis anterior and lumbar paraspinal muscles EMG activity onsets, reflecting the head-body forward movement. Take-off occurred at a rather constant latency after onset of activity in the lumbar paraspinal muscles (168 ± 19 ms).

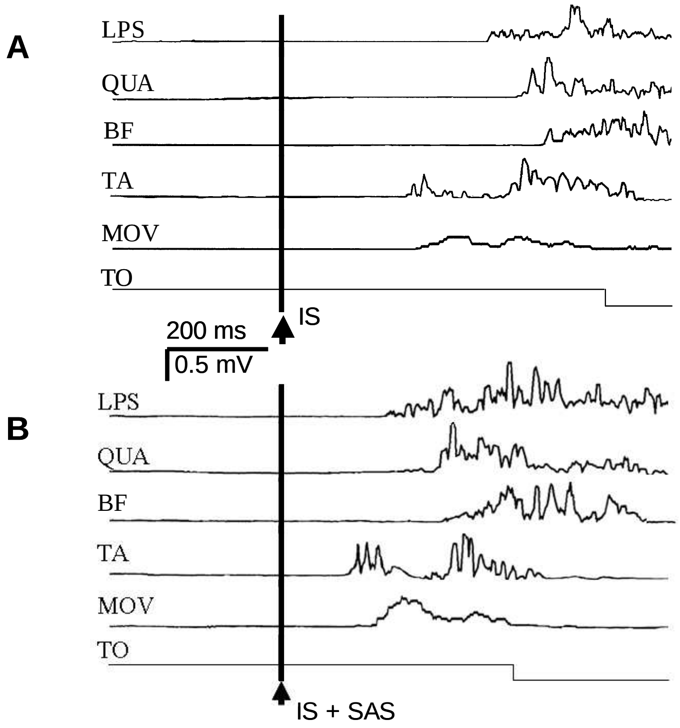

Figure 2.1. Reaction time in control and test trials. Representative examples of movement recordings from one subject. A, Control trial. B, Test trial in which SAS is delivered at the same time (0 ms) as the imperative signal. Note the marked shortening of reaction time for all events with maintenance of their temporal pattern. For this and the remaining figures: LPS lumbar paraspinal muscle, QUA quadriceps muscle, BF biceps femoris muscle, TA tibialis anterior muscle, MOV signal recorded by the accelerometer attached to the forehead, TO time of take-off, IS imperative signal, SAS startling auditory stimulus. TO is represented as a downward shift of the recording.

A noticeable latency shortening, involving the whole manoeuvre, was observed in all subjects when SAS was delivered together with the imperative signal, i.e. at an interval of 0 ms (Figure 2.1B). Take-off shortened to a mean of 75.7% of the control values and values between 51.5 and 68.6% were observed in the EMG recordings of all muscles. Latency shortening was also evident, although less marked, when SAS was delivered at 50 and 100 ms following the imperative signal, but it was not apparent when SAS was delivered at intervals of 150 and 200 ms. No evident modification of the sequence of events was observed by simple inspection of the graphs in any of the trials. Numerical relation of the data for all intervals is shown in Table 2.1. Figure 2.2 shows the graphical representation of the mean percentage change in test trials at each interval.

Table 2.1. Mean onset latency for control and test trials.

	Control	0 ms	50 ms	100 ms	150 ms	200 ms
TA	192(56)	99(16)	121(18)	158(22)	180(24)	195(45)
MOV	241(62)	144(28)	154(39)	189(51)	229(50)	238(32)
LPS	407(74)	261(45)	297(65)	328(80)	388(60)	399(44)
QUA	434(70)	276(42)	321(88)	356(94)	418(65)	426(70)
BF	458(62)	314(51)	340(85)	373(48)	446(61)	454(65)
TO	585(69)	443(39)	479(29)	522(53)	572(54)	578(37)

Onset latency of EMG activity in tibialis anterior (TA), lumbar paraspinal (LPS), quadriceps (QUA) and biceps femoris (BF), as well as for the signal recorded by the accelerometer (MOV) and the time of take off from the chair (TO).
Data are the mean values (with one SD within parenthesis) expressed in ms for all control and test trials.

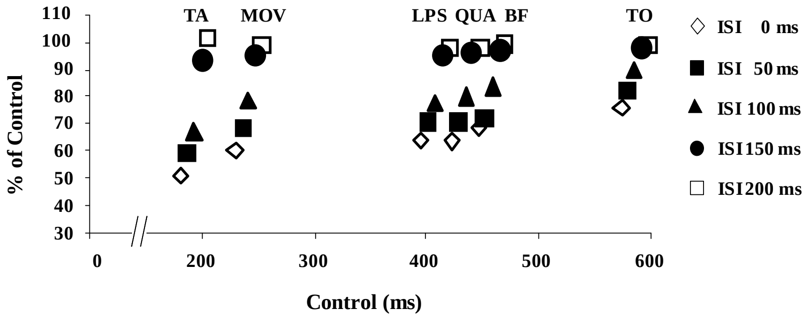

Figure 2.2. Relationship between control and SAS conditions delivered at different time intervals from the imperative signal (ISI). Mean latencies for onset of TA, MOV, LPS, QUA, BF, and TO are shown in the horizontal axis, while the effect of SAS in test trials is shown for each interval in the vertical axis as the percentage shortening with respect to control. Events labelled as in Figure 2.1.

Statistical analysis showed a significant effect of interval on the latency shift for each muscle ($P < 0.05$ for all). Differences were significant for onset of EMG in tibialis anterior ($F_{5,40} = 43.7$), lumbar paraspinal ($F_{5,40} = 29.0$), quadriceps ($F_{5,40} = 19.2$), biceps femoris ($F_{5,40} = 13.0$), movement ($F_{5,40} = 30.3$), and take-off ($F_{5,40} = 30.6$). Post-hoc analysis showed that the mean values for all events were significantly shorter for test trials than for control trials at the intervals 0, 50, and 100 ms, but not at 150 and 200 ms.

The temporal relationship among all events was maintained in all trials. Figure 2.3 shows the mean latency difference between each of the events and take-off for each interval. There was no significant effect of interval on the latency difference between onset of EMG activity in each muscle, or movement, and take-off, with $F_{5,40} = 2.2$ for tibialis anterior, $F_{5,40} = 1.7$ for lumbar paraspinal, $F_{5,40} = 2.1$ for quadriceps, $F_{5,40} = 0.8$ for biceps femoris, and $F_{5,40} = 2.1$ for movement ($P > 0.05$ for all comparisons).

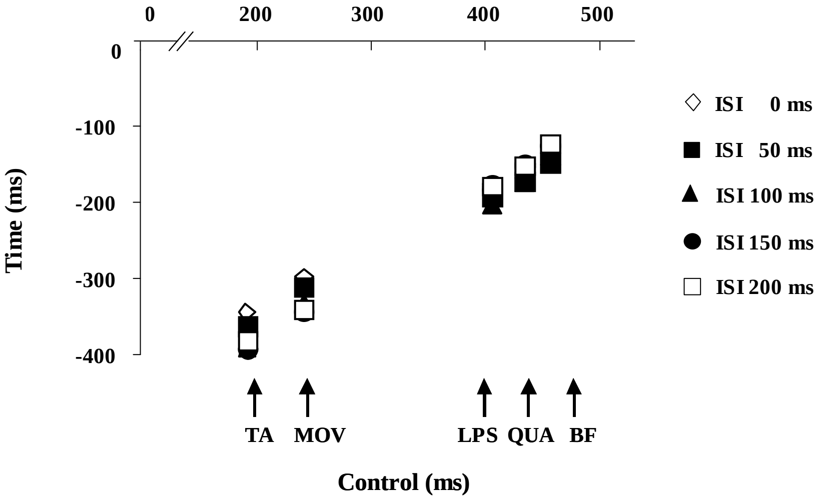

Figure 2.3. Time difference with respect to take-off (ms) for each event at different SAS conditions. Events labelled as in Figure 2.1.

The area of the initial 100 ms of the EMG activity and of the signal recorded by the accelerometer had a large variability among subjects but was, in general, larger in test trials than in control trials for all muscles (Table 2.2). Statistical comparison showed significant differences only for tibialis anterior ($F_{5,40}$ = 3.9) and movement ($F_{5,40}$ = 3.1). Post-hoc analyses indicated larger area in test with respect to control trials at intervals of 0, 50, and 100 ms but not at 150 and 200 ms.

Table 2.2. Mean size of the rectified EMG and accelerometer signals.

	Control	0 ms	50 ms	100 ms	150 ms	200 ms
TA	1.06 (0.49)	2.24 (0.45)	1.88 (0.52)	1.77 (0.33)	1.28 (0.23)	1.25 (0.19)
MOV	0.43 (0.84)	0.84 (0.23)	0.70 (0.27)	0.63 (0.17)	0.51 (0.18)	0.46 (0.11)
LPS	0.76 (0.33)	1.10 (0.44)	0.95 (0.51)	0.90 (0.34)	0.85 (0.30)	0.89 (0.21)
QUA	1.26 (0.51)	1.74 (.052)	1.52 (0.41)	1.46 (0.26)	1.33 (0.23)	1.36 (0.18)
BF	1.27 (0.55)	1.55 (0.36)	1.48 (0.42)	1.37 (0.29)	1.40 (0.22)	1.33 (0.15)

Data are the mean of the root mean square (with one SD within parenthesis), calculated for the first 100 ms after onset latency for all EMG and accelerometer signals in control and test trials. TA: Tibialis anterior; MOV: movement signal from the accelerometer; LPS: lumbar paraspinal; QUA: quadriceps; BF: biceps femoris.

2.4 Discussion

The sit-to-stand manoeuvre involves changing from a relatively stable position to one relatively unstable. The movement is usually performed by first repositioning the center of gravity and then activating a chain of axial muscles, whose combined action causes extension of the pelvic girdle and stretching of the trunk to reach the standing position. The results of our study show that the whole sit-to-stand manoeuvre was executed significantly earlier when a SAS was presented together with the imperative signal but no significant interference was observed if SAS was presented when the execution of the manoeuvre has already started. Apart from latency shortening, SAS did not induce other significant changes. In particular, the temporal pattern of the manoeuvre did not change. In fact, our subjects did not experience more disequilibrium in test than in control trials, and executed the manoeuvre similarly in both conditions. The EMG bursts of the tibialis anterior and the accelerometric signal showing the body movement were larger in test trials at intervals between 0 and 100 ms in comparison to control trials. Such an enhancement has been reported previously for wrist movements (Kumru and Valls-Sole 2006). It may be due to the fact that at the time of preparation, there is a sustained increase in subcortical motor pathways excitability (Kumru and Valls-Sole 2006). The StartReact effect seen in our study is similar to the effects reported previously for other motor actions (Valls-Sole et al. 1995; 1999; Siegmund et al. 2001; Carlsen et al. 2004a; 2004b). It is considered to be due to the early triggering of a motor program and not a reaction to the SAS because no such a reaction occurs when SAS is given without motor preparation.

The role of APA muscles has been recognized for a long time (Belen'kiĭ et al. 1967; Cordo and Nashner 1982; Bouisset and Zattara 1987; Massion 1992; 1994; Krishnamoorthy and Latash 2005). It is considered that this preparatory activity is based on estimations of expected perturbations that may take place when performing the task, and generates muscular activity resulting in a force that opposes the expected perturbations (Friedli et al. 1984; Bouisset and Zattara 1987). In the sit-to-stand task, the tibialis anterior likely acts as an early APA muscle that advances the body forward and fixates the ankle to permit the action of more rostral muscles. The movement signal, recorded from the accelerometer attached to the forehead, likely reflected the APA activity also, since moving the head forwards likely contributes to forward displacement of the trunk in preparation for the transition phase (Millington et al. 1992).

The time difference between activation of APA muscles and prime movers probably varies according to the task. The most frequent values reported in the literature for postural leg muscles when performing upper limb tasks are 50–150 ms (Bouisset and Zattara 1987; Massion 1992). However, longer APA delays have been also described (Lee et al. 1990; De Wolf et al. 1998). In our subjects, the delay between onset of tibialis anterior EMG activity and take-off ranged between 350 and 400 ms. In fact, it makes sense to have a relatively long delay between onset of activation of APA muscles and that of prime movers in sit-to-stand where subjects have to reposition their centre of body mass, likely involving profuse sensory processing and further adjustments. If the muscles erecting the body are activated too fast, subjects may risk disequilibrium and fall. Probably, activation of APA muscles is prepared in a feedforward mode for it to be a precise manoeuvre acting to adjust body posture to limit the consequences of expected future perturbations.

Two different models for the relationship between APA and prime movers have been proposed: a single-process control model and a dual-process control model. According to the first, the control modules for APA and prime movers are linked together in a single process (Aruin and Latash 1995; Toussaint et al. 1997a; 1997b). Also, studies using correlation procedures between prime movers and postural muscles showed a unique controller for both (Lee 1980; Cordo and Nashner 1982). In our study, SAS shortened the latency of the whole manoeuvre by a certain amount, with the prime movers following the activation of the tibialis anterior with the same proportional delay with respect to take-off as in control trials. The relative time difference between activation of prime movers and take-off is similar in control and test trials at all intervals, in keeping with the fact that they belong to the same motor program. We cannot completely rule out, however, that the tibialis anterior participates in the upward motion to reach the standing posture, since it acts in the same mechanical chain as the prime movers.

The second model is supported by results of studies allowing for timing differentiation between APAs and prime mover muscle activation using self-paced and simple reaction time trials. Dissociation between APAs and prime movers activities has been seen in patients with Parkinson’s disease (Dick et al. 1986; Bazalgette et al. 1987) and in those with motor cortex lesions (Viallet et al. 1992; Massion et al. 1999). Therefore, it has been speculated that the supplementary motor area and the basal ganglia are involved in modulation of postural muscles, whereas the contralateral cortex commands prime movers. According to our results, activation of subcortical structures can advance APAs activity and shorten the movement, which supports the hypothesis that the whole task, including APAs and prime mover activation, is fully prepared at a subcortical level (Valls-Sole et al. 1999). The fact that the shortening was not observed when SAS was applied just before expected activation of prime movers also supports the idea that a tight temporal link should exist between postural and prime mover muscles for specific manoeuvres.

We conclude that the sit-to-stand manoeuvre responds as a single block of combined motor programs to the presentation of a SAS. The SAS-induced patterned shift to earlier latencies affects APA and prime mover muscles alike. This suggests that, even if APA and prime mover muscles were initiated independently (Slijper et al. 2002), they end up having a common modulation at a subcortical level. This subcortical loading supports the idea that postural adjustments may be considered as prepared in an internal forward model (Wing et al. 1997). The persistence of the temporal link between APA and prime movers when a startle is applied during the time lag between their respective activation suggests that the muscles examined in this study constitute a common motor program that, once launched, is resistant to unexpected external perturbations. This is compatible with the existence of an active inhibitory process over the reflex reaction of subcortical motor structures during an ongoing motor action. Further studies on descending inhibitory control of reflexes during complex motor manoeuvres should help with examining such a hypothesis.

This chapter has been adapted from: Exp Brain Res 185: 603-609, 2008.

CHAPTER 3

SPEEDING UP GAIT INITIATION AND GAIT-PATTERN WITH A STARLING STIMULUS

3.1 Introduction

Gait initiation is the transition from upright quiet stance to walking (Carlsoo 1966; Crenna and Frigo 1991; Malouin and Richards 2000). This is a delicate task brought about by a fine tuned neuromuscular mechanism that activates different muscles in an adequate sequence allowing the center of gravity of the body to move toward the swing limb first and then to the stance limb (Mann et al. 1979). Crenna and Frigo (1991) reported that gait initiation includes a basic single motor pattern that starts with inhibition of the soleus and activation of the tibialis anterior. At present, however, it is unclear what part of such motor program is generated as brain commands and what part is reflex in nature. Usually, we start walking without thinking on it, being capable of maintaining a regular speed and cadence quite automatically, suggesting that subcortical structures play an important role in gait.

Walking consists in the repetition of activation of several muscles in a sequenced pattern. The automatic maintenance of a walking pattern is likely regulated at a spinal level. Although the concept of central pattern generators emerged in the early 1960s (Hughes and Wiersma 1960; Wilson 1961) it has not been until the last decades when the presence in humans of a central pattern generator for locomotor activity has been considered (Duysens and Van de Crommert 1998). Studies of invertebrates and lower vertebrates have substantially contributed to give insights on their mechanisms (Barbeau and Rossignol 1991; Cazalets et al. 1992). However, little is known about the relation between the launch of the motor program for gait initiation and the generation of the walking pattern.

Whether subcortical motor structures are prepared or not for execution of a given motor task can be assessed using the StartReact effect (Valls-Sole et al. 1995; 1999; Carlsen et al. 2004b; Tresilian and Plooy 2006). This phenomenon consists in the involuntary activation of prepared motor programs by an unexpected loud SAS delivered at the same time as the imperative signal for executing the task. The phenomenon has been mainly studied in basic motor tasks but it is also present in tasks requiring complex patterned movements such as the sit-to-stand manoeuvre (Queralt et al. 2008a), stepping (MacKinnon et al. 2007; Reynolds and Day 2007) or obstacle avoidance (Queralt et al. 2008b).

In the present study we wanted to know whether the StartReact effect is present in gait initiation and whether or not the effects are carried over to the subsequent steps integrated in the ensuing gait-pattern. By knowing this, we aimed to expand our knowledge regarding motor control during gait and clarify if the neural structures involved in the preparation and execution of gait initiation are also involved in the establishment of gait-pattern. We hypothesized that carry over of the StartReact effect to involve gait-pattern would suggest that the two tasks are linked with each other. Therefore, in a simple reaction time task paradigm, we aimed at characterizing the motor preparation of gait initiation and of gait-pattern by means of examining the effects of an unexpected SAS delivered together with a visual imperative signal to start walking.

3.2 Methods

3.2.1 Participants

Eight subjects participated in our study after giving their consent. None of them suffered from any hearing, neurological or motor disorder that could interfere with the experiments. They were aged 23 to 50 years (mean =30.9 ± 10.6), their mean height was 172.3 ± 12.8 cm and their mean weight was 65.3 ± 13.9 kg. The study was approved by the Ethical Committee of the Hospital Clinic and all subjects gave written informed consent to participate in it.

3.2.2 Recording and stimulation

Subjects were requested to maintain a stationary standing posture, in preparation to perform a rapid initiation of gait with their right leg at the appearance of a visual imperative signal and take at least 3 complete steps. The imperative signal was a white 5 cm^2 square appearing on a black computer screen situated at eye level at about 2 m distance slightly lateral to the left of the expected subjects walking path. It was preceded by a verbal warning with a variable foreperiod of 3 to 5 seconds. An electromyograph oscilloscopic sweep was triggered simultaneously with the imperative signal. A SAS was obtained by discharging the coil of a MagStim 200 magnetic stimulator on top of a metallic platform (Valls-Sole et al. 1999). The sound produced in this way, measured at a distance of 1 m from the source with a Brüel and Kjaer Impulse Precision Sound Level Type 2204, was of an intensity of 130 dB sound pressure level.

EMG activity of the tibialis anterior (TA), soleus (SOL), rectus femoris (RF) and biceps femoris (BF) of the right limb was recorded with pairs of surface silver/silver chloride electrodes (0.7 cm diameter). We also recorded the time of each step by placing adequate switches on the floor and on the sole of the foot, one on the heel and the other at the level of the head of the first metatarsal bone. In this way, we recorded toe-off and heel-on during gait phases. Because we were interested in determining if the effects on gait initiation were different from those on gait-pattern, we considered gait initiation to be limited to the very initial events, including only the ‘standing’ phase, lasting from appearance of the imperative signal to the first toe-off of the right limb. For gait-pattern, we considered all the events included in the phases ‘swing’ and ‘stance’, defined, respectively, as the time period from toe-off until the subsequent heel-on and the time period from heel-on until the subsequent toe-off.

All recordings were done with an electromyograph Mystro5Plus (Vickers Medical, Surrey, London) supplied with conventional recording electrodes connected to home-made shielded cables long enough for allowing the subject to move freely along the space. The band-pass frequency filter was set at 50 to 1000 Hz for the EMG activity and a gain of 500 µV per division, with an analysis time window of 5 s. The signal was fed into a personal computer provided with an analysis program (Acknowledge, MP100; Biopac Systems, Bionic, Barcelona). Sample rate was 1.000 Hz.

3.2.3 Procedure

Subjects standing still were requested to react as fast as possible to the visual trigger imperative signal by initiating gait and perform at least 3 steps at their own pace. In some trials at random, a SAS was delivered at the same time as the imperative signal. We collected a total of 20 trials per subject, 15 control trials (without SAS) and 5 test trials (with SAS). Subjects were warned that there could be an external auditory stimulus at the same time as the presentation of the imperative signal, and were instructed to concentrate in responding to the imperative signal, regardless of the presence or absence of SAS. Before beginning with the experiment subjects performed the task a few times to get accustomed to it, and received a few SAS with no instruction to move to be aware of the type of interfering stimuli.

3.2.4 Data analysis

We assigned time 0 to the moment of imperative signal appearance and measured the latency of all events to that point. Onset latency was measured at the first deviation from the baseline larger than 20 µVs, offset latency at the point in which the EMG activity became lower than 20 µVs, and duration as the time between onset and offset. Area of EMG bursts was measured from onset to offset latencies. Toe-off and heel-on were used to calculate the duration of gait phases (standing, swing, and stance phases). The EMG events occurring during each of the phases were also identified according to their onset latency and duration. Events that occurred in the standing phase (for instance TA_{st}) had the subscript ‘st’, except for the inhibition of the tonic SOL activity in which the subscript ‘in’ was used (SOL_{in}). All these events corresponded to the gait initiation phase. For the subsequent swing and stance phases, the events were named according to the order of their appearance (for instance TA_1, TA_2).

Data were grouped for each condition (control and test). Absolute differences between control and test trials were calculated for each event. For statistical comparison between control and test trials we used a repeated-measures one-factor ANOVA. Differences in the amount of anticipation among events were tested by means of paired t tests. Statistical significance was chosen at P = 0.05.

3.3 Results

When SAS was delivered with no instruction to move, no reactions were observed in leg muscles except for a small burst of tibialis anterior activity in the very first trial in 3 subjects. As in the study of Schepens and Delwaide (1995) these responses were clearly different with respect to the ones observed in gait. Representative control and test trials of individual gait recordings are shown in Figure 3.1. In control trials, the first event of gait initiation was SOL_{in}. This was followed at short latency by onset of TA_{st}, RF_{st} and SOL_{st}, before the first toe-off that marked the end of the gait initiation. After gait initiation there was a patterned series of muscular activations and displacements as the gait-pattern was established.

3.3.1 Effects of SAS in gait initiation

All events related to gait initiation followed the same sequence as those in control trials but occurred earlier (Figures 3.1 and 3.2). Mean EMG values are reported in Table 3.1. Statistical analysis showed a significant latency shortening in test compared to control trials for SOL_{in} ($F_{1,7} = 103.76$, $P < 0.001$) and all EMG bursts ($F_{1,7} = 270.71$, $P < 0.001$ for TA_{st}; $F_{1,7} = 178.65$, $P < 0.001$ for RF_{st}; $F_{1,7} = 109.67$, $P < 0.001$ for SOL_{st}). The first toe-off occurred significantly earlier in test than in control trials (368.27 ± 96.82 ms vs 573.97 ± 78.44 ms; $F_{1,7} = 212.36$, $P < 0.001$).

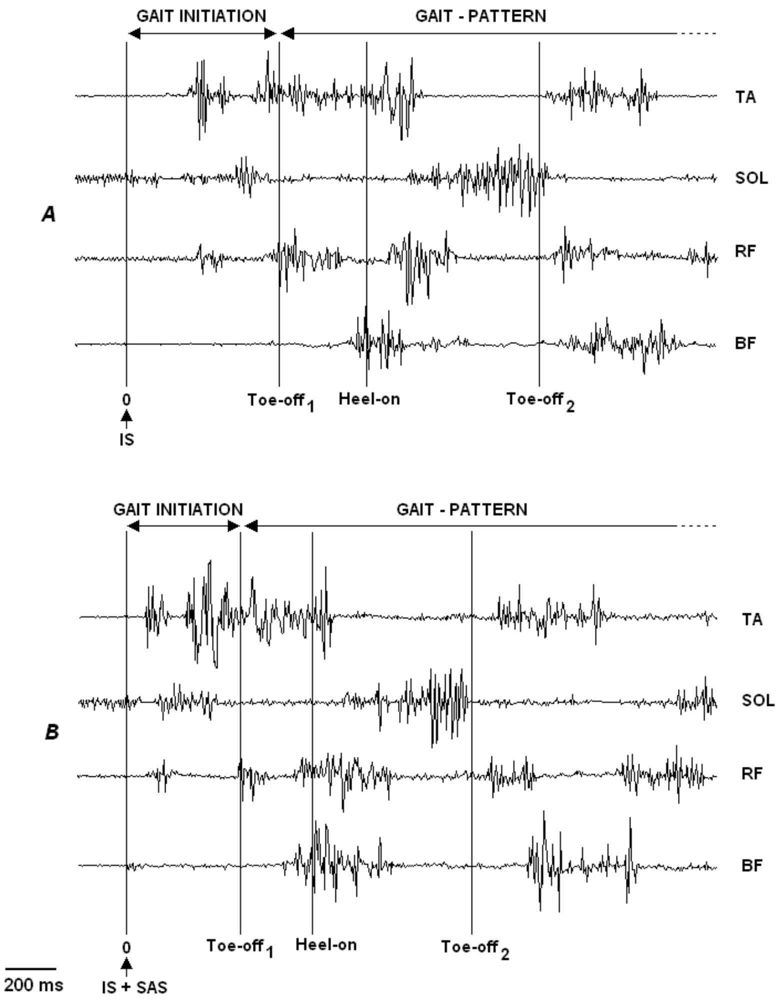

Figure 3.1. Representative examples of gait recordings from one subject. *A*, Control trial. *B*, Test trial

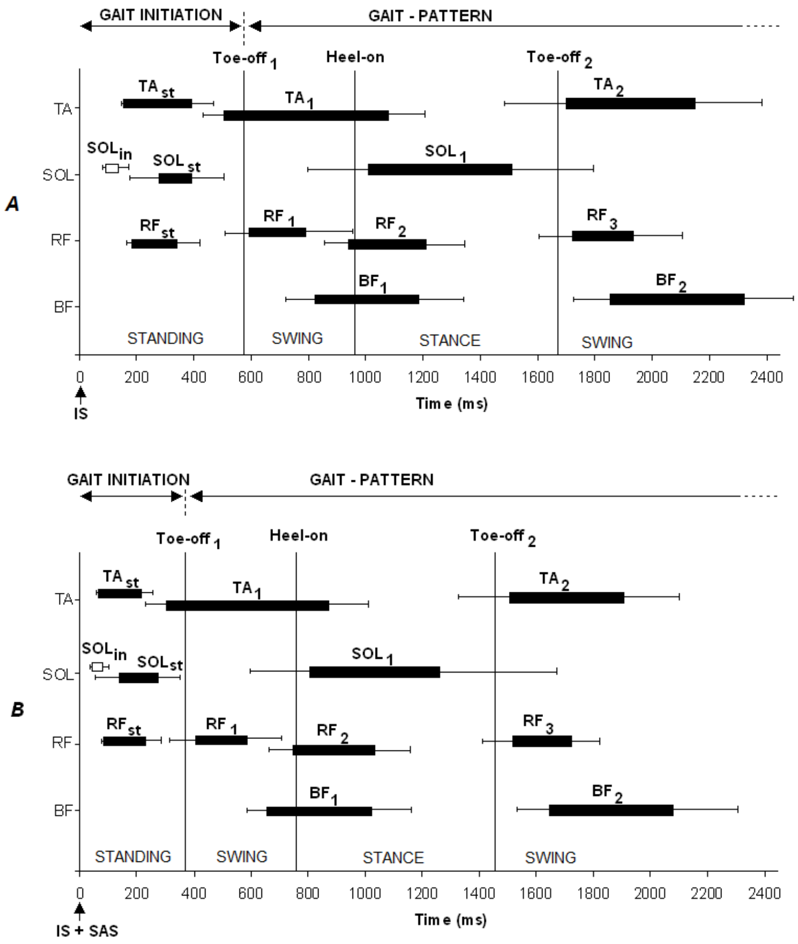

Figure 3.2. Bar representation of latency and duration of EMG events along the walking phases analyzed (N=8). *A.* Control trial. *B.* Test trial. The whisker at the left of each bar represents the standard deviation of the mean onset latency while the whisker at the right side of the bar represents the standard deviation of the mean offset latency. Some bars have been slightly moved from their straight alignment to avoid overlapping of standard deviation markers. The empty bar for SOL_{in} indicates inhibition of tonic activity in opposition to the indication of bursts of activity in the rest of the events. Vertical lines show the latency of kinematic events.

Table 3.1. Mean onset latencies, durations and area of the EMG bursts, with SD within parenthesis of the main events recorded during gait initiation.

	Onset latency		***Duration***		***Area***	
	Control	Test	Control	Test	Control	Test
SOL_{in}	91.58 (19.11)	49.97 (12.90) *	53.09 (26.50)	39.44 (26.78)	-	-
TA_{st}	149.24 (12.71)	63.75 (11.31) *	240.78 (69.23)	150.31 (40.91) *	2.43 (1.22)	3.21 (1.05)
RF_{st}	178.61 (23.30)	76.98 (14.71) *	159.08 (80.38)	156.09 (49.94)	0.71 (0.44)	1.74 (1.00) *
SOL_{st}	271.30 (107.66)	135.00 (86.89) *	120.74 (40.19)	139.22 (47.96)	0.80 (0.45)	1.03 (0.38)

* $P < 0.01$

When SAS was applied, duration of SOL_{in} was reduced (Table 3.1). In addition, the activity of TA_{st} was also shortened. Statistical analysis showed a significant effect only in TA_{st} ($F_{1,7} = 14.13$, $P < 0.01$). In contrast to duration, the amount of EMG activity was larger in test trials than in control trials for all muscles (Table 3.1). Statistical analysis showed a significant effect only in RF_{st} ($F_{1,7} = 15.88$, $P < 0.01$ for RF_{st}).

3.3.2 Effects of SAS on gait-pattern

All events after the first toe-off, considered to be part of the gait-pattern, occurred at shorter latency in test than in control trials. Differences in onset latencies were significant for all EMG bursts ($F_{1,7} = 472.54$, $P < 0.001$ for

TA_1; $F_{1,7} = 133.92$, $P < 0.001$ for RF_1; $F_{1,7} = 157.06$, $P < 0.001$ for BF_1; $F_{1,7} = 217.43$, $P < 0.001$ for RF_2; $F_{1,7} = 264.78$, $P < 0.001$ for SOL_1; $F_{1,7} = 856.97$, $P < 0.001$ for TA_2; $F_{1,7} = 148.10$, $P < 0.001$ for BF_2; $F_{1,7} = 37.22$, $P < 0.001$ for RF_3) as can be seen in Table 3.2. However, there was no significant effect for area of the EMG bursts, nor for duration of swing and stance phases ($P > 0.05$ for all). There was also an anticipation effect on heel-on in SAS trials (756.18 ± 97.27 ms) when compared to control trials (961.77 ± 93.12 ms). It was also observed for toe-off_2 (1457.50 ± 155.32 ms for SAS trials and 1671.03 ± 155.26 ms for control trials). Statistical analysis showed significant effects between conditions ($F_{1,7} = 51.55$, $P < 0.001$ for heel-on; $F_{1,7} = 164.89$, $P < 0.001$ for toe-off_2). Mean latency values for all events recorded during gait initiation and the first swing and stance phases are shown in Figure 3.2. Note that the pattern of kinematics and muscle activations is not different in control and test trials.

Table 3.2. Mean onset latencies, durations and area of the EMG bursts, with SD within parenthesis of the main events recorded during gait-patterned walking.

	Onset latency		Duration		Area	
	Control	Test	Control	Test	Control	Test
TA_1	497.48 (78.93)	301.20 (77.15) *	574.89 (91.06)	572.50 (120.63)	0.99 (0.26)	1.11 (0.45)
RF_1	588.97 (87.26)	401.49 (96.74) *	173.78 (66.70)	186.43 (45.27)	0.80 (0.56)	0.83 (0.38)
BF_1	847.01 (85.05)	654.24 (72.15) *	367.71 (139.68)	369.31 (160.30)	1.13 (0.53)	1.34 (0.83)
RF_2	937.85 (85.90)	745.63 (88.29) *	269.65 (98.75)	290.99 (68.01)	1.06 (1.05)	1.09 (0.99)
SOL_1	1006.78 (213.85)	802.45 (211.91) *	522.49 (136.07)	527.14 (163.41)	1.13 (0.45)	1.16 (0.35)
TA_2	1699.90 (192.13)	1501.79 (184.94) *	445.40 (116.04)	413.75 (44.87)	1.20 (0.24)	1.13 (0.37)
RF_3	1731.00 (125.37)	1517.47 (130.43) *	199.00 (74.49)	136.75 (93.30)	0.58 (0.38)	0.75 (0.84)
BF_2	1851.03 (131.50)	1647.50 (116.45) *	475.11 (287.29)	433.47 (289.41)	1.28 (0.63)	1.38 (0.55)

* $P < 0.001$

3.3.3 Different effects of SAS on gait initiation and on gait-pattern

In order to compare the amount of shortening in gait initiation and gait-pattern, time differences between control and test trials were analysed. Figure 3.3 shows the differences for both movement events and EMG onset latencies. Mean absolute differences for the EMG bursts that correspond to gait initiation (SOL_{in}, TA_{st}, RF_{st} and SOL_{st}) were between 40 ms and 150 ms, while those included in the gait-pattern, were overall around 200 ms.

Statistical analyses showed significant differences between the amount of anticipation of all gait initiation events and any EMG or movement events of the gait-pattern ($P > 0.05$). Not significant differences were found among the degree of anticipation of toe-off$_1$ (end of gait initiation) and all the following gait-pattern events ($P > 0.05$ for all).

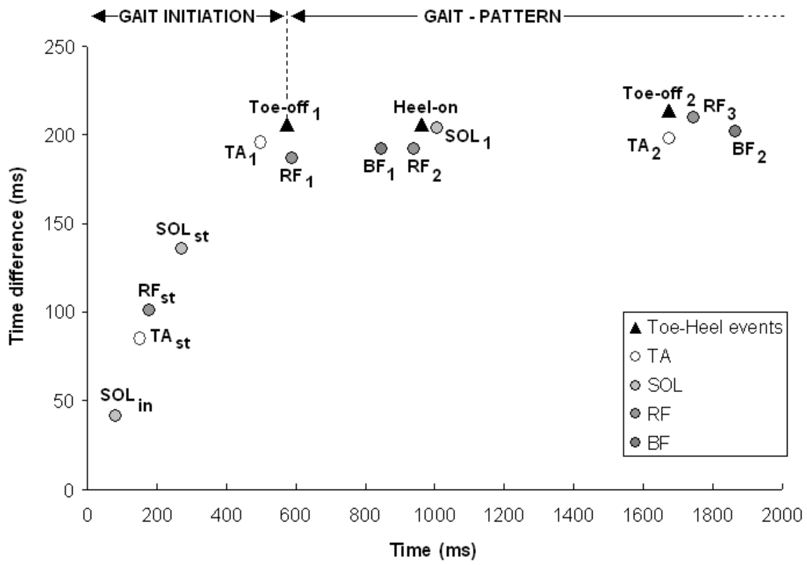

Figure 3.3. Time differences (between control and test trials) for EMG onset latencies. The horizontal axis indicates time along the values of control trials in which the events would be initiated at the mean latency represented by each symbol. The vertical axis indicates the mean latency difference found between control and test trials at each of the events. Note that the absolute mean differences increase up to the end of gait initiation and remain stable during gait-patterned walking.

3.4 Discussion

In this report, we studied the effects of a SAS on gait initiation and on the establishment of the gait-pattern sequence of walking. Gait initiation is mainly described as the joint action of muscles displacing the centre of gravity to start walking. Following the first toe-off, a series of events are repeated as part of the gait-pattern sequence of movements. Our main result is that both tasks are speeded-up when a SAS was presented together with the imperative signal to initiate gait. However, gait-pattern and the sequence of swing and stance phases were unmodified with respect to the last event considered as part of the gait initiation, i.e., the moment of the first toe-off. This suggests that the preparation and release of a triggered reaction (gait initiation) leads to the early activation of the motor program for locomotion. We could consider that the pattern generated for gait is actually not changed between control and test trials but in these it is initiated by a task that has been advanced in latency by SAS.

Basic and complex motor actions are anticipated when a SAS is added to the imperative signal, in the so-called StartReact effect (Valls-Sole et al. 1999; Carlsen et al. 2004a; MacKinnon et al. 2007; Reynolds and Day 2007; Queralt et al. 2008a; 2008b). With the study presented here, we have demonstrated that the

StartReact effect is also present for gait initiation, considered as a single motor program composed by the basic EMG sequence of SOL inhibition-TA burst activation (Crenna and Frigo 1991). The speeding-up of events in gait initiation is accompanied by an increase in the size and a decrease in duration of EMG bursts, which may indicate a higher synchronization of activity in the StartReact effect (Valls-Sole et al. 1999). The suggested physiological mechanism underlying the StartReact effect is that motor programmes are represented in subcortical structures where they are accessible to a startling stimulus (Valls-Sole et al. 1999; Carlsen et al. 2004a). Also, the combined stimulation of two different sensory modalities could lead to intersensory facilitation, which could contribute to some extent to the shortening of the initial reaction. The superior colliculus is a potential site for this facilitation (Reynolds and Day 2007).

This study expands the initial finding of MacKinnon et al (2007) who reported that tibialis anterior activity was advanced with startle stimuli applied together with the imperative signal for gait initiation. We describe that the speeding up of the activity occurs in all lower limb muscles engaged in gait initiation. In addition, we suggest that although the ensuing motor pattern is also shifted in time, this shifting is secondary to an early activation of gait initiation. This result is in line with the one from Delval et al

(2005) who found no differences, in terms of kinematic data, in the subsequent steps between self-paced and triggered gait initiation, although attention should be paid to the fact that our subjects were requested to prepare the program to be launched.

After gait initiation, the muscular and movement events considered in the gait-pattern were also speeded-up but there was no more progressive latency shortening. It remained steady for the whole recorded epoch beyond the first toe-off. To explain this finding, we should consider that gait-pattern is mainly dependent on specialized neural circuits included in the concept of central pattern generators. The probable existence of central pattern generators producing rhythmic movements has been considered for a large number of vertebrates (MacKay-Lyons 2002). The evidence for their existence in humans is indirect through studies on spinal cord injury subjects (Wernig and Müller 1992; Barbeau et al. 1998). We consider that the anticipation of gait-pattern may either be due to a direct influence of SAS over the central pattern generator of gait maintenance or be a secondary consequence of the effects of SAS on gait initiation, which would then trigger the muscle activation sequence of the gait-pattern.

Afferents from peripheral nerves may operate on central pattern generators (Clarac 2008; Crapse and

Sommer 2008). Therefore, it could be suggested that startle-induced kinematic changes may affect the central pattern generators for gait. However, Nieuwenhuijzen et al. (2000) reported that startle was well integrated during gait, with only discrete kinematic changes that did not modify its course. In the same line, the results of Schepens and Delwaide (1995) indicated that the step cycle was not modified when an unexpected loud sound was applied. Therefore, we consider that the afferent information from proprioceptors to the spinal cord would not be differently processed between control and test conditions in our study. Furthermore, the fact that anticipation of gait-pattern is tightly linked to gait initiation supports the view that the proprioceptive information may not be responsible of that.

The effects of SAS are conveyed through the reticular system (Davis et al. 1982). During locomotion, Drew et al. (1991) demonstrated in cats that the central pattern generator for gait maintenance receives inputs from the reticular formation. This observation supports the view that there may be a direct influence of SAS on the central pattern generator activity which would possibly explain part of the findings of our study. In any case, our results in test trials suggest that before the imperative signal the central pattern generator for gait should have been prepared for its activation after gait initiation. If this were not the case, the anticipation of the events induced by SAS would have caused a distortion in the integration of sensory inputs generated during the gait initiation into the program for gait-pattern. We suggest that the subcortical motor circuits responsible for gait-pattern were already prepared beforehand, with no need for any additional influence from peripheral information. This may be necessary to protect the motor program from unwanted sensory information and maintain the stability of gait, which could be distorted if proprioceptive information was let to impinge on the central pattern generator.

This chapter has been adapted from a submission to Gait & Posture.

CHAPTER 4

THE EFFECTS OF AN AUDITORY STARTLE ON OBSTACLE AVOIDANCE DURING WALKING

4.1 Introduction

When a SAS is applied at the same time as the imperative signal in a simple reaction time task experiment, subjects execute the required task significantly faster while maintaining the basic motor program undisturbed (Valls-Sole et al. 1995; 1999; Carlsen et al. 2004a; 2004b). The underlying physiological mechanisms of this phenomenon, termed StartReact effect (Valldeoriola et al. 1998; Valls-Sole et al. 1999), are not completely clear yet. It is suggested that, during preparation, simple reaction time motor programmes become fully represented in subcortical motor structures, where they are accessible to activation by external stimuli (Valls-Sole et al. 1999; Carlsen et al. 2004a; 2004b; Kumru and Valls-Sole 2006; Castellote et al. 2007). This may also explain the observation of Carlsen et al. (2004a) who found no significant effect of an auditory startle in choice reaction time tasks, in which the pre-programming of a response may not be possible. However, this seems not always to be the case since many authors have reported on the speeding up of movements in some forms of choice reaction time tasks (Valls-Sole 2004; Kumru et al. 2006; Oude Nijhuis et al. 2007; Reynolds and Day 2007). Another possibility to explain the StartReact effect is that the energy of the stimulus used as imperative signal increases with the presence of the startle, inducing the so-called intersensory facilitation (Nickerson 1973; Gielen et al. 1983; Schmidt et al. 1984) and attributing the responses to the joint stimulation of multiple sensory modalities.

A few studies have reported on the effects of an auditory startle on some complex automatic movements such as walking (Schepens and Delwaide 1995; Nieuwenhuijzen et al. 2000), gait initiation (MacKinnon et al. 2007) and sit-to-stand (Queralt et al. 2008a). In most instances, latency shortening was the only change observed in the patterned activity. This suggests again that the subcortical motor structures responsible for the execution of automatic or overlearned motor tasks were activated by a SAS. A recently published example of such effect is the startle-induced shortening of reaction time when adjusting a stepping movement to the right or to the left (Reynolds and Day 2007). The direction of the adjustments was not known in advance and was guided by the visual stimulus. Reynolds and Day (2007) suggested that shortening of stepping reactions could be particularly relevant in situations, such as obstacle avoidance, when fast stepping adjustments are of utmost importance. Avoiding a suddenly appearing obstacle during walking is a reaction time task where subjects have to perform fast gait adjustments. The strategy for obstacle avoidance to be adopted, i.e. lengthening or shortening of the stride is influenced by the ongoing gait phase. This is an important difference with respect to the results reported by Carlsen et al. (2004a) who used a choice reaction time paradigm requiring simple ballistic movements. In our work and in that reported by Reynolds and Day (2007), a choice reaction time task was implemented in an ongoing movement. These obstacle avoidance reactions are faster than voluntary reactions (Weerdesteyn et al. 2004), suggesting that subcortical pathways might be involved. However, so far, nothing is known about gait adjustments to an obstacle when an auditory startle is given. Therefore, the present study was carried out to investigate the effects of a SAS on obstacle avoidance at different phases of the gait cycle. We aimed at expanding our knowledge regarding motor control during gait. Further specific goals were to assess if SAS speeds up the impending movement in a situation of choice reaction time task under the constraints of time and the functional implications of the presence of an auditory startle in obstacle avoidance tasks. Another goal of the present study was to study how perturbations can affect gait. From previous work it is known that startle responses can be integrated surprisingly well in normal gait (Nieuwenhuijzen et al. 2000). However, it is unknown how such responses affect more complex gait, such as occur when stepping over obstacles. Such questions are important, for example for our understanding of how gait perturbations can lead to a fall.

A second related question was whether the actual observation of the obstacle movement was an absolute requirement for a StartReact effect on obstacle avoidance. Some studies reported that when the acoustic stimulus was delivered during the foreperiod of a reaction time experiment, the reaction was indistinguishable from the one observed when the startle was delivered together with the imperative signal (Valls-Sole 2004; Kumru and Valls-Sole 2006). Similarly, MacKinnon et al. (2007) found that subjects were already prepared for right leg step initiation even before the imperative stimulus for a choice reaction was given. These seemingly ‘inappropriate’ reactions indicate that SAS releases involuntarily a subcortically prepared motor programme. Based on these observations we hypothesized that obstacle avoidance reactions could be elicited even in the absence of the obstacle actually falling. To test this idea, we used two conditions: one in which the obstacle was not present at all and another one in which the obstacle was visibly present but did not fall into the subject’s path.

4.2 Methods

4.2.1 Participants

Twelve healthy adults (10 women, 2 men, mean age 25.67 ± 6.69 years) participated in the study. None of them suffered from any hearing, neurological or motor disorder that could interfere with the experiments. None had participated in previous experiments implying the methods used in this study, which was approved by the local medical ethics committee and was conducted in accordance with the Declaration of Helsinki. All subjects gave written informed consent to participate in the study.

4.2.2 Procedure

Two experiments were done in separate sessions. In the first experiment, participants walked on a treadmill at a fixed speed of 3 km/h wearing flexible gymnastic shoes and binaural earphones (Figure 4.1). The obstacle, a wooden board of 40x30x1.5 cm, was suspended from a bridge via a small metallic piece attached to the middle part of the obstacle, held by a computer-operated electromagnet (Schillings et al. 1996; 1999; 2000; Weerdesteyn et al. 2003) that could be released by a trigger from the computer. It was placed in front of the subject at a distance of approximately 10 cm from the most anterior position reached by the toes in the swing phase.

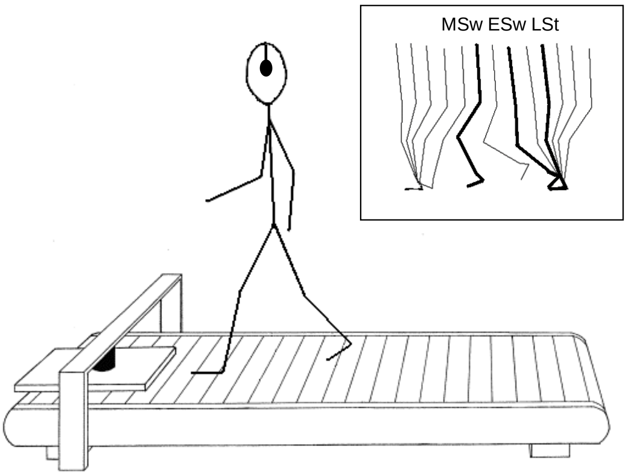

Figure 4.1. Schematic diagram of the experimental setup. The electromagnet is attached to a bridge over the front of the treadmill. The obstacle falls onto the treadmill in front of the subject's left foot after the electromagnet has been switched off by a trigger from the computer. The three obstacle release phases were Late Stance (LSt), Early Swing (ESw) and Mid Swing (MSw).

After release, the obstacle always dropped in front of the left foot. Three reflective markers (diameter 14 mm) were attached to the left foot at heel, hallux and external maleolus. A fourth marker was placed on top of the obstacle. Marker positions were recorded by a 6-camera 3-D motion analysis system (Vicon®) at a sample rate of 100 Hz. These marker positions were processed in real time in order to determine the moment of obstacle release related to gait phase. The obstacle was only released when a regular walking pattern was observed and after at least five unperturbed strides had been taken from the start of the trial. Stride regularity was defined as a maximum difference of 50 ms between two consecutive strides. The obstacle was dropped randomly at 3 different moments of the step cycle (Figure 1): Late Stance (45-59% of the step cycle), Early Swing (60-69%), or Mid Swing (70-85%). Note that the later the obstacle is released along the step cycle, the time allowed for the reaction is shorter and the condition becomes more challenging.

A custom-made noise generator delivered unexpected startling stimuli through binaural earphones, consisting of 50 ms white noise with an intensity of 110 dB. The experimental procedure consisted of 60 obstacle avoidance trials, 20 in each of the previously defined phases of the step cycle. The SAS was delivered in 5 trials (Obstacle Avoidance trials with startle), interspersed among the remaining 15 trials (Obstacle Avoidance trials without startle) for each step cycle. Startle was delivered at a latency of 40 ms after obstacle release.

The participants were requested to step over the obstacle, and stepping aside from it was specifically discouraged. Any contact with the obstacle was noted as a failure. Surface EMG data were collected from the biceps femoris, the rectus femoris, the tibialis anterior and the gastrocnemius medialis of the left leg. We also recorded the EMG activity from the sternocleidomastoid to check for the presence of a startle reaction. Self-adhesive Ag/AgCl electrodes (Tyco Arbo® ECG) were placed approximately 2 cm apart and longitudinally on the belly of each muscle, according to European guidelines (Hermens et al. 1999). The EMG signals were sampled synchronously with the marker data at 1000 Hz.

The second experiment was conducted in five of the twelve subjects. The procedure was similar to the first experiment. Subjects performed trials in which the obstacle was released in the same three phases of the step cycle as in the first experiment. Randomly, we presented twenty-one trials in which an auditory startle was delivered at Late Stance. In five of them the obstacle was not present (No Obstacle trials), in eight the obstacle was visibly present but it did not fall (Stationary Obstacle trials), and in the remaining eight trials startle was applied as in the first experiment, 40 ms after obstacle release.

In both experiments the number of trials in which the SAS was applied represented no more than 25 per cent of the trials to ensure that subjects did not habituate to the stimulus (Siegmund et al. 2001; Carlsen et al. 2003; Queralt et al. 2008a). To be aware of the type of interfering stimuli, subjects performed a few obstacle avoidance trials before beginning with the experiments and they also received a few isolated SAS.

4.2.3 Data analysis

EMG activity was full-wave rectified and low-pass filtered at 25 Hz (zero-lag, second order Butterworth filter). The EMG characteristics were determined for each of the selected muscles as the mean of 30 trials in the stride before obstacle release, which was used as the control stride. Onset latency of the EMG activity was determined by a combination of a computer algorithm and visual observation as the time between obstacle release and the instant at which EMG activity exceeded the average control stride plus 2 SD. For each muscle, we determined the rate of response occurrence as the percentage of trials in which an onset latency was detected. Average EMG amplitude was calculated over 100 ms following the muscle onset latency. Response amplitude was normalized with respect to the average activity of the control stride for each muscle. Averages and standard deviation of EMG onset latencies and EMG amplitudes were calculated for all subjects and phases of obstacle release.

During the experiment we noted whether subjects selected a long step strategy or a short step strategy (Chen et al. 1994; Weerdesteyn et al. 2004; 2005) in avoiding the obstacle and the corresponding percentage of trials for each category was calculated. However, as in the second experiment there were trials in which the obstacle did not fall or trials without obstacle, the percentage of stride shortening or lengthening was calculated with respect to the previous step. We also noted whether the trial was successful or unsuccessful and avoidance success rates were calculated for each Obstacle Avoidance condition.

In order to analyze whether EMG onset latencies, amplitudes and proportions of avoidance strategies were different between both Obstacle Avoidance conditions (presence or absence of startle) and gait phases, repeated-measures ANOVA was conducted in the first experiment. Differences in stride length modifications between trials with and without startle were tested by means of paired *t* tests. Wilcoxon Signed Ranks test was also conducted to compare success rates between both conditions because these were not normally distributed due to frequently reaching 100% of success. For the second experiment, due to the small sample size, a Friedman test on the three startle conditions (No Obstacle, Stationary Obstacle and Obstacle Avoidance) was performed and, if appropriate, *post hoc* Wilcoxon Signed Ranks test was conducted to determine differences among conditions. Statistical significance was chosen at $P = 0.05$.

4.3 Results

The first muscle activated in all Obstacle Avoidance trials was biceps femoris. This muscle had the highest rate of response occurrence (75.7%). In line with previous studies (Weerdesteyn et al. 2007), the biceps femoris was considered the prime mover of the obstacle avoidance task. After biceps femoris, there was no consistent patterned activation of other muscles which we recorded from. The rates of response occurrence in other muscles were 53.8% for rectus femoris, 64.9% for tibialis anterior and 47.2% for gastrocnemius medialis. Mean values revealed earlier responses in all subjects when an auditory startle was delivered together with the imperative signal. EMG responses in sternocleidomastoid were present in 77.2 % of the auditory startle trials and the average onset latency was 56.1 ± 7.4 ms. Startle habituation was not observed.

4.3.1 The effect of SAS on obstacle avoidance

Onset latencies

A noticeable shortening of the response onset was observed in all subjects when an auditory startle was delivered with the imperative signal. Two single representative Mid Swing trials are shown in Figure 4.2. This effect was seen for all muscles and conditions (Figure 4.3A). The percentage of shortening taking all obstacle release conditions together was 20.0% for biceps femoris, 19.6% for rectus femoris, 20.9% for tibialis anterior and 9.4 % for gastrocnemius medialis, which numbers correspond to earlier responses of 30.7, 31.1, 33.0 and 14.4 ms, respectively. Differences in EMG onset latencies between trials with and without startle were also seen in the second experiment. The percentage of shortening was 17.7% for biceps femoris, 15.4% for rectus femoris, 13.0% for tibialis anterior and 10.7% for gastrocnemius medialis, with earlier responses of 28.6, 25.1, 19.9 and 19.1 ms, respectively. Statistical analysis for the first experiment showed that the effect of startle was significant for all muscles ($F_{1,11} = 32.83$, $P < 0.001$ for biceps femoris; $F_{1,9} = 24.50$, $P < 0.005$ for rectus femoris; $F_{1,10} = 44.52$, $P < 0.001$ for tibialis anterior; $F_{1,9} = 6.60$, $P < 0.05$ for gastrocnemius medialis). There was no significant effect of phase ($P > 0.05$), except for biceps femoris ($F_{2,22} = 5.71$, $P < 0.05$), with earlier responses in Mid Swing condition followed by Early Swing and Late Stance conditions.

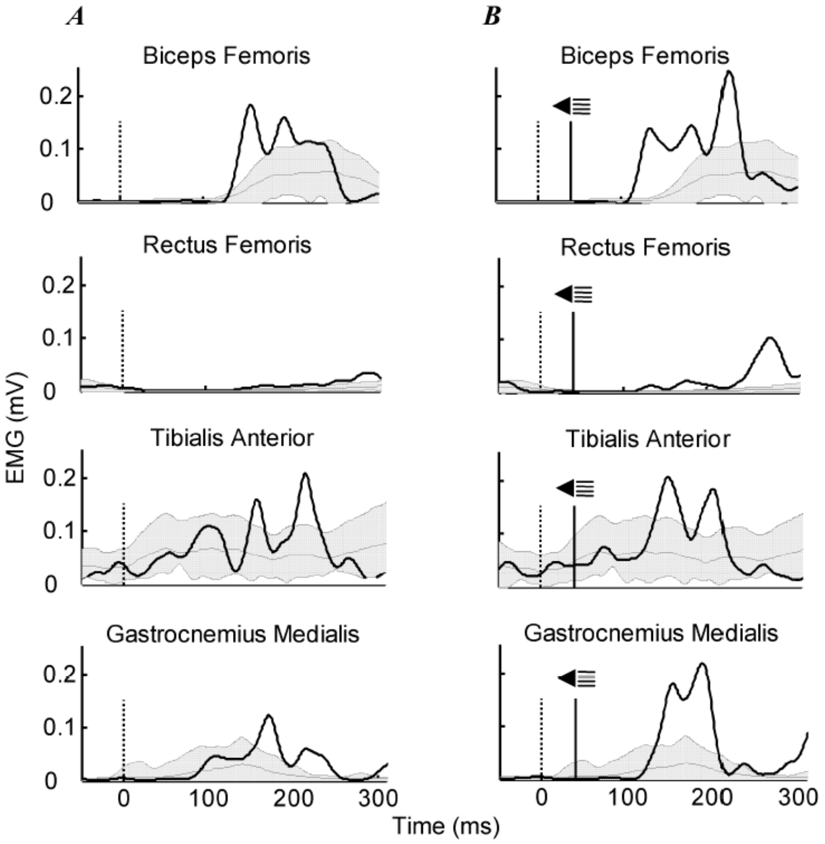

Figure 4.2. Examples of EMG responses for obstacle avoidance. EMG activity of biceps femoris, rectus femoris, tibialis anterior and gastrocnemius medialis in response to an obstacle release at Mid Swing. Representative trials from one subject. *A*, No startle trial. *B*, Startle trial. The vertical dotted line indicates the obstacle release moment. The vertical full line shows when the startle was given. The shaded area represents mean and ± 2 SD. of EMG activity of the control stride. Superimposed (full line) is the trace of the representative trial. The obstacle was released at 72.8% of the step cycle in *A* and at 71.1% of the step cycle in *B*, which accounts for the slight delay of the control stride in *B* with respect to *A* (difference of 20 ms).

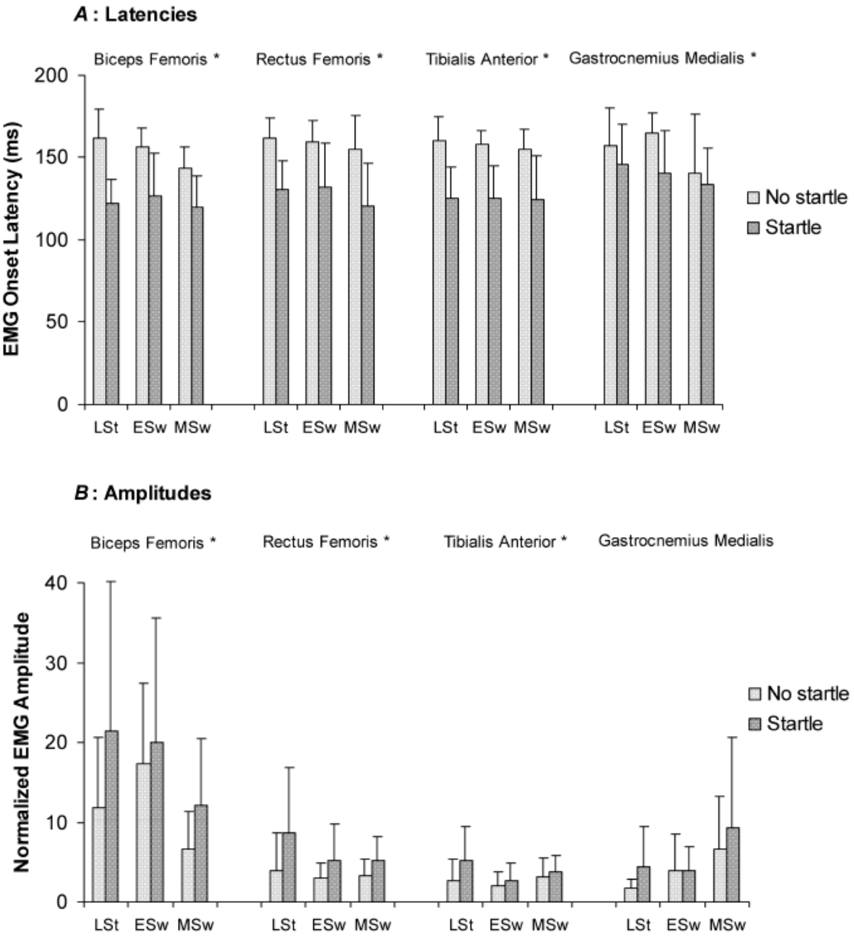

Figure 4.3. EMG effects of SAS on obstacle avoidance. Mean values and standard deviation of onset latencies (*A*) and amplitudes (*B*) of EMG activity in biceps femoris, rectus femoris, tibialis anterior and gastrocnemius medialis muscles in response to an obstacle for no startle and startle trials. Obstacle release phases were Late Stance (LSt), Early Swing (ESw), and Mid Swing (MSw).
* $P < 0.05$ between startle and no startle conditions.

Amplitude of EMG bursts

The response to the approaching obstacle in trials with startle was also characterized by larger amplitudes of EMG bursts in comparison to those without startle (Figure 4.3B). Differences in response amplitudes were significant in biceps femoris ($F_{1,11} = 10.98$, $P < 0.05$), in rectus femoris ($F_{1,9} = 14.31$, $P < 0.005$) and in tibialis anterior ($F_{1,10} = 6.61$, $P < 0.05$). Overall, there was no consistent phase-dependency in the startle-related change of EMG amplitudes. As expected, EMG amplitudes of trials with startle were also significantly larger than those without startle in the second experiment.

Stride modifications and success rates

Obstacle avoidance strategies differed according to gait phase. Mean percentages of long step strategy are presented in Table 4.1. Generally, long step strategy was less often used if the time pressure increased (main effect of phase, $F_{2,10} = 11.34$, $P < 0.005$). The presentation of an auditory startle together with the imperative signal caused a significant change in strategy, increasing the use of long step strategy by 13.7% (Late Stance trials), 19.5% (Early Swing trials) and 2.5% (Mid Swing trials) (main effect of startle, $F_{1,11} = 13.97$, $P < 0.005$). There was no interaction effect between phase and startle. In the second experiment, in which only Late Stance trials were performed together with startle, long step strategy was used in 45.6% of trials without startle and in 62.1% of those with startle. Therefore, the results were similar to experiment 1, where increased incidence of long step strategy was observed when an auditory startle was given. Within each strategy the amount of stride shortening or lengthening of the obstacle avoidance stride was affected by startle as well. Both percentages of stride shortening (in case of short step strategy) and lengthening (in case of long step strategy) were higher when the obstacle was presented together with an auditory startle in any of the obstacle release conditions (Figure 4.4). These changes were significant in stride shortening for Early Swing and Mid Swing conditions (P = 0.015 for Early Swing, P = 0.002 for Mid Swing).

Table 4.1. Mean percentages of long step strategy for obstacle avoidance (OA).

	LSt	ESw	MSw
OA trials	48.0 (44.2)	15.6 (28.4)	9.0 (28.8)
OA_{SAS} trials	61.7 (38.3)	35.1 (44.0)	11.5 (29.5)

Data are the mean (SD) for each phase of the step cycle: Late Stance (LSt), Early Swing (ESw) and Mid Swing (MSw).

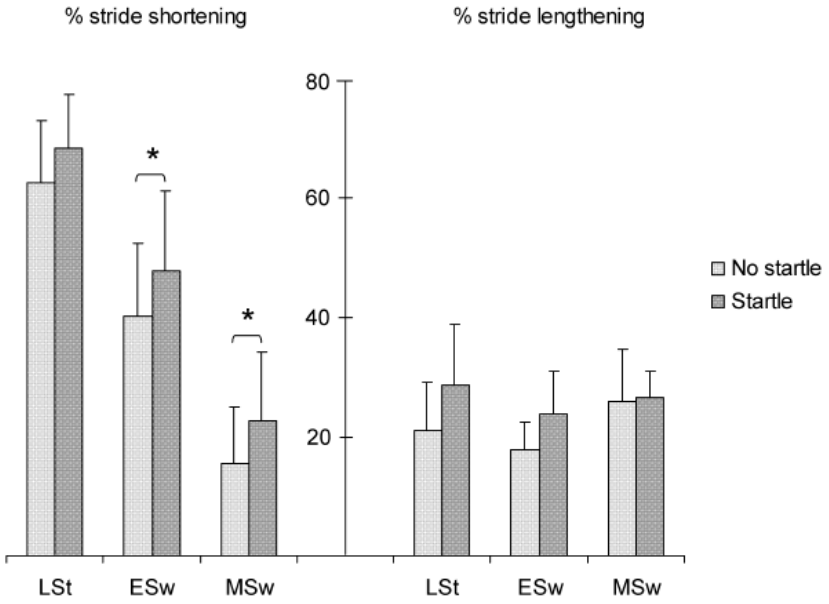

Figure 4.4. Stride modification effects of SAS on obstacle avoidance. Mean percentages and standard deviation of stride shortening or lengthening for no startle and startle trials. Obstacle release phases were Late Stance (LSt), Early Swing (ESw) and Mid Swing (MSw). * $P < 0.05$
Note: the number of trials in each condition was different (see Table 4.1) since there were few Late Stance trials in which subjects performed a short step strategy (or Early Swing and Mid Swing trials in which subjects performed a long step strategy). This may partly explain why significance was only obtained for Early Swing and Mid Swing in stride shortening.

Success rates in Obstacle Avoidance trials without startle were high, for all phases (Late Stance 99.4%; Early Swing 99.5%; Mid Swing 92.7%). However, when a SAS was presented along with obstacle release, success rate was 100% at all phases (Late Stance, Early Swing, Mid Swing). Wilcoxon Signed Ranks test revealed that success rates in Obstacle Avoidance trials with startle were significantly higher ($P = 0.025$) than in those without startle.

4.3.2 Responses to SAS in obstacle conditions

The average normalized EMG responses in the three startle conditions are shown in Figure 4.5A together with the Obstacle Avoidance condition without startle (added for comparison). Onset latencies were clearly similar in conditions in which an auditory startle was delivered. Statistical analysis showed that differences in EMG onset latencies were not significant for any muscle ($P > 0.05$). Therefore, the mean onset latencies when a startle was applied together with the obstacle were not significantly different with respect to mean onset latencies measured when the stimulus was applied but the obstacle did not fall or it was not present (Figure 4.5A). However, the rate of response occurrence was different for each condition. For instance, activation of biceps femoris, prime mover of the obstacle avoidance task, was observed in 52.0% of No Obstacle trials, in 100.0% of Stationary Obstacle trials and in 90.0% of Obstacle Avoidance trials. Also, the mean amplitude of EMG activity was different in the three startle conditions. The largest EMG amplitude was observed in Obstacle Avoidance trials, followed by Stationary Obstacle trials, while the smallest amplitude was observed in No Obstacle trials. These amplitudes were significantly different in biceps femoris (Friedman's statistic [2] = 10.00, P < 0.05) and rectus femoris (Friedman's statistic [2] = 6.63, P < 0.05). Post hoc analysis revealed that the amplitudes of biceps femoris in any of the three conditions were significantly different from each other. Furthermore, if we observed the time window indicated by a box in Figure 4.5A, it is clear that the obstacle avoidance response when a startle was given was not just a summation of startle and obstacle avoidance separately. For this area, EMG amplitude of the Obstacle Avoidance condition with startle was 76.1% higher than the sum of Stationary Obstacle and Obstacle Avoidance without startle conditions.

The percentages of stride shortening and lengthening are shown in Figure 4.5B. In the Obstacle Avoidance condition the stride was clearly shortened (when a short step strategy was performed) or lengthened (when a long step strategy was performed). Barely perceptible modifications were observed in No Obstacle condition. However, the tendency to shorten and lengthen the stride in Stationary Obstacle condition was present. Both percentages of stride shortening and lengthening were significantly different among conditions (Friedman's statistic [2] = 10.00, P < 0.05).

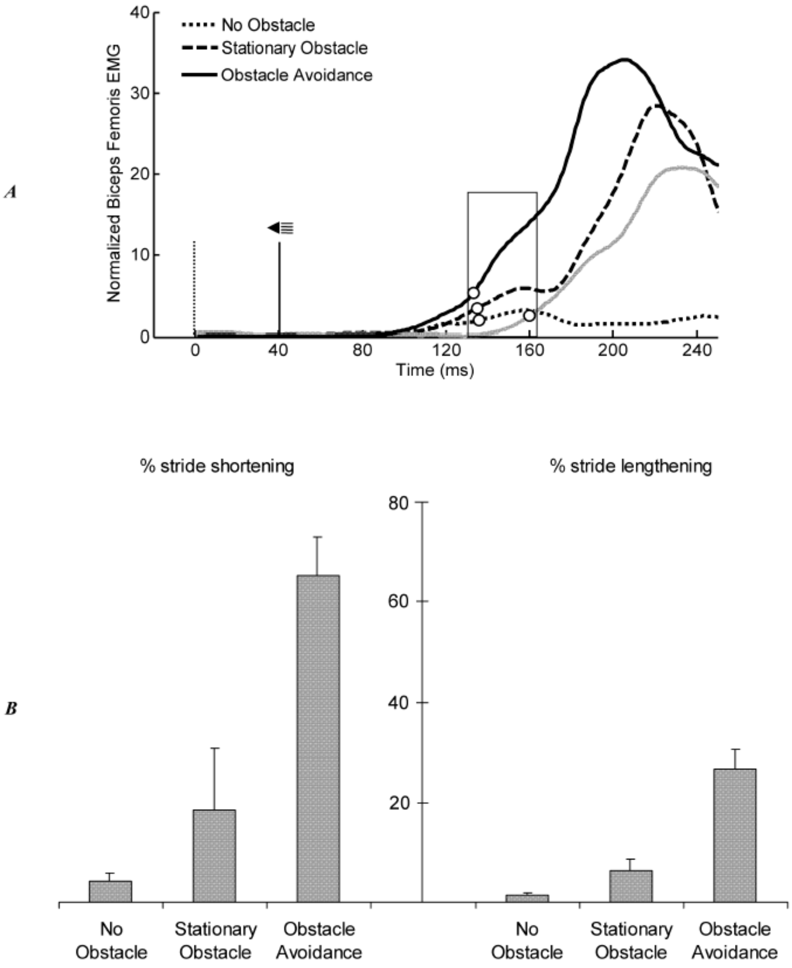

Figure 4.5. Responses to SAS in obstacle conditions. *A,* averaged EMG data of all subjects for biceps femoris in three different startle conditions (No Obstacle, Stationary Obstacle and Obstacle Avoidance). Obstacle Avoidance condition without startle (grey trace) is added for comparison. Open circles in the traces indicate mean onset latency of each condition. The vertical dotted line indicates the obstacle release moment. The vertical full line shows when the startle was given. The time window used to compare the amplitudes of the various conditions is indicated by a box. *B*, mean percentages and standard deviation of stride shortening or lengthening for startle conditions.

4.4 Discussion

To our knowledge, this is the first study to investigate the effects of an auditory startle on the response to an obstacle avoidance task. Our main results are that when the SAS was applied together with the obstacle, subjects not only reacted faster but also had a more effective performance with fewer errors.

4.4.1 Response latencies and amplitudes

The onset latency of the EMG bursts recorded in startle trials requiring obstacle avoidance was shorter than in those without startle, an effect that was most strongly seen in the biceps femoris. The biceps femoris is also the most consistently activated muscle in avoidance responses following obstacle release (Weerdesteyn et al. 2007). This is in line with the speeding up of a reaction without its perturbation, as seen in the StartReact effect. The fact that in obstacle avoidance tasks, gait adjustments are done faster than other voluntary reactions (Weerdesteyn et al. 2004) led to the suggestion that subcortical motor structures may already be prepared to react with a patterned program to the presentation of an external visual stimulus. The present data are in line with this suggestion. Not only onset latencies benefited from the startle but also response amplitudes. Enhancement of amplitudes to a startle has been found in preparation for movements in simple reaction time tasks and is assumed to result from a sustained level of enhanced excitability in startle pathways preceding the onset of movement (Kumru and Valls-Sole 2006).

In a separate experiment, we investigated whether such startle-induced effects on latencies and amplitudes were also present in the absence of the imperative stimulus. Subjects were given a startle when the obstacle was either not present, or was present but did not fall. The results clearly showed that the rate of response occurrence in biceps femoris was low when the obstacle was not present. However, in the presence of the obstacle subjects expect it to fall and engage in preparation of the appropriate motor program. In this situation, the SAS would trigger the prepared subcortical response without the obstacle actually falling, as it has been observed in simple reaction time experiments when the auditory startle was presented before the imperative signal (Valls-Sole 2004; Kumru and Valls-Sole 2006). In our experiment, the reaction to the startle, when subjects were expecting the obstacle to fall, had the same latency as the reaction to the obstacle combined with startle. Furthermore, we also observed a tendency of shortening or lengthening the stride in the trials in which subjects did not have an obstacle to avoid but the obstacle was present. In contrast, when the obstacle was not present, subjects did not make any gait adjustments when an auditory startle was given (Figure 4.5B). These findings further strengthen the hypothesis of subcortically prepared responses triggered by an auditory startle.

It should be emphasized, nevertheless, that the response to a startle in trials with a stationary obstacle was smaller in amplitude than in trials that required obstacle avoidance. Such difference could be explained by assuming that the actual observation of the obstacle moving is a potent visual stimulus that provides a powerful extra input to the neural structure involved in generating the response. This may well be evidence of an intersensory facilitation hypothesis, in which facilitation occurs when inputs from various modalities (auditory startle and visual input, in this case) are added (Nickerson 1973; Terao et al. 1997; Siegmund et al. 2001). Intersensory facilitation can only explain a small part of the StartReact effect (Valls-Sole et al. 1995; 1999; Sanegre et al. 2004). The data gathered in the present study suggest that the two effects may be complementary to each other. When a startle was applied with a stationary obstacle, latencies of the reaction were shortened to a similar extent as in trials in which an obstacle had to be avoided, suggesting a StartReact effect. However, the amplitude of the EMG activity became larger when avoiding the obstacle, which suggests a further role of visual inputs in augmentation of the response, a feature compatible with intersensory facilitation.

4.4.2 Startle and stride modifications

If the obstacle was released in the Late Stance phase our subjects selected more frequently the long step strategy than in Early Swing and Mid Swing phases. The finding that the proportion of long step strategies increases when the obstacle is presented earlier in the step cycle is in line with the studies of Chen et al. (1994) and Weerdesteyn et al. (2005). Patla et al. (1999) proposed that the main criterion for this selection of alternate foot placement is the minimal displacement of the foot from its original landing position. Despite that, interindividual differences have been reported (Weerdesteyn et al. 2004; 2005). In our subjects, the SAS resulted in a more frequent use of the long step strategy. One explanation for this tendency could be related to the startle-induced shortening of the response onset latencies that shifts the response to a slightly earlier phase in the step cycle. This would increase the likelihood of using a long step strategy. Furthermore, some authors described the startle as a generalized motor response where flexor activity dominates (Landis and Hunt 1939; Rossignol 1975; Davis 1984). In addition, a characteristic of the StartReact effect is that muscles highly prepared to react are indeed those that are activated first when an auditory startle is presented together with the imperative signal (Valls-Sole et al. 1999). The biceps femoris, which is one of the main knee flexor muscles, is also a prime mover for the obstacle avoidance task (Weerdesteyn et al. 2007). Furthermore, the SAS preferentially activates upper leg muscles such as biceps femoris (Nieuwenhuijzen et al. 2000). This predicts that the biceps femoris would be more rapidly and strongly activated in trials with startle, as was indeed shown by the present study. The result would be a faster and stronger knee flexion, which may more easily lead to a long than to a short step strategy.

4.4.3 Functional significance

In the present obstacle avoidance task, quick and large activation of the prime movers may be a determining factor to achieve success. In fact, in a study of Weerdesteyn et al. (2007), shorter latencies and larger response amplitudes were significantly associated with higher success rates. The shortening in latency and the increase in amplitude in trials with a SAS could provide a functional advantage in avoiding obstacles during gait. In addition, slow reaction times in choice stepping tasks have been identified as an excellent predictor of falls (Lord and Fitzpatrick 2001). As a consequence, some authors have used step training to improve the speed of voluntary step initiations in both young and old subjects (Rogers et al. 2003). In their study, step initiation times could be reduced up to 17% but elderly consistently took longer steps than young subjects, presumably to extend their stability margin. The reduced step times were linked to the potentially startling waist pulls used for the training. Hence it is conceivable that an auditory StartReact effect would yield similar results if incorporated in a training program (see also Valls-Sole et al. 1999). The success of such intervention will probably be linked to the ability to solve the problem of an increased threat to stability in the populations concerned. For example, it can be predicted that vestibular loss patients will have greater difficulty with such training because they probably are less equipped to perceive the increased risk of instability linked to a fastened stepping response.

Regarding balance, it should be mentioned that speeding up stepping responses may also have consequences for stability. As pointed out by Reynolds and Day (2005), the stability during gait depends on predictive mechanisms, which result in a pre-step throw of the body (Lyon and Day 2005; see also MacKinnon et al. 2007). Rapid changes in foot trajectory (because of on-line adjustments after seeing an obstacle) have the potential to disturb this process. This may be especially hazardous for elderly people. For example, using a choice stepping response over an obstacle, St George et al. (2007) showed that elderly were much more likely to contact the obstacle when asked to quickly step over it. Furthermore, it was shown that elderly subjects with a history of falls were much more likely to perform slowly on this type of task than non-falling elderly (Lord and Fitzpatrick 2001). In addition, one should take into account that startle stimuli have the potential to inhibit the motor cortex (Kühn et al. 2004), thereby further increasing the risk of suppressing potentially important cortical reactions aimed at restoring stability. Whether startle stimuli may indeed override these critical balance recovery reactions in those cases where people reach their limits of stability needs to be established in further research, preferentially including groups of patients with balance disorders. Particularly neurological patients of whom the localisation of the disorder is well described would be of great interest, as a loss of balance induced by conditions with a startle could provide insight into the brain areas involved in the weighting of task-induced and balance demands. In this respect, the vestibular system would be a good candidate to be considered.

In conclusion, our study shows that a SAS induces a speeded up activation of the main muscle executors used for obstacle avoidance tasks. This finding, along with the observation that obstacle avoidance can be triggered in the absence of an imperative signal (moving obstacle), strengthens the hypothesis that the motor programmes used for obstacle avoidance tasks are fully represented at a subcortical level, where they are readily accessible to a SAS. Intersensory facilitation may play a role in the execution of the entire motor program. There are also clear behavioural effects of an auditory startle on obstacle avoidance tasks. The improvement of success rate, the favouring of long step strategy and the increase of stride shortening (in case of short step strategy) or lengthening (in case of long step strategy) are all elements that may be related to a more effective activation of the prime movers leading to a biologically relevant advantage.

This chapter has been adapted from: Journal of Physiology 586: 4453-4463, 2008.

CHAPTER 5

CONCLUSIONS AND FINAL REMARKS

Conclusions and final remarks

Understanding the basic mechanisms of the control and coordination of voluntary human movements is an extensive theme that contributes to expanding knowledge regarding motor control. After performing the previous research studies in relation to preparation and execution of selected motor activities (sit-to-stand, gait initiation and gait-pattern, and obstacle avoidance during walking) it is concluded that:

1. **Subcortical motor structures are involved in the preparation and execution of complex voluntary activities performed in a context of a reaction time task**.

The previous general conclusion is inferred from the conclusions obtained from each study. The following are the main conclusions of each chapter.

2. **The sit-to-stand manoeuvre responds as a single block of combined motor programmes to the presentation of a startling auditory stimulus.**

3. **The startle-induced shift of the sit-to-stand pattern to earlier latencies affects anticipatory**

postural adjustments and prime mover muscles alike.

4. **Muscles involved in the sit-to-stand activity constitute a common motor program as, once launched, it is resistant to unexpected external perturbations.**

5. **Subcortical stimulation induces a latency shortening not only for gait initiation but also for gait-pattern generation.**

6. **The anticipation of gait-pattern generation seems to be a secondary consequence of the startle effects on gait initiation, which triggers the muscle activation of the gait-pattern.**

7. **A startling auditory stimulus induces a speed up activation of the muscles used to avoid obstacles during walking.**

8. **The motor programmes used for obstacle avoidance tasks are fully represented at subcortical level although intersensory facilitation may play a role in the execution of the entire motor program.**

9. **The improvement of success rate, the favouring of long step strategy and the increase of stride shortening or lengthening are behavioural effects of the auditory startle on obstacle avoidance tasks that may be related to a more effective activation of prime movers.**

What is new in this thesis is that voluntary human activities may be launched with stimulation that activates subcortical areas. Subcortical structures are then highly involved in the preprogramming and execution of complex voluntary and everyday movements. This contribution to the field of motor control suggests that future studies should take into account other neural structures apart from motor cortex when studying motor programming.

Although the studies performed in this thesis are focused on physiological mechanisms of the nervous system, practical applications should be possible. They could be oriented to neurological diseases to analyse the impaired functions and the neural structures involved, and would contribute to find more appropriately retraining strategies for some everyday activities such as sit-to-stand and gait-pattern. In addition, subcortical stimulation could have functional benefits on obstacle avoidance, which is one of the tasks widely studied in elderly and some patient groups such as Parkinson’s disease, stroke, amputees and visually impaired subjects. Other practical applications of subcortical stimulation are related to physical activity and sports where improving reaction time is basic to higher performance.

It is the hope that the present contribution may also help future studies to solve questions in motor control and related areas that nowadays are not completely understood.

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RESUMEN

Resumen

La implicación de los centros motores subcorticales en actividades voluntarias en humanos

1. Introducción

Históricamente las ciencias se han desarrollado para dilucidar y explicar fenómenos de la naturaleza. Con este propósito general, sus diferentes ramas han analizado en profundidad sus propios campos con la tarea posterior de sintetizar y así, acercarse a la naturaleza. Dentro del área de la fisiología, la investigación sobre el movimiento se ha centrado tradicionalmente en el estudio de partes concretas del organismo para establecer reglas básicas sobre los sistemas musculares y articulares. De alguna forma, las conclusiones de estos estudios han proporcionado conocimientos importantes sobre el funcionamiento motor del ser humano. Sin embargo, algunas partes del comportamiento motor todavía no están completamente claras. El ser humano está formado por un elevado número de músculos y articulaciones, todas ellas controladas durante la ejecución de movimientos funcionales coordinados. La realización de tareas motoras, o el movimiento humano en general, deriva de la interacción de múltiples procesos incluyendo aquellos relacionados con la percepción, la cognición y la acción.

En las últimas décadas el desarrollo de nuevas técnicas, tales como la resonancia magnética y cámaras de alta velocidad, ha fomentado una profunda comprensión de conceptos básicos y ha ofrecido abundante literatura. Los principales avances han sido realizados en la comprensión de tareas intencionales como el apoyo en miembros inferiores y la estabilidad del tronco durante bipedestación (e.j. Crenna et al. 1987; Keshner et al. 1988; Mouchnino et al. 1992; Allum et al. 2001; Gill et al. 2001); la marcha (e.j. Perry 1992; Harris y Wertsch 1994; Ounpuu 1994); la sedestación (e.j. Brogren et al. 1998; Genthon et al. 2007; van Geffen et al. 2008) y sus transiciones (e.j. Goulart y Valls-Sole 1999; Janssen et al. 2002; Roy et al. 2007; Nadeau et al. 2008); destrezas del miembro superior como el alcance y el agarre (e.j. Paulignan et al. 1991a; 1991b; Castiello y Begliomini 2008) y la manipulación (e.j. Johansson y Cole 1992; Johansson et al. 2001; Valero-Cuevas 2005; Flanagan et al. 2006); y el control visual en la percepción y la acción (Goodale y Milner 1992; Bardy y Warren 1997).

En relación con la participación cerebral, se han realizado diferentes aproximaciones en lo relativo al control motor y han sido explorados conceptos fundamentales como la posición y el movimiento (Brooks 1983; Henatsch 1985); niveles de voluntariedad y conciencia en la tarea (Posner y Rothbart 1998; Wegner y Erskine 2003); diferenciación entre tareas iniciadas por el propio sujeto y aquellas solicitadas externamente en las que los procesos cognitivos tienen un papel central (Jahanshahi et al. 1995; Jenkins et al. 2000); y la complejidad de la respuesta -siendo posible elegir entre varias respuestas o responder únicamente con una acción predeterminada- (Goodrich et al. 1990; Henderson y Ditrich 1998). Estas aproximaciones han facilitado el estudio y la diferenciación de niveles de automatización y aprendizaje de tareas teniendo gran influencia en las áreas del entrenamiento humano para un mayor rendimiento físico.

Por tanto, la investigación del control motor, normalmente estudiada en relación con actividades específicas, proporciona una visión de los principios por los cuales se dirigen dichos movimientos. Entender el control de la acción implica entender las órdenes motoras del sistema nervioso hacia los músculos (Shummway-Cook y Woollacott 2001).

Control motor de actividades humanas voluntarias

El análisis de los movimientos voluntarios es una forma de intentar entender cómo el sujeto toma decisiones y cómo las ejecuta (Latash 1998). En la vida diaria realizamos gran variedad de tareas funcionales que requieren movimientos voluntarios. El tipo de movimientos necesarios está determinado, en parte, por la naturaleza de la tarea que va a ser realizada. Entender el control del movimiento requiere concienciarse de cómo las tareas regulan, o constriñen, el movimiento (Shummway-Cook y Woollacott 2001).

Estos movimientos son normalmente la consecuencia de la reacción a un estímulo interno o externo. En la vida diaria las personas están acostumbradas a reaccionar ante diversos estímulos principalmente visuales, auditivos, mecánicos. Algunos de ellos conllevan expectación (por ejemplo, cuando estamos esperando a que el semáforo cambie de color para cruzar la calle) pero otros no (accidentalmente una botella cae al suelo detrás de nosotros). En ambos casos, el movimiento será ejecutado como reacción a un estímulo externo, visual en el primer caso, auditivo en el segundo. Además del estado mental, en el que la expectación juega un papel relevante, el movimiento también está influido por lo que la persona esté haciendo cuando se presenta el estímulo (pudiendo encontrarse en una situación estática o dinámica).

Por lo general, los movimientos voluntarios van acompañados por ajustes posturales, cuyas características podrían concretarse en tres (Massion 1984): son anticipatorios en relación al movimiento, adaptables a las condiciones en las cuales éste se ejecuta y están influidos por las instrucciones dadas al sujeto en relación a cómo ejecutar la tarea. Por tanto, estos ajustes posturales, conocidos como ajustes posturales anticipatorios (APAs), preceden a las perturbaciones posturales planificadas y las minimizan con correcciones anticipatorias. Desde el primer estudio de Belenkii et al. (1967) que mostró cambios en la actividad electromiográfica de los músculos posturales, han sido realizados numerosos estudios relacionados con APAs. Teniendo en cuenta los resultados de éstos, Aruin (2002) sugiere que hay tres componentes principales que influyen en los APAs: acción motora, perturbación y tarea postural. Como cualquier movimiento voluntario, y especialmente uno rápido, induce perturbaciones posturales (Aruin 2002), los APAs deben ser considerados al estudiar la preparación y la ejecución de movimientos voluntarios.

Los movimientos voluntarios no sólo pueden ser únicos sino también repetitivos. En este sentido, se hará especial mención a las actividades rítmicas musculares. Los patrones cíclicos necesarios para andar, correr, respirar u otras actividades rítmicas son generados por redes neuronales especializadas en la repetición de acciones concretas (Duysens y Van de Crommert 1998). El término patrón generador central se utiliza normalmente cuando uno se refiere a esas redes neuronales para la locomoción. Hay suficientes estudios en animales que dirigen al supuesto de la existencia de un patrón generador central subyacente al control central de la locomoción (revisiones de Duysens y Van de Crommert 1998; Grillner et al. 2008). Sin embargo, ha sido en las últimas décadas cuando se ha considerado la presencia de un patrón generador central en la actividad locomotora humana (Calancie et al. 1994; Dimitrijevic et al. 1998; Gerasimenko et al. 2002). Han sido propuestas pruebas sobre la existencia de esa determinada red neuronal, por ejemplo, en estudios con lesionados medulares o experimentos en los que la médula espinal ha sido estimulada eléctricamente en puntos específicos.

Propiedades diferenciales de las tareas motoras

Las tareas motoras pueden ser clasificadas teniendo en cuenta características específicas inherentes a cada una. Shummway-Cook y Woollacott (2001) consideran las siguientes tareas: tareas discretas versus continuas, tareas estáticas versus dinámicas, tareas abiertas versus cerradas; valoran además el estado atencional. En relación al miembro superior, también mencionan el grado de manipulación que requiera la tarea, no siendo su explicación pertinente en nuestro estudio.

Una tarea puede ser clasificada como discreta o continua. Levantarse de una silla o tumbarse en la cama son ejemplos de tareas discretas en las que se reconoce el principio y el final de la tarea. Por el contrario, en una tarea continua, como andar o correr, el final de la tarea es decidido de forma arbitraria por su ejecutor.

Las tareas estáticas como la sedestación o la bipedestación son realizadas en una base de sustentación fija o inmóvil. Por el contrario, en las tareas dinámicas como andar o correr hay una base de sustentación variable o móvil.

Los movimientos también se clasifican en función de la demanda atencional. En principio, las tareas estáticas posturales son las que menor demanda atencional requieren mientras que en las tareas dinámicas como andar o evitar obstáculos las demandas atencionales están incrementadas.

Las tareas cerradas se caracterizan por patrones de movimiento fijos y son realizadas en ambientes relativamente constantes. Sin embargo, las tareas abiertas son realizadas en ambientes cambiantes, dificultando la capacidad para planificar un movimiento. Los términos tarea *abierta* y tarea *cerrada* se utilizan también en otros contextos relacionados con el movimiento. Los términos *con o sin retroalimentación* son utilizados para describir dos modos de control del movimiento. Los movimientos *sin retroalimentación* no son sensibles a la información del ambiente y en el control *con retroalimentación* el movimiento sí es sensible al entorno. Además, los términos *cadena abierta* y *cadena cerrada* también han sido utilizados para caracterizar el movimiento. Un movimiento de cadena abierta es aquel en el que la articulación distal está libre de movimiento mientras que en un movimiento de cadena cerrada el segmento distal encuentra resistencia en el entorno.

Además, en el contexto de tareas de tiempo de reacción, donde es posible estudiar la preparación del movimiento, se debe diferenciar en función de la complejidad de la respuesta (Klapp 1996). En los experimentos de tiempos de reacción simple, la respuesta requerida es identificada previamente y, a continuación, la señal imperativa indica que la respuesta debe ser realizada. Por el contrario, los experimentos de tiempos de reacción electiva no incluyen indicaciones previas; únicamente la señal imperativa informa de la respuesta que debe ser realizada. Por tanto, en tareas de tiempos de reacción electiva la programación previa de la respuesta no sería posible y el tiempo de reacción es mayor que en tareas de tiempo de reacción simple.

Estudios de estimulación subcortical

Comúnmente se acepta que cuando las personas reaccionan a un estímulo, las áreas premotoras y motoras suplementarias de la corteza cerebral tienen un papel esencial en la preparación y ejecución de movimientos voluntarios. Sin embargo, si se requiere una rápida ejecución motriz, es posible que los centros motores subcorticales estén involucrados en la aceleración de actividades motoras voluntarias (Valls-Sole et al. 2008). En esta situación de preparación, un estímulo brusco e inesperado podría lanzar la respuesta motora a través de una activación directa de las estructuras subcorticales ya preparadas, fenómeno conocido como 'StartReact' (Valls-Sole et al. 1995; 1999; Carlsen et al. 2004a; 2004b). Tal estímulo es conocido como sobresalto (startle). La consecuencia de una reacción al sobresalto es una respuesta motora involuntaria que consiste en una contracción muscular generalizada (Landis y Hunt 1939). Entre esta serie de movimientos musculares generalizados, la reacción de parpadeo es la más rápida, fiable y resistente a la habituación del reflejo de sobresalto en humanos (Landis y Hunt 1939). En general, esta reacción de sobresalto es considerada como unas de las reacciones motoras más rápida en humanos y animales.

Por tanto, con el objetivo de averiguar las implicaciones subcorticales en la preparación y ejecución de movimientos voluntarios, se han realizado estudios de estimulación subcortical. La estimulación con sobresalto ha sido utilizada en dichos estudios ya que la reacción de sobresalto ocurre a través de mecanismos reflejos subcorticales y las entradas sensoriales activan la formación reticular y el tracto retículo-espinal descendente a la médula espinal (Davis et al. 1982). Normalmente, en humanos, la reacción de sobresalto es inducida a través de estimulación auditiva, aunque se han utilizado otros métodos como la estimulación visual o cutánea (Berg y Balaban, 1999).

En un contexto de una tarea de tiempo de reacción simple los sujetos son capaces de preparar los programas motores con suficiente antelación para una ejecución rápida al percibir la señal imperativa (Valls-Sole et al 1995; 1999; Siegmund et al. 2001; Carlsen et al 2004a; 2004b). Después, se puede observar una reacción rápida y voluntaria. Sin embargo, cuando un sobresalto auditivo o estímulo auditivo de alta intensidad es aplicado al mismo tiempo que la señal imperativa, los sujetos ejecutan la tarea requerida y preparada con mayor rapidez mientras que el programa motor básico no se ve modificado (Valls-Sole et al 1995; 1999; Siegmund et al. 2001; Carlsen et al. 2004a; 2004b). Sin ninguna duda, este efecto ‘StartReact’ está presente en tareas de tiempos de reacción simple. En tareas de tiempos de reacción electiva, en las que la programación previa de la respuesta no sería posible, el efecto ‘StartReact’ está también presente, aunque con reservas, tal como ha sido observado en algunas formas de tareas de tiempos de reacción electiva y no en otras (Valls-Sole 2004; Kumru et al. 2006; Oude Nijhuis et al. 2007; Reynolds y Day 2007). Valls-Sole et al (2008) sugieren que hay algún grado de preparación motora subcortical en paradigmas de tareas de tiempos de reacción electiva.

Por consiguiente, la programación previa de respuestas voluntarias puede ser analizada con el efecto ‘StartReact’. Este efecto ha sido ampliamente investigado en acciones relativamente simples, como movimientos balísticos (p.e. Valls-Sole et al. 1999), movimientos de cuello (p.e. Siegmund et al. 2001; Oude Nijhuis et al. 2007), o movimientos de un sólo dedo (p.e. Carlsen et al. 2004a; 2004b). Existen escasas investigaciones sobre movimientos relativamente complejos, como ponerse de puntillas -tip-toeing- (Valls-Sole et al. 1999) o los recientes experimentos de MacKinnon et al. (2007) y Reynolds y Day (2007). Por tanto, que sepamos, ésta es la primera vez que se estudia el efecto ‘StartReact’ en algunos movimientos voluntarios más complejos como son: el paso de sedestación a bipedestación, el patrón de locomoción y la evitación de obstáculos al caminar. No se conoce si esos programas motores se preparan y ejecutan de la misma forma que los modelos ‘StartReact’ previos, ni tampoco -siendo de mayor interés- cómo son la programación previa a nivel tanto de la coordinación con APAs, como de los patrones motores posteriores a otros (como el patrón de locomoción tras el inicio de la marcha) y de las estrategias de evitación de obstáculos.

Actualmente, se consideran dos opciones en relación a los mecanismos fisiológicos subyacentes al efecto ‘StartReact’ (Valls-Sole et al. 2008). Uno sugiere que los programas motores están representados en estructuras motoras subcorticales y, por tanto, accesibles a la activación a través del estímulo de sobresalto (Valls-Sole et al. 1999; Carlsen et al. 2004b; Sanegre et al. 2004). La segunda posibilidad es que la energía del estímulo procedente de la señal imperativa se ve aumentada con la presencia del sobresalto. Esto último se ilustra a través de la facilitación intersensorial (Nickerson 1973; Gielen et al. 1983) y las respuestas son atribuidas a la unión de estímulos de múltiples modalidades sensoriales.

2. Parte principal

La presente investigación está centrada en actividades humanas realizadas voluntariamente. Se han seleccionado intencionadamente tres tareas diferentes para estudiar en profundidad la preparación y ejecución de movimientos humanos voluntarios. Las tres son actividades de la vida diaria relacionadas entre sí a nivel funcional pero con características diferenciales únicas.

Teniendo en cuenta las diversas propiedades tratadas previamente, se seleccionaron tres tareas motoras para formar parte de la tesis. Para cada una de las tareas se realizó un experimento, abordando objetivos específicos en cada uno de ellos.

La primera tarea es la maniobra **sit-to-stand**, una tarea discreta en la que el sujeto pasa de sedestación a bipedestación. Las posiciones tanto de inicio como de final de esta tarea son estáticas y estables, y no requiere de demandas atencionales elevadas. Es una tarea cerrada ya que se realiza en un contexto fijo. El experimento se realizó en un contexto de tiempo de reacción simple y se prestó especial atención a la relación entre los músculos que realizan APAs y los principales ejecutores del movimiento.

La segunda tarea es el inicio de la marcha **(gait initiation),** seguida del patrón de locomoción **(gait-pattern)**. Los sujetos empezaban a andar desde una posición estática de bipedestación y libremente realizaban al menos tres pasos. En este caso, la posición inicial era también estática y estable pero la posición final era decidida por el ejecutante. Por tanto, este movimiento comparte características de tareas motoras discretas y continuas. Al igual que la maniobra de paso de sedestación a bipedestación, no requiere demandas atencionales elevadas. Es también una tarea cerrada realizada en un contexto de tiempo de reacción simple. Se prestó especial atención tanto al establecimiento del gait-pattern después de una manipulación externa de la temporalidad del inicio de la marcha, como al concepto de patrón generador central.

La tercera tarea es la evitación de obstáculos durante la marcha **(obstacle avoidance during walking)**. Los sujetos, que andaban en un tapiz rodante, debían evitar obstáculos que aparecían inesperadamente en su camino. Contrariamente a las tareas previas, la evitación de obstáculos durante la marcha es una tarea claramente continua y dinámica realizada en una base de sustentación variable. Además es una tarea abierta, al realizarse en un contexto cambiante, y supone mayores demandas atencionales. El experimento es considerado como de tiempo de reacción electiva ya que los sujetos debían elegir entre dos estrategias para evitar los obstáculos: estrategia de paso corto o estrategia de paso largo.

El objetivo general de la presente tesis doctoral es **analizar las implicaciones subcorticales en la preparación y la ejecución de movimientos voluntarios complejos**. Para ello se han realizado tres estudios: paso de sedestación a bipedestación como una actividad de tiempo de reacción simple para analizar los APAs y la coordinación muscular; inicio de la marcha y patrón de locomoción como una actividad compleja para añadir el análisis de un patrón motor precedido de otro; y estrategias de evitación de obstáculos para analizar las respuestas electivas en una situación dinámica. A continuación se presenta un resumen de cada uno de los estudios realizados.

“**Los efectos del sobresalto en la maniobra de paso de sedestación a bipedestación**”

En contextos en los que se realizan tareas de tiempo de reacción, los movimientos balísticos simples son ejecutados con mayor rapidez cuando la señal imperativa va acompañada de un estímulo auditivo de alta intensidad (sobresalto). Se examinó si este efecto ocurre también en movimientos complejos como en la tarea de paso de sedestación a bipedestación, teniendo en cuenta tanto los músculos que realizan ajustes posturales anticipatorios como los principales ejecutores del movimiento. Nueve voluntarios sanos realizaron la tarea en respuesta a una señal visual imperativa, presentada bien de forma aislada (registros control) o acompañada del estímulo auditivo de alta intensidad (registros test). El tiempo de reacción, medido como el tiempo entre la señal imperativa y el despegue desde el asiento, se anticipó de forma significativa en los registros test cuando el sobresalto fue aplicado con un intervalo de 0 ms respecto a la señal imperativa. Las latencias de la actividad electromiográfica, registradas en los músculos tibial anterior, paraespinal lumbar, cuádriceps y bíceps femoral, se redujeron de forma proporcional a la anticipación del momento del despegue. De todas formas, estos efectos no fueron observados si el estímulo era aplicado 150 ms después de la señal imperativa, cuando la tarea ya estaba iniciada. Los resultados sugieren que los estímulos que actúan a nivel de las estructuras motoras subcorticales anticipan, aunque no interfieren, la ejecución de los programas motores de la maniobra de paso de sedestación a bipedestación.

“**Anticipación del inicio de la marcha y del patrón de locomoción al aplicar un estímulo auditivo de alta intensidad**”

La locomoción humana integra un patrón motor repetitivo que aparece después del inicio de la marcha. Mientras que el mantenimiento automático de la locomoción se cree que está bajo el control de centros motores subcorticales, el inicio de la marcha parece requerir una orden voluntaria de otro patrón diferenciado. El objetivo de este estudio es examinar cómo los dos programas motores responden a la manipulación experimental de la temporalidad del inicio de la marcha. Los participantes debían iniciar la marcha tan pronto como percibieran la señal imperativa que, en algunos registros intercalados, iba acompañada de un estímulo auditivo de alta intensidad. Se sabe que este método anticipa la latencia de ejecución de una tarea motriz preparada. Se pensó que, si los dos programas motores eran lanzados a la vez, la secuencia del patrón de locomoción respondería al estímulo de la misma forma que para el inicio de la marcha. Se registraron las fases de la marcha y la actividad electromiográfica de cuatro músculos del miembro inferior que la iniciaba. En los registros acompañados del estímulo auditivo, la latencia de todos los eventos relacionados con el inicio de la marcha mostraron una anticipación significativa y la actividad electromiográfica tuvo mayor amplitud y menor duración que en los registros sin el estímulo. Los eventos relacionados con el patrón de locomoción se anticiparon pero no se vieron modificados. El hecho de que todos los efectos del estímulo auditivo de alta intensidad estuvieran vinculados al inicio de la marcha sugiere que el sobresalto puede afectar de forma selectiva a las estructuras implicadas en el inicio de la marcha. Además, la anticipación proporcional de la secuencia del patrón de locomoción respecto a la finalización del inicio de la marcha refuerza la idea de que el inicio de la marcha debe de ser el estímulo de entrada (input) necesario para la generación del patrón de locomoción humana.

“Los efectos del sobresalto auditivo en la evitación de obstáculos durante la marcha”

El efecto StartReact ha sido recientemente estudiado en una tarea concreta como es el ajuste del paso al requerir una selección rápida de movimientos en una tarea de tiempo de reacción electiva. Por tanto, se hipotetiza que el inducir un efecto StartReact puede ser beneficioso en la evitación de obstáculos bajo presión temporal, cuando los sujetos deben realizar rápidos ajustes de la marcha. Doce adultos jóvenes, todos ellos sanos, anduvieron en un tapiz rodante en el que se fueron dejando caer obstáculos en determinados momentos del ciclo de la marcha. La latencia de activación electromiográfica del bíceps femoral se redujo de media un 20 % mientras que la amplitud aumentó un 50 %, en registros en los que el sobresalto acompañó a la evitación del obstáculo. La presentación del sobresalto incrementó la probabilidad de utilizar la estrategia de paso largo, se hicieron más evidentes las modificaciones del paso y aumentó el éxito en la evitación del obstáculo. También se examinaron los efectos del sobresalto comparando entre una condición en la que el obstáculo no estaba presente con otra en la que el obstáculo estaba presente pero no caía. En esta última condición, la reacción con el fin de evitar el obstáculo fue realizada con una latencia similar pero con menor amplitud que en registros en los que el obstáculo se dejaba caer realmente en el tapiz. Los resultados sugieren que los programas motores utilizados para la evitación de obstáculos son susceptibles de estar preparados en estructuras subcorticales. Es posible que la liberación de estos programas motores debido al estímulo auditivo de alta intensidad combine la facilitación intersensorial y el efecto StartReact.

3. Conclusiones

El entender los mecanismos básicos del control y la coordinación de movimientos humanos voluntarios es un área extensa de estudio que contribuye al desarrollo de conocimientos en relación al control motor. Después de la realización de los estudios de investigación descritos previamente, en relación a la preparación y la ejecución de determinadas actividades motoras (paso de sedestación a bipedestación, inicio de la marcha y locomoción humana, y evitación de obstáculos), se concluye que:

1. Las estructuras motoras subcorticales están involucradas en la preparación y ejecución de actividades voluntarias complejas realizadas en contextos de tareas de tiempos de reacción.

La conclusión general previa se deduce de las principales conclusiones obtenidas en cada estudio, detalladas a continuación:

2. La maniobra de paso de sedestación a bipedestación responde a la presentación de un estímulo auditivo de sobresalto como un solo bloque de programas motores combinados.

3. La anticipación, inducida por el sobresalto, de las latencias de activación muscular del patrón de paso de sedestación a bipedestación afecta de igual forma a los músculos que realizan APAs que a los principales ejecutores de movimiento.

4. Los músculos implicados en la actividad de paso de sedestación a bipedestación constituyen un programa motor común que, una vez lanzado, es resistente a perturbaciones externas inesperadas.

5. La estimulación subcortical induce una anticipación de latencias de activación muscular no sólo en el patrón de inicio de la marcha sino también en la generación del patrón de locomoción humana.

6. La anticipación del patrón de locomoción humana parece ser una consecuencia secundaria de los efectos del sobresalto sobre el patrón de inicio de la marcha, provocando éste la activación muscular del patrón de locomoción.

7. El estímulo auditivo de sobresalto anticipa la activación de los músculos que se utilizan para evitar obstáculos durante la marcha.

8. Los programas motores utilizados en la tarea de evitación de obstáculos están representados en su totalidad a nivel subcortical aunque la facilitación intersensorial puede estar implicada en la ejecución del programa motor completo.

9. El aumento de la tasa de éxito, la tendencia a utilizar la estrategia de paso largo y el incremento del acortamiento o alargamiento del paso son efectos comportamentales del sobresalto auditivo en la tarea de evitación de obstáculos, que pueden

estar relacionados con una activación más efectiva de los principales ejecutores del movimiento.

La principal aportación de la presente tesis es el hecho de que las actividades humanas voluntarias pueden ser provocadas a través de la estimulación subcortical. Las estructuras subcorticales están altamente implicadas en la programación previa y en la ejecución de movimientos complejos voluntarios realizados habitualmente. Esta contribución en el campo del control motor sugiere que, para futuras investigaciones, se deban considerar otras estructuras nerviosas como las subcorticales, diferentes a la corteza motora, al estudiar la programación motora.

Aunque los estudios realizados en esta tesis doctoral están centrados en mecanismos fisiológicos del sistema nervioso, deberían ser posibles ciertas aplicaciones prácticas. Éstas podrían estar orientadas a enfermedades neurológicas para analizar la limitación funcional y las estructuras nerviosas implicadas, así como contribuir a elaborar estrategias de reentrenamiento para actividades cotidianas como levantarse de una silla o andar. Además, la estimulación subcortical puede tener beneficios funcionales en la evitación de obstáculos, una de las tareas ampliamente estudiadas en personas mayores y en algunos grupos de pacientes como son aquellos con Parkinson, enfermedades cerebrovasculares, amputados o sujetos con limitaciones visuales. Otras aplicaciones prácticas de la estimulación subcortical podrían estar relacionadas con la actividad física y el deporte donde la mejora del tiempo de reacción es fundamental para un mayor rendimiento.

Se espera que el presente trabajo pueda ayudar a estudios futuros que traten de dar explicación a aspectos aún por resolver en control motor y campos próximos.