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THE CONTROL AND COORDINATION OF HUMAN STEPPING

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I, Matthew James Bancroft confirm that the work presented in this thesis is my own. Where information has been derived from other sources, I confirm that this has been indicated in the thesis.

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Abstract

Walking is a simple task for most humans. However, the act of lifting a foot from the ground to take a step, as when walking, destabilises the body and threatens a loss of balance. This thesis details a series of studies designed to investigate the control and coordination of a step. In each experiment, the body was voluntarily translated from stationary to the location of a visually-presented target. It is first shown that the movement of the body before a step is modulated by the future location of the foot, even when the location of a step target is made to change unexpectedly before the stepping foot lifts. This pre-step movement provides the body with an initial position and velocity at the start of a step from which it begins to fall under gravity. It is then demonstrated that the movement of the body during the step is largely determined by its initial conditions and the influence of gravity. However, the trajectory of the body is also modified by mid-step ankle torques, which seem particularly important in controlling forwards motion. Next, it is shown that the movement of both the body and leg during a step is variable between steps to the same location. This variability is organised to reduce foot placement error, demonstrating that the body and leg are precisely coordinated to land the foot accurately on its intended target. Surprisingly, this was still the case when visual feedback was denied during the step. Finally, the coordination of a step is investigated in subjects with a genetically determined and pure form of cerebellar degeneration. Foot placement error was increased in subjects with cerebellar dysfunction, with the results suggesting that this originated from both impaired coordination and increased variability in the body and leg movements used during a step.

Impact Statement

This thesis details a series of studies designed to investigate how humans take a step from one location to another. This task is a basic human action that underlies functions such as locomotion, walking and reorientation of the body. As such, this thesis offers a unique insight into the control of human movement and could be used to benefit individuals with movement problems through impacting both basic and clinical science.

A key issue when taking a step concerns the control of balance. This thesis argues, and provides evidence that, standing balance is relinquished when a foot is lifted from the ground to take a step and that the body is falling under gravity when supported on only one leg during the step. The trajectory of the body is controlled by a movement immediately prior to the lift of the stepping foot which acts to ‘throw’ the body into the step. The body then falls along a planned path determined by the throw. During the step, the stepping leg swings and aims to move the foot to its intended target. A successful step requires the body to be thrown along an appropriate trajectory for the intended placement of the foot. It also requires the stepping leg to move the foot accurately to its target in order for the body to be caught and balance to be regained.

This framework has important implications for the study of walking and balance. It implies that error in the execution of the body throw, leg swing and/or their coordination could lead to a complete loss of balance and an unintended fall.

Perhaps most significantly, it offers a basis within which to examine an individual’s movement for the purpose of highlighting specific deficits. The experimental paradigm presented in this thesis (the act of a step from one location to a visually-presented target location) encapsulates each source of potential movement error and could provide a useful screening test. For example, if a specific deficit was found for an individual, a clinician, physiotherapist or other allied health professional could use this information to estimate an individual’s fall risk, design informed training or rehabilitative programs to improve specific movement deficits and prevent falls.

The experimental paradigm presented in this thesis could also provide a useful tool with which to train specific aspects of movement. It has the advantage of being a simple task which can be adapted to the ability of the individual, as low cost as simply fixing a piece of paper to the floor and compact enough to be performed safely in areas with limited space.

Furthermore, the knowledge amassed in this thesis on how humans control and coordinate a step could be used to impact the design of robotic assistive-devices, prostheses and exoskeletons aimed at improving gait in neurologically impaired populations and others with gait and balance problems.

In each of these ways, it is hoped that this thesis can impact the lives of individuals with movement problems and improve quality of life.

Acknowledgements

Forty-seven thousand words, twenty-five thousand steps (each one watched intently and analysed meticulously) and four years of work have gone into this thesis. I am forever indebted to the following people, without whom none of it would have been possible.

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DayLab has been a hugely enjoyable place to work, due both to Brian and the many people I consider myself extremely lucky to have co-habited an office with. My time in the lab overlapped most with Chris Dakin, Irene Di Giulio and Amy Peters, and all three deserve special commendation for their generosity, expert advice, remarkable kindness, and, most importantly, humour. I would also like to thank Dan Voyce for engineering the electronics for the target lights that underpin every part of this thesis.

Outside of the lab I have also received incredible support from my close friends and family. The unwavering belief that my flatmates, past and present, have shown in me has been the rock upon which this thesis has been built. Tom (Wood, in press), Gaz, Alex (Malcolm, 2017), Dan, Charlotte and Medhavi (aka St. Cheese Club): I cannot thank you enough. I would also like to thank Mark for being an ever-reliable friend and Eleanor, who has been an absolute star in helping me to get over the finish line and who kindly proof read part of this thesis.

Although this thesis reflects my past four years in London, it equally reflects the previous twenty-one years of my life, during which time my parents and grandparents taught me most of what I know. The grounding they gave me allowed me the strength with which to complete this thesis. At times the demands of this PhD have taken me away from them but their continued faith in me has been of great solace. Rightly, I dedicate this thesis to them all.

Finally, I must thank the wonderful people who kindly gave up their time to participate in the experiments described in this thesis and who let me watch and record their many, many steps. The humility shown by all, perhaps most remarkably in the SCA6 patients, was truly inspirational. I hope you enjoyed taking part as much as I enjoyed your company.

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Abbreviations

ANOVA	Analysis of Variance
AP	Antero-posterior
cm	centimetres
CoM	Centre of Mass
CoP	Centre of Pressure
GVS	Galvanic Vestibular Stimulation
HC	Healthy control
Hz	Hertz
kg	kilograms
m	metres
ML	Medio-lateral
mm	millimetres
ms	milliseconds
N	Newtons
PLATO	Portable Liquid crystal Apparatus for Tachistoscopic Occlusion
s	seconds
SARA	Scale for the Assessment and Rating of Ataxia
SCA	Spino-cerebellar ataxia
SCA6	Spino-cerebellar ataxia type 6
SD	Standard deviation (of the mean)
SE	Standard error (of the mean)

1 Chapter 1: General Introduction

1.1 The balance problem

Walking is an action many of us take for granted. For the most part, humans are able to walk and avoid losing balance without great difficulty. On the one hand, walking could be considered a simple action given its everyday nature and apparent ease. In reality it is a remarkable feat given the number of muscles that must act in concert to move the body and legs, all whilst ensuring the body does not topple over. For humans, the ability to maintain balance is complicated by the preference to walk on two, rather than four, limbs. In comparison to quadrupeds like dogs and cats, this bipedal posture results in the human body's centre of mass (CoM) being positioned high above the ground and over a relatively small base of support. Subsequently, the human body is inherently unstable.

The difficulty in maintaining balance can be seen all around us in everyday life; for example, when attempting to maintain upright stance on a moving bus or when watching a toddler's stumbling gait. Indeed, failing to maintain balance and falling is a considerable problem for many people. It is estimated that around a third of over 65 year olds suffer at least one fall a year, with this figure increasing with advancing age and in persons with neurological disease such as Parkinson's, stroke and spinocerebellar ataxia (Roller *et al.*, 1989; O'Loughlin *et al.*, 1993; Forster & Young, 1995; Fonteyn *et al.*, 2010). Frequently falling is also a problem for many people as an estimated 31% of fallers fall multiple times a year (Nevitt *et al.*, 1989).

A fall can cause serious physical injury, or even death. Common injuries resulting from a fall include concussion and fractures, particularly of the hip (Lord *et al.*, 2007). Such injuries can cause prolonged immobility, which can reduce a person's independence and quality of life (Lord *et al.*, 2007). The treatment of these injuries leaves a substantial economic burden on health and social care services (Heinrich *et al.*, 2010). In the United Kingdom alone it has been estimated that falls cost the government £1billion annually (Scuffham *et al.*, 2003), with an average cost of £202 per fall (Collerton *et al.*, 2012). Understanding the root cause of a fall is of critical importance in preventing falls in order to reduce their impact on both individuals and society. To understand the cause of a fall, we need to understand how movement is controlled to enable balance to be maintained.

In what scenarios do individuals often fall? To attempt to answer this, Robinovitch *et al.* (2013) set-up-video cameras inside two care homes and noted the activity at the time of a fall and the cause of the loss of balance. The authors reported that individuals lost balance and fell during many activities, including standing quietly and sitting down, but the most frequent activity leading to a fall was walking. The causes of falls ranged from trips and stumbles to bumping into external objects and loss of support. However, the most frequent cause of a loss of balance and a fall was incorrect weight shifting. These two factors may be linked given that walking involves the shifting of weight between the feet.

1.2 A single step

A fundamental part of walking is a step, which is the act of lifting a foot from the ground to move it to a new location. Humans are required to step in many different scenarios, for example when walking, to transition from standing to walking or simply to reorient the body. A single step has much in common with a step during walking but differs in that the body starts from no momentum rather than entering with momentum from the previous step. Importantly, a single step contains common elements of the causes of falls noted by Robinovitch *et al.* (2013): prior to a step weight must be shifted and, like during walking, a foot must be lifted from the ground. For this reason, a single step offers a useful tool with which to study the interaction of movement and balance. Stepping behaviour has also been shown to dissociate between individuals who have fallen and those who have not (Lord & Fitzpatrick, 2001), suggesting that the study of a single step is relevant to the problem of understanding real-world falls.

1.3 Mechanics of a step

For a stationary object to be considered to be stable, its centre of mass (CoM) must lie directly over its base of support. For a standing human, the base of support comprises the area around the two feet in contact with the ground. The body's CoM is the weighted mean position of the CoM of each of the body's segments (Winter, 1995), which when stood upright is located approximately at the level of the navel. During stance, the CoM is kept over the base of support by the application of force on the ground via the feet. The location that force is applied to the ground is termed the centre of pressure (CoP). In order to take a step, a foot must be lifted from the ground. In so doing, the base of support is reduced in size from the area enclosing two feet to the size of the one foot still in contact with the ground.

Presumably then, humans would opt to step and walk in a manner that was stable; in other words, by keeping the CoM over the base of support (the stance foot) during a step. In reality this is not the preferred strategy. During a step, when only one foot is in contact with the floor, the CoM typically lies medially to the base of support (Jian *et al.*, 1993; MacKinnon & Winter, 1993; Lyon & Day, 1997, 2005). The body is therefore not stable but is falling sideways, away from the stance foot, under the influence of gravity during a step. Given that the body is falling about the stance foot during a step, the human body can be considered to move like an inverted pendulum. Whilst this means the body is unstable and at risk of a complete loss of balance, it does seem to be the most efficient mode of movement for bipeds and substantially reduces the energy required for locomotion (Srinivasan & Ruina, 2006). In this context, gravity can simultaneously be considered our greatest friend and greatest foe.

Prior to a step, the body's mass is positioned above its base of support, spanning the area enclosed by the feet, and the body is balanced. In order to take a step, a foot must lift from the ground and the body's static balance disrupted. Before the stepping foot lifts, force is exerted on the ground to accelerate the body and generate momentum for the step (Carlsöö, 1966; Mann *et al.*, 1979; Crenna & Frigo, 1991; Jian *et al.*, 1993; MacKinnon & Winter, 1993; Lyon & Day, 1997, 2005). Typically, this results in the body moving forwards and towards the stance-side by the time the stepping foot lifts. When the foot lifts, the mass is rarely positioned over its new base of support defined by the foot still in contact with the ground (Jian *et al.*, 1993; MacKinnon & Winter, 1993; Lyon & Day, 1997). The body is therefore unbalanced and falling under the influence of gravity during a step. This poses a significant control problem for the brain as a complete loss of balance (i.e. a fall) needs to be prevented. How is the motion of the body controlled during a step?

1.4 The throw-and-catch model of human stepping

The throw-and-catch model of human stepping has been proposed to explain how the motion of the body is controlled during a step. This hypothesis states that the pre-step activity represents a 'throw', which gives the body a specific position and momentum at the time of foot lift. At this point, the body enters a ballistic phase during the step where it falls under gravity along a trajectory determined by the pre-step activity, just as a ball would after being thrown. The direction and magnitude of the throw is finely tuned to take into account the initial state of the body and the intended final position of the stepping foot. Thus, during the step, the stepping foot swings towards its intended target while at the same time being optimally placed when it lands to 'catch' the body and regain balance.

1.5 Movement errors

Presumably error in one or both of the throw and catch can lead to a complete loss of balance. One way in which error in movement has been examined is by experimentally inducing it. In the case of a step this has most frequently been achieved by making the location of a step target change unexpectedly. When a target changes location at the instant the stepping foot lifts, the throw of the body is no longer appropriate for the new intended step location. In response the trajectory of the foot is altered rapidly in an attempt to land the foot on the new target (Reynolds & Day, 2005a, 2007; Kim & Brunt, 2009; Tseng *et al.*, 2009; Nonnekes *et al.*, 2010; Kim & Brunt, 2013). However, the magnitude of the adjustment of the foot is directionally dependent: medial adjustments are unable to be as large as lateral adjustments. This reflects that the body is falling laterally under gravity during the step and that the catch of the body must still be incorporated into movement.

Another way of exploring movement error is to study diseased populations with movement difficulties. Gross errors are apparent in populations with neurological disease by their increased frequency of losing balance and falling in comparison to healthy, non-diseased populations (Roller *et al.*, 1989; O'Loughlin *et al.*, 1993; Forster & Young, 1995; Fonteyn *et al.*, 2010). Finer errors can be seen by abnormal movement patterns. One such abnormal movement pattern is of that after damage to the cerebellum. The behavioural hallmarks of cerebellar damage are unsteadiness and movement ataxia, literally meaning movement without order. Together, this manifests as a distinctive staggering gait that resembles a person who is drunk. For this reason, the role of the cerebellum has received much attention. In humans, however, damage to the cerebellum is often accompanied with damage to other areas of the brain or peripheral nervous system. It can therefore be tricky to pinpoint the input that the cerebellum has on behaviour such as gait ataxia. However, some forms of damage to the cerebellum are genetically determined and therefore have a pathology that is well defined (Solodkin & Gomez, 2012).

1.6 Spino-cerebellar ataxia type 6 (SCA6)

Spino-cerebellar ataxia type 6 (SCA6) is one such pathology. SCA6 is somewhat unique in that it causes damage almost exclusively to the cerebellum, most notably to Purkinje cells which are the output neurons of the cerebellum (Gomez *et al.*, 1997; Stevanin *et al.*, 1997; Solodkin & Gomez, 2012). For this reason it has been described as a pure form of cerebellar disease and offers a useful population with which to study the influence of the cerebellum in movement.

1.7 Aim and experimental approach

This thesis aims to investigate the control and coordination of a human step. It is asked how the body and leg move when stepping from one location to another. A single step from a stationary starting position is used as a model with which to study dynamic balance control. A single step contains all the constituent parts of walking: the lift of a foot, a shift of the mass and swing of the leg. The use of a single step also has the advantage, over the study of stepping during walking, that the body begins the step in a controlled and repeatable stationary state.

This thesis starts by examining how the body moves before a step to different locations (Chapter 3). A novel method is used where the location of a step target is made to unexpectedly jump to a new location shortly after the initiation of the body’s pre-step movement. Crucially, this target jump is made to occur long before the stepping foot lifts. It is asked whether the pre-step movement (the throw) is adjusted to take account of the new target location.

It then proceeds in Chapter 4 to examine how the movement of the body before the step relates to its movement during the step. The body is modelled during the step in order to ascertain whether the body throw completely determines its motion during the step or whether the motion of the body is modified during the step.

Chapters 5 and 6 then investigate how a step is coordinated. First, Chapter 5 asks how the movement of the body (the throw) and leg (the catch) are coordinated during the step in a healthy, young population without balance difficulties. Chapter 6 then applies this method to a population with movement and balance difficulties (SCA6) to investigate movement error in relation to the throw and catch model.

2 Chapter 2: General Methods

2.1 Introduction

The experiments outlined in this thesis were each performed in a single session lasting approximately 2-3 hours. All experiments involved subjects stepping onto a visually presented target within a floor-bound display. This chapter will describe the apparatus used in the experiments, the techniques used to quantify stepping performance and outline how the resulting data was analysed.

All investigations were funded by a UCL Grand Challenge studentship. The experimental procedures were explained to each subject before written informed consent was obtained. The experiments were approved by the UCL Research Ethics Committee and conformed to the *Declaration of Helsinki*.

2.2 Apparatus

2.2.1 Target lights

The step targets were made from strips of electroluminescent paper (Light Tape UK Limited; Barnsley, Yorkshire, UK), which provided a clean, cool-to-the-touch and low-profile (< 1 mm thickness) light source. The electroluminescent paper strips were affixed to a thin sheet of similarly-coloured cardboard with circular cut-outs (2.5 cm diameter) in the desired locations of the targets. A transparent plastic sheet was placed over the cardboard and electroluminescent paper to protect the targets. The entire display was secured to the floor to prevent the targets moving after being stepped on. Different target layouts were used depending on the experiment and are outlined in the relevant experimental chapters.

It was unknown whether the electroluminescent paper would illuminate immediately upon instruction or whether there was a delay between an instruction to illuminate and the target actually illuminating. To establish this, an experiment was performed to calculate any inherent delay. A single target was made to illuminate for 100 ms whilst the light emitted from the target was measured (Figure 2.1). The instruction to illuminate and extinguish the target was controlled by a computer program (the same process as was used in all experiments) and the timing of the computer’s command signal was recorded by changing the voltage of an analogue channel. A voltage greater than zero signified the instruction for the target to be illuminated. To measure when the target responded to the signal, a photodiode (1.75mm IPL 10530DAL [with lens] photodiode with integrated amplifier) was placed over the target which would output a voltage proportional to the amount of light hitting it. Thus, the timing of the target's instruction to illuminate and the target actually illuminating could be recorded precisely and any delay measured. Fifty trials were recorded at a sampling frequency of 10 kHz. The photodiode output was digitally low-pass filtered using a 2nd order, dual-pass Butterworth filter with a cut-off frequency of 100 Hz.

The illumination delay was estimated with Matlab's *risetime* function (The Mathworks Inc.; Natick, MA, USA). In brief, *risetime* estimated the photodiode output's high- and low-state by examining the (bimodal) distribution of the signal (Figure 2.1: blue inset). The two peaks identified by *risetime* were designated the low- (0%) and high-state (100%). The target was considered illuminated when the photodiode output

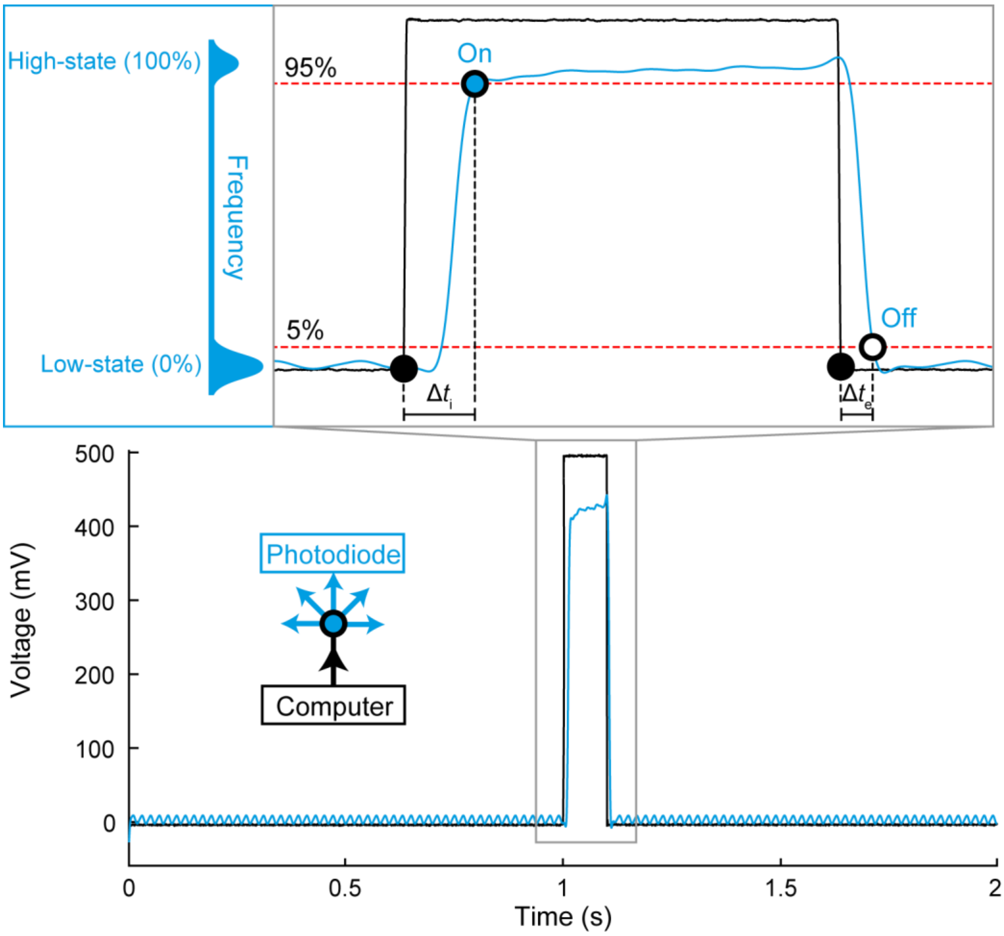

Figure 2.1. Calculation of target illumination delay. A single trial where a target was instructed to illuminate for 100 ms is depicted (bottom). The light emitted from the target was measured by a photodiode (blue trace). The delay between a computer's signal for the target to illuminate (black trace) and the target actually turning on (Δt_i) or off (Δt_e) was calculated. The thresholds for when the target was on or off were defined by Matlab's *risetime* function, which estimated the peaks (0% and 100%) of the photodiode's bimodal distribution (blue inset, top left).

reached 95% of its transition from low- to high-state and extinguished when it was below 5% of its transition from high- to low-state.

The delay between the signal for a target to illuminate or extinguish and the target actually turning on (Δt_i) or off (Δt_e) was calculated at 16.3 (0.3; mean (SD)) ms and 7.1 (0.2) ms respectively. Knowledge of these delays was particularly useful in Chapter 3 to allow for estimation of when a target jump was perceptible to the subjects and subsequently from when a step modulation could have been expected. These delays are accounted for in all experimental analyses.

2.2.2 Body motion

Movement of the subjects' body and limbs during a step was measured using a Coda motion capture system (Coda cx-1; Charnwood Dynamics, Leicestershire, UK). Several different set-ups were used, depending on the experiment, and are explained in detail within the relevant experimental chapters (Chapters 3, 4, 5 and 6). The Coda system consisted of several motion capture units, each of which contained three cameras. The cameras tracked the movement of infrared-emitting diode markers, herein termed markers, which were attached to the subjects. The markers would either be directly attached to the subjects using double-sided tape or attached in a 'cluster' of four markers, which were non-collinearly placed on a rigid structure and firmly strapped onto the body. The laboratory coordinate system was defined by the Coda system.

2.2.2.1 Virtual body landmarks

In addition to tracking 'real' marker locations, virtual body landmarks could also be tracked. These 'virtual' landmarks were calculated using the locations of marker clusters. To calculate the virtual landmark locations, a pointer, containing four markers, was placed over the relevant body landmark. The location of the pointer's markers and the markers on the relevant cluster(s) were then briefly recorded. The virtual landmark location could then be associated to the cluster marker locations and reconstructed at any time using a rigid body transformation. For example, when constructing the left-foot 1st toe landmark, the pointer would be placed over the 1st metatarsal head and its location would be associated with the left-foot markers. For landmarks adjoined by two segments with marker clusters (for example the knee being adjoined by the upper and lower leg which each had a cluster), two virtual landmarks were reconstructed based on the locations of each segment's cluster markers. Rigid body transformations were implemented by Python scripts provided

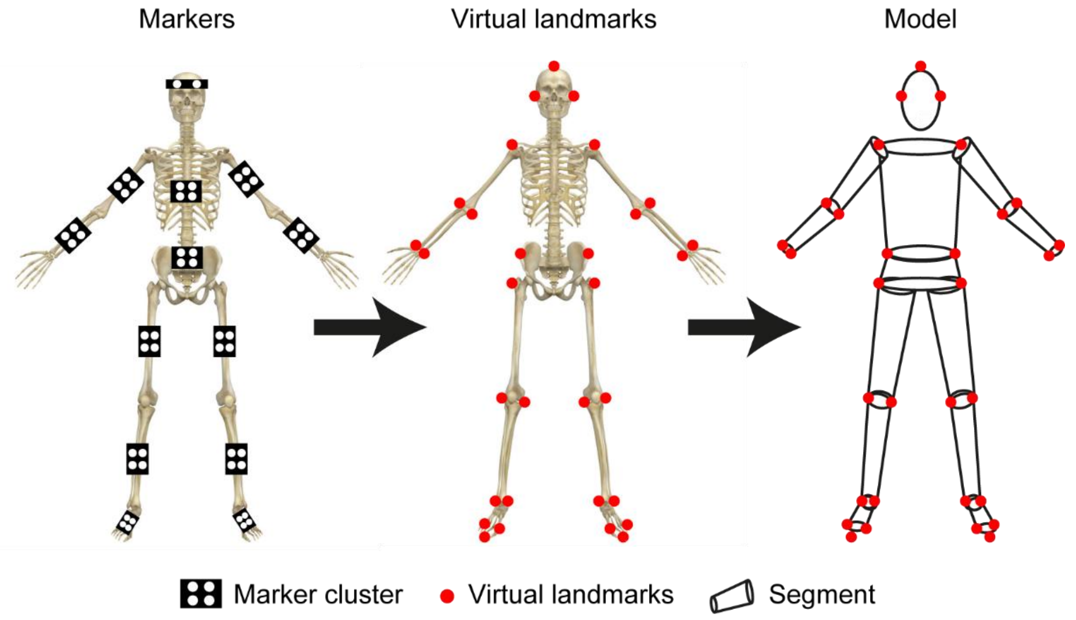

Figure 2.2. Whole-body set-up. When modelling the whole-body, rigid clusters of markers were attached to the body (left). These markers were used to track the positions of virtual landmarks (middle) which defined the locations of each body segment for whole-body modelling (right). The white circles in the marker clusters represent the markers. The head cluster was attached to a head band with two front-facing markers (depicted) and two back-facing markers (not depicted). The pelvis and trunk clusters were attached to the back but are depicted from the front here for simplicity.

within Coda's recording software. Virtual landmark locations were calculated using filtered marker data. The filtering techniques employed are outlined in Chapter 2.4.

Tracking the movement of virtual landmarks was useful in order to construct a whole-body model of each subject during a step (Figure 2.2). The virtual landmark locations were chosen so that the location of the body's segments could be reconstructed and the whole-body's centre of mass (CoM) estimated. A six degrees of freedom, thirteen segment model consisting of the feet, upper and lower arms and legs, pelvis, torso and head was constructed based on the virtual landmark locations. The location of the each hand was not tracked. The model was implemented using Visual 3D modelling software (C-Motion; Germantown, MD, USA), which estimated each segment's CoM and inertial properties using calculations from Dempster (1955) and Hanavan Jr (1964). The segments, its relative weighting for the whole-body CoM location, its geometric shape in the model and the corresponding virtual landmarks used to define its location are outlined in Table 2.1. The segment weightings were Visual 3D's default values, based on Dempster's regression equations (1955).

2.2.2.2 Reliability of motion capture data

Modern motion capture systems are extremely precise and are generally considered to provide sub-millimetre accuracy and precision (Whittle, 1996; Windolf *et al.*, 2008). However, in practise several sources of error can decrease the accuracy and reliability of kinematic data measured using motion capture technology. The technique involves placing markers on a subject's skin or clothes which emit near infra-red light. Specialised cameras are then able to locate the position of the markers and track their motion over time, with the aim of quantifying the movement of selected anatomical landmarks. Several sources of potential error have been reported in the literature: (1) instrumentation error (Chiari *et al.*, 2005); (2) soft-tissue artefacts (Leardini *et al.*, 2005); and (3) marker placement error (Della Croce *et al.*, 2005).

Instrumentation error relates to the intrinsic precision of the motion capture system, the calibration of the cameras and the hardware of the cameras (Chiari *et al.*, 2005). The motion capture cameras used in all experiments presented within this thesis were calibrated by the manufacturer and are estimated to resolve a marker's position to within approximately 0.05 mm when operating without error (Charnwood Dynamics Ltd, 2016). One known source of error in the camera's hardware is that the photo-detector in each of the cameras which locates the markers in space is susceptible to distortion due to the frequency of room lighting and electrical noise. This presents as high-frequency fluctuations in the marker position signal even when a marker is motionless (Charnwood Dynamics Ltd, 2016). The degree of error from the camera hardware in the present set-up was estimated by recording the position of a static marker over 5 seconds. This was repeated multiple times and at the two sampling frequencies (100 Hz and 200 Hz) that were used in the experiments in this thesis. The fluctuation in marker position was found to be small (root-mean-squared error of <0.1 mm in x, y and z dimensions) and was approximately halved by low-pass filtering marker positional data (see Chapter 2.4 for filtering techniques). It should be noted that the level of instrumentation error associated with the motion capture system used here is miniscule in comparison to the movement of the human body, leg and foot measured during the steps studied in this thesis and also in comparison to the variation present between repeated steps. As such, the motion capture system's instrumentation error is unlikely to have significantly impacted the reliability of the data presented in this thesis.

Larger errors can be introduced through soft-tissue artefacts (Leardini *et al.*, 2005; Peters *et al.*, 2010). The term soft-tissue artefacts describes the fact that markers attached to the skin can move with respect to the underlying anatomical (i.e.

skeletal) landmark that they are intended to represent (Leardini *et al.*, 2005). The level to which soft-tissue artefacts influences marker positional error depends on the body segment and the task performed (Leardini *et al.*, 2005). Peters *et al.* (2010) conducted a systematic review to estimate lower-limb soft-tissue artefacts in the published literature and showed that markers affixed to the upper leg (thigh) display greatest (>10 mm) imprecision. However, the use of marker clusters (as described in Chapter 0) reduces the effect of soft-tissue artefacts substantially (Peters *et al.*, 2010). The position of the foot was a key variable in all experiments in this thesis but soft-tissue artefacts only moderately effect markers placed on the feet (Peters *et al.*, 2010), with those on the metatarsals being erroneously displaced by less than 3 mm on average (Maslen & Ackland, 1994).

Incorrect placement of the markers on the intended anatomical landmark can also introduce error into measurements made using motion capture technology (Della Croce *et al.*, 2005). Error can result from variation between different experimenters' ability to locate the landmarks (inter-experimenter) or from variation in the same experimenter's ability to locate the landmarks over repeated experiments (intra-experimenter). All measurements in the experiments within this thesis were made by the same experimenter (the applicant, MJB) and, as such, the influence of error resulting from inter-experimenter variation can be ruled out. Inter-experimenter variability has been shown to be greater than intra-experimenter variability when locating lower limb and pelvic landmarks (Della Croce *et al.*, 1999), suggesting that the exclusion of inter-experimenter variability will have removed a major error source.

Intra-experimenter variability can be substantial though and tends to vary depending on the landmark's prominence. For example, Della Croce *et al.* (1999) asked experimenters to locate various landmarks over the pelvis and lower limb and reported that intra-experimenter variability in determining landmark location was least for particularly bony landmarks like the metatarsals (up to 9 mm imprecision) and greatest for landmarks surrounded by soft-tissue such as the pelvis and greater trochanter (up to 21 mm imprecision).

Despite this, intra-experimenter variability in locating anatomical landmarks is most relevant for studies where measurements are taken from the same subject over multiple sessions as erroneous placement of the marker can give the illusion of a difference between sessions. This was not the case here as all experiments were conducted in a single session and all analyses were based on measures recorded with the same marker placement. Of greater issue in the present experiments was that the markers stayed in a consistent location over the landmark across the experimental session. As previously discussed, markers can move with respect to the underlying landmark when a subject moves. Moreover, markers can become dislodged or slip out of position over the course of an experiment. For much of the data in this thesis, markers were attached to the skin directly using double-sided tape to prevent them becoming dislodged or slipping. When markers were attached onto clothes, the clothes were tight-fitting to ensure that the marker was as close to the anatomical landmark as possible. When clusters of markers were used, the location of the cluster on the body segment was marked with tape or pen to give a visual representation of any cluster slippage. Additionally, marker clusters were strapped tightly onto the body segment. In all cases, the position of the markers and clusters were systematically rechecked over the course of an experimental session to ensure that their placement remained as accurate as possible.

Additional errors can be introduced when estimating the location of the whole-body's CoM. The method employed to achieve this (described in Chapter 0) uses mathematical models developed by Dempster (1955) and Hanavan Jr (1964) based on standard anatomical tables to estimate the inertial properties of each of a subject's body segments. Inevitably, no subject measured in the present experiments will have had an identical body build, shape and distribution as the subjects from which Dempster (1955) and Hanavan Jr (1964) developed their models and some error in estimating each segment's inertial properties can be expected. Hanavan Jr (1964) estimated that the horizontal whole-body CoM location to be accurate within 1.8 cm and the moments of inertia to be correct within 10%. Similarly, Plagenhoef *et al.* (1983) estimated error whole-body CoM inertia of between 10% and 15% when using these methods.

2.2.3 Ground reaction forces

Ground reaction forces were also recorded in addition to tracking segmental body motion. Prior to a step subjects stood with each foot over separate force platforms (Type: 9281C1, Kistler; Winterthur, Switzerland) which were embedded in the floor. The platforms measured the force exerted on the floor by the subjects in three dimensions. Each force platform contained piezoelectric sensors in each of its four corners which would output a voltage proportional to the force exerted upon the sensors. This voltage was amplified, recorded, converted to force and subsequently transformed from force platform coordinates into laboratory coordinates, as defined by the Coda system.

Ground reaction forces were sampled at 1000 Hz before being filtered to remove noise. Two filtering methods were employed: firstly, an analogue filter consisting of a seven stage low-pass Butterworth filter with a 50 Hz cut-off frequency was used to prevent aliasing of waveforms; secondly, a zero-lag, second-order Butterworth low-pass digital filter with a 30 Hz cut-off frequency was used to remove noise. The force platforms are prone to drift over time and as such were systematically reset after each block of experimental trials.

Table 2.1. Whole-body model.

Segment	Properties	Virtual landmarks
Foot	Weighting: 0.0145 Shape: Cone	- 1st toe (metatarsal head) - 5th toe (metatarsal head) - Medial ankle (tibial medial malleolus) - Lateral ankle (fibular lateral malleolus)
Lower leg	Weighting: 0.0465 Shape: Cone	- Medial ankle (tibial medial malleolus) - Lateral ankle (fibular lateral malleolus) - Medial knee (femoral medial condyle) - Lateral knee (femoral lateral condyle)
Upper leg	Weighting: 0.10 Shape: Cone	- Medial knee (femoral medial condyle) - Lateral knee (femoral lateral condyle) - Greater trochanter - Radius: 25% of the distance between greater trochanters
Pelvis	Weighting: 0.142 Shape: Cylinder	- Left greater trochanter - Right greater trochanter - Left hip (posterior superior iliac spine) - Right hip (posterior superior iliac spine)
Trunk	Weighting: 0.355 Shape: Cylinder	- Left hip (posterior superior iliac spine) - Right hip (posterior superior iliac spine) - Left shoulder (acromion process) - Right shoulder (acromion process)
Lower arm	Weighting: 0.016 Shape: Cone	- Elbow (medial humeral epicondyle) - Elbow (lateral humeral epicondyle) - Wrist (radial styloid process) - Wrist (ulnar styloid process)
Upper arm	Weighting: 0.028 Shape: Cone	- Shoulder (acromion process) - Elbow (medial humeral epicondyle) - Elbow (lateral humeral epicondyle) - Radius: 50% of the distance between medial and lateral humeral epicondyles
Head	Weighting: 0.081 Shape: Ellipsoid	- Left ear (meatus) - Right ear (meatus) - Top of the head - Radius: 50% of the distance between the left and right ears

2.2.3.1 Centre of pressure

The point of application of the ground reaction force (termed centre of pressure (CoP)) was also calculated for each force platform according to the manufacturer’s guidelines. The CoP from each platform was then combined to give a resultant CoP vector location. This was calculated by weighting each force platform’s CoP location according to the vertical force exerted on each platform:

$$Equation\ 2.1: \qquad CoP = CoP_1 \frac{Fz_1}{Fz} + CoP_2 \frac{Fz_2}{Fz}$$

where *CoP* is the location of the combined CoP vector, $CoP_{1/2}$ is the location of the CoP vector from force platform 1 and 2 respectively, $Fz_{1/2}$ is the vertical force measured by force platform 1 and 2 respectively and *Fz* is the summed vertical force from force platforms 1 and 2.

2.2.3.2 Reliability of ground reaction force data

The equipment used in this thesis to measure ground reaction forces is considered of gold-standard in the analysis of human gait and balance (Whittle, 1996). There a several factors that can limit the accuracy and precision of ground reaction force data however.

The recorded ground reaction forces measured by the force plates used in all experiments presented within this thesis are prone to drift over time. For example, if one of the force plates was left unloaded (and no forces other than gravity were acting upon it) the outputted force should equal zero across *x*, *y* and *z* dimensions. However, what is actually seen is that the recorded forces progressively drift away from zero despite no additional force acting on the surface of the force plate. Two methods were employed to remove drift errors from force recordings. Firstly, as mentioned in Chapter 2.2.3, the force platforms were systematically reset after each experimental block of trials to remove time-dependent drift in force recordings. Further to this, an offset was calculated offline for each trial to remove any further drift error. The algorithm (provided in Appendix 9.1) estimated when a foot was not in contact with a force platform in a single trial and calculated the median force across this time period for each of the ML, AP and vertical dimensions. This offset was subtracted from the recorded forces and these corrected forces were used to calculate foot lift, foot land and the resultant CoP location as described above (Chapter 2.2.3.1).

Another known problem is in the determination of the CoP. The accuracy of determining the CoP location systematically varies over the surface of the force plate and is greatest in the four corners of the plate where the piezoelectric sensors are placed and least in the centre of the plate (Bobbert & Schamhardt, 1990; Schmiedmayer & Kastner, 2000). It should be noted that each foot was placed over separate force platforms and that each foot was placed near the centre of the plate in the experiments within this thesis. As such, minimal error in locating the CoP can be expected in the present results. In addition, algorithms have been employed to improve the systematic error in CoP determination according to the manufacturer's guidelines and the expected remaining error is of the magnitude of 1 mm (Sommer *et al.*, 1997). Imprecision in CoP determination could have influenced the accuracy of torque calculations presented in Chapter 4. As an illustrated example of this, a single trial was randomly selected from Chapter 4 and the CoP location was altered from the recorded value by ±1 mm, which caused the calculated torque to vary by up to 12%.

2.2.3.3 Online event detection

All experiments described in this thesis required the detection of specific events during a trial in order for different experimental manipulations to be triggered. In Chapter 3 the onset of the pre-step postural activity required detection to trigger a target jump whilst in Chapters 5 and 6 the lift of the stepping foot required detection to trigger occlusion of vision. The analogue signal from the force platforms was used to detect these events in all experiments. Figure 2.3 summarises the methods used. Firstly, the voltage outputted from each force platform's four vertical sensors were summed using an electronic summer. This estimated the total vertical force exerted on each platform. For detection of the onset of the pre-step postural activity, the difference in vertical force between the two force platforms was then calculated by subtracting one force platform's vertical force from the other using an electronic inverter. This signal, or simply the summed vertical force for each platform when foot-lift required detection, was then inputted to a Schmitt trigger. For detection of the onset of the pre-step postural activity, the Schmitt trigger's threshold was set at a voltage equating ±80 N. Accordingly, the positive threshold was broken when a right-foot step was being initiated and the negative threshold was broken when a left-foot step was being initiated. For the detection of foot-lift, the threshold was broken when the vertical force was below a voltage equating 10 N. The Schmitt trigger would output a digital signal when its threshold was broken which triggered the desired events in each experiment.

More precise methods were used offline when analysing the data to detect these events and are described in Chapter 2.3 and the methods sections of each experimental chapters.

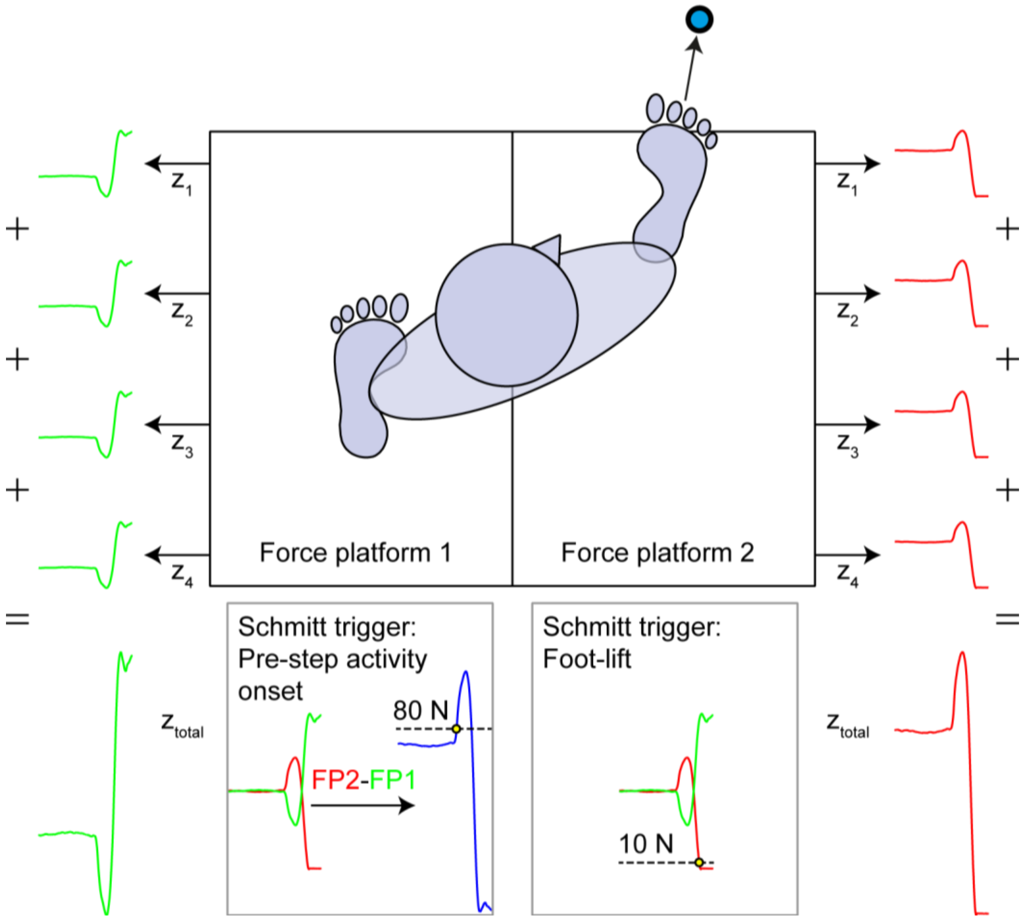

Figure 2.3. Online event detection. An example of a right-foot leading trial is depicted. Analogue outputs of vertical force ($z_{1\text{-}4}$) were summed (z_{total}) for each force platform. The insets show how these summed traces were inputted to a Schmitt trigger and the trigger's thresholds. All traces are voltage over time from the start of the trial until shortly after the stepping foot lifted.

One potential disadvantage with the method described above to detect the pre-step activity's onset is that small asymmetries in the distribution of weight between the two feet can bias the timing of the event's detection. Consider the example vertical force traces presented in the left-hand inset of Figure 2.3. In this case the subject is stood with equal weighting between the left (green trace) and right (red trace) feet, the difference in vertical force between the two force plates equals zero and the Schmitt trigger threshold would be broken when the difference equalled 80 N (i.e. when 40 N of weight was transferred from one leg to the other). If the subject was stood asymmetrically with greater weight on the right side, the difference in vertical force between the feet would be closer to the 80 N threshold than when stood symmetrically and, assuming the same rate of weight shift, the threshold would be broken sooner. On the other hand, if the subject was stood asymmetrically with greater weight on the left side, the difference in vertical force between the feet would be further from the 80 N threshold than when stood symmetrically and the threshold would be broken later. Likewise, the timing of the pre-step activity's onset based on this method depends on the rate of the weight shift, with more rapid weight shifts being detected sooner and slower weight shifts detected later.

Previous studies have used set time-delays after a cue to initiate a step to estimate approximately when the pre-step activity begins (Tseng *et al.*, 2009; Mouchnino *et al.*, 2012; Kim & Brunt, 2013). However, such methods do not account for trial-to-trial variability in response time after the cue, are not based on movement of the subject and often require the subject to initiate movement as fast as possible. These major disadvantages were found to be unacceptable for the present studies in which a normal, temporally unconstrained step was to be studied. In practise, the method adopted here based on the difference in vertical force underneath the left and right feet was found to be far superior in comparison to using a set time delay.

The absolute force difference of ±80 N was set at a relatively small proportion (~6-9%) of the actual weight shift that occurs during the pre-step activity, which allowed a rapid detection of the pre-step activity onset after its initiation. To attempt to minimise the effect of stance asymmetry, the weight distribution was monitored on a trial-by-trial basis and subjects were told to stand with a more equal weight distribution if any asymmetry was noticed. Due to a combination of small asymmetries in the initial weight distribution that remained and trial-to-trial difference in the rate of weight shift, the pre-step activity's onset was detected online at a variable time, but consistently with short latency (mean and standard deviation provided in Chapter 3.3.5) after the pre-step activity's actual initiation (calculated as described in Chapter 2.4). The online detection of the pre-step activity's onset was found to be appropriate in the vast majority of trials, with only a few trials (1% of trials in Chapter 3.3.7) were requiring exclusion due to incorrect detection of the pre-step activity's onset.

2.2.4 Visual occlusion

Visual occlusion was achieved with PLATO (Portable Liquid crystal Apparatus for Tachistoscopic Occlusion) spectacles (Translucent Technologies; Toronto, Canada). PLATO spectacles are lightweight goggles that can be electronically controlled such that their lenses are either transparent (to allow vision) or opaque (to occlude vision; Figure 2.4A). Subjects wore the spectacles and looked downward towards the target lights during a trial in the experiments in Chapters 5 and 6. Although the PLATO spectacles occlude the majority of the visual field, it was possible that subjects would attempt to look downward and underneath the frame of the spectacles

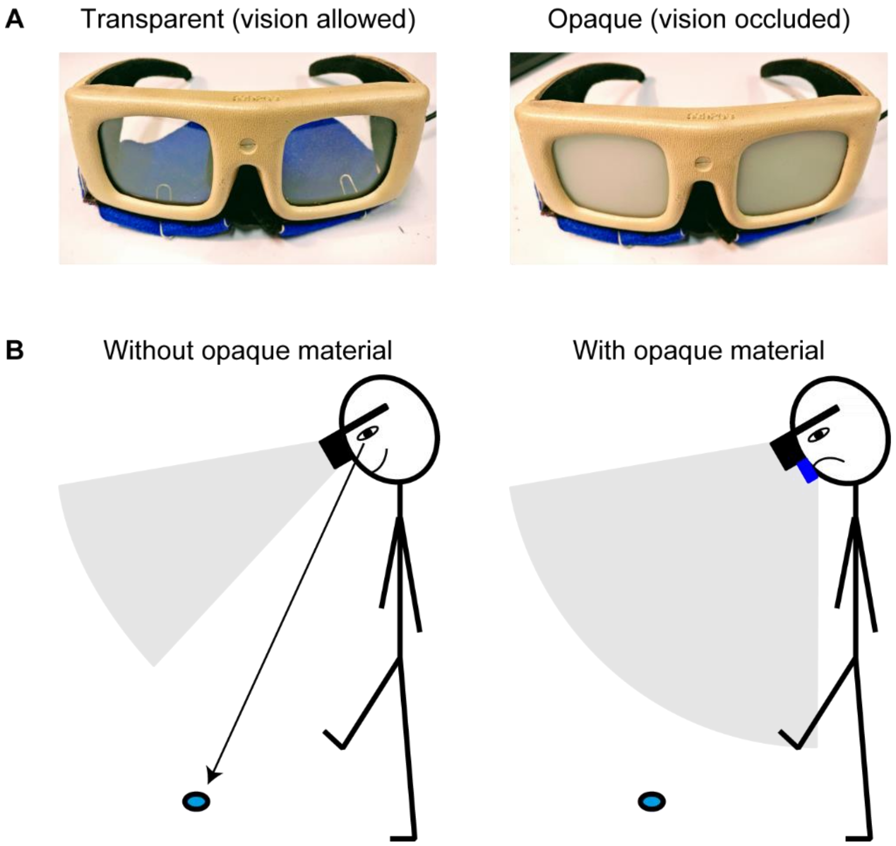

Figure 2.4. Visual occlusion. (**A**) The PLATO spectacles and opaque material (blue on the underside of the spectacles) when the lenses were transparent (left) and opaque (right). (**B**) When opaque the PLATO spectacles occluded much of the visual field but subjects could have retained vision of the target and/or their body by looking underneath the glasses' frame (left). The opaque material ensured that this was not possible (right). The grey areas signify the area of the visual field occluded.

to retain vision of the target and/or their body when vision was occluded (Figure 2.4B). To avoid this possibility, opaque material was attached to the underside of the spectacles to force subjects to look through the lenses at all times, ensuring that vision was actually occluded when desired.

The delay between a signal and the spectacles transitioning from transparent to opaque states is rapid (~7 ms (Translucent Technologies Inc., 2012)), allowing precise control of the timing of visual occlusion. The signal to occlude vision at foot-lift was provided by the Schmitt trigger pulse outlined in Chapter 2.2.3.3. The inherent delay between the signal and the lenses becoming opaque is included in all analyses.

2.3 Protocol

In all experiments, subjects were instructed to step to the location of a target as accurately as possible. An accurate step to each target was self-defined by all participants prior to each experiment. To achieve this, participants would place the appropriate foot over each target without time constraints in a manner they deemed accurate. For targets on the left of the subject, a left-foot leading step was required; for targets to the right, a right-foot leading step was required. For the accuracy trials, subjects were allowed to adjust their foot's position until they felt it represented an accurate step to a target. The accuracy step was redone if the subject or experimenter felt it necessary. Subjects were instructed to land their foot in this way for all subsequent steps and the position of their foot when it landed was compared to this ideal position.

The final position of the stepping foot was emphasized as being paramount and non-adjustable following foot landing in all experimental trials. After the stepping foot landed subjects were required to step with the trailing foot and bring it alongside their stepping foot. The final position of the trailing foot does not affect the performance of the initial step (Lyon & Day, 2005) so no specific instruction was given as to where to place the trailing foot. However, subjects were encouraged to finish the step in a balanced state, similar to which they started.

2.4 Data analysis

All data was acquired using Codamotion's Odin software suite. Once acquired, the data was exported to Matlab for further analysis using custom written scripts. Force data was filtered as described in Chapter 2.2.3. Marker position was filtered using a low-pass, second order Butterworth filter with a cut-off frequency of 15 Hz. The specific analyses and variables computed are described in each experimental chapter. Several key step events were calculated in all analyses:

Pre-step activity onset: To the best of my knowledge, no published studies have assessed the reliability of methods to detect the onset of pre-step activity. However, the first biomechanical event associated with the onset of pre-step activity is typically the movement of the CoP backwards and laterally towards the forthcoming stepping-side heel (Mann *et al.*, 1979; Breniere *et al.*, 1987; Jian *et al.*, 1993). Previous studies have used this signal to detect the pre-step activity's onset either by visual inspection of the CoP trace (for example Brunt *et al.*, 1991) or by an algorithm. Such algorithms tend to use the CoP velocity to differentiate between the natural movement of the CoP during quiet stance and the onset of the pre-step activity (for example Caderby *et al.*, 2014; Yiou *et al.*, 2016). When stood quietly with the eyes open and feet separated by 15 cm (as was the posture prior to a step in all experiments here), mean medio-lateral (ML) CoP velocity is approximately 1 cm/s in healthy populations but can fluctuate substantially (Day *et al.*, 1993). For this reason, the onset of the pre-step activity was qualified by: (1) ML CoP velocity being substantially greater (at least 5 cm/s) than the normal level seen by Day *et al.* (1993); (2) the ML CoP velocity being directed towards the stepping foot; and (3) both of conditions 2 and 3 being satisfied for at least 50 ms. These three conditions ensured that the onset of the pre-step activity was not triggered during quiet stance. Individual trials were inspected to ensure that gross errors were not encountered.

Foot lift: the time the stepping-foot lifted from the ground was calculated offline and compared to the online detection outlined in Chapter 2.2.3. Foot lift was defined as the first time vertical force went below 1% of a subject's body weight.

Foot land: the step targets were placed differently in different experiments; this meant that for some experiments the subjects would step off the force platforms and that the force platforms could not be used to estimate when the foot landed on the ground in all steps. When this was the case foot land was estimated using the speed of the stepping foot and defined as the first time after foot lift that the ML, AP and vertical speed of the hallux marker went below 2 cm/s. Otherwise, when the stepping foot landed on the force platform, foot land was defined as the first time after foot lift that the vertical force exceeded 1% of body weight. The method used is specified in each experimental chapter.

The detection of foot lift and foot land based on vertical force recordings is considered a gold-standard measure against which the precision and reliability of all other methods are compared (Taborri *et al.*, 2016). It should be noted that in the experiment where foot-land was calculated based on the hallux marker speed (Chapter 3), the timing of foot-land was not of primary interest and a highly precise detection of foot-land was not necessary. In all other cases, the lift and land of the stepping-foot was calculated from the vertical force from the plate beneath the stepping-foot.

These events were used to define key variables, such as the location of the foot when it landed to determine step accuracy or the CoM velocity when the foot lifted.

2.5 Statistical analysis

In general, computed variables fell under two categories: directional and non-directional data; each were analysed using different statistical methods.

Non-directional data: these variables were univariate, for example temporal variables or one-dimensional measures of variability. Non-directional data was submitted to *t*-tests or repeated-measures analysis of variance (ANOVA) depending on the number of conditions being compared, which were performed using SPSS statistical software (IBM Corporation; New York, NY, USA). Greenhouse Geisser correction was used in ANOVAs when the assumption of sphericity was violated.

Directional data: these variables were bivariate, for example two-dimensional foot location, or circular, such as angles. Directional data was analysed using statistical methods designed for directional data. Ideally a repeated-measures ANOVA capable of analysing directional data would be used to test for effects between more than two conditions. However, to my knowledge, no such test exists. Instead Hotelling's tests were used. A Hotelling's test is a generalised *t*-test capable of detecting differences between two conditions of directional data. For bivariate data like foot location, Hotelling's tests are advantageous in comparison to analysing the data in two dimensions separately as power is increased (Batschelet, 1981) and no *a priori* assumptions are required about which dimension of the data an effect is expected. Normality of directional data was assessed by Mardia's test of skewness and kurtosis (Mardia, 1970). Descriptive statistics of circular variables were calculated using circular methods (Zar, 2010) from the CircStat Matlab toolbox (Berens, 2009).

Statistical significance was set at an alpha level of 0.05 after Bonferroni correction for multiple comparisons in all analyses.

2.6 Sample size estimation

In each experimental chapter a power analysis of relevant data from previously published studies has been performed to estimate the expected effect size and required sample size to detect any effect. The relevant study or studies is reported in each chapter. In all cases the power analysis was performed using G*Power version 3.1.9.2 (Faul *et al.*, 2007; Faul *et al.*, 2009). Power analyses were performed for use with two-tailed *t*-tests as previously reported data was univariate in nature. Chapters analysing within-subject effects (Chapters 3, 4 and 5) use dependent-sample *t*-tests, whereas chapters analysing between-subject effects (Chapter 6) use independent-samples *t*-tests. A chance of type I error of 0.05 and type II error of 0.2 is generally considered conventionally acceptable (Zar, 2010). For all power analyses here, the chance of type I error (α) was set at 0.05 but the chance of type II error (1-β) was set at 0.1. The reason for this choice of lower type II error rate (greater power) was that both univariate and bivariate statistical methods were used in each chapter (see Chapter 2.5) and it was unclear how power analysis for univariate statistics (*t*-tests) would relate to bivariate statistical power. A conservative approach was therefore favoured.

G*Power requires Cohen's *d* (Cohen, 1969) to be calculated as a measure of effect size in order to estimate required sample sizes for *t*-tests. In the dependent-samples case, Cohen's *d* (termed d_z in G*Power) was calculated as:

$$Equation\ 2.1 \qquad d_z = \frac{|\mu_z|}{\sigma_z} = \frac{|\mu_x - \mu_y|}{\sqrt{\sigma_x^2 + \sigma_y^2 - 2\rho_{xy}\sigma_x\sigma_y}}$$

where μ_x, μ_y denote the population means from two dependent groups, σ_x and σ_y are the standard deviation in either population, ρ_{xy} is the correlation between the two populations and μ_z, σ_z are the mean and standard deviation of the difference (*z*) between the two populations, respectively (Faul *et al.*, 2007; Faul *et al.*, 2009). The correlation between population means was assumed to equal zero when it could not be estimated from the previously reported data (as in Chapters 3 and 5).

In the independent-samples case, Cohen's *d* (termed *d* in G*Power) was calculated as:

$$Equation\ 2.2 \qquad d = \frac{\mu_1 - \mu_2}{\sigma}$$

where μ_1, μ_2 denote the population means of two independent groups and

$$Equation\ 2.3 \qquad \sigma = \sqrt{\frac{\sigma_1^2 + \sigma_2^2}{2}}$$

where σ_1, σ_2 denote the standard deviation in each population (Faul *et al.*, 2007; Faul *et al.*, 2009).

For each of the dependent and independent samples cases, the population means and standard deviations were taken either from the reported text and tables or, when this was not possible, were extracted from reported figures. Data from figures was extracted using Engauge Digitizer Software version 10.4 (Mitchell *et al.*, 2018), which imports image files containing graphs and is able to extract the underlying data points.

2.7 Conclusion

Subjects stepped onto a target as accurately as possible in all experiments. Their stepping movement was evaluated using ground reaction forces and motion capture technology. Ground reaction forces were used online to detect specific events within a step and trigger experimental manipulations, such as a target jump or the occlusion of vision

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3 Chapter 3: Pre-step postural activity is coupled to the step location

3.1 Abstract

Postural activity normally precedes the lift of a foot from the ground when taking a step, but its function is unclear. The throw-and-catch hypothesis of human gait proposes that the pre-step activity is organized to generate momentum for the body to fall ballistically along a specific trajectory during the step. The trajectory is appropriate for the stepping foot to land at its intended location while at the same time being optimally placed to catch the body and regain balance. The hypothesis therefore predicts a strong coupling between the pre-step activity and step location. Here, this coupling was examined when stepping to visually-presented targets at different locations. Ten healthy, young subjects were instructed to step as accurately as possible onto targets placed in five locations that required either different step directions or different step lengths. In 75% of trials, the target location remained constant throughout the step. In the remaining 25% of trials, the intended step location was changed by making the target jump to a new location 96 ms ± 43 ms after initiation of the pre-step activity, long before foot lift. As predicted by the throw-and-catch hypothesis, when the target location remained constant, the pre-step activity led to body momentum at foot lift that was coupled to the intended step location. When the target location jumped, the pre-step activity was adjusted (median latency 223 ms) and prolonged (on average by 69 ms), which altered the body's momentum at foot lift according to where the target had moved. This chapter concludes that whenever possible the coupling between the pre-step activity and the step location is maintained. This provides further support for the pre-step postural activity functioning to throw the body into the step.

The work described in this chapter has been published and permission has been obtained for it to be included here:

Bancroft MJ & Day BL. (2016). The throw-and-catch model of human gait: evidence from coupling of pre-step postural activity and step location. *Frontiers in Human Neuroscience.* 10.

3.2 Introduction

When taking a step, postural activity usually precedes the lift of the stepping foot by around half a second. It modulates the force between the feet and ground to accelerate the body sideways and forwards, and is observed during single steps as well as during locomotion (Carlsöö, 1966; Mann *et al.*, 1979; Crenna & Frigo, 1991; Jian *et al.*, 1993; MacKinnon & Winter, 1993). What is the function of this pre-step activity? One possibility is that its job is to move the body mass directly over the upcoming stance foot, allowing the stepping foot to be lifted freely without compromising balance. However, this is not what is usually observed during single steps or locomotion. At the instant the stepping foot is lifted, the vertical projection of the body's centre of mass (CoM) commonly lies outside and medial to the base of support formed by the stance foot (Jian *et al.*, 1993; MacKinnon & Winter, 1993; Lyon & Day, 1997, 2005). This means that the body is not balanced, but is falling sideways under gravity during a step.

An alternative function of the pre-step activity has been proposed by the throw-and-catch model of human gait (Lyon & Day, 1997). This hypothesis states that the pre-step activity represents a 'throw', which gives the body a specific position and momentum at the time of foot lift. At this point, the body enters a ballistic phase during the step where it falls under gravity along a trajectory determined by the pre-step activity, just as a ball would after being thrown. The direction and magnitude of the throw is finely tuned to take into account the initial state of the body and the intended final position of the stepping foot. Thus, during the step, the stepping foot swings towards its intended target while at the same time being optimally placed when it lands to 'catch' the body and regain balance.

The throw-and-catch model predicts that the pre-step activity depends on both the body's initial conditions and the intended step location. In support of this are the findings that the resulting position and velocity of the body's CoM at the point of foot lift depend on both the initial stance width (Lyon & Day, 1997) and whether the step is to a forward or diagonal location (Lyon & Day, 1997, 2005), but are not influenced by the final position of the trailing foot (Lyon & Day, 2005). However, the predicted coupling between the pre-step activity and the intended step location has been shown to be breakable under certain circumstances. If the intended step location changes after the stepping foot leaves the ground, for example by shifting the position of a target, it is possible for the foot to land at a location different to that originally planned (Reynolds & Day, 2005a, 2007; Kim & Brunt, 2009; Tseng *et al.*, 2009; Nonnekes *et* *al.*, 2010; Kim & Brunt, 2013). This ability to de-couple the pre-step activity from the step location represents a challenge to the throw-and-catch hypothesis.

3.2.1 Hypothesis

Here, the strength of coupling between the pre-step activity and the step location is investigated under conditions previously unexplored. First, stepping onto five (for each foot) possible target locations is studied, either demanding different step directions with the same step length, or demanding different step lengths with the same direction. The throw-and-catch hypothesis predicts that the pre-step activity will differ and be unique for each target location. Second, the initial target is occasionally made to jump to another location just after the pre-step activity has been initiated, but before the stepping foot has been lifted. This timing of target jump potentially allows the pre-step activity to be adjusted should it be advantageous to do so. The crucial question, therefore, is whether the pre-step activity is adjusted to take account of the new target location, or is unchanged such that all necessary adjustments are made later during the step, similar to that observed with later target jumps. Support for the throw-and-catch hypothesis would be obtained if: (1) the pre-step activity were modulated by the target jump; and (2) the modulation were dependent on the final location of the target.

3.3 Methods

3.3.1 Sample size estimation

Lyon and Day (1997) conducted a similar study examining the motion of the CoM at foot-lift when stepping in different directions from an initial narrow or wide stance width. The authors reported means and standard deviations of ML CoM velocity (forward v diagonal step) of 0.099±0.020 v 0.052±0.015 m/s for the narrow stance and 0.160±0.030 v 0.104±0.023 m/s for the wide stance, equalling an effect of step location of size 1.97 and 1.47, respectively (Cohen's *d*; see Equation 2.1 in Chapter 2.6). Using the latter as a conservative estimate of effect size and a two-tailed dependent-samples *t*-test with the chance of type I error (α) set at 0.05 and the chance of type II error (1-β) set at 0.1, the estimated sample size required in the present experiment was eight. More subjects than this were recruited because the additional effects of step length and target jump were unknown.

3.3.2 Subjects

Ten human subjects (7 male; 24 ± 2 years; 64 ± 7 kg; mean ± standard deviation (SD)) participated in the experiment. No subject reported any known neurological, sensory, muscular or orthopaedic disorders. All subjects were naïve to the purpose of the study.

3.3.3 Protocol

Subjects performed a step onto a floor-bound target. Prior to the step, subjects stood barefoot and still with both feet parallel. The medial borders of the feet were

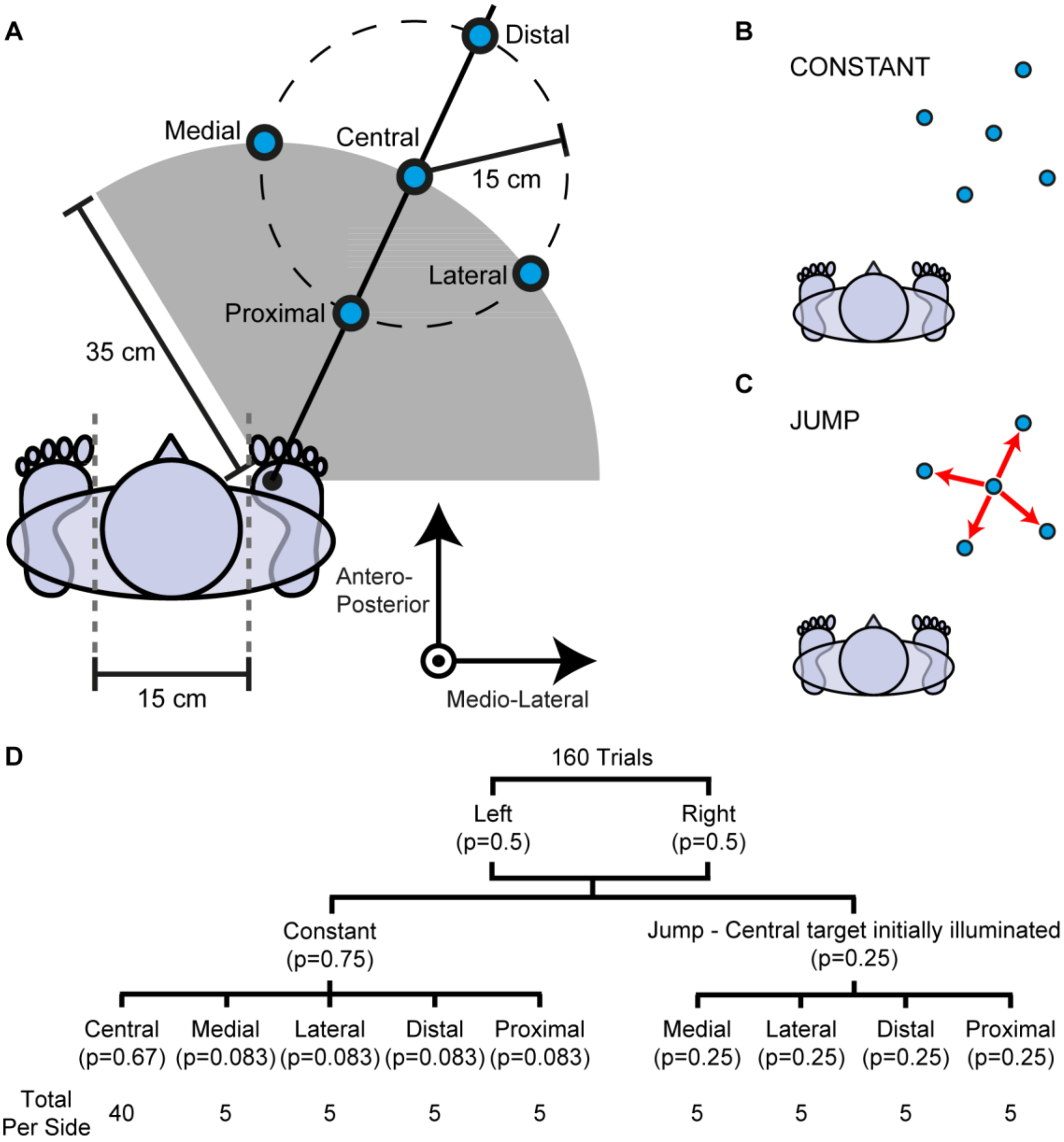

Figure 3.1. Experimental set-up. *A*: Right-sided targets are depicted; an identical configuration was present on the left side. The vertical axis protrudes directly out of the page. Subjects were instructed to step to a visually-presented target (blue circles). In most trials a target illuminated on either the left or right side and its location did not change (*B*). In some trials the target jumped 15 cm from the central target to one of four peripheral targets (medial, lateral, distal or proximal) shortly after initiation of the pre-step activity (*C*). *D*: Probability tree outlining the number of trials and probability per condition. A target jump occurred with a probability of 0.33 after illumination of the central target.

separated by 15 cm. This starting position was chalk-marked to ensure a consistent starting location for all steps. The positions of the targets required a forwards movement, with five targets located on each of the left and right sides (Figure 3.1). Subjects were instructed to step as accurately as possible to the target, and bring the trailing foot alongside. An accurate step was self-defined by each participant prior to the experiment, as described in Chapter 2.3. By instructing subjects to step accurately to the targets, rather than as quickly as possible, stepping foot placement, and thereby step location, variance would be minimised and any coupling between step location and the pre-step activity preserved. Multiple targets on both left and right sides were used to prevent prediction of target jump location or stepping side, thereby ensuring unbiased conditions at the time of target presentation and target jump.

A trial began with an audible beep, which was followed by a random delay and illumination of a step target. Illumination of the target acted as a cue for the subject to initiate a step to its location in their own time. The stepping targets were oriented so that step length and direction could be independently manipulated (Figure 3.1A). That is, for medial, central and lateral targets, step length was constant (35 cm) but step direction was different (0°, 25°, 50° forward of the stepping foot respectively). Equally, for proximal, central and distal targets, step direction was constant (25° forward of the stepping foot) but step length was different (20 cm, 35 cm, 50 cm respectively).

3.3.4 Experimental conditions

In 75% of trials, one of the five targets on either the left or right side was selected pseudo-randomly and illuminated for the duration of the step (constant condition; Figure 3.1B). The central target was selected most frequently (probability = 0.67), whereas the peripheral targets were selected less often but each with equal frequency (probability = 0.083).

In 25% of trials, the central target was illuminated on either the left or right side and was made to unpredictably jump to one of its four peripheral targets selected pseudo-randomly (jump condition; Figure 3.1C). The peripheral targets were selected with equal frequency when a target jumped to a new location (probability = 0.25). After illumination of the central target, the probability of it jumping was 0.33.

The target jump was achieved by simultaneously extinguishing the central target and illuminating one of the four peripheral targets. Target jumps were triggered when the difference in vertical force between the stepping and trailing foot sides exceeded 80 N. This related to a mean (SD) of 7.8 (0.9)% (range: 5.7%–8.8%) of total body weight. The new target appeared shortly after the initiation of the pre-step activity (mean (SD) latency: 96 (43) ms), long before the stepping foot lifted. The locations of the new targets meant that the required magnitude of foot adjustment remained constant (15 cm) but either step direction (medial- or lateral-jump) or length (distal- or proximal-jump) required modification.

A total of 160 trials were completed and performed in 10 blocks of 16 steps. The number of trials and its probability for each condition is summarized in Figure 3.1D.

3.3.5 Apparatus

Ambient light conditions were dim (<0.1 Lux; Isotech 1332A Digital Illuminance Meter, Southport, Merseyside, UK) to eliminate potential distractors and ensure that the target light was compelling. Three infrared-emitting diode markers were placed at the base of the first metatarsal and head of the first (hallux) and fifth metatarsals of each foot. Marker positions were tracked at 200 Hz by two motion capture units (Codamotion cx-1, Charnwood Dynamics, Leicestershire, UK). At the start of a trial, subjects stood with each foot over separate force platforms (9281C1, Kistler, Winterthur, Switzerland) which were embedded in the floor. Force was acquired at 1000 Hz.

3.3.6 Data analysis

Both marker position and force data were digitally low-pass filtered using a zero-lag, second order Butterworth filter with 15 Hz and 30 Hz cut-off frequencies respectively. An anti-aliasing analogue filter was used on force data prior to this.

The two force platforms were summed to evaluate the net force acting on the body in three-dimensions. From Newton’s Second Law of Motion, the acceleration of the body’s CoM was calculated by dividing net force by a subject’s mass. The net acceleration of the body’s CoM while the subject stood still (from the beginning of a trial until target illumination) was assumed to be zero and used as a baseline for the remainder of the trial. CoM velocity at foot lift, which has previously been shown to be an important variable in stepping (Lyon & Day, 1997, 2005), was then estimated by numerical integration of the CoM acceleration during the pre-step activity (trapezoidal method).

The timing of the pre-step activity’s initiation and the lift of the stepping foot were calculated, as outlined in Chapter 2.2.3.3. Pre-step activity duration was the time from its initiation to stepping foot lift. The target locations meant that for some steps the stepping foot would land beyond the force platforms. Therefore, the time the stepping foot landed was calculated using the stepping foot hallux marker speed, as outlined in Chapter 2.4. Speed was calculated as the absolute value of the first derivative of marker position. Step duration was the time from foot lift to foot land. The final position of the stepping foot was the mean position of the three foot markers upon landing.

To investigate whether the pre-step activity was modulated when the intended step location changed, the body's horizontal (AP and ML) motion in jump trials was compared to constant-central (the initial target in a jump trial) steps over time after alignment. All trials were aligned to the initiation of the pre-step activity and CoM acceleration was differentiated to calculate jerk. Two-dimensional 95% confidence intervals (confidence ellipses) were then generated at each time point for the constant-central condition. Figure 3.2 shows an example of this for one subject. The latency of any modulation was defined as the first time, at least 100 ms after a target jump, that a jump trial diverged from the constant-central confidence interval. The delay of 100 ms after a target jump was chosen as this relates to the shortest reported latencies to adjust lower limb trajectory or modulate ground reaction forces in visuomotor tasks (Reynolds & Day, 2005a, 2007; Leonard *et al.*, 2011). Modulation latency was measured for each jump condition and subject.

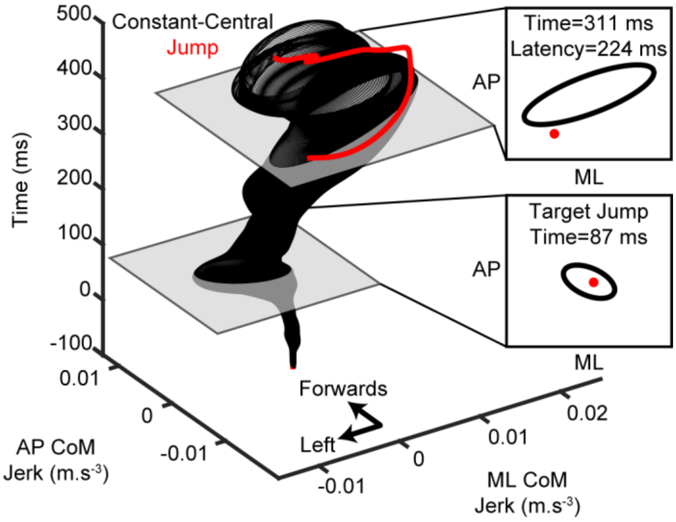

Figure 3.2. Calculation of modulation latency. An example is shown for one subject's step to the right-side lateral target after the target jumped (red). Medio-lateral (ML) and antero-posterior (AP) centre-of-mass (CoM) jerk traces were aligned to the initiation of the pre-step activity (time = 0) and 95% confidence ellipses were calculated at each time point for the constant-central steps (black). A modulation was detected when a jump trial diverged from the confidence ellipse. In this example the modulation occurred 224 ms after the target jumped and before the stepping foot lifted (time = 488).

Sixteen jump trials (1% of total trials, 4% of jump trials) were excluded from the analysis due to the target jump being triggered either before the initiation of the pre-step activity or shortly before the stepping foot lifted.

3.3.7 Statistical analysis

No bias was found between the left and right sides or dominant and non-dominant legs in the latency of the target jump from the pre-step activity's initiation, final position of the stepping foot, CoM velocity at foot lift, or duration of the pre-step activity (all $p > 0.05$). Therefore left-sided steps were reflected about the laboratory AP axis and combined with right-sided steps. All steps are reported as if they were right-sided.

Foot placement and CoM velocity at foot lift contained both ML and AP components and as such are directional variables. Therefore, one-sample (paired) Hotelling's tests (Batschelet, 1981; Zar, 2010) were used to test for differences between conditions. CoM velocity at foot lift was paired within-subject by subtracting the mean of the constant-central condition from all other stepping conditions. Unidimensional temporal variables (pre-step activity duration, step duration and modulation latency) were submitted to repeated-measures ANOVA with the within-subject factor of step location.

3.4 Results

3.4.1 Steps when the target location remained constant

All subjects were able to land the stepping foot on or near the target when its location remained constant. On average, the final position of the foot was not different to each subject's self-defined ideal step, which was the case when stepping to all target locations (Figure 3.3, black symbols; all $T^2(2,8) < 5.3$, $p > 0.7$). This indicated that a successful step was taken to all targets. Step duration was effected by the step target (Table 3.1; $F(4,36) = 19.2$, $p < 0.001$), with step duration increasing with step length ($p < 0.01$) but not step direction ($p > 0.05$).

	Step target location					
	Central	Medial	Lateral	Distal	Proximal	**Mean**
Constant	641(79)	644(76)	639(90)	697(88)	574(62)	**639(44)**
Jump	-	649(98)	671(92)	734(91)	590(91)	**661(59)**

Table 3.1. Step duration (ms; group mean (SD)).

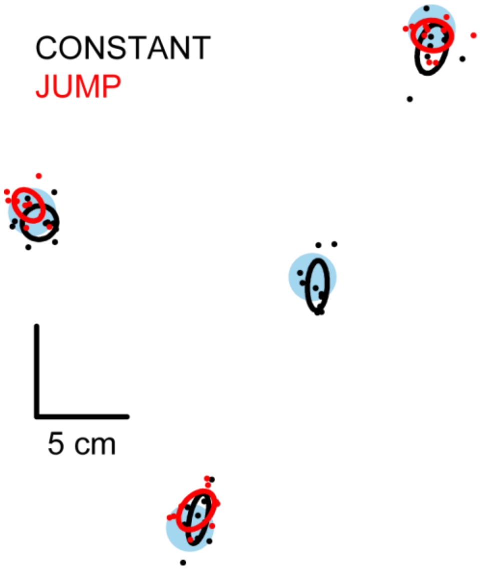

Figure 3.3. Final position of the stepping foot. Filled blue circles are the stepping targets. Filled black and red circles are each subject's mean final position of the stepping foot for the constant and jump conditions respectively. Ellipses are Hotelling's 95% confidence ellipses of the group mean. The size and spacing of the stepping targets is to scale.

In order to land the foot in this position, all subjects produced pre-step activity that accelerated the body sideways, away from the stepping foot, and forwards. The mean (SD) time from the pre-step activity's initiation until foot lift was 561 (89) ms and was not consistently affected by the step location (F(4,36) = 0.8, $p = 0.520$).

However, the pre-step activity that accelerated the CoM differed with target location (Figure 3.4). Figure 3.4A and Figure 3.4C depict the mean CoM acceleration for one subject and shows activity before the lift of the stepping foot. Figure 3.4B and Figure 3.4D show that for this subject the pre-step acceleration resulted in the body gaining velocity that was specific for each intended step location. For the group analysis, each subject's mean CoM velocity at foot lift for steps to the central target was subtracted from the mean value for steps to each peripheral target. The resulting two-dimensional (AP and ML) representation of relative CoM velocity at foot lift showed a target-specific organization that resembled the relative positions of the targets in Cartesian coordinates (Figure 3.4E). The confidence ellipses of CoM velocity at foot lift for steps to medial, lateral, distal and proximal locations were all significantly different from each other (all $T^2(2,8) > 82.5$, $p < 0.001$), indicating that the pre-step activity was coupled to the planned step location.

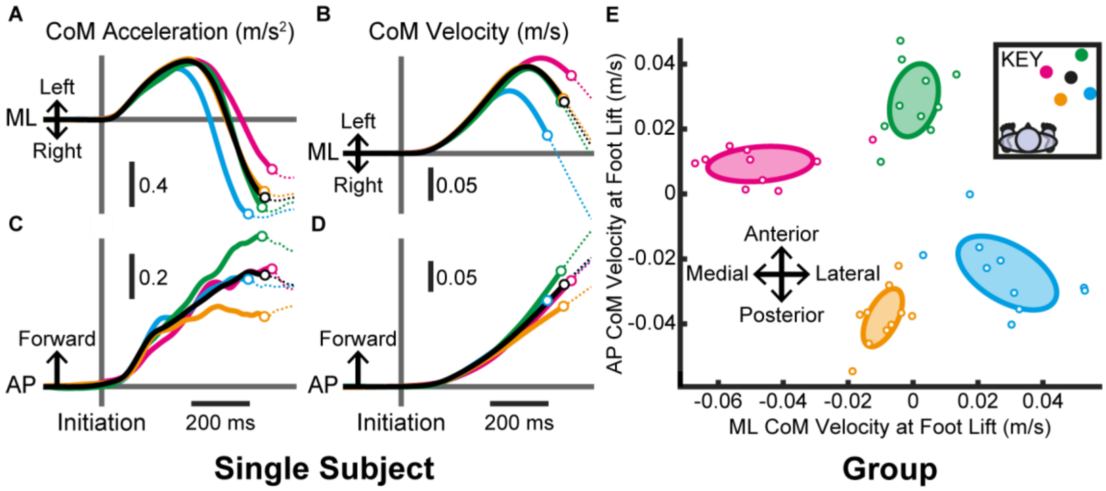

Figure 3.4. Centre-of-mass (CoM) motion when the target location remained constant. *A–D:* Mean estimated CoM acceleration (*A*,*C*) and velocity (*B*,*D*) over time from an individual subject in the ML (*A*,*B*) and AP (*C*,*D*) dimensions. Trials were aligned to the time of pre-step activity initiation. The circles denote the mean time the stepping foot lifted in steps to each target and the traces are dotted thereafter. *E*: Estimated CoM velocity at foot lift for the group after within-subject pairing by subtracting the constant-central mean. The circles are each subject's mean estimated CoM velocity at foot lift for each target. Ellipses are Hotelling's 95% confidence ellipses of the group mean. As per the key, black = central; magenta = medial; blue = lateral; green = distal; yellow = proximal.

3.4.2 Steps when the target location changed

All subjects adjusted their step when the target jumped to a new position shortly after initiation of the pre-step activity. This was demonstrated by the final position of the foot being different to that originally planned (constant-central steps) for steps to all target-jump locations (Figure 3.3, red symbols; all $T^2(2,8) > 1900$, $p < 0.001$). Furthermore, the mean final position of the foot was not different to each subject's self-defined ideal step for any target jump location (all $T^2(2,8) < 8.0$, $p > 0.3$), indicating that the step adjustments were successful and accurate. The final position of the foot after a target jump was mostly the same as when stepping without a target jump (lateral, distal and proximal all $T^2(2,8) < 10.5$, $p > 0.18$), however medial steps were modestly but significantly different from each other (mean vector distance = 1.1 cm; $T^2(2,8) = 49.2$, $p = 0.002$). Step duration was slightly increased in steps with a target jump in comparison to without (23 (31) ms increase; Table 3.1); $F(1,9) = 5.5$, $p = 0.044$).

To determine whether the pre-step activity was modulated in response to a change in step location, the CoM motion when subjects stepped to the constant-central target was compared with that when the target jumped (see Figure 3.2 for details). An initial modulation could be reliably detected in 94% of all jump trials, with 6% of trials being excluded because their jerk trace lay outside the constant-central ellipse at the time of the target jump. The first detectable modulation occurred before the foot lifted from the ground in the vast majority (93%) of the remaining trials, with a modulation after foot lift in 7% of trials (Figure 3.5). The median modulation latency was 223 ms (interquartile range = 158) and was not affected by the new target's location (F(3,27) = 1.0, *p* = 0.41).

Subjects would also delay the lift of the stepping foot to elongate the pre-step activity in response to the change of target location. When compared with steps to the constant-central target, foot lift was significantly delayed by 69 (55) ms in jump trials (*p* = 0.003), but did not depend on target-jump location (F(3,27) = 1.8, *p* = 0.178). The stepping foot was also lifted later in jump trials than in steps to the same location without a target jump (F(1,9) = 10.9, *p* = 0.009). The mean (SD) pre-step activity duration of steps with a target jump was 629 (129) ms.

Typically, the initial response to a change in target location acted to reduce the forward acceleration of the body, as shown for a single subject in Figure 3.6C. This 'braking' effect was apparent for all target jump locations even if an increase in forward acceleration seemed more appropriate, for example during a jump that required an increased step length. The initial non-specific response was rapidly followed by a target-specific acceleration of the CoM (Figure 3.6A and Figure 3.6C) leading to different CoM velocities at the point of foot lift (Figure 3.6B and Figure

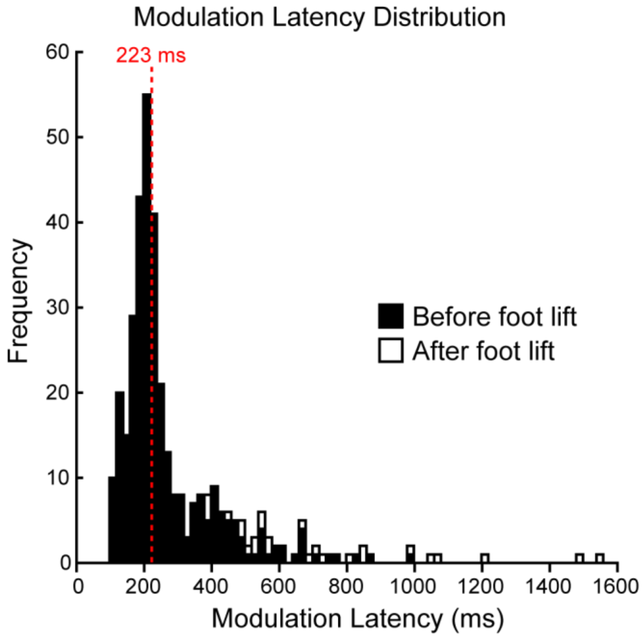

Figure 3.5. Distribution of modulation latencies. A histogram of all jump trials for all subjects is depicted. The distribution was skewed and the average modulation latency was determined by the median (223 ms, red dashed line). Filled bars represent modulations occurring before the lift of the stepping foot and open bars represent modulations occurring after the lift of the stepping foot. Each bin is 20 ms.

3.6D). For the group, the confidence ellipses of the change in CoM velocity at foot lift for steps with a medial, lateral, distal and proximal target jump were all significantly different from each other (Figure 3.6E; all $T^2(2,8) > 83.9$, $p < 0.001$) demonstrating that the pre-step activity modulation was target-specific. The modulated CoM velocity at foot lift reflected the positions of the new stepping target, similar to that observed when the target position remained constant, suggesting that an attempt was made to re-couple the pre-step activity and step location.

3.5 Discussion

The experiments were designed to test the throw-and-catch hypothesis of human gait. This was achieved by measuring the coupling between the pre-step activity (the throw) and the final stepping-foot position (the catch). The hypothesis states that the two actions are intimately coupled such that the pre-step activity differs with the planned step location. This was verified in the experiment where the final location was known to the subject throughout the movement. For the experiment in which the final location changed just after the throw was initiated, which effectively de-coupled the two actions, the throw was found to be adjusted so that it was re-

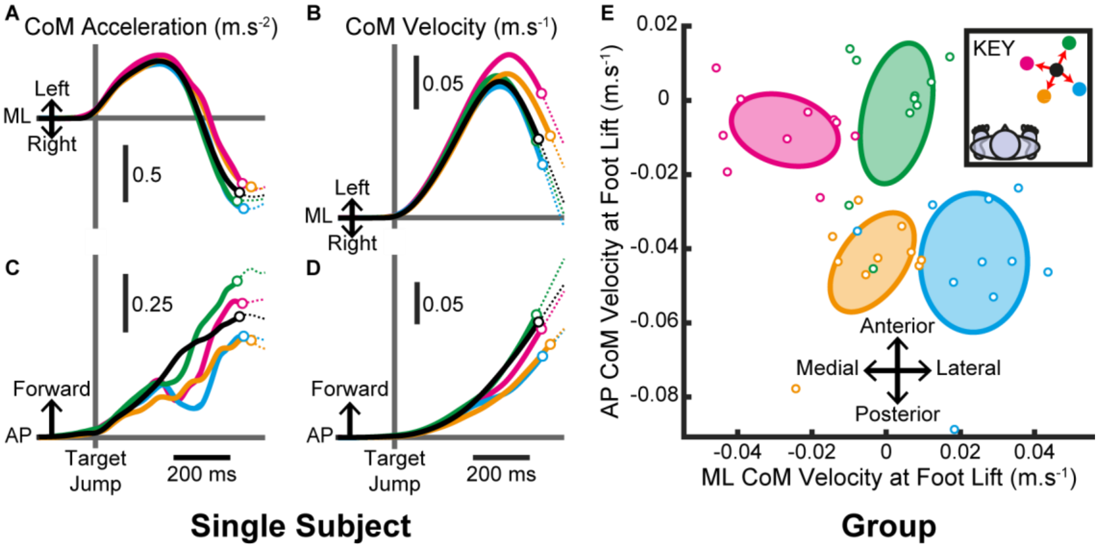

Figure 3.6. Centre-of-mass (CoM) motion when the target location changed. *A–D*: Mean estimated CoM acceleration (*A*,*C*) and velocity (*B*,*D*) over time from an individual subject in the ML (*A*,*B*) and AP (*C*,*D*) dimensions. Trials were aligned to the time a target jumped. The circles denote the mean time the stepping foot lifted in steps to each target and the traces are dotted thereafter. *E*: Estimated CoM velocity at foot lift for the group after within-subject pairing by subtracting the constant-central mean. The circles are each subject's mean estimated CoM velocity at foot lift for each target. Ellipses are Hotelling's 95% confidence ellipses of the group mean. As per the key, black = constant-central; magenta = medial; blue = lateral; green = distal; yellow = proximal.

coupled to the new step location. Together these results provide support for the throw-and-catch hypothesis of human gait.

3.5.1 Steps when the target location remained constant

The throw-and-catch model predicts that the pre-step activity depends on the intended step location. This is because the direction and magnitude of the body throw would need to be tuned differently in order for the body to fall towards its target during steps to different locations. Previous research identified a coupling between the pre-step activity and step location for forwards and diagonal steps (Lyon & Day, 1997, 2005). This experiment sought to investigate whether this finding, and the throw-and-catch model, generalized to steps of different lengths and directions. The resulting data therefore required that both ML and AP body motion was analysed together using multidimensional statistics (Hotelling's tests and confidence ellipses). The results confirmed that the pre-step activity systematically differed with target location in steps of both different lengths and directions (Figure 3.4). The net result of these changes was such that when the stepping foot lifted from the ground, the body had gained velocity, and therefore momentum, that was specific to the intended step location. Lyon and Day (1997) demonstrated that the body's momentum at the point of foot lift is a key factor that predicts the body's trajectory during the step. The coupling between the body's momentum and step location in the present results suggests that this ballistic model generalizes and the throw is fine-tuned for steps of different lengths and directions.

In order to test the throw-and-catch model's generality, steps were initiated from an imposed initial posture which allowed both step length and direction to be precisely controlled. Although the initial posture may not have been a natural stance width or foot angle for all subjects, it is unlikely to have affected their behaviour significantly. The step was otherwise natural for each subject as the initiation and duration of the step was unconstrained. This lack of temporal constraint is unlikely to have affected the use of a ballistic strategy, as it has been demonstrated both for temporally unconstrained steps (Lyon & Day, 1997, 2005) and when initiating gait as quickly as possible (Yiou *et al.*, 2016). It is possible that differences in step duration may have influenced the throws to different targets (Zettel *et al.*, 2002a, b; Yiou *et al.*, 2016). However, this is unlikely to explain the results because although step duration changed with step length, it did not change with step direction. In exploring the throw-and-catch in steps of different lengths and directions, subjects would often step beyond the force platforms. Subsequently, CoM position was unable to be reliably estimated (for a discussion of CoM position estimation from force data see Lyon &

Day, 1997). The position from which the body initiates its fall is an important aspect of the throw (Lyon & Day, 1997, 2005) but, by demonstrating a step location-specific change in CoM velocity, the present results show that the pre-step activity is tuned to the future foot position.

The between-subject variability of the throw in this experiment (Figure 3.4E) and in Lyon and Day (1997) shows that there is no ‘one-size-fits-all’ throw to achieve a successful step. Even for the same subject, different throws could successfully be caught by identical foot-landing positions. This likely reflects both the ability to make mid-step adjustments (Reynolds & Day, 2005a, 2007; Kim & Brunt, 2009; Tseng *et al.*, 2009; Nonnekes *et al.*, 2010; Kim & Brunt, 2013) and the numerous solutions that exist to catch the body without losing balance (Koolen *et al.*, 2012). However, the present results show that there is pressure to maintain the throw within limits which differ for different step locations. This suggests there is some advantage in coupling the pre-step activity and step location.

3.5.2 Steps when the target location changed

The pre-step activity and the step location can be uncoupled, for example by changing the location of a target. In this scenario the body throw and step location become uncoupled if the pre-step activity remains unchanged while the foot position changes. Previous work has shown that if the target is made to jump after the foot leaves the ground, so that the pre-step activity cannot be changed, the final position of the stepping foot can still be altered, albeit with varying degrees of success depending on the extent and direction of the target jump (Reynolds & Day, 2005a, 2007; Kim & Brunt, 2009; Tseng *et al.*, 2009; Nonnekes *et al.*, 2010; Kim & Brunt, 2013). This de-coupling does not necessarily disprove the throw-and-catch hypothesis, but may be interpreted as there being some flexibility in the coupling which can be exploited under certain circumstances. A better test of the hypothesis is to measure whether there is an attempt to re-couple the pre-step activity with the new step location under conditions when the pre-step activity has an opportunity to be adjusted. Here the target was made to change location during the pre-step activity, long before the stepping foot left the ground, thus allowing time for a re-coupling of the pre-step activity with the new target location. The target jump was unpredictable, as more often than not the target location did not change and could be to any one of four locations when it did. This procedure resulted in substantial uncertainty and rendered attempts at anticipating the target jump unlikely to be of value to the subject. It will be argued that an attempt to re-couple the pre-step activity with the new step location would provide support for the throw-and-catch hypothesis given that an adjustment could be initiated after the foot leaves the ground.

Previous research is conflicted on whether the pre-step activity can be modulated. Experiments that unpredictably perturbed the trajectory of the body during the pre-step activity via mechanical pulls have returned mixed results, with muscle activity being altered to correct the body's trajectory in response to resistive (Mouchnino *et al.*, 2012; Mille *et al.*, 2014) but not assistive perturbations (Mouchnino *et al.*, 2012). Additionally, stimulation of proprioceptive (Ruget *et al.*, 2008) and vestibular (Bent *et al.*, 2002) afferents were found not to affect the pre-step activity, suggesting it may be immutable once it has been initiated. This was not found to be the case in the present experiment, since the pre-step activity was modulated in the vast majority of trials when prompted by a visual cue. Furthermore, the precise modulation of the pre-step activity depended on the new target location. This suggests that an attempt was made to re-couple the pre-step activity to the new target location and provides causal evidence that the pre-step activity is fine-tuned to take the final position of the foot into account. According to the throw-and-catch hypothesis, re-coupling the pre-step activity to the new target location would have promoted a more appropriate fall of the body towards its intended target after the lift of the stepping foot. This does not rule out the possibility that further adjustments were made during the step.

Although the net adjustment of the pre-step activity was different depending on where the target jumped, a non-specific initial response to the perturbation was evident that reduced the forward acceleration of the body. Similar 'braking' responses to visual cues have been reported after the lift of the stepping foot during both single steps and locomotion (Kim & Brunt, 2013; Potocanac *et al.*, 2016). In the present experiment, this braking was used irrespective of where the target moved. Although the braking could have been expected when the step length required shortening, it was surprising that it was also used when a longer step was required. This is because greater forward acceleration was observed for longer steps when the target did not move (Figure 3.4). The braking may have enabled a pause whilst the necessary actions for a successful step were reconsidered (Potocanac *et al.*, 2016), which would explain the increase in pre-step duration that was observed when a target jumped. Mille *et al.* (2014) also report a similar delay in stepping after a mechanical pull to the body prior to a step. Presumably, in the current experiments, the extra time was needed to re-program and adjust the body throw so that it was re-coupled to the new final foot location.

3.5.3 What Advantage Does the Throw-and-Catch Coupling Offer?

Stepping can be considered a ballistic action if, as suggested here, gravity drives the fall of the body during the step with its trajectory being controlled by the pre-step activity. The ballistic nature of stepping is sometimes misinterpreted as sensory information not being attended to or usable during the step. This interpretation is clearly false given that adjustments to the step are possible both before the lift of the stepping foot, as shown in this experiment, and after foot lift when suitable sensory cues are provided (Reynolds & Day, 2005a, 2007; Kim & Brunt, 2009; Tseng *et al.*, 2009; Nonnekes *et al.*, 2010; Kim & Brunt, 2013). However, the magnitude and direction of mid-step adjustments are limited by the fall of the body and the subsequent balance constraints. For example, the size of medially-directed foot adjustments cannot be made as large as laterally-directed adjustments (Reynolds & Day, 2005a). This limitation may underlie the incentive to maintain the coupling between the pre-step activity and final foot location demonstrated in the present experiment. At the same time, the ability to rapidly alter the intended foot position mid-step offers a degree of flexibility in the coupling, which would be essential for responding to an unexpected environmental threat or maintaining foot landing accuracy in the presence of error in the initial throw.

3.6 Conclusion

The results show a close coupling between the pre-step activity and final foot position during unperturbed steps of different lengths and directions. Furthermore, there is pressure to maintain this coupling when the demanded step location unpredictably changes shortly after initiation of the pre-step activity. I conclude that these results support the throw-and-catch hypothesis of human stepping.

4 Chapter 4: The control of body motion during a step

4.1 Abstract

In theory, the initial conditions are able to control the trajectory of the body during a step, with only gravity driving the body after the stepping foot lifts. However, the stance foot remains in contact with the ground during the step and is presumably able to generate torques about the ankle joint to influence the trajectory of the body. How is the motion of the body controlled during a step? Are the initial conditions able to determine the trajectory alone or are ankle torques also used to achieve the desired trajectory? Here I investigate this by comparing the motion of the body during a step to that of a simulated model. The model was given the initial position and velocity of the centre of mass at the instant the stepping foot lifted and was then allowed to fall under the influence of gravity for the same duration that the stepping foot was airborne in the observed step. The model was generally able to reproduce the sideways motion of the body observed during the step with reasonable accuracy. However, the model substantially overshot the observed step in the forwards direction. When the ankle torque generated during the step was added, the model reproduced the observed body motion with reasonable accuracy in both medio-lateral and forwards directions. This suggests that mid-step torques are used to influence the trajectory of the body during a step, and are particularly important in controlling forwards motion.

4.2 Introduction

In Chapter 3, it was demonstrated that the body enters a step with a different initial velocity depending on where the person intends to step. It was proposed that the body then begins to fall under the influence of gravity along a trajectory determined by the initial position and velocity of the mass. In theory, these initial conditions are able to control the trajectory of the body during a step, with only gravity driving the body after the stepping foot lifts. Here I will explore this possibility in greater detail. In doing so, this chapter will investigate the control of body motion during a step.

Prior to a step, the body's mass is positioned above its base of support, spanning the area enclosed by the feet, and the body is balanced. In order to take a step, a foot must lift from the ground and the body's static balance disrupted. Before the stepping foot lifts, force is exerted on the ground to accelerate the body and generate momentum for the step (Carlsöö, 1966; Mann *et al.*, 1979; Crenna & Frigo, 1991; Jian *et al.*, 1993; MacKinnon & Winter, 1993; Lyon & Day, 1997, 2005). Typically, this results in the body moving forwards and towards the stance-side by the time the stepping foot lifts. When the foot lifts, the mass is rarely positioned over its new base of support defined by the foot still in contact with the ground (Jian *et al.*, 1993; MacKinnon & Winter, 1993; Lyon & Day, 1997). The body is therefore unbalanced and falling under the influence of gravity during a step. This poses a significant control problem for the brain as a complete loss of balance (i.e. a fall) needs to be prevented. How is the motion of the body controlled during a step?

Given that the body is falling under the influence of gravity during a step, one possibility is that the body's trajectory is determined by its initial conditions when the stepping foot lifts. The body's mass could be moved to a position, relative to the stance foot, and given a velocity at the instant the stepping foot lifted to provide suitable initial conditions for the step. If the initial conditions were set appropriately, gravity could drive the body along its desired trajectory without the need for further modification during the step. If this was true then normal stepping could be considered a ballistic action, analogous to the throw of a ball.

Support for this ballistic hypothesis is provided both from observations and simulations of the body's motion during a step. Importantly, the body's initial conditions are modulated according to the future location of the stepping foot (Chapter 3; Lyon & Day, 1997, 2005; Bancroft & Day, 2016). The body therefore begins the step in a different state depending upon the intended step location, from which a fall along the desired trajectory could develop. This is further supported by evidence that ballistic models, which are given the same initial conditions as a step and are only acted on by gravity, are able to reproduce the observed medio-lateral motion of the body during a step (Lyon & Day, 1997; Yiou *et al.*, 2016). The initial conditions alone therefore seem appropriate to determine the body's trajectory. However, ballistic models have thus far only examined medio-lateral motion of the body. It is therefore unclear whether the ballistic model of stepping is completely true; that is, whether it can accurately describe both medio-lateral and forwards motion.

Studies of robotic gait suggest that the forwards motion of the body could also be produced ballistically. Robots that are made to walk down a slight incline are able to mimic the forwards motion of the body during gait whilst being driven only by gravity (McGeer, 1990; Kuo, 1999; Collins *et al.*, 2001). Such machines require no control once they have been set off, utilising only passive dynamics to produce and maintain remarkably stable and human-like gait. In order to walk over level terrain however, a 'push off' impulse is required on each step, analogous to the impulse provided by the initial conditions of the body. Robots inspired by the passive-dynamic down-slope walkers that generate a push-off impulse are also able to produce stable and human-like gaits (Collins *et al.*, 2005; Kim & Collins, 2017).

A ballistic strategy may not be completely true in humans though and mid-step adjustments could be important in controlling body motion. One foot remains in contact with the ground during a step and can presumably influence the body's trajectory by exerting force on the ground and generating torque about the ankle joint. Support for the role of mid-step adjustments is provided by evidence that the trajectory of the foot can be modified during a step. For example, when a target is made to change location when the stepping foot lifts, the foot's trajectory is rapidly altered to move the foot towards the new target location (Weerdesteyn *et al.*, 2004; Reynolds & Day, 2005a, b, 2007; Nonnekes *et al.*, 2010). Moreover, vision is used to guide the foot towards its target during the step, as evidenced by an increase in foot placement error when visual feedback is denied after the stepping foot lifts (Reynolds & Day, 2005b). Given that the stepping foot is part of the whole-body's mass, presumably the trajectory of the mass can be altered similarly. This is in agreement with the fact that mid-step ground reaction forces applied through the stance foot are adjusted after a change in step target location (Tseng *et al.*, 2009). This raises the possibility that the motion of the body is adjusted during the step to achieve its desired trajectory. In addition to the mid-step adjustments outlined above, which are examples of the active control of movement, mid-step adjustments could also be made passively. Muscles and tendons have an intrinsic mechanical stiffness, like a spring, which can generate torque and influence movement. This passive control of ankle torques is known to be important in maintaining balance in quiet stance (Winter *et al.*, 1998; Loram & Lakie, 2002) and may play a role in influencing mid-step body motion.

4.2.1 Hypothesis

This chapter asks how the motion of the body during a step is controlled. It is hypothesised that the trajectory of the body during a step is determined by the initial conditions of the body. By setting the initial position and velocity of the body when the stepping foot lifts, the body could be driven by gravity along its desired trajectory during the step. This hypothesis is tested by comparing the observed motion of the body during a step to a model which is given the initial conditions of the body and falls freely under gravity during a step. Support for the hypothesis would be provided if the motion of the model closely reflected the observed motion of the body during a step. Alternatively, mid-step adjustments may be important in controlling body motion. This is tested by a model which is given the initial conditions of the body and falls freely under gravity during a step but its trajectory is able to be modified by torques about the stance-foot ankle.

4.3 Methods

4.3.1 Sample size estimation

As will be described shortly, the performance of the model with and without ankle torques was compared. To estimate the required sample size, I consider a meaningful difference between model simulations with and without ankle torques to be 5% of the required step length (0.05 x 35 cm = 1.75 cm). Whilst Lyon and Day (1997) did not compare model simulations with and without ankle torques, they did compare the motion of a similar model under conditions with and without the same initial medio-lateral CoM velocity as the body. The regression parameter intercepts in each of these simulation conditions (Table 2 in Lyon and Day (1997)) are used here to estimate the expected variability between the different model simulations (SD of the difference = 0.58 cm). Assuming a mean difference of 1.75 cm with a standard deviation of 0.58 cm between conditions, an effect of size 3.0 was expected (Cohen's *d*; Equation 2.1 in Chapter 2.6). Using a two-tailed dependent-samples *t*-test with the chance of type I error (α) set at 0.05 and the chance of type II error ($1-\beta$) set at 0.1, the estimated sample size required in the present experiment is four.

4.3.2 Subjects

Five healthy, young subjects (3 male; 25±2 years; 65±14 kg; 1.71±0.07 m) participated in the experiment. All subjects reported as right-foot dominant.

4.3.3 Protocol

Subjects performed a step onto the location of a floor-bound target. A trial started with the subject stood still and barefoot with the medial borders of the feet 15 cm apart (Figure 4.1A). The initial positions of the feet were chalk-marked onto the floor to ensure a consistent starting location. An audible beep alerted the subject that a trial was to begin and after a random delay a target would illuminate. The illumination of a target acted as a cue for the subject to initiate a step accurately to the location of the target in their own time.

The targets were placed ahead of the feet and required a forwards movement in different directions (Figure 4.1A). Each target was 35 cm from either the left or right foot, meaning that the required step length was equal when stepping in each direction. When a target illuminated to the left, a left-foot-leading step was required and when a target illuminated to the right, a right-foot-leading step was required. Subjects were instructed to step to the location of the illuminated target and bring their trailing foot alongside the stepping foot. The final location of the trailing foot does not affect the motion of the body during the initial step (Lyon & Day, 2005) so no instruction was given as to where to land the trailing foot. Subjects were encouraged to finish the step in a balanced posture with their feet roughly separated by the same distance as before

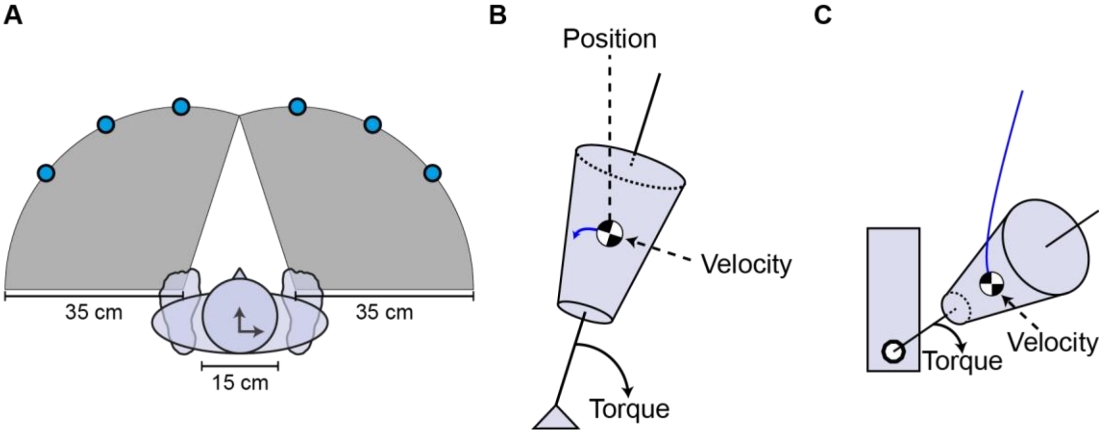

Figure 4.1. Step targets and model. *A*: Bird’s-eye view of the subject’s initial stance prior to a step and the step targets (blue circles). *B*, *C*: Frontal- and horizontal-plane views of the model, respectively. The model’s CoM (black and white circle) was given the same initial conditions (position and velocity) as the body’s CoM at the instant the stepping-foot lifted from the ground. The model was then allowed to fall about a pivot under gravity for the duration of the step either with or without modification from the mid-step torques generated about the stance-side ankle joint. The stance-foot is depicted as a triangle, with the ankle joint at its apex in *B*, whereas in *C* the stance-foot is depicted as a rectangle, with the ankle joint at the centre of the unfilled circle within the rectangle. The curved blue lines show a typical trajectory of the model’s CoM. The initial conditions and torques were inputted to the model in three dimensions.

the step. The trials were presented in a randomised order and each subject performed a total of 120 trials, equalling 20 steps to each target.

4.3.4 Apparatus

The step targets were circular (2.5 cm diameter) and illuminated via electroluminescent paper (see Chapter 2.2.1 for further details). A total of fifty-two infrared-emitting diode markers were attached to each subject to track the motion of the whole body. Marker locations were recorded by three motion capture cameras (Coda cx-1; Charnwood Dynamics, Leicestershire, UK) and sampled at 100 Hz. The markers were attached via thirteen rigid clusters, each containing four markers, and placed on the following segments: head, back, pelvis, feet, upper and lower arms and upper and lower legs (Figure 2.2). The locations of the clusters were associated with landmarks on the body by a pointer to create virtual marker locations (Table 2.1). The virtual marker locations defined the location of each of the body's major segments. A thirteen-segment model of the body was then created using Visual 3D software (C-Motion; Germantown, MD, USA) and the location of the whole-body's CoM and its inertia estimated (see Chapter 2.2.2 for further details). The subjects initiated a step with each foot over a force platform, which was embedded within the floor. Ground reaction forces were sampled at 1000 Hz. The centre of pressure was calculated from the force plates (see Chapter 2.2.3.1 for further details).

4.3.5 Model

The whole-body's CoM was modelled as a single-segment in the shape of a truncated cone (Figure 4.1B & C). The cone was attached via a massless leg to a pivot which represented the stance-foot ankle and was free to rotate about the pivot during a step. The model was similar to previously published ballistic models (Lyon & Day, 1997; Yiou *et al.*, 2016). The position of the pivot was fixed, which assumes the stance ankle does not move significantly during a step. For each step, the model was given the three-dimensional position and velocity of the body's CoM at the instant the stepping foot lifted, the three-dimensional moments and products of inertia of the body's CoM, the position of the stance-ankle at foot-lift and the mass of the body. The moments and products of inertia were estimated using a function within Visual 3D (C-Motion, 2014). In brief, the function calculated the inertia of each of the body's segments (Table 2.1) relative to the CoM and then summed the inertia of each segment to estimate the whole-body CoM inertia. Proofs of the calculations used within the Visual 3D function are provided by (Yeadon, 1993a, b, c, d). Given these initial conditions, the model was released and allowed to move for the same duration as a step.

Two variants of the model were simulated. In the first variant, the model fell under gravity but was not acted upon by any other forces during the step (termed *without torques*). In the second variant, the model fell under gravity but was also acted upon by the torque generated about the ankle joint during a step (termed *with torques*). This second model was identical to the first model except for the addition of the calculated mid-step ankle torques. The motion of the model's mass as it fell about its pivot was predicted by a fourth-order Runge-Kutta algorithm. The motion of the model was then compared to the observed motion of the body. The model was implemented using Simscape Multibody, which is MATLAB and Simulink's mechanical modelling software (The Mathworks Inc.; Natick, MA, USA).

4.3.6 Data analysis

Foot-lift and foot-land were calculated with the force-plate methods described in Chapter 2.4. The duration of a step was the time from foot-lift to foot-land. The position of the stance ankle at the instant the stepping-foot lifted (the location of the model's pivot) was the centroid of the medial and lateral stance-ankle virtual landmarks (Table 2.1). Marker position and force plate data were filtered as outlined in Chapter 2.4.

Torque about the ankle joint during a step was calculated as:

$$Equation\ 4.1: \qquad \tau = r\ x\ F$$

where τ is torque, r is the three-dimensional distance between the point of application of force (CoP) and the pivot (the stance ankle), and F is the three-dimensional ground reaction force under the stance foot. Force and CoP were down-sampled to the same sampling frequency as marker position data to calculate torque.

The ability of the model to predict body motion was first estimated by comparing the end-point of the model's CoM and the body's CoM at the end of a step. This was calculated as the absolute Euclidean distance between these two points for each step, and is herein referred to as absolute error. Although a useful marker of the model's ability, this measure does not reflect error in predicting body motion during a step. In other words, the model could correctly predict where the CoM ended the step but take an entirely different trajectory to get to this end-point. In this case, the model would seem to have no absolute error but in reality would not reflect the motion of the body during a step. Therefore, the ability of the model to predict body motion during a step was further estimated by comparing the length of the path taken by the model's

CoM and the body's CoM during a step. The length of the model's path was expressed as a percentage of the body's path length and termed relative error:

$$Equation\ 4.2: \qquad Relative\ error = \frac{Model\ path\ length}{Body\ path\ length}\ x\ 100$$

The path length of the model and the body's CoM was calculated using Matlab's *arclength* function (D'Errico, 2012). With relative error, a value of 100 would signify that the model's path was the same length as the body's path during a step, with an increase or decrease from 100 reflecting a longer or shorter path, respectively. An identical path length and no absolute error would suggest that the model was able to perfectly simulate the motion of the body during a step.

4.3.7 Statistical analysis

For statistical analysis, left-sided steps were reflected about the laboratory antero-posterior axis so that they appeared as right-sided steps. The effect of step-side and step-direction on the initial conditions and final location of the body's CoM was analysed by paired Hotelling's tests. The effect of step-side and step-direction on the model's absolute and relative error was analysed by repeated-measures ANOVA. Greenhouse Geisser corrections were used when the assumption of sphericity was violated. Paired *t*-tests were used when *post-hoc* analyses were required. Bonferroni correction for multiple comparisons was used with Hotelling's tests and *post-hoc* analyses. Simple linear regression was also performed to compare the modelled and observed CoM location at the end of the step. Normality of data was checked by either χ^2 goodness of fit tests for univariate data or by Mardia's test of skewness and kurtosis (Mardia, 1970) for bivariate data.

4.4 Results

4.4.1 Observed body motion

Figure 4.2A shows typical positions of the stepping-foot when it landed on the target. As presented in Chapter 3, postural activity preceded the lift of the stepping foot. Figure 4.2B shows that the CoM first moved forwards and towards the stance-side before the stepping-foot was lifted from the ground (depicted by the bolder section of each trace in Figure 4.2B). This pre-step movement gave the CoM a position and velocity by the time the stepping-foot lifted.

Both the position and velocity of the CoM at the instant the stepping foot lifted were significantly different when stepping to each target (all comparisons: $T^2(2,3\ ) > 67.3$; $p < 0.04$). Figure 4.2C & Figure 4.2D show that the position and velocity of the

CoM at foot-lift were specific to the intended step location. At the instant the stepping-foot lifted, the CoM had moved closest to the stance-side in steps to the target directly ahead of the stepping-foot, less so in steps to the target diagonally ahead of the stepping-foot, and least in steps to the most lateral target (pink, black and blue respectively in Figure 4.2C).

The velocity acquired by the CoM at foot-lift was modulated by the future position of the foot in a similar way. Figure 4.2D shows data from a single subject where the CoM velocity was directed forwards and towards the stance-side in steps to the target directly ahead of the stepping-foot, less forwards and slightly away from the stance-side in steps to the target diagonally ahead of the stepping-foot, and least forwards and away from the stance-side in steps to the most lateral target (pink, black and blue respectively in Figure 4.2D). By comparing the coloured footprints in Figure

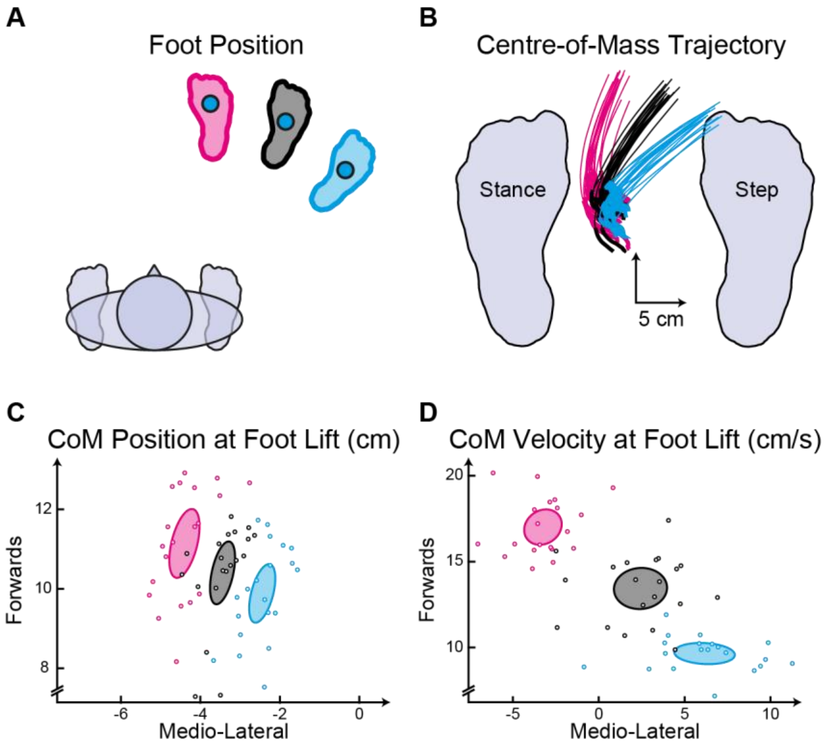

Figure 4.2. Observed centre-of-mass (CoM) motion. *A*: Typical final foot positions from a single trial when stepping to each of the right-side targets. The colour of each foot-print defines the colour scheme for *B*, *C* and *D*. *B*: Horizontal-plane view of the CoM trajectory from a typical subject during right-foot-leading steps to each target. Each trace is thickened prior to the instant the stepping-foot lifted from the ground and ends at foot-land. The foot-prints are the estimated locations of the feet prior to the step, based on the mean positions of the virtual landmarks on the feet. The origin is located at the intersection of the two arrows, which was approximately midway between the left and right ankles. *C*, *D*: Initial conditions of the CoM for the same steps as depicted in *B*. Each circle is a single step. Ellipses are Hotelling's 95% confidence ellipses of the mean. For the medio-lateral axis of both *C* and *D*, negative is leftward (towards the stance side) and positive is rightward (towards the step side).

4.2A and the coloured ellipses in Figure 4.2C and Figure 4.2D, it can be seen that both the position and velocity of the CoM at foot-lift reflected the future location of the foot in Cartesian coordinates. The medio-lateral CoM velocity varied between subjects. For example, the medio-lateral CoM velocity at foot-lift was always directed towards the stance-side in some subjects, whereas for others it could be directed away from the stance-side in steps to the more laterally located targets. However, the medio-lateral CoM velocity would always display the same relative relationship as seen in Figure 4.2D.

The initial conditions were significantly different between left- and right-sided steps (position: $T^2(2,3) = 30.5$, $p = 0.039$; velocity: $T^2(2,3) = 297.8$, $p = 0.002$). In comparison to left-sided steps, the body had moved further towards the stance-foot and acquired less forwards and lateral velocity towards the stance-side by the instant the stepping-foot lifted in right-sided steps.

Once the stepping foot lifted from the ground, the body travelled along a different trajectory when stepping to each target location (Figure 4.2B). The duration of the step was not effected by stepping side or direction ($F(1,4) = 0.063$; $p = 0.815$, ($F(2,8) = 0.798$; $p = 0.483$, respectively) and on average lasted 424±58 ms. There was no difference between left- and right-sided steps in the location of the CoM when the stepping-foot landed ($T^2(2,3) = 7.6$; $p = 0.202$). The CoM finished the step in a different location depending on the step target (all comparisons: $T^2(2,3) > 491.0$; $p < 0.01$), with the CoM ending further from the stance-side with increasing step width (Figure 4.2B). As with the CoM's initial conditions, the position of the CoM at the end of the step reflected the location of the foot when it landed.

4.4.2 Ankle torques

At the instant of foot-lift, the torque about the stance ankle was not consistently effected by step side ($T^2(2,3) = 5.8$; $p = 0.259$) or direction (all comparisons after Bonferroni correction $T^2(2,3) < 18.4$; $p > 0.227$), although a significant effect of step direction may have been detected with a larger sample size. The torque at foot-lift when normalised for body mass was -0.06±0.08 Nm/kg in the medio-lateral direction and 0.29±0.07 Nm/kg in the antero-posterior direction.

4.4.3 Modelled body motion

Figure 4.3A shows the motion of both the body and the model's CoM for a typical trial. The model was given the initial conditions of the body and either allowed to fall freely under the influence of gravity alone (blue trace) or allowed to fall under gravity and be acted upon by the torque about the ankle joint during the step (red

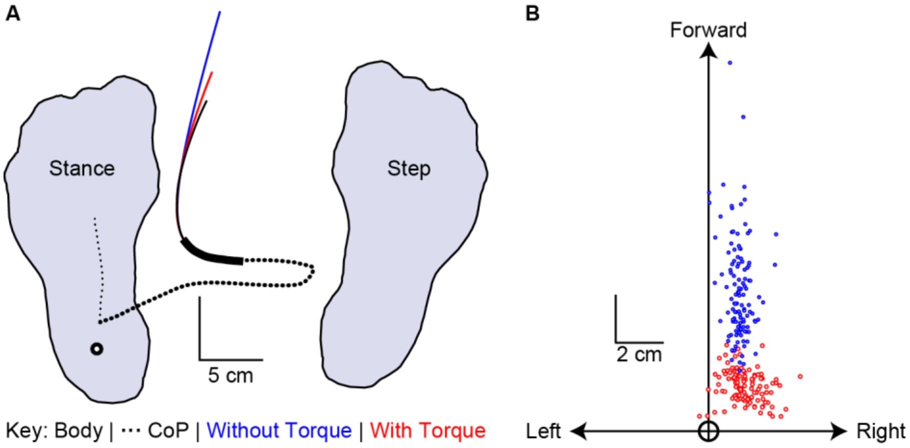

Figure 4.3. Modelled centre-of-mass (CoM) motion. *A*: Trajectory of the body and model’s CoM for a single representative trial from a typical subject. A right-foot step to the target directly ahead of the stepping foot is depicted (pink in Figure 4.2). The traces are thickened prior to the lift of the stepping foot. The broken line is the trajectory of the centre of pressure (CoP). The foot-prints have been placed over the positions of the virtual landmarks on the feet prior to the step. The circle within the stance-foot is the location of the stepping-ankle, which was used to calculate torque about the ankle and acted as the model’s pivot. *B*: Final position of the model’s CoM relative to the body’s CoM at the end of the step in all trials from the same subject.

trace). The torque was calculated for each trial using the centre of pressure (dashed trace), location of the ankle joint (open circle) and ground reaction forces (see Chapter 0 and Equation 4.1 for details). When allowed to fall freely under gravity without the mid-step torques, the model would typically overshoot the observed motion of the body’s CoM (Figure 4.3A, blue). Across all trials, the model’s CoM would consistently end the step substantially further forward than the body’s CoM (Figure 4.3B, blue). On average, the model’s path without modification from mid-step torques was roughly 50% longer than the body’s path during a step (relative error: 151±26 %) and its CoM ended the step 6.8±3.7 cm from the location of the body’s CoM (absolute error; Figure 4.4, blue).

The model was better able to replicate the motion of the body during a step when mid-step torques could modify its motion whilst it fell under gravity. The red trace in Figure 4.3A shows that the trajectory of the model’s CoM was much closer to the observed body motion during a step when mid-step torques were added. Subsequently, the model’s CoM finished the step nearer to the location of the body’s CoM, although the model still slightly overshot the observed motion of the body (Figure 4.3B). The addition of mid-step ankle torques to the model resulted in a significant decrease in both absolute and relative error ($p < 0.05$; Figure 4.4). On average, the model’s CoM finished 2.1±0.3 cm away from the body’s CoM at the end of a step (absolute error) and took a slightly longer path (relative error: 116±4 %;

Figure 4.4). Neither absolute nor relative error were effected by stepping side (F(1,4) < 1.2; $p > 0.330$), stepping direction (F(2,8) < 1.1; $p > 0.392$) or an interaction of stepping side and direction (F(2,8) < 1.1; $p > 0.365$) in each of the model simulation conditions.

Figure 4.5 shows a comparison of the model's prediction of CoM position and the body's observed CoM position at the end of the step in both the medio-lateral and forwards directions. The grey line denoted 'Observed = Predicted' is where the model would have predicted the CoM to be located had body motion been simulated without error (i.e. the line of identity). Table 4.1 summarises the regression lines depicted in Figure 4.5. Like previous models (Lyon & Day, 1997; Yiou *et al.*, 2016), the present model was able to predict the final medio-lateral CoM position with reasonable accuracy, both with and without the ankle torques. This can be seen in Figure 4.5A by each of the blue and red regression lines lying close to the grey line of equality, which was also generally true of each subject (Figure 4.5C). Broadly, the addition of torques to the model made only a minor difference to the predicted medio-lateral CoM position at the end of a step (Figure 4.5C). In all cases, the medio-lateral regression line's gradient approximated one, indicating a close relationship between the model's prediction and the body's actual CoM position at the end of a step (Table 4.1). Moreover, the model accounted for almost all of the variability in the body's final medio-lateral CoM position, as displayed by the tight clustering of each trial around their respective regression lines and high adjusted r^2 values (Figure 4.5A: without

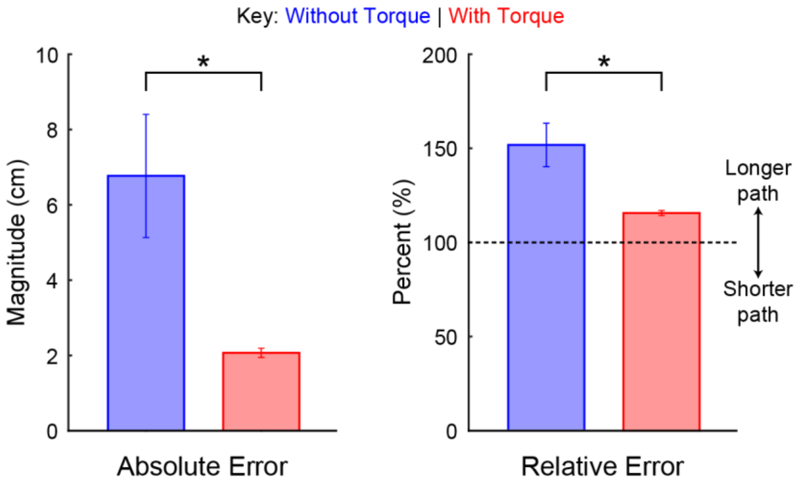

Figure 4.4. Model error. Absolute and relative error in the model's simulation of the body's CoM motion. Error bars are standard error of the group mean. Blue bars are when the model was given only the same initial conditions as the step, without the mid-step torques; red bars are when the model was given the initial conditions with the mid-step torques. * $p < 0.05$

torques = 0.96, with torque = 0.99; Table 4.1). A similar relationship was seen in all subjects (Table 4.1: Medio-Lateral).

Conversely, the addition of torques to the model substantially improved the predicted forwards CoM position. When the model was simulated without the mid-step torques, it was a poor predictor of the body’s final position. This is shown in Figure 4.5B by the loose clustering of points around the blue regression line, the corresponding low

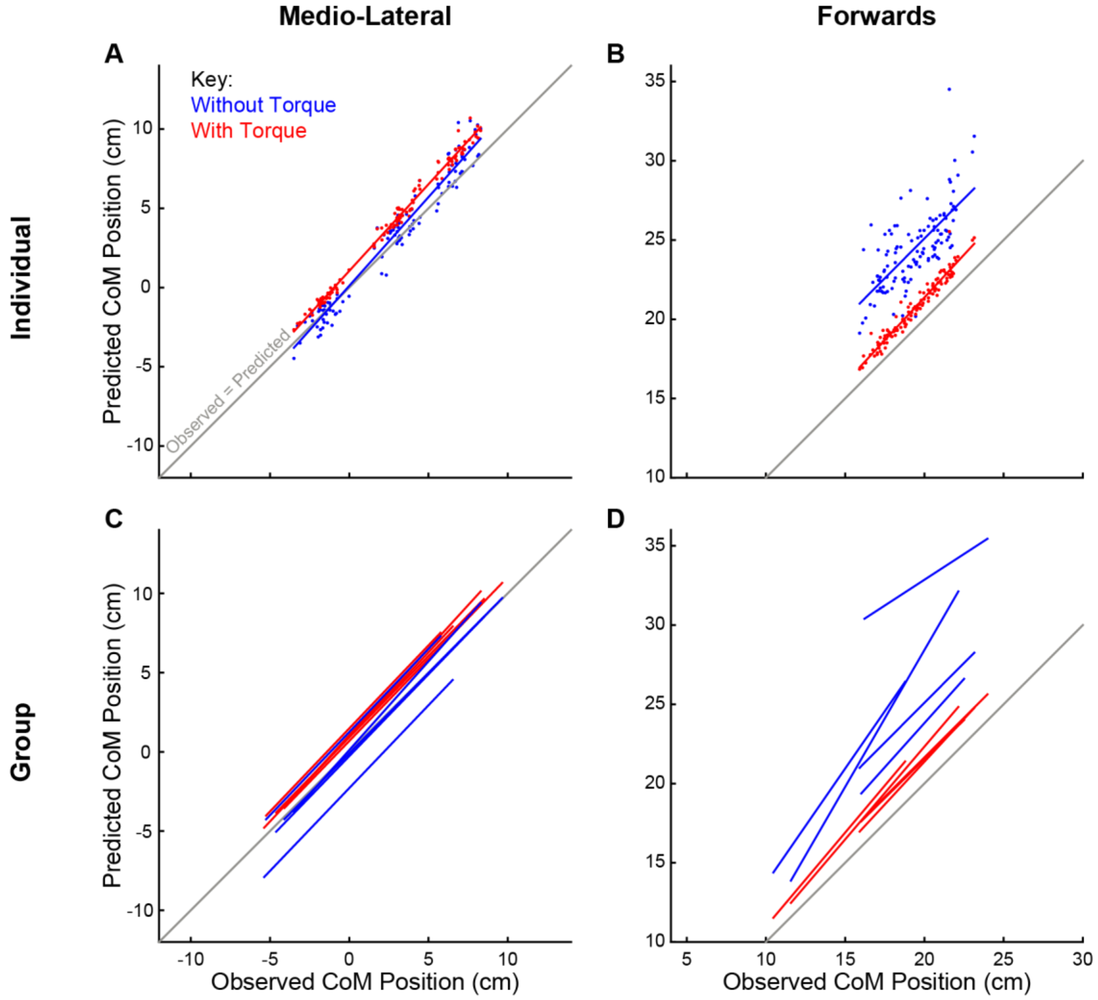

Figure 4.5. Observed (body) versus predicted (model) CoM position at foot-land. *A*, *C*: Model performance in the medio-lateral direction, where negative is towards stance side and positive is towards stepping side. *B*, *D*: Model performance in the forwards direction. The coordinate scheme used is the same as in Figure 4.2B, where (0,0) approximates the centroid between the ankles. *A* and *B* show all trials (circles) and the least-squares fit regression line from a typical subject (#4) both when the model was with (red) and without (blue) the mid-step ankle torques. *C* and *D* show the least-squares fit regression lines for all subjects. For each panel, the grey line is where observed equals predicted CoM position. In *A* and *C*, above this line is further right and below this line is further left of the actual CoM position. In *B* and *D*, above this line is further forwards of the actual CoM position. The range of each plot’s axes are equal to allow a visible comparison between the model’s ability to predict medio-lateral and forwards motion. Regression parameters are summarised in Table 4.1.

r^2 values for each subject (Table 4.1: Forwards) and the considerable distance between the blue regression line and grey line of identity (Figure 4.5D). The slope of the regression line also varied substantially between subjects and was often not approaching one (Figure 4.5D; Table 4.1: Forwards), further showing a poor relationship between the model without torques and the observed final CoM position. In both Figure 4.5B and Figure 4.5D, it can be seen that the red regression lines lie closer than the blue to the grey line of equality, showing that the model with torques was a better predictor of final CoM position. Further, in Figure 4.5B the clustering of the red points is much tighter than the blue around their respective regression line. In general, the addition of torques meant the regression slope was closer to one and its r^2 value was greater than the model without torques.

4.5 Discussion

This chapter aimed to investigate how the motion of the body is controlled during a step. It was hypothesised that the trajectory of the body is determined by its initial conditions (position and velocity) at the beginning of the step when the stepping foot lifts. Gravity could then drive the body along its desired trajectory during the step. The results suggest that this is partly true, but that the body's trajectory is also modified during the step. Evidence for this conclusion is firstly provided by observations of the body's initial conditions and secondly by model simulations of body motion during a step.

4.5.1 Initial conditions and observed body motion during a step

In this chapter, unlike Chapter 3, a whole-body kinematic analysis of stepping was performed with both the position and velocity of the CoM being measured across

	Subject	**Gradient**		**Intercept (cm)**		**Adjusted r^2**	
		Without	With	Without	With	Without	With
Medio-Lateral	1	1.05	1.07	-2.28	0.95	0.85	0.94
	2	1.05	1.05	1.25	1.48	0.98	0.95
	3	1.03	1.03	-0.27	0.91	0.93	0.97
	4	1.12	1.09	0.11	1.05	0.96	0.99
	5	1.02	1.03	-0.10	0.69	0.97	0.99
Forwards	1	0.65	1.00	19.85	1.68	0.04	0.89
	2	1.45	1.19	-0.76	-0.89	0.75	0.96
	3	1.73	1.17	-6.13	-1.08	0.64	0.90
	4	1.00	1.08	5.02	-0.19	0.50	0.95
	5	1.11	0.99	1.52	1.83	0.45	0.92

Table 4.1. Observed versus predicted regression parameters.

the step. The experiment was designed to test whether the body's initial conditions can determine its trajectory during a step. If the initial conditions were important in controlling the motion of the body during a step, it would be expected that they would be different depending upon the intended step location. This is because the initial conditions (either or both of the mass' position and velocity) would need to be tuned differently in order to throw the body into the step and for gravity to then drive the body towards its target during the step. The results show that both the position and velocity of the mass are specifically modulated according to the intended step direction (Figure 4.2). This confirms the findings of Chapter 3 and previous experiments that demonstrate that the state of the body when the stepping foot lifts from the ground is different depending on the future location of the foot (Lyon & Day, 1997, 2005).

Subjects stood still and balanced prior to a step and initiated their movement from the same starting location in each trial. The required step was of a constant length in one of three directions. Due to the constant step length required, the duration of the step was the same when stepping to each target. The modulation of the initial conditions cannot therefore be explained by differences in posture prior to the step's initiation or changes to the duration of the step. The movement was also entirely volitional so the body was actively moved in such a way that the initial conditions were specific to the intended step location.

The results demonstrate that the initial conditions broadly differ into set classes depending on where you intend to step. However, both the position and velocity vary between steps to the same location (Figure 4.2C and Figure 4.2D). The initial conditions are therefore not set-in-stone. In Figure 4.2D for example, on average the CoM velocity was directed away from the stance-side when stepping to the most lateral target (as seen by the blue ellipse positioned greater than zero on the medio-lateral axis). For a single step however, the CoM velocity was directed towards the stance-side (leftmost blue circle), yet there is no immediate outlier when examining the trajectory of the CoM in steps to the same location (Figure 4.2B, blue traces). Likewise, there is substantial between-subject variability, showing that the throw of the body into the step must be appropriate for the individual. This between-subject variability was particularly apparent in the medio-lateral CoM velocity when the stepping foot lifted. For some subjects, the velocity of the body at foot-lift was always directed towards the stance side. For others however, the body's velocity could, on average, be directed away from the stance-side when stepping to the more lateral targets (for example the black and blue ellipses in Figure 4.2D). Together, the within and between subject variability acts as a reminder that the initial conditions are task and subject specific. As such, generalised statements of what is ‘typical’ should be used with care.

Like in Chapter 3, both the medio-lateral and forwards components of the initial conditions were analysed and plotted together (Figure 4.2B and Figure 4.2C). This revealed the close correspondence between the initial conditions and future location of the foot. As a result, the body began the step from a position and with momentum that was tuned to the intended step location. After the stepping foot lifted the body continued to move along a different trajectory in steps to each target (Figure 4.2A). The specificity of the initial conditions to the step location suggested that the initial conditions could be, at most, the sole determinant of or, at least, an important controller of the body’s trajectory during a step. To verify which of these options was true, the motion of the body during a step needed to be modelled.

4.5.2 Model simulations of body motion during a step

The body was modelled as a single segment that was free to rotate about a pivot (representing the ankle joint) under the influence of gravity during a step. The model was based on previously published ballistic models that have been used to predict medio-lateral motion of the CoM during a step (Lyon & Day, 1997; Yiou *et al.*, 2016). Similar inverted pendulums and ballistic models have also been used to either simulate human-like robotic gaits and predict forwards motion of the mass during gait (McGeer, 1990; Collins *et al.*, 2001). Here, the model was used to predict both medio-lateral and forwards motion of the CoM simultaneously. In doing so, the control of body motion during a step was able to be examined in greater detail than previous experiments. The model was provided with the same initial conditions as the body and allowed to move for the same duration as the step. Two model simulations were performed: (1) when the model fell freely under gravity during the step (without torques), and (2) when the model fell freely under gravity but its trajectory could be influenced by mid-step torques (with torques).

In common with previous findings (Lyon & Day, 1997; Yiou *et al.*, 2016), the model without torques (that is, a purely ballistic model) was able to predict medio-lateral motion of the body with reasonable accuracy. Addition of mid-step torques that could modify the body’s trajectory whilst it fell under gravity did little to improve the prediction of medio-lateral motion. This suggests that the medio-lateral motion of the body during a step is largely determined by the initial conditions of the body when the stepping foot lifts and that mid-step adjustments are not used under normal circumstances.

On the other hand, the model without torques poorly predicted forwards body motion and overshot observed body motion substantially. Error in predicting forwards motion accounted for most of the model's error. The addition of mid-step torques to the model reduced the forwards motion and overshoot of the model's CoM (Figure 4.3, Figure 4.5B and Figure 4.5D). Subsequently, the model with torques was a better predictor of forwards body motion and did so with reasonable accuracy. This suggests that the initial conditions alone did not determine the body's trajectory during a step and that mid-step adjustments were important in modifying body motion. Overall, model error was significantly reduced by the addition of mid-step torques. Consequently, a ballistic model of stepping does not seem to fully explain the observed motion of the body.

Inferential statistics were not performed on the regression data presented in Figure 4.5 and Table 4.1 due to their non-normality. Figure 4.5A shows that the distribution of the CoM's location was not continuous, as can be seen by the three distinct clusters of points around the regression lines. The experiment required a step to three distinct locations with each foot and thus the CoM ended the step in three roughly distinct locations. Given that a continuous distribution of CoM locations would have been expected if the subjects were asked to step in all directions, I argue that the use and interpretation of regression lines as a descriptive measure is justified here. Hypothetically, it would also be expected that if the model were able to reliably predict the motion of the body, a one-to-one linear relationship would be present across steps in all directions, the model would account for the variability in final CoM location and its regression line would lie close to the line of identity (i.e. a regression slope and r^2 of approximately one and intercept approaching zero). This strong *a priori* expectation seems to be true of the data presented here, particularly when the model was provided with mid-step torques. Inspection of the descriptive statistics of Table 4.1 and the depiction of this data in Figure 4.5 shows that the relationship between observed and modelled CoM position seemed to be linear, further justifying the use of regression here.

4.5.3 Why did the mid-step torques influence forwards more than medio-lateral body motion?

One reason could be the shape and mechanics of the foot. To exert influence on the body's trajectory during a step, force must be exerted on the ground via the stance foot. The application of force generates a torque about the ankle joint. The torque generated is the product of the magnitude of the force applied and the distance it is applied from the pivot (i.e. the ankle joint). So, for example, a force applied at the toes would generate a greater torque than the same force applied mid-way along the foot as the distance between the point of application of the force (i.e. the centre of pressure) and the pivot (the ankle joint) is larger. Given that the foot is much longer than it is wide, the centre of pressure is able to move further from the ankle joint along the length of the foot (forwards) than it can sideways (medio-laterally). As a result, the magnitude of torque about the ankle is able to be larger in the forwards in comparison to medio-lateral direction. It can also be seen from Figure 4.3A that the centre of pressure moves much more along the antero-posterior axis (i.e. towards the toes) than it does medio-laterally during a typical step.

4.5.4 The causes of mid-step torques

The torque generated about the stance-leg ankle joint during a step acted to adjust the body's trajectory but could have originated from several sources. Broadly, these separate into either active or passive control mechanisms. Active control refers to the neural control of muscle. By actively changing the firing rate of neurons innervating muscle, the nervous system can alter the torque generated about a joint. Firing rate can be altered based on spinal-level reflexes, such as muscle stretch reflexes, or higher-level input based on feedforward control or ongoing sensory information. Active control of mid-step adjustments based on ongoing sensory information has previously been demonstrated by both the increase in foot placement error when visual feedback is denied and the rapid adjustment of the foot's trajectory when a step target changes location (Weerdesteyn *et al.*, 2004; Reynolds & Day, 2005a, b, 2007; Nonnekes *et al.*, 2010). Active control implies a step-specific refinement of the ongoing movement based on a prior motor programme or the perception of error.

However, muscles and tendons display an intrinsic mechanical stiffness and, much like a spring, can generate torque without neural control. The muscles and tendons of the ankle joint, and possibly other joints, could therefore have generated torque passively to resist movement. Passive control implies a specific adjustment of the ongoing movement based on the state of the musculature, but non-specific with regards to error present in the movement. The level to which active and passive mechanisms influenced the observed torque here is unknown, although both will have played a role in adjusting the motion of the body during the step. It has previously been suggested that passive mechanisms contribute comparatively less than active mechanisms to ankle torques during normal gait, although passive mechanisms can exert greater influence than normal in cases where the ankle joint is stiffened by pathology (Siegler *et al.*, 1984).

The main muscles governing the ankle joint are the tibialis anterior, which dorsi-flexes the ankle, the gastrocnemius and soleus, which both plantar-flex the ankle. Whilst, to my knowledge, the role of the stance-leg ankle dorsi- and plantar-flexors have not previously been studied in a single step similar to the present experiment, they have been extensively studied in gait initiation and walking. Such studies suggest that when initiating a step from a stationary posture, like in the present experiment, the ankle plantar-flexors are initially inhibited relative to their tonic level in quiet stance (Herman *et al.*, 1973; Crenna & Frigo, 1991). The tibialis anterior are then activated, which causes ankle dorsi-flexion, the movement of the CoP backwards and a subsequent propulsive torque about the ankle that accelerates the body forwards (Herman *et al.*, 1973; Crenna & Frigo, 1991; Winter, 1995). Once the body is in motion and the stepping-foot is airborne, the stance-leg plantar-flexors contract eccentrically or isometrically whilst the body moves forward during the step (Hof *et al.*, 1992; Kepple *et al.*, 1997; Neptune *et al.*, 2001).

For the present results, the mid-step plantar-flexor activity is important as it is thought to resist forward motion of the body (Simon *et al.*, 1978; Sutherland *et al.*, 1980; Hof *et al.*, 1992; Neptune *et al.*, 2001), which is consistent with how the torque influenced the model's motion here. The role of the plantar-flexors during a step can therefore be likened to that of a car brake whereby applying the brake when the car is in motion causes it to slow. The car brake analogy is more complete when considering the motion of a car as it descends a slope. This is because in this case the car, like the body during a step and the model simulation here, is being accelerated by gravity. In this analogy, applying the brake as the car descends the slope would resist the gravity-driven acceleration of the car. In the same way, contracting the plantar-flexors can control the gravity-driven fall of the body during the step and attenuate the forwards motion of the body.

The purely ballistic (without torques) model simulation condition presented here is analogous to the complete removal of all muscle (including plantar-flexor) activity during a step. In the car brake analogy, this would amount to disabling the brake, after which the car would be expected to enter an uncontrolled downhill acceleration. Experiments that have disabled the stance-leg plantar-flexors with a paralytic tibial-nerve blockage have noted that the CoM velocity at the end of the step is increased compared to normal, indicating that without stance-leg plantar-flexor input the body's fall under gravity is unable to be resisted (Simon *et al.*, 1978; Sutherland *et al.*, 1980). The present results are in agreement with this. For a given step, the two model simulations were identical in terms of duration, yet the model had travelled further forward in the same time when it was allowed to fall without modification. Thus, the velocity of the model's CoM was greater when it underwent an unconstrained fall.

It therefore seems reasonable to suggest that the ankle plantar-flexors were significant contributors to the mid-step torques measured in the present experiment. However, it is important to note that the forces measured in this experiment are the net sum of all forces acting on the body's centre of mass. As such, the measured torque about the stance ankle will have resulted from the net sum of the action of all muscles across the whole-body. Whilst the stance-leg plantar-flexors are likely to have significantly influenced the torque, and thereby body motion, the relative contributions of the plantar-flexors and other muscles cannot be determined from the present results. The use of electromyography may have been useful in indicating whether plantar-flexor activity was consistent with the observed torque, but it should also be noted that the relationship between a muscle's activity and the force it produces is not simply estimated when using non-invasive methods (Erdemir *et al.*, 2007). Complex computational models can be used to infer force production dynamics at individual joints (Zajac *et al.*, 2002; Erdemir *et al.*, 2007) but estimated force magnitudes differ considerably between models (Trinler *et al.*, 2018).

4.5.5 Variability in model predictions

As previously discussed, the initial conditions differ between subjects. The magnitude of the effect of mid-step torques on the model also differed between subjects. For example, the model's prediction in subject four (a typical subject, depicted in Figure 4.5A and Figure 4.5B) was not greatly affected by the mid-step torques in the medio-lateral direction (the regression parameters were broadly similar, Table 4.1) but was affected in the forwards direction (slope closer to one and increase in r^2 values, Table 4.1). On the other hand, the model performed relatively poorly in both medio-lateral and forwards dimensions for subject one when the model fell freely under gravity but the addition of mid-step torques had a profound effect. This raises the possibility that different people utilise different stepping strategies. With this logic, subjects two to five would seem to rely more heavily on the initial conditions to determine the body's trajectory during a step , whereas subject one seems to rely more heavily on mid-step adjustments of the body's trajectory.

The addition of mid-step torques to the model also reduced both within- and between-subject variability of error in predicting the final location of the body's CoM. The reduction of within-subject variability can be seen in Figure 3B by the tighter clustering of the red in comparison to the blue points. Likewise, this is shown by the tighter clustering of each red point around its regression line and an increased adjusted r^2 values when the model was with torques in comparison to without (Figure 4.5A & Figure 4.5B and Table 4.1). The reduction of between-subject variability can be seen in Figure 4.5C and Figure 4.5D by the tighter clustering of the red regression lines in comparison to the blue and also in Figure 4.2 by the smaller error bars on the red bars in comparison to the blue. The reduction in within-subject variability shows that the model with torques provided a more precise and accurate estimate of the body's final position than when it fell freely without modification from mid-step torques. The reduced between-subject variability showed that the remaining error was relatively consistent across subjects. Together, this suggests that a small constant error was present after the model was simulated with mid-step modification from ankle torques. However, it should be noted that for such a simple model, it simulates such a complex action with remarkable accuracy.

4.5.6 Limitations and assumptions

The model has several limitations and assumptions that could potentially explain this remaining constant error. Firstly, there could be small errors in estimation of the kinematics of the step; for example the location of the body's CoM, its inertia or the location of the stance-foot ankle which defined the location of the model's pivot. The model assumes that the location of the pivot does not move during a step. In reality, the stance ankle does move slightly during a step (typically between 3 and 10 mm) which could potentially alter the motion of the body. The model also assumes that the body moves as a single unit during a step. However, each body segment can move relative to the mass during the step. The movement of a segment relative to the CoM could affect the mass' inertial properties and therefore its motion. An analogous example can be seen in the angular motion of a rotating ice skater. By moving the arms closer to or further from their body, the skater can alter their inertia and subsequently increase or decrease their angular velocity, respectively. Reorganisation of the body's segments about its CoM could act in a similar way during a step to alter the body's motion.

The limitations in the design of this experiment must also be considered when interpreting its results. Subjects were required to take a single step to a target location and bring their trailing foot alongside. The movement was performed without imposed time constraints and gait was not initiated after the steps. The task was simple and seemed to elicit a natural and self-initiated movement for each subject. However, it is unclear how well a single step generalises to steady-state gait. The two acts do have many similarities, most notably the need to lift one foot from the ground, the mass typically lying medially to the base of support defined by the stance foot during a step and the body therefore being unstable and falling sideways under gravity. There are some differences between the steps in the current experiment and steps to initiate or maintain gait however. When stepping to initiate gait, the CoM typically reaches a velocity of approximately 1 m/s in the direction of travel by the time the stepping foot lands on the ground (Breniere & Do, 1991). The CoM's velocity can increase or decrease depending on the intended gait speed and step length and in slow gaits is typically approximately 0.8 m/s (Breniere & Do, 1986; Lepers & Breniere, 1995).

In the present experiment, the CoM velocity at foot land was substantially less than this (horizontal Euclidean velocity (group mean±SD): 0.44±0.04 m/s). As can be seen in Figure 4.3 & Figure 4.2, the mid-step torques also acted to decrease the forwards motion of the mass. It is therefore possible that, because gait need not be initiated, the subjects could have used mid-step torques in an abnormal way to temper their step and reduce the body's velocity. However, subjects need not have done this and instead could have reduced the magnitude of the throw of the body into the step. The experiment was designed to reduce this possibility. Subjects were required to step with the trailing foot after the initial step and produce a natural, fluid movement where one step seamlessly transitioned to the next, rather than two separate steps. Subsequently, the mass was required to move continuously from the initiation of movement until after the second step with the trailing foot.

Nevertheless, whilst a single step may not be able to be directly extrapolated to stepping during gait, the present results do show that mid-step modifications of the body's trajectory seem to be used during a step. It remains to be seen whether mid-step modifications are of similar importance in other types of steps; for example stepping as quickly as possible, non-goal directed stepping, stepping down a step or incline, stepping to initiate gait, or stepping to maintain steady-state gait.

4.6 Conclusion

This chapter shows that the body's initial conditions are modulated depending on the intended step location. The body therefore enters the step travelling along a different trajectory when taking a step in different directions. The motion of the body during a step was then simulated using a model. The model could not fully explain the observed motion of the body during a step when acted upon by the initial conditions and gravity alone. Instead, body motion could be simulated with reasonable accuracy when the model was acted on by the initial conditions, gravity and mid-step ankle torques. Thus, whilst the initial conditions are important in controlling body motion during a step, mid-step ankle torques are also used to modify the body’s trajectory as it falls under gravity.

5 Chapter 5: Coordination between the body and leg during a step

5.1 Abstract

During a step, the body is in a state of imbalance as it falls laterally along its intended trajectory. Whilst the body falls, the foot swings and aims to land in a location that enables the body to be caught and balance to be regained. Given that the foot is attached to the body via the leg, the position of the foot at the end of the step depends on the movements of the body and the leg. How are the body and leg coordinated to land the foot accurately on its target? This chapter examines this by instructing subjects to step as accurately as possible to different target locations either with or without visual feedback during the step. The results show that foot placement error was increased when visual feedback was denied during the step. Regardless of visual feedback, a step location-dependent body and leg movement was used to land the foot on its target. Both the final body and leg position varied between steps to the same location which landed the foot in a variable location. Foot variance was far less than that expected had the body and leg varied independently or had body and leg movement errors summed. Rather, the body and leg seemed to be organised to reduce foot placement error, even when visual feedback was denied. It is concluded that, although vision is important in guiding the foot towards its target, the coordination between the body and leg is predominantly non-visual.

5.2 Introduction

When repeating an action many times it is extremely rare, if not impossible, for the action to be repeated exactly the same twice. Bernstein (1967) demonstrated this when repeatedly hitting a nail with a hammer and noted that the hammer's trajectory in space is variable, despite the hammer starting in the same location and ending accurately on the nail. This action requires movement across multiple joints to be controlled and a chain of body segments to be coordinated to move the hammer onto the nail. Stepping is a similar but somewhat unique action. Like hitting a nail with a hammer, a chain of body segments must be coordinated to move an end-effector (the foot) to its target. However, unlike hitting a nail with a hammer, movement must be coordinated with the need to keep balance when taking a step.

The challenge of coordinating multiple segments during a step is complicated by the fact that the body is unstable during a step. Prior to lifting a foot to take a step, the body's CoM is shifted forwards and towards the forthcoming stance side (Carlsöö, 1966; Mann *et al.*, 1979; Crenna & Frigo, 1991; Jian *et al.*, 1993; MacKinnon & Winter, 1993). However, the mass typically lies medially to the stance foot when the stepping foot is lifted and the body therefore begins to fall laterally under gravity during the step (Jian *et al.*, 1993; MacKinnon & Winter, 1993; Lyon & Day, 1997). To counter this instability, the motion of the falling body is firstly controlled by the position and velocity of the mass at the instant the stepping foot lifts (Chapter 4; Lyon & Day, 1997, 2005). The initial position and velocity of the mass is closely coupled to the intended step location (Chapters 3 and 4; Lyon & Day, 1997, 2005; Bancroft & Day, 2016) which sets the body in motion along a trajectory that is appropriate for the future location of the foot. The motion of the body is then modified during the step by applying torques about the stepping-foot ankle (Chapter 4).

During the step, the leg moves on the body and aims to swing the foot towards its target. Provided the foot moves accurately to its target and its location is appropriate for the body's motion, the falling body is 'caught' and balance is regained. In order for the foot to land in an appropriate location, the movement of the body and leg need to be coordinated during a step. The coordination between the leg and body must therefore enable the foot to land accurately and precisely on its target. How does the brain coordinate the body and leg to achieve foot accuracy and precision?

One way could be to use online sensory information to update the ongoing movement and guide the foot towards its target. The brain has multiple channels of information at its disposal which can be used to correct movements. For goal-directed actions, such as hitting a nail with a hammer or stepping to a target, vision is perhaps the most important sense in guiding movement. In the case of stepping, the denial of visual feedback during the step increases foot placement error and leads to the foot landing in a more variable location (Reynolds & Day, 2005b). Experiments that make a step target change location when the foot lifts from the ground also show that visually-triggered corrections can be incorporated into the step rapidly (latency: ~120 ms; Weerdesteyn *et al.*, 2004; Reynolds & Day, 2005a, 2007). Together, this suggests that vision may play a role in coordinating the body and leg movements used during a step.

Movement is still variable, even with vision available however, which poses a problem for the brain. Figure 5.1 shows three different potential organisations of the trial-to-trial variation in the body and leg movements. Each dot shows the final location of the body, foot-relative-to the body (leg) and foot in a single trial. The variance in the body and leg movements is identical in each panel (A, B, C). The pink dots and vectors highlight a single step. The same body movement is highlighted in each panel but the leg movement it is coupled with differs in A, B and C. Each panel therefore demonstrates a different form of organisation between the body and leg, with each having different predictions. In each, the body and leg movements sum to land the foot in a location.

In A, the variances of the body and leg are independent. When two distributions sum (such as the body and leg), the variance of the resulting distribution (the foot) is the sum of the two variances. This predicts that the variance of the foot would sum to be larger than the variance of the body or the leg. Independent variances would also predict that the variance in the body and leg would have no systematic relationship. If this was true, the angular difference between the body and leg vectors would be randomly distributed and have no meaningful direction. Independent variances would mean that the observed variability in the body and leg was random, which would suggest that randomly pairing the body and leg movements used (as in a randomisation test) would not change the observed variance of the foot. This strategy could be true given that random noise is present in every part of movement, from the processing of sensory information to inform action through to its execution (Faisal *et al.*, 2008).

In B, the variances of the body and leg are dependent and positively correlated. The variance of the sum of two dependent distributions that are positively correlated is greater than the sum of the two variances. This predicts the variance in

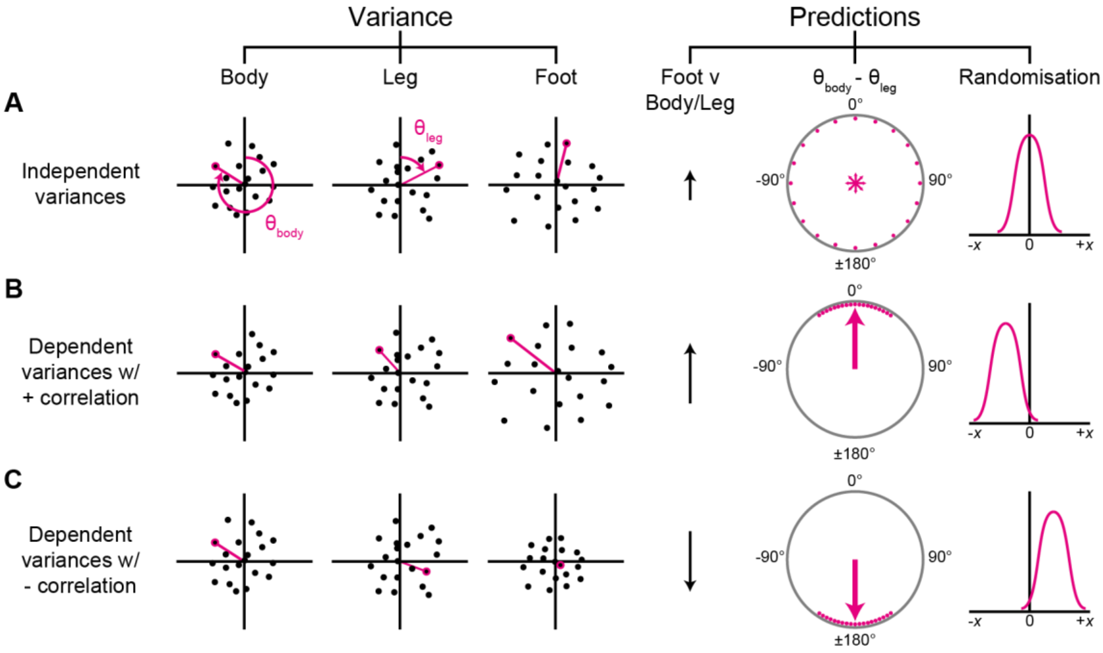

Figure 5.1. Random variation and co-variation. Hypothetical trial-by-trial variance of the body, leg and foot at the end of steps to the same target. Dots are single trials. Pink dots and vectors in the left-hand panel indicate a single step. Each row (*A*, *B*, *C*) has a different coupling between the body and leg movement, which predicts different effects on foot (in comparison to body/leg) variability, the angular difference between the body and leg vector angles and randomisation tests. The pink arrows in the right-hand panel are the mean angular difference between body and leg vectors across repeated steps.

the foot to also be greater than the body or leg movements, but more so than that predicted by independent variances (Figure 5.1A). A positive correlation also predicts the body and leg vectors to be oriented in the same direction and the angular difference between the two to be 0°. This would mean that, for example, a body movement that deviated in one direction (leftward in Figure 5.1B) was coupled with a leg movement that deviated in the same direction. Moreover, randomly coupling the body and leg movements in a randomisation test would destroy the positive correlation between the body and leg and reduce the variance of the foot in comparison to that actually observed (leftward shifted bell-curve in Figure 5.1B). Dependent variance with a positive correlation could be true given that the foot is the end-effector in a chain of segments where each segment contains movement error which would be expected to sum and increase error in the end-segment location.

In C, the variances of the body and leg movements are dependent and negatively correlated. The variance of the sum of two dependent distributions that are negatively correlated is less than the sum of the two variances. This predicts that the variance in the foot would not be greater than the body or leg movements. A negative correlation also predicts the body and leg vectors to be oriented in opposite directions and the angular difference between the two to be ±180°. This would mean that, for example, a body movement that deviated in one direction (leftward in Figure 5.1B) was coupled with a leg movement that deviated in the opposite (rightward) direction. The variation in the body and leg sum and cancel out. Moreover, randomly coupling the body and leg movements in a randomisation test would destroy the negative correlation between the body and leg and increase the variance of the foot in comparison to that actually observed (rightward shifted bell-curve in Figure 5.1B). Dependent variance with a negative correlation would suggest that the body and leg were organised to reduce end-point error in foot placement.

5.2.1 Hypothesis

This chapter asks how the movements of the body and leg are coordinated during a step. The task is a goal-directed step, analogous to hitting a nail with a hammer with the upper limb, performed either with or without visual feedback during the step. It is hypothesised that the body and leg are coordinated to reduce foot placement error, as predicted by the body and leg variances being dependent and negatively correlated (Figure 5.1C). It is also hypothesised that vision is important in coordinating the body and leg during a step and that denial of visual feedback increases foot placement error.

5.3 Methods

5.3.1 Sample size estimation

No relevant data has been published where the coordination of the body and leg has been analysed, as in the present experiment. However, Reynolds and Day (2005b) conducted a similar study of goal-directed stepping and examined the effect of visual feedback on foot placement variability during fast and slow steps. The authors report means and standard deviations (vision on v off) of 7.7±1.6 v 11.5±0.7 mm for slow steps and 9.7±1.2 v 11.8±2.0 mm for fast steps, which equals an effect of vision on foot placement variable error of size 2.16 for slow steps and 0.88 for fast steps (Cohen's *d*; see Equation 2.1 in Chapter 2.6). Neither the variability of nor coordination between the body and leg movements was reported. The smaller of the two reported effect sizes (fast steps) was used here to compute a conservative estimate of the required sample size. Using a two-tailed dependent-samples *t*-test with the probability of type I error (α) set at 0.05 and type II error ($1-\beta$) set at 0.1, a sample size of sixteen was required.

5.3.2 Subjects

Sixteen healthy, young subjects (9 male; 26±5 years; 66±11 kg; 1.74±0.10 m) participated in the experiment. Fifteen out of sixteen subjects reported as either being right-foot dominant or having no side preference, with one subject expressing left-foot dominance.

5.3.3 Protocol

Subjects performed a step to the location of a floor-bound target. Before initiating the step, subjects stood still and barefoot with both feet parallel and separated by 15 cm. The initial position of the feet was chalk-marked to ensure a consistent starting location. Three targets were placed ahead of the left and right feet in the same orientation as Chapter 4 (T1, T2, T3; Figure 5.2A). Each target was placed 35cm from the stepping foot in different directions. Thus, each target required a forwards movement in a different direction but with a constant step length. Subjects were instructed to step accurately to the location of the target and bring their trailing foot alongside. An accurate step was self-defined by each participant prior to the experiment. This was achieved by placing the foot over each target without time or movement constraints and recording its position. The ideal accurate step was repeated if the subject or experimenter felt it necessary. Foot placement accuracy was compared to this ideal accurate foot placement in all experimental trials.

An audible beep alerted the subject that a trial was to begin. After a short random delay a target light would illuminate, which acted as a cue for the subject to initiate a step to its location in their own time. No instruction was given about where to land the trailing foot. However, subjects were encouraged to make a natural stepping movement and to finish the step in a balanced state, similar to their posture

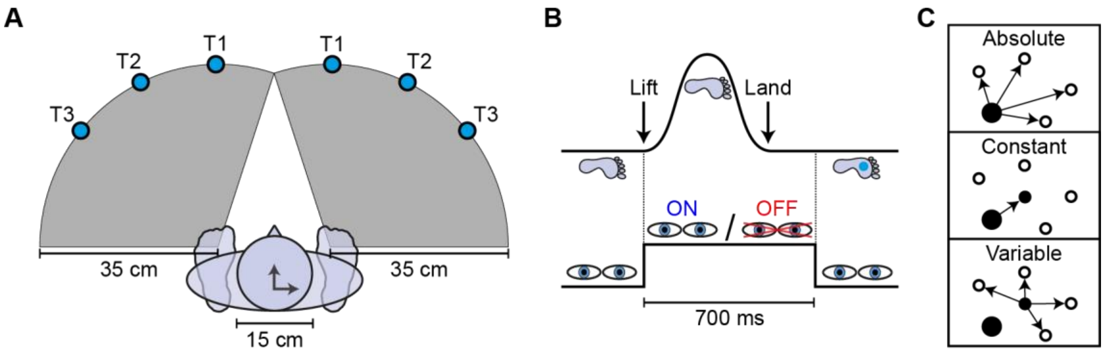

Figure 5.2. Experimental set-up and measures of error. *A*: Target lay-out. Three targets (T1-3) were placed 35 cm from each foot. *B*: Timing of visual occlusion. *C*: Absolute, constant and variable foot placement error (Reynolds & Day, 2005b). Unfilled circles show the foot's position, the smaller filled circled shows the mean foot position and the larger filled circle shows the ideal accurate foot position.

prior to the step. Each subject completed a total of 240 trials in randomised order. In 50% of randomly selected trials, visual feedback was denied during the step by occluding vision from the instant the stepping foot lifted for 700 ms (Figure 5.2B). Thus, 20 steps to each target were performed both with and without visual feedback during the step. A delay of 700 ms in returning vision was chosen as this was comfortably greater than the duration of similar steps in Chapter 3 and other experiments (Reynolds & Day, 2005a, b). Inspection of each trial confirmed that vision was successfully occluded during every step, with vision always being returned after the stepping foot landed. Subjects were still required to land their stepping foot accurately on the target when visual feedback was denied. Visual feedback of final foot placement was allowed after vision was returned to the subject.

5.3.4 Apparatus

The step targets were circular (2.5 cm diameter) and illuminated via electroluminescent paper (see Chapter 2.2.1 for further details). Infrared-emitting diode markers were placed on the feet and hip to quantify leg and body movement, respectively. Three markers were placed on each foot, located at the base of the first metatarsal and head of the first and fifth metatarsals. One marker was placed on each of the left and right anterior superior iliac spine of the hip. The hip markers were used because the pelvis has been shown to approximate the location of the whole-body CoM during gait (Saini *et al.*, 1998; Eames *et al.*, 1999; Huntley *et al.*, 2017) but its location, unlike the CoM, is independent of the movement of the leg. Marker locations were recorded by two motion capture cameras (Coda cx-1; Charnwood Dynamics, Leicestershire, UK) and sampled at 200 Hz. The subjects initiated a step with each foot over a force platform, which was embedded within the floor. Ground reaction forces were sampled at 1000 Hz. PLATO spectacles were used to occlude vision during a step (see Chapter 2.2.4 for details). The spectacles were triggered to occlude vision when the vertical force beneath the stepping foot went below 10 N, which provided a precise signal of foot lift (see Chapter 2.2.3.3 for details).

5.3.5 Data analysis

Foot-lift and foot-land were calculated offline with the force-plate methods described in Chapter 2.4. The step was considered the time from foot-lift to foot-land. The instantaneous position of the foot was the mean of the three markers on the stepping foot. The instantaneous position of the body was considered the location of the stepping-side hip marker. The foot is attached to the rest of the body (i.e. the hip) via the leg. The position of the foot in space therefore depends on the position of the body and the movement of the leg on the body. In mathematical form this equates to:

$$Equation\ 5.1: \qquad Body + Leg = Foot$$

where each of *Body*, *Leg* and *Foot* are three-dimensional vectors defining the position of the body in space, the movement of the leg on the body and the position of the foot in space, respectively. Given that the positions of the body and foot in space were measured, the movement of the leg was calculated as the foot relative to body position, or in mathematical form:

$$Equation\ 5.2: \qquad Leg = Body - Foot$$

Foot placement error was evaluated with three different measures: absolute, constant and variable error (Schmidt & Lee, 1999). Absolute error was the Euclidean distance between the stepping foot when it landed and the ideal stepping foot placement, reflecting step accuracy. Constant error was the Euclidean distance between the mean stepping foot position when it landed and the ideal stepping foot placement, reflecting step bias. Variable error was the Euclidean distance between the foot position when it landed and the mean stepping foot position when it landed, reflecting consistency. These three measures are depicted in Figure 5.2C.

Coordination was investigated by examining the variability around the mean of each of the body and leg movements. For this, the mean position of the body or foot-relative-to-body was calculated from steps in a condition and subtracted from each step in the same condition. This returned a spread of steps about the mean like those in Figure 5.1. For a single step, the azimuth angle of its vector from the ‘North’ (forwards) direction was calculated for each of the body and leg movements (pink vectors in Figure 5.1). The angular difference between the body and leg vectors from the same step was then calculated. Variability in body and leg movements was calculated in the same way as variable error in foot placement and is used as an analogous measure to variance. Note that variability of foot placement is termed variable error because the goal of the task was to land the foot as accurately as possible. Variability in body and leg movements is not termed error as the body and leg movements did not have independent goals. In other words, the body and leg were allowed to take any trajectory to land the foot on the target and therefore variability in their movement cannot be directly equated with error.

5.3.6 Statistical analysis

For univariate variables (step duration and measures of error and variability), repeated-measures ANOVAs were used to analyse the effects of step side (left/right), direction (T1/T2/T3) and vision (on/off). Greenhouse Geisser corrections were used when the assumption of sphericity was violated. Paired *t*-tests were used when *post-hoc* analyses were required. Bivariate variables (two-dimensional body and leg positions, angular data) were analysed by paired Hotelling's tests (Batschelet, 1981; Zar, 2010). Angular means and standard deviations were computed using methods appropriate for circular data (Batschelet, 1981; Zar, 2010). Bonferroni correction for multiple comparisons was used with Hotelling's tests and *post-hoc* analyses.

The organisation of the body and leg movements was also examined using a series of repeated-measures randomisation tests (repeated-measures ANOVAs with random data permutation in Manly, 2007). Independent variance of the body and leg (as in Figure 5.1A) predicts that in steps to the same target a random body movement is coupled with a random leg movement. The foot then ends the step in a more variable location than the body and leg. If this was true then coupling a body movement with a randomly selected leg movement would not change the variation in the foot location. On the other hand, if the coupling between the body and leg was important (i.e. the variances were dependent), randomly coupling the 20 body and leg movements would affect the computed variability of the foot (see this Chapter's Introduction and Figure 5.1 for predicted effects). A total of 5000 permutations of the data were performed per randomisation test. A permutation consisted of coupling a body movement with a randomly selected leg movement. The resulting foot positions were calculated for each step (using Equation 5.1) and the mean variable error of the 20 steps computed**.** The permuted mean variable error was then compared to the 'real' variable error from the measured data. The test statistic and *p* value calculation is explained in the Results. One-hundred-and-ninety-two randomisation tests were performed (16 subjects x 2 sides x 3 targets x 2 visual conditions). The random coupling was performed with replacement and each randomisation test was independent.

5.4 Results

5.4.1 Body and leg movements in steps to different targets

Figure 5.3 shows the trajectory of the body and foot-relative-to-the-body during right-sided steps and the location of the foot when it landed for a typical subject. The body moved along a different trajectory depending on the step location, as seen by the distinct separation between each colour's traces. By the time the stepping foot landed, the body had moved into a location that was significantly different when stepping to each target (all comparisons $T^2(2,14) > 385$, $p < 0.001$). The foot would swing towards its target whilst the body moved during the step. The inset of Figure

5.3 shows the movement of the foot-relative-to-the-body, denoting the movement of the leg during a step. Like the trajectory of the body, the trajectory of the foot-relative-to-the-body differed with the step location. The foot ended the step in a location that was significantly different when stepping to each target ($T^2(2,14) > 1900$, $p < 0.001$). The trajectory and final location of the body and foot-relative-to-the-body reflected the intended step location in Cartesian coordinates, showing that the body and leg movements used during a step were specific to the step location. Both the movement of the body and leg were variable, which landed the foot in a variable location.

5.4.2 Foot placement error

Even when visual feedback was present during the step, foot placement contained error (vision ON absolute (mean±SD): 30.3±12.0 mm; constant: 26.5±13.3 mm; variable: 14.2±1.7 mm). This can be seen in Figure 5.3 by the variable final location of foot placements and the cluster of foot placements being located away from the ideal accurate foot placement (filled circles). Foot placement error was no different between each step direction ($F(2,30) > 0.2$, $p > 0.2$). Absolute and constant error were not affected by the stepping side ($F(1,15) > 0.4$, $p > 0.5$) but the foot landed in a more variable location in right-sided steps than left (15.2±1.8 v 14.3±1.9 mm; $F(1,15) = 10.1$, $p = 0.006$). The denial of visual feedback during a step significantly increased absolute, constant and variable foot placement error (Figure 5.4A; $F(1,15) = 10.2$, $p = 0.006$; $F(1,15) = 5.8$, $p = 0.029$; $F(1,15) = 12.2$, $p = 0.003$, respectively).

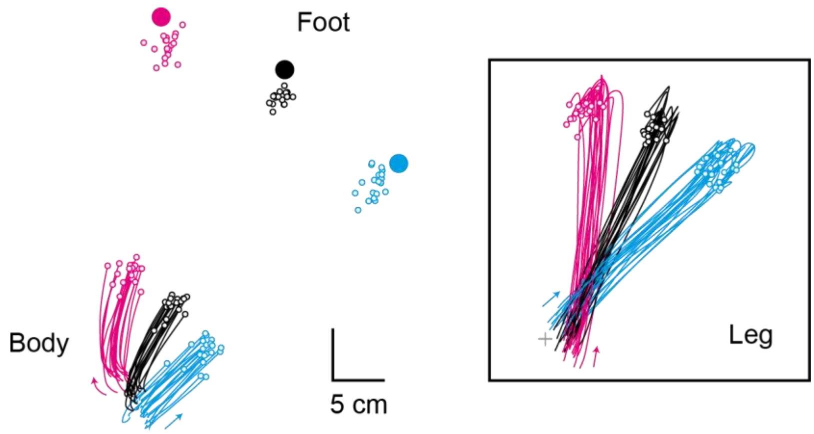

Figure 5.3. Trajectory of the body and leg during a step. Right-sided steps with vision ON to T1 (pink), T2 (black) and T3 (blue) from a typical subject. The unfilled circles are the position of the body, foot and foot-relative-to-the-body (leg movement) when the stepping foot landed. The large circles are the ideal accurate foot position. Body and leg traces are from foot-lift to foot-land. The arrows point in the direction of movement over time. In the leg inset, the grey '+' is the instantaneous position of the body (hip). The main figure and inset are on the same scale.

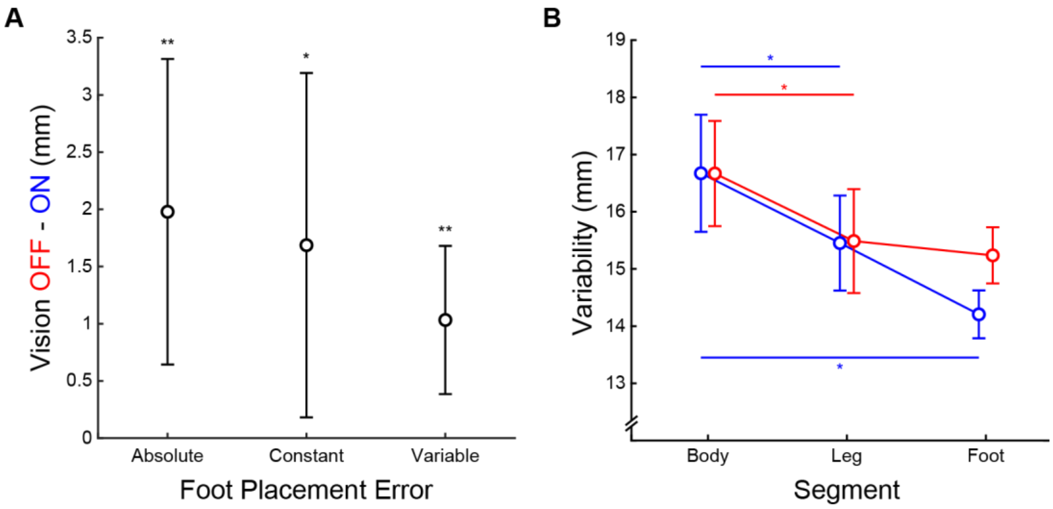

Figure 5.4. Effect of vision on step performance. *A*: Mean and 95% confidence intervals of the pairwise difference (Vision OFF – ON) for the three measures of foot placement error. None of the confidence intervals overlap zero, indicating a significant increase in error without vision. *B*: Group mean (±SE) of body, leg (foot relative to body) and foot variability at foot-land. Blue indicates steps with vision (ON) and red without vision (OFF). *$p < 0.05$; **$p < 0.01$

The magnitude of the increase in error can be seen in Figure 5.4A, but was generally small (~1-2 mm). No interaction was found between vision and step side or direction (all $p > 0.05$).

5.4.3 Segment variability

The variability of the body and leg movements for a single subject can be seen in Figure 5.3 by the spread of trajectories and final locations of the body and foot relative to the body. For the group, variability of the body and leg movements was not affected by step side, direction or vision (F(1,15) < 3.2, $p > 0.1$; F(2,30) < 3.5, $p > 0.05$; F(1,15) < 0.02, $p > 0.9$, respectively). Figure 5.4B compares the variability of the body, leg and foot at the end of the step. The difference in variability between segments was affected by vision (segment x vision: F(2,30) = 6.0, $p = 0.006$). *Post-hoc* tests revealed that the body was more variable than the leg in steps both with and without visual feedback. The variability of the foot was no different from the leg in steps both with and without vision ($p > 0.05$) and as variable as the body in steps without vision ($p > 0.05$). The foot was less variable than the body in steps without vision ($p < 0.05$).

5.4.4 Organisation of the body and leg movements

5.4.4.1 Angular difference

Figure 5.5 shows the mean group angular difference between the orientation of body and leg vectors in steps with (blue) and without (red) vision. The further the data is from the centre of the graph (i.e. a greater *r* value), the greater the

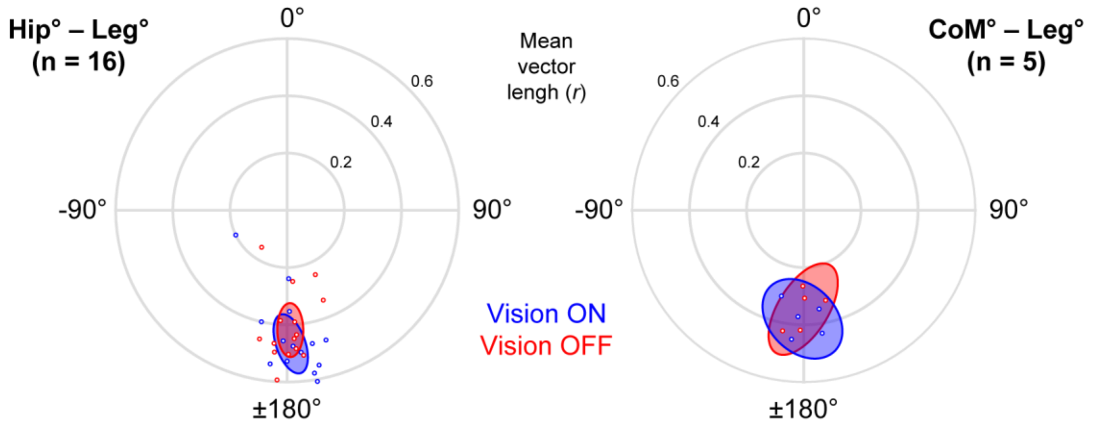

Figure 5.5. Co-variation of body and leg movements. Angular difference between the foot-relative-to-hip (leg) and either the hip (*left*) or centre of mass (CoM; *right*) vectors. Each circle represents the mean of a single subject either with (blue) or without (red) vision. Ellipses are 95% Hotelling's ellipses of the group mean.

concentration of the data on a given angle. The left-hand side of Figure 5.5 shows the angular difference between the hip and foot-relative-to-hip position vectors, as measured in this chapter. The 95% confidence ellipses of steps with and without vision did not overlap the centre of the figure (where $r = 0$), indicating that their mean angles were not randomly distributed and had a meaningful direction. The average angular difference was 178.5±1.2° ($r = 0.47$) in steps with vision and 178.5±1.3° ($r = 0.42$) in steps without vision. There was no difference between vision ON and OFF in the mean angle or its variability ($T^2(2,14) < 3.8$, $p > 0.2$). The group angular difference was not different from ±180° either with or without vision, as seen by the confidence ellipses overlaying ±180° ($p > 0.05$).

To test whether this result was simply an artefact of the body position being estimated by the hip and not the whole-body, the same analysis was performed on the data from Chapter 4. The right-hand side of Figure 5.5 shows the angular difference between the CoM and foot-relative-to-hip position vectors as measured in Chapter 4. These five subjects also participated in the experiment in this Chapter. The same relationship was found between the whole-body CoM and leg movements as with the hip: the mean angular difference between their vectors was not different from ±180° in steps with or without vision and no difference was present between visual feedback conditions ($p > 0.05$).

5.4.4.2 Randomisation tests

Figure 5.6A outlines the procedure of a randomisation test. For the test, the 20 measured body and leg movements in a condition were randomly coupled and the resulting variable error of the foot computed (see Chapter 5.3.6). Figure 5.6B and Figure 5.6C show examples of the two typical distributions of foot variable error that

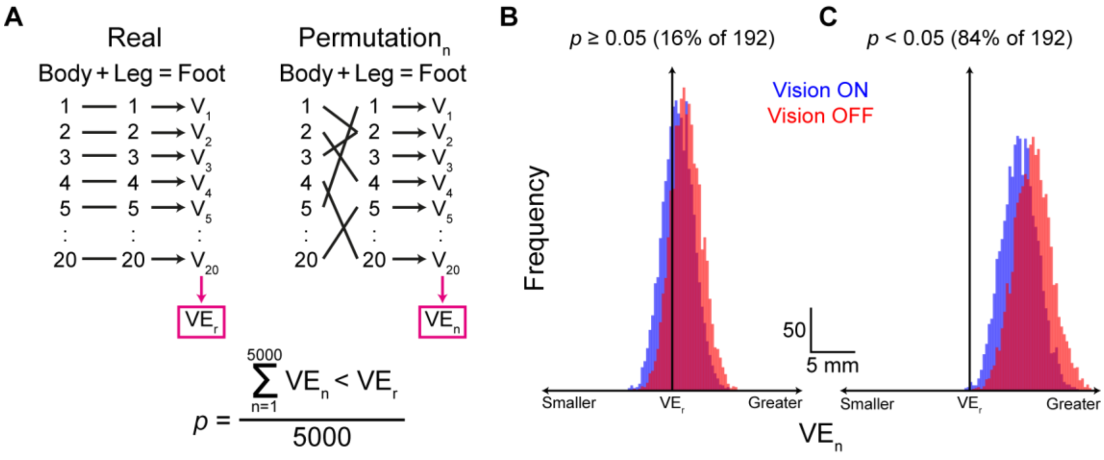

Figure 5.6. Randomisation tests. *A*: A permutation consisted of randomly coupling the 20 body and leg movements and computing the resulting foot placement variable error. The *p* value was the proportion of the 5000 permutations which returned a variable error which less than reality. *B*,*C*: Histograms of the distribution of four of the 192 randomisation tests. *B* shows right-sided steps to T1 from one subject; *C* shows the same condition from a different subject.

the randomisation tests returned. The distribution in Figure 5.6B corresponds to that predicted in Figure 5.1A, whereas the distribution in Figure 5.6C corresponds to Figure 5.1C. Note, a leftward shifted distribution (as in Figure 5.1B) was not observed in any randomisation test. Given this, the *p* value of the test was the proportion of permutations where foot placement variable error was less than the foot placement variable error in the real data. Figure 5.6B shows two randomisation tests (one from a condition with vision and one without from a single subject) which returned non-significant *p* values, whereas Figure 5.6C shows tests which returned significant *p* values (from the same conditions in a different subject as Figure 5.6B).

The vast majority (161/192; 84%) of randomisation tests returned a significant *p* value, as in Figure 5.6C. The remaining tests were not significant and appeared like Figure 5.6B. There was a roughly equal split in significant randomisation tests between conditions where vision was ON (83/161) and OFF (78/161). In Figure 5.6C the *p* value returned was less than or equal to 0.001, which was also the case the majority of permutation tests (111/192; 58%). In ten out of sixteen subjects, the permutation test was significant at the 0.05 level across all conditions.

5.5 Discussion

This chapter aimed to investigate the coordination between the body and leg movements used during a step. The results show that: (1) both a step-target-dependent body and leg movement is used to land the foot in the intended location; (2) the variation within the body and leg of steps to the same location are not random but are dependent and systematically co-vary; and (3) foot placement error increases when visual feedback is denied during a step. It will be argued that the body and leg are organised to reduce error in foot placement and that, although vision is important in guiding the foot to its target, the coordination between the body and leg is predominantly non-visual-feedback based.

5.5.1 Body and leg movements in steps to different targets

In this chapter subjects stepped as accurately as possible to target locations whilst the position of the hip and foot were tracked. The step was self-initiated and self-paced. The trajectory of the hip, approximating the body and CoM, was different depending on the step direction. This result mirrors the results of Chapter 4 where the whole-body CoM moved along a different trajectory when stepping to the same targets. The trajectory of the hip was similar to that of the whole-body CoM seen in Chapter 4 (compare Figure 5.3 and Figure 4.2B), suggesting that the hip was a reasonable proxy for the position of the body.

Unlike Chapter 4, this chapter aimed to investigate the coordination of the body and leg during a step that moved the foot to its target. To do this, the movement of the leg was measured as the foot relative to hip position. The results showed that the foot finished in a different location relative to the hip when stepping to each target. Therefore, in addition to a target-dependent body movement, a target-dependent leg movement was used during a step. This need not have been the case however. Conceivably, the same leg movement could have been used when stepping to each target, with the body's displacement being used to achieve the foot's location. For example if the leg movement in steps to T1 (directly forward) had been used in steps to more lateral targets (T2/3) then the body would have had to be displaced more laterally (rightward in Figure 5.3) than that observed to achieve the same foot location. Presumably the use of a target-dependent body and leg movement is a more optimal strategy for stability.

The stability of the body at foot-land, and thereby the ability of the body to be caught and for balance to be regained, depends on the placement of the foot relative to the motion of the body (Hof *et al.*, 2005). To achieve the same level of stability, the stepping foot needs to be placed further laterally with increasing lateral position and velocity of the body (Hof *et al.*, 2005). It is likely that, had the same leg movement been used in steps to all targets, the position and velocity of the body would have been inappropriate for the position of the foot and stability would have been threatened. Given that there seem to be optimal foot placement locations to catch the moving body successfully (Koolen *et al.*, 2012), it is possible that the target-dependent leg movement moved the foot into a location that was optimal for the state of the body. Given that no subject lost their balance during the experiment, the foot location was at least appropriate for the motion of the body.

5.5.2 Coordination between the body and leg movements during a step

The body and leg movements varied between repeated steps to the same location. Subjects started each step from the same chalk-marked location to minimise the variability in both the hip and foot position before a step. The trial-to-trial variability observed can therefore be attributed to the stepping movement itself and not due to a different starting position. The subjects were explicitly instructed to place their foot on the target as accurately as possible, which would have further reduced trial-to-trial movement variability. The coordination between the body and leg was investigated by examining the relationship between the variance of each movement in repeated steps to the same location.

Three forms of organisation between the variance of the body and leg were proposed, each of which had different predictions (see this Chapter’s Introduction and Figure 5.1). The organisation of the variances in Figure 5.1A and Figure 5.1B predicted the foot to land in a more variable location than the body and leg. The results clearly show this not to be true. Variability of the foot was no different from the body and leg even when visual feedback was denied during the step, and was less than the body in steps with visual feedback (Figure 5.4B). This level of variability is far less than that expected if the variances of the body and leg summed, as per Figure 5.1A and Figure 5.1B, and seemed consistent with the prediction of Figure 5.1C (dependent variances which were negatively correlated).

Next the trial-to-trial organisation within the variance of the body and leg movements was examined. Again, different forms of organisation predicted different relationships between the body and leg vectors depicted in Figure 5.1. The results clearly showed that the body and leg movements were not coupled in a random manner, as the confidence ellipses in Figure 5.5 did not overlap the centre of the figure (where $r = 0$). Rather, the body and leg vectors were systematically oriented oppositely to one another both when visual feedback was allowed and denied during a step. This was verified by examining the angular difference between the leg and both the hip vector, as measured in this Chapter, and whole-body CoM vector, as measured in Chapter 4. This confirmed that a body movement that deviated in one direction was coupled with a leg movement that deviated in the opposite direction, or *vice versa*. This strongly demonstrated that the variance between the body and leg was negatively correlated, as predicted by Figure 5.1C. The body and leg movements thereby compensated for each other and summed to reduce foot placement error.

Randomisation tests were also performed to further test the predictions in Figure 5.1. The randomisation test comprised of randomly coupling the body and leg movements in steps to the same target and asked whether the resulting foot placement was more or less variable than that seen in the real data (when the body and leg were coupled correctly). In a minority of cases, randomly coupling the body and leg movements did not significantly alter the variability in the foot's position (Figure 5.6B), as was predicted in Figure 5.1A. This suggested that, in these steps, the body and leg were not specifically coupled to one another but there was a degree of randomness in their relationship. This would perhaps be expected given that movement results from noisy neural signals (Faisal *et al.*, 2008). However, in the vast majority of cases the test indicated that the variability in foot placement was greater than reality when the body and leg were randomly coupled (a rightward shifted distribution, like in Figure 5.6C). This result aligned with the prediction of Figure 5.1C and was not consistent with those in Figure 5.1A and Figure 5.1B. This showed that, more often than not, the coupling of body and leg movement was important and that the body and leg movements used were specific to one another in order to reduce foot placement variability. Moreover, for the majority of subjects randomisation tests were always significant suggesting that the specificity of the coupling between the body and leg movements was important and the prevailing strategy.

Together, the results suggested that the body and leg co-varied to reduce foot placement error. For example, if the body had moved further in one direction than average, a leg movement that was further than average in the opposite direction was used. The variance of the body and leg were therefore dependent and summed to cancel each other in order to maintain foot placement accuracy. The finding that the body and leg were organised to co-vary agrees with studies of locomotion where lower-limb joint angles have been demonstrated to co-vary (Winter, 1984; Ivanenko *et al.*, 2005; Hicheur *et al.*, 2006; Dominici *et al.*, 2007; Ivanenko *et al.*, 2008). If this covariation resulted from passive biomechanical effects it would be expected to be present in all gaits (Ivanenko *et al.*, 2008). However, whilst it is true of many gaits, it can be violated by, for example gaits involving stooping to the floor to pick up an object or the locomotion of toddlers (Ivanenko *et al.*, 2005; Dominici *et al.*, 2007; Ivanenko *et al.*, 2008). This suggests that the covariation of the body and leg here, and between the joints of the leg in studies of locomotion, is due to active control from the central nervous system. One potential source of this active control was from visual feedback during the step.

5.5.3 Visual feedback reduces foot placement error

Foot placement accuracy and precision decreased when visual feedback was denied during the step, as shown by significant increases in absolute, constant and variable error (Figure 5.4A). Vision was therefore used during a step to guide the foot towards its target. These results agree with a similar precision stepping study which demonstrated increases in foot placement error when visual feedback was denied during the step (Reynolds & Day, 2005b). Despite this, the importance of visual feedback during a step is often neglected. Recently, the idea of a ‘critical phase’ for visual information in locomotion has been suggested where vision of the future foot target must be available from mid-stance of the previous step until foot-lift of the ‘current’ step (Matthis *et al.*, 2017). This implies that visual feedback is of no use during the ‘current step’. Whilst the present results and those of Reynolds and Day (2005b) are not in disagreement with the concept of a ‘critical phase’, they do reiterate that visual information *can* be of use in guiding the foot during the ‘current’ step. The importance of online visual guidance of the foot is likely to be greater when the environment demands it, for example walking over rocky terrain where inaccuracy and imprecision in foot placement is of greater consequence to balance.

5.5.4 Visual feedback and coordination

Both the variability of the hip and foot-relative-to-hip positions were unaffected by the denial of visual feedback during the step (Figure 5.4B). The increased variability in foot position without vision cannot therefore be accounted for by a simple effect of vision on either the body or leg movement. Rather, the loss of vision seemed to cause a slight imprecision in the coupling between the body and leg movements. Despite this, a tight coupling between the body and leg movements was still apparent without vision, as seen by the lack of effect of vision on the angular difference between hip and leg vectors (Figure 5.5) and comparable results in the randomisation tests in conditions with and without vision (Figure 5.6B and Figure 5.6C). Generally, the body and leg movements were tightly coupled regardless of the presence or absence of visual feedback during the step. The coordination of the body and leg with and without vision seemed remarkably similar. If visual feedback was not a major contributor to the coordination of a step in the present results, what could have been? Non-visual sensory information could have been used to continually guide movement and ensure an accurate foot placement.

The vestibular system provides information about the acceleration of the head-in-space and contributes to knowledge of where the body is. Vestibular information is known to be able to update movement so could potentially have been used during a step in the present experiment. For example, when performing a goal-directed body tilt, perturbation of vestibular afferents causes the body's trajectory to change showing that vestibular information is incorporated online into the movement (Day & Reynolds, 2005). Further, the trajectory of the arm on the body can be updated by vestibular information as shown by changes to its trajectory after either artificial perturbation of vestibular afferents or whole-body and head rotation (Bresciani *et al.*, 2002a; Bresciani *et al.*, 2002b; Bresciani *et al.*, 2002c; Smith & Reynolds, 2017). Whilst these studies clearly show that vestibular information can update body and arm trajectory, it is less clear that the same is true of the lower limb during a step. What is clear is that vestibular information can influence locomotion. For example, Fitzpatrick *et al.* (1999) asked subjects to walk 4m towards a floor-bound target with their eyes closed. In contrast to control trials, the subjects veered off course when vestibular afferents were perturbed by an electrical stimulus. Similarly, Bent *et al.* (2002) instructed subjects to initiate gait with their eyes closed whilst their vestibular afferents were perturbed with a similar electronic stimulus. Again, the walking trajectory was altered when vestibular afferents were perturbed. However, in both cases, although the perturbation started before the first step, no effect was seen until several steps into gait. Therefore, although vestibular information is able to influence the trajectory of the body and upper limb, it is not clear whether vestibular information could have been used in a single step here to preserve movement accuracy.

Another source of sensory feedback is proprioception, which provides the brain with information about where the body is in space and the relative movement of the limbs. Online proprioceptive information is known to be useful for the control of walking as the loss of proprioceptive feedback from the neck down makes walking extremely difficult (Cole & Sedgwick, 1992). Additional loss of neck proprioceptive feedback renders walking nigh on impossible, even with continuous visual monitoring of movement and substantial conscious effort (Forget & Lamarre, 1987; Cole & Paillard, 1995). Verschueren *et al.* (2002) asked subjects with normal proprioceptive function to walk along a memorised path without vision whilst their proprioceptive afferents were perturbed by muscle vibration. Vibration of lower limb muscles altered joint displacement and thus their gait pattern, showing that online proprioceptive information was used to control locomotion. Additionally, Sorensen *et al.* (2002) asked subjects to step over an obstacle whilst vibration was applied to their stance-side

Achilles tendon. Their results showed that vibration resulted in alterations to the CoM trajectory during the step and further demonstrated that proprioception can influence ongoing stepping movement.

Presumably, either independently or in concert, vestibular and proprioceptive information could have provided a powerful tool to update the ongoing movement when visual information was not available. For example, one or both of the vestibular and proprioceptive senses could have detected if the body was moving too far in one direction and could have relayed this information to the brain in order for the leg to move further in the opposite direction and preserve foot placement accuracy.

5.5.5 Limitations

Whilst the present results are in agreement with those of Reynolds and Day (2005b) there are some subtle, but potentially important, differences. These can be summarised as the present results displaying much larger foot placement error in all conditions and a lesser effect of vision here than in Reynolds and Day (2005b). In their paper, the authors report that absolute and constant error approximately doubled and variable error increased by ~33% with the denial of visual feedback. In steps with vision, absolute, constant and variable error were approximately 10, 5 and 9 mm respectively. In comparison, the absolute, constant and variable error of steps with vision in the present results was much greater (30, 27, 14 mm, respectively). Perhaps due to this raised level of baseline error, the effect of vision was much less here than in Reynolds and Day (2005b), with only an approximate 7% increase in each of absolute, constant and relative error. Whilst small, the effect was still large enough to reach statistical significance for all measures of foot placement error.

Why was this? One reason could be that the step targets in this experiment were smaller than those in Reynolds and Day (2005b) and not shaped like the foot. The perceived requirement of foot placement precision could therefore have been less in the present experiment. To try to avoid this each subject was required to define an accurate step prior to the experiment placing their foot on each target without time constraints. The foot’s position was allowed to be adjusted until the subject was happy that it reflected an accurate step and subjects were explicitly told to attempt to land their foot in this way for all subsequent experimental trials. Foot placement was compared to this ideal foot placement for the calculation of absolute and constant error. It is possible that subjects forgot where their ideal step was placed over the course of the experiment, making the intended target ambiguous and enhancing foot placement error. An argument against this is that using the target light position as the intended target did not reduce the magnitude of absolute and constant foot placement error (data not shown), suggesting that ambiguity in the intended target was not a problem. This does not rule out that the variability of the foot could have been enhanced by an ambiguous target location however. It is also possible that significant differences between vision ON and OFF could have been seen in the coordination of the body and leg movements (for example Figure 5.5) had the effect of visual occlusion been greater.

5.6 Conclusion

This chapter aimed to investigate how the movements of the body and leg were coordinated during a step. It is concluded that the body and leg are organised to co-vary in order to reduce foot placement error. The body and leg movements used in a step are tightly coupled to achieve a precise foot placement. Whilst vision is used to guide the foot towards its target, the coordination between the body and the leg seems to be achieved through non-visual mechanisms.

6 Chapter 6: The effect of cerebellar dysfunction on the coordination of a step

6.1 Abstract

Balance is relinquished when a foot is lifted from the ground to take a step and the body begins to fall under the influence of gravity. At the same time, the foot swings and aims to land in a location that enables the body to be caught and balance to be regained. In order to land the foot on its intended target, the movement of the body and leg must be coordinated. The cerebellum may play a critical role in this process as it has previously been implicated in the coordination of movement. Here, the effect of cerebellar dysfunction on the coordination between the body and leg during a step is investigated. The performance of a goal-directed step was compared between individuals with a genetically determined and pure form of cerebellar degeneration, spino-cerebellar ataxia type 6 (SCA6), and sex- and age-matched healthy controls (HC). SCA6 subjects stepped with increased foot placement error in comparison to HC. This was in part due to increased variability in both the body and leg movements used during a step in SCA6. However, the increased foot placement error could not be explained by increased movement variability alone. Instead, the coupling between the body and leg was less precise in SCA6 subjects than HC, resulting in a disproportionate increase in foot placement error in SCA6. Despite this impaired coordination, the body and leg movements used by SCA6 subjects were still organised to minimise foot placement error, even when visual feedback was denied during the step. However, both the increased variability of movement and impaired coordination seen in SCA6 subjects could be due to enhanced movement execution error. Therefore, it remains to be seen whether ataxia results from impaired coordination in cerebellar dysfunction.

6.2 Introduction

The experiments in this thesis so far have investigated the control of movement and balance of a step in young, healthy subjects. This population generally does not have a problem with maintaining balance. In contrast, older individuals and people with neurological disorders frequently lose balance, especially during activities such as stepping and walking (Robinovitch *et al.*, 2013). To better understand movement and balance, and thereby falls, populations with balance difficulties need to be studied. This chapter aims to extend the work in Chapter 5 (the coordination between the body and leg during a step) into a population with significant movement and balance difficulties: spino-cerebellar ataxia type 6 (SCA6).

SCA6 is a genetically determined (autosomal dominant) degenerative neurological disorder that impacts the cerebellum (Gomez *et al.*, 1997; Yang *et al.*, 2000; Mantuano *et al.*, 2003; Craig *et al.*, 2004). The cerebellum is a neural structure located in the hindbrain which receives inputs from multiple sensory channels, the brain stem and cerebral cortex and outputs signals to the brain stem and thalamus in order to influence movement (Gray *et al.*, 1995; Clarke & Lemon, 2016). SCA6 causes atrophy of the cerebellar cortex and nuclei (Stefanescu *et al.*, 2015) with profound Purkinje cell loss but little or no damage to extra-cerebellar areas (Gomez *et al.*, 1997; Stevanin *et al.*, 1997; Solodkin & Gomez, 2012), even after many years of disease (Stevanin *et al.*, 1997; Jacobi *et al.*, 2015). This makes SCA6 an ideal model with which to study the role of the cerebellum in human movement.

A classical sign of cerebellar damage is movement ataxia, literally meaning movement ‘without order’. This can be debilitating and lead to difficulties maintaining standing balance and an increased risk of falling (Fonteyn *et al.*, 2010). Ataxia is perhaps most striking when an individual with cerebellar damage walks. Cerebellar gait has been described as appearing ‘drunken’ due to its unstable, stumbling and erratic nature resembling that of someone who is intoxicated. Ninety percent of SCA6 patients display gait ataxia as an initial symptom (Solodkin & Gomez, 2012). Studies of cerebellar gait have noted that the timing and trajectory of limb movements are more variable than normal gait, leading to increased foot placement variance and erratic walking paths (Ilg *et al.*, 2007; Serrao *et al.*, 2012; Ilg & Timmann, 2013; Hoogkamer *et al.*, 2017). Individuals with SCA6 display increased variability in step width and length (Rochester *et al.*, 2014), reflecting greater foot placement variance. However, the origin of gait ataxia still remains unclear.

In order to take a step during gait, a foot must be lifted from the ground. In doing so, balance is temporarily relinquished and the body begins to fall under the influence of gravity. During the step the foot swings and aims to land in a location that enables the body to be caught and balance to be regained. The movement of the body and leg during the step must be coordinated to land the foot in its intended target. This gives rise to three potential sources of movement error from which cerebellar gait could result: error in body movement, leg movement or the coordination between the body and leg. What aspect of movement is impaired in cerebellar gait?

The term ataxia implies that cerebellar gait results from a lack of coordination and thereby that the cerebellum is directly involved in the coordination of movement. However cerebellar gait ataxia need not originate from impaired coordination. In Chapter 5, it was demonstrated in healthy, young subjects that the movement of the body and leg during a step is variable but coordinated in a manner that reduces foot placement error. In cerebellar dysfunction, it could be that the movement of the either the body, leg or both have increased variance but the coordination between the body and leg is normal. As a result, the foot would land in a more variable location yet the body and leg would still be organised to minimise foot placement error, like that seen in Chapter 5. On the other hand, the coordination between the body and the leg could be impaired in cerebellar dysfunction. This would manifest as a disproportionate increase in foot placement error above any increase in body or leg movement variability. If the lack of coordination was severe, there could even be no systematic organisation of the body and leg, with the variance in each being independent, leading to greatly increased foot placement error.

6.2.1 Hypothesis

This chapter aims to investigate the effect of cerebellar dysfunction on the coordination of a step. To do this the body, leg and foot movements during a step are compared in subjects with and without cerebellar dysfunction. It is hypothesised that foot placement error will be increased in subjects with cerebellar dysfunction. It is asked whether this is due to increased error in body movement and leg movements, a dyscoordination between the body and leg during a step or both increased error in and dyscoordination between the body and leg.

6.3 Methods

6.3.1 Sample size estimation

Few experiments have studied walking or stepping in SCA6, with one potentially relatable study failing to report statistics from which effect sizes can be estimated (Rochester *et al.*, 2014). Similarly, there are few reported data sets on goal-directed stepping in cerebellar diseased populations as a whole. Therefore, reliably estimating a required sample size is difficult for the present experiment. However, two somewhat relatable studies were conducted by Morton and Bastian (2003) and Ilg *et al.* (2008). In both experiments, subjects with and without cerebellar dysfunction were required to step accurately to a target with their weight supported during the movement and foot placement error was measured. The reported means and standard deviations of foot placement error (control v cerebellar) in each study are 16.0±5.6 v 30.0±18.4 mm (Morton & Bastian, 2003) and 14.3±2.6 v 19.6±4.3 mm (Ilg *et al.*, 2008), which equates to an effect of cerebellar dysfunction sized 0.87 and 1.50, respectively (Cohen's *d*; see Equations 2.2 and 2.3 in Chapter 2.6). Based on these estimates of effect size and the use of a two-tailed independent-samples *t*-test with the chance of type I error (α) set at 0.05 and the chance of type II error (1-β) set at 0.1, the required sample size in each of the SCA6 and control groups in the present experiment ranges between 11 (for the data from Ilg *et al.*, 2008) and 29 (for the data from Morton & Bastian, 2003). Two factors render these sample size estimates likely to be overly conservative: firstly, the aforementioned studies (unlike the present experiment) used heterogeneous cerebellar diseased populations, which likely increased between-subject variability in the cerebellar group and as a result reduced the reported effect size; and secondly, the removal of balance constraints by allowing weight to be supported during the step would have simplified the task and likely reduced the effect of cerebellar dysfunction on performance.

6.3.2 Subjects

Ten participants (4 female) with spinocerebellar ataxia type 6 (SCA6) were recruited from the Ataxia Centre at the National Hospital of Neurology and Neurosurgery and completed the experiment. Ten sex- and approximately age-matched healthy control (HC) subjects were recruited from the local population via an advertisement. Inclusion criteria were that all subjects: (1) were between the ages of 18 and 80; (2) were proficient in the English language; (3) had no neurological or orthopaedic conditions (other than SCA6); (4) were not pregnant; (5) were not registered blind; (6) were able to complete the stepping task without falling; and (7) were competent to provide consent. Two SCA6 subjects were excluded from the current analysis due to an inability to complete the experimental task: one subject frequently lost balance during the stepping task; another subject expressed unease at vision being occluded during the step and requested to complete the remainder of the experiment with vision available in all steps. Thus, eight SCA6 patients are included in the analysis. There was no significant difference in age between the remaining SCA6 subjects and HC group (SCA6 v HC (mean±SD): 65±7 v 64±7; $p > 0.05$). On average, SCA6 patients were taller and weighed more than HCs (1.77±0.11 v 1.66±0.05 m; 82.0±12.1 v 68.5v7.3 kg; both $p < 0.05$), but no differences were present between groups in body mass index (BMI: 26.3±2.9 v 24.8±2.8; $p > 0.05$). SCA6 subjects scored 6.9±3.1 out of 40 on the Scale for the Assessment and Rating of Ataxia (SARA; Schmitz-Hübsch *et al.*, 2006). The experiment was approved by the National Research Ethics Service Committee.

6.3.3 Protocol

The experimental protocol was broadly the same as previously described in Chapters 4 and 5. Subjects were required to step to the location of a floor-bound target as accurately as possible. Before the step, each subject began with the feet facing forward and separated by 15 cm (Figure 6.1A). This starting position was chalk-marked to ensure a consistent starting location. An audible beep alerted the subject that a trial was to begin and, after a short random delay, a target illuminated. The target illumination acted as a cue for the subject to initiate a step to its location in their own time. An accurate stepping-foot placement was emphasised as of paramount importance. No instruction was given as to where to land the trailing foot, except that subjects were encouraged to bring their trailing foot alongside the stepping foot such that their stance was similar to that prior to the step. Subjects self-defined an accurate step by placing their foot over each target without time or movement constraints prior to the experiment. The position of the foot over each target was recorded and foot placement accuracy was compared to this ideal foot placement in all experimental trials. An accurate foot placement trial was repeated if the subject or experimenter felt it necessary.

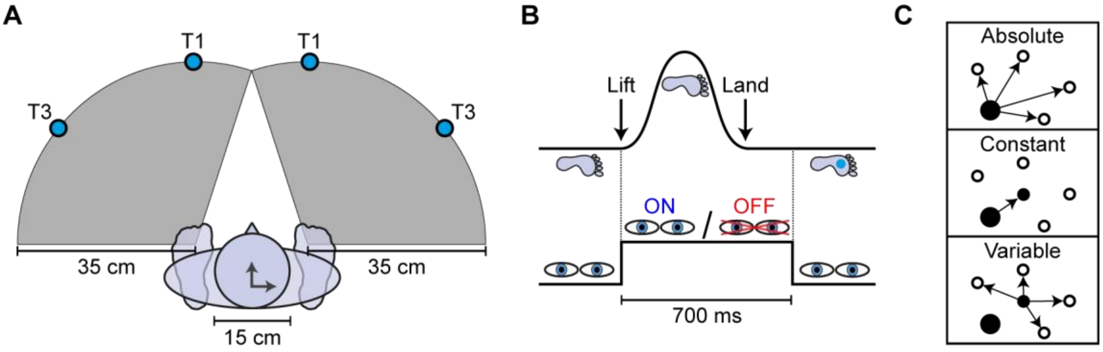

Figure 6.1. Experimental set-up and measures of error. *A*: Target lay-out. Two targets (T1, T3) were placed 35 cm from each foot. *B*: Timing of visual occlusion. *C*: Absolute, constant and variable foot placement error (Reynolds & Day, 2005b). Unfilled circles show the foot's position, the smaller filled circled shows the mean foot position and the larger filled circle shows the ideal accurate foot position.

A reduced set-up was used here in comparison to Chapters 4 and 5 due to concerns that 240 steps may cause SCA6 and older HC subjects to fatigue, to the detriment of their stepping performance. To try and avoid this, subjects completed fifteen steps (rather than twenty) to each of four (rather than six) targets. The targets were placed 35 cm from the stepping foot in two directions (T1 and T3 from Chapters 4 and 5; Figure 6.1A). The required step length was constant across all targets. As in Chapter 5, vision was occluded in 50% of randomly selected experimental trials from the instant of foot-lift for 700 ms (Figure 6.1B). This delay was adequate to occlude vision until after the stepping-foot landed in all trials. This reduced set-up resulted in each subject completing a total of 120 trials.

Prior to the ideal foot placement and experimental trials, subjects completed two thirty-second trials of quiet standing to quantify stance instability. These trials were completed with the medial borders of the feet touching and eyes closed.

6.3.4 Apparatus

The step targets were circular (2.5 cm diameter) and illuminated via electroluminescent paper (see Chapter 2.2.1 for further details). The stepping movement was measured using a whole-body set-up (the same as that described in Chapter 4). This consisted of fifty-two infrared-emitting diode markers being attached to each subject. Marker locations were recorded by three motion capture cameras (Coda cx-1; Charnwood Dynamics, Leicestershire, UK) and sampled at 100 Hz. The markers were attached via thirteen rigid clusters, each containing four markers, and placed on the following segments: head, back, pelvis, feet, upper and lower arms and upper and lower legs (Figure 2.2). The locations of the clusters were associated with landmarks on the body by a pointer to create virtual marker locations (Table 2.1). A thirteen-segment model of the body was then created using Visual 3D software (C-Motion; Germantown, MD, USA) and the location of the whole-body’s CoM and its inertia estimated (see Chapter 2.2.2 for further details). The subjects initiated a step with each foot over a force platform, which was embedded within the floor. Ground reaction forces were sampled at 1000 Hz. The centre of pressure (CoP) was calculated from the force plates (see Chapter 2.2.3.1 for further details). PLATO spectacles were used to occlude vision during a step (see Chapter 2.2.4 for details). The spectacles were triggered to occlude vision when the vertical force beneath the stepping foot went below 10 N, which provided a precise signal of foot lift (see Chapter 2.2.3.3 for details). All subjects also wore a harness that was attached to the ceiling to prevent a fall in case of a loss of balance. The harness did not restrict the stepping movement.

6.3.5 Data analysis

The timing of foot-lift and foot-land was calculated offline with the force-plate methods described in Chapter 2. The instantaneous position of the foot was the location of the first metatarsal virtual marker, the position of which was determined by a cluster of four markers on the stepping foot (Table 2.1). The instantaneous position of the hip was the location of the posterior superior iliac spine virtual marker, the position of which was determined by a cluster of four markers on the pelvis (Table 2.1). As in Chapter 5, the movement of the leg was considered the foot-relative-to-hip position (Equation 5.2).

Foot placement error was evaluated with three different measures: absolute, constant and variable error (Schmidt & Lee, 1999). Absolute error was the Euclidean distance between the stepping foot when it landed and the ideal stepping foot placement, reflecting step accuracy. Constant error was the Euclidean distance between the mean stepping foot position when it landed and the ideal stepping foot placement, reflecting step bias. Variable error was the Euclidean distance between the foot position when it landed and the mean stepping foot position when it landed, reflecting step consistency. These three measures are depicted in Figure 6.1C.

As in Chapter 5, the variability around the mean of the body and leg movements was examined to investigate coordination. The mean hip or foot-relative-to-hip positions in a condition were subtracted from the trials in the same condition. The angular difference between the angular displacement of the body and leg vectors was calculated, as in Chapter 5 (see Figure 5.1 for details). Variability of the body and leg was calculated in the same manner as foot placement variable error.

Stance instability was quantified as the standard deviation of the CoP velocity in each of the medio-lateral and antero-posterior directions across the quiet standing trials. A previous study found no differences between CoP and kinematic measures (such as 7th cervical vertebra position) in quantifying stance instability of SCA6 patients and healthy controls (Bunn *et al.*, 2013). As such, the CoP was used for simplicity. Given that subjects started each trial stood still and that stance instability is increased in SCA6 subjects, it was possible that SCA6 subjects would start each step from a more variable location. To evaluate this the variability of the body and foot was also examined before the step. The time-point used for this was 1 s into the trial, which was shortly before the stepping target illuminated and before the initiation of any stepping movement.

6.3.6 Statistical analysis

For statistical analysis, left-sided steps were reflected about the laboratory antero-posterior axis so that they appeared as right-sided steps. The effect of between-subject (group: HC/SCA6) and within-subject (side: left/right; direction: T1/T3; vision: ON/OFF; time-point: pre-step/foot-land) factors on univariate variables was analysed by repeated-measures ANOVA. Greenhouse Geisser corrections were used when the assumption of sphericity was violated. For angular data, between-subject (group) differences were analysed by two-sample Hotelling's tests (analogous to the linear independent samples *t*-test) and within-subject differences (side/direction/vision) were analysed by paired-sample Hotelling's tests (analogous to the linear paired-samples t-test; Batschelet, 1981; Zar, 2010).

As in Chapter 5, randomisation tests were performed to analyse the effect of the coupling between the body and leg movements used to land the foot on its intended target. The procedure was the same as that described in Chapter 5.3.5 and Figure 5.6A. In brief, the body and leg movements used in steps within the same condition were randomly coupled and the resulting foot placement computed using Equation 5.1. The foot placement variable error was then calculated for this permutation and compared to the observed foot placement variable error from the real data (when the body and leg movements were not randomly coupled, but as they were in the observed data). Each randomisation test consisted of 5000 permutations of the data. Each random coupling of the body and leg was performed independently and with replacement. The *p* value of the randomisation test was the proportion of the permuted variable error that was less than the real permuted variable error. Randomly coupling the data made the variance in the body and leg movements independent of each other. Thereby, a non-significant *p* value (≥ 0.05) would indicate that the coupling between the body and leg movements was no better than random and therefore the variances were independent. A significant *p* value (< 0.05) would indicate that the coupling between the body and leg movement was not random and therefore the variances were dependent.

The effect of each factor (group, side, direction and vision) on the results of the randomisation tests were also analysed. Between-subject (group) differences were analysed by the Mann-Whitney *U* test, which is a non-parametric analogue of the independent samples *t*-test. Within-subject differences (side, direction and vision) were analysed by Wilcoxon's Signed-Rank test, which a non-parametric analogue of the paired samples *t*-test. The data inputted to these tests was the number of significant randomisation tests in a factor for each subject, which ranged from zero to four and was not normally distributed. For example, if all 4 (2 sides x 2 directions) randomisation tests with vision ON were significant for one subject a value of 4 would be inputted to the test, whereas if 1 was significant and 3 non-significant a value of 1 would be inputted, and so on. This was calculated for each level of the factor for each subject and inputted to the relevant statistical test.

Statistical significance was considered at the level of $p < 0.05$ for all tests. Bonferroni adjustments were used to correct for multiple comparisons.

6.4 Results

6.4.1 Stance instability

Figure 6.2A shows the trajectory of the CoP during a representative quiet stance trial from a typical SCA6 subject and their sex- and age-matched HC. As can be seen, the range of movement of the CoP under the feet was much greater in the SCA6 subject than HC as they attempted to maintain standing balance. Figure 6.2B shows the stance instability for each group. The standard deviation of CoP velocity was much greater in SCA6 subjects in comparison to HCs (group: F(1,16) = 26.0, $p < 0.001$; Figure 6.2B), reflecting the greater instability in SCA6. Both groups were as stable in the medio-lateral as the antero-posterior direction, as shown by the lack of significant effect of direction (F(1,16) = 2.9, $p = 0.108$) or group by direction interaction (F(1,16) = 0.2, $p = 0.648$).

6.4.2 Foot placement error

Figure 6.3 shows the body (hip) and leg (foot-relative-to-hip) movements used during steps with vision to each of the right-sided targets and the position of the

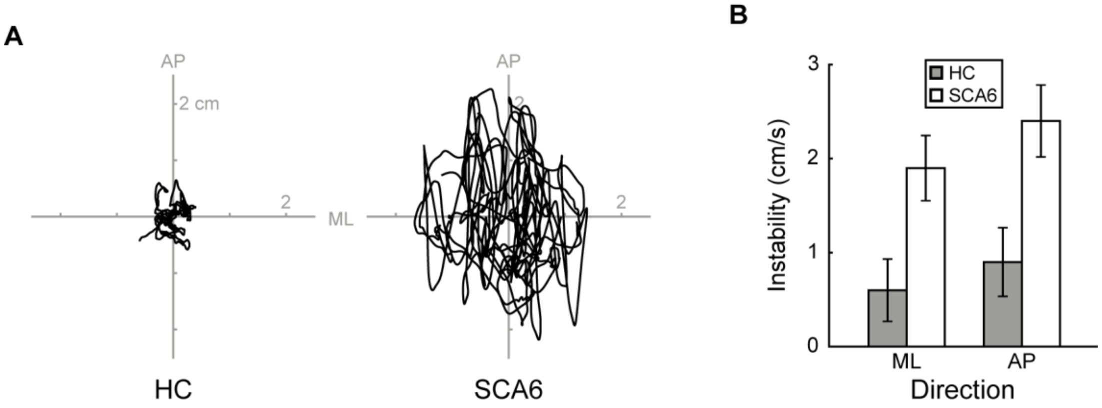

Figure 6.2. Stance instability. *A*: CoP trajectory during 30 s standing with the feet together and eyes closed from a representative SCA6 subject (69 year-old male, SARA: 5.5) and their sex- and age-matched healthy control (HC; 69 year-old male). *B*: Medio-lateral (ML) and antero-posterior (AP) instability (SD of CoP velocity) for each group. Error bars are 95% confidence intervals of the group mean.

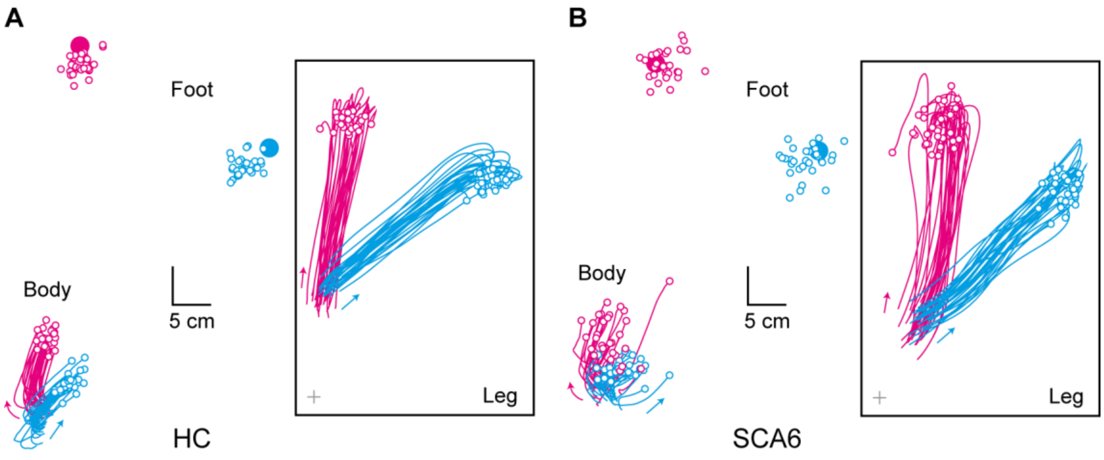

Figure 6.3. Trajectory of the body and leg during a step. Right-sided steps with vision ON to T1 (pink) and T3 (blue) are depicted from a representative SCA6 subject (*B*, SARA: 9.5) and their sex- and age-matched healthy control (HC, *A*). Both subjects are 51 year-old females. The unfilled circles are the position of the body (hip), foot and leg (foot-relative-to-hip) when the stepping foot landed. The large, filled circles are the ideal accurate foot position. Body and leg traces are from foot-lift to foot-land. The arrows point in the direction of movement over time. In the leg insets, the grey '+' is the instantaneous position of the body. The main figures and insets are on the same scale.

stepping foot when it landed in a representative SCA6 subject (Figure 6.3B) and their sex- and age-matched HC (Figure 6.3A). In this example, it can clearly be seen that the spread of foot placement locations was much greater in the SCA6 than the HC subject, reflecting increased foot placement error. Figure 6.4A shows the effect of group on foot placement error. SCA6 subjects stepped with greater absolute, constant and variable foot placement error than HCs (F(1,16) = 6.9, *p* = 0.018; F(1,16) = 5.6, *p* = 0.031; F(1,16) = 12.4, *p* = 0.003; respectively; Figure 6.4A). A significant effect of vision was seen in absolute (F(1,16) = 5.5, *p* = 0.032) but not constant or variable foot placement error (F(1,16) = 2.5, *p* = 0.135; F(1,16) = 0.4, *p* = 0.526, respectively). For absolute error, both HC and SCA6 subjects tended to step with increased error when vision was OFF but this did not reach statistical significance when groups were tested separately (HC (mean±SD): 22.3±16.9 v 25.0±14.8 mm, *p* = 0.051;SCA6: 41.8±16.9 v 44.7±14.8 mm, *p* = 0.238). No effect of side or direction, nor any interactions, were seen in absolute and constant error (all F(1,16) < 4.2, *p* > 0.05). A significant group by side interaction was seen for variable foot placement error (F(1,16) = 5.0, *p* = 0.039). *Post-hoc* tests revealed that variable foot placement error was greater in left- than right-sided steps of SCA6 subjects (24.5±6.2 v 21.4±4.6 mm, *p* = 0.008) but not in HCs (*p* = 0.996).

6.4.3 Segmental variability

In Figure 6.3 it can be seen that the body and leg movements used during a step were variable between steps to the same target location in both HC and SCA6 subjects. In this example it appears the trajectory of both the body and leg was generally more variable in the SCA6 (Figure 6.3B) than the HC subject (Figure 6.3A). This was also true of the HC and SCA6 groups. Figure 6.4B shows the variability of each of the body, leg and foot placement at foot-land in each group. SCA6 displayed greater variability across all segments (group: F(1,16) = 15.6, $p = 0.001$). However, there was a group by segment interaction (F(2,32) = 3.5, $p = 0.042$). *Post-hoc* tests revealed that the source of this interaction was the foot being less variable than the leg movement in HCs ($p = 0.016$). In contrast, the foot was equally as variable as the leg in SCA6 patients ($p > 0.5$). The body was equally as variable as the leg and foot in HC subjects and equally as variable as the foot in SCA6 subjects (all $p > 0.280$).

As shown in Figure 6.2, SCA6 subjects were more unstable during quiet stance than HCs. Did this mean that the body started the step from a more variable location in SCA6? To investigate this, the variability of the body was compared before and after the step (pre-step v foot-land). Figure 6.4 shows this data for each group and also for the variability of the foot at the same time-points. The starting body position was more variable in SCA6 subjects than HCs (group: both F(1,16) = 21.0, $p < 0.001$), as expected due to their increased instability. The variability of the body increased by the time the foot landed in both SCA6 and HC subjects (time-point: F(1,16) = 89.2, $p < 0.001$) and this increase was not different between groups (group x time-point: F(1,16) = 1.6, $p = 0.219$). The foot also started in a more variable location in SCA6 subjects (group: F(1,16) = 12.6, $p = 0.003$) and variability increased by the time the foot landed in both SCA6 and HCs (time-point: F(1,16) = 135.2, $p < 0.001$).

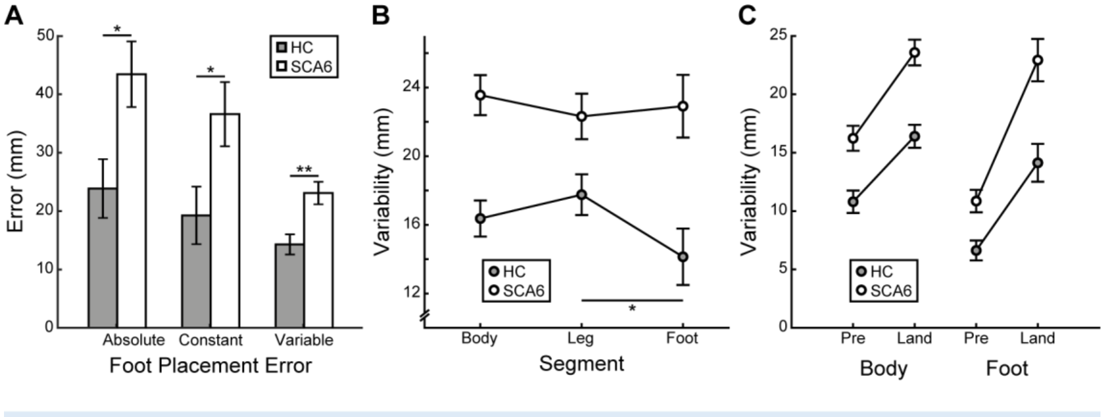

Figure 6.4. Effect of cerebellar dysfunction of step performance. *A*: Group foot placement error. *B*: Group variability of the body (CoM), leg (foot relative to hip) and foot at foot-land. Error bars are standard errors of the group mean. *C*: Variability of the body and foot before the step (pre) and at foot-land (land). *$p < 0.05$; **$p < 0.01$

However, there was a significant group x time-point interaction (F(1,16) = 7.4, p = 0.015) whereby SCA6 foot variability increased more than HCs over time. This interaction suggested the body and leg movements were not as tightly coupled in SCA6 subjects, leading to a disproportionate foot placement error.

6.4.4 Organisation of the body and leg movements

6.4.4.1 Angular difference

Figure 6.5 shows the difference in orientation of the body and leg vectors in each group in steps with vision ON and OFF. As seen previously in healthy young subjects (Chapter 5), the vectors were oppositely directed in HC and SCA6 subjects both with and without visual feedback during the step. This was true both when using the hip and CoM as a marker of the body's position. No differences were present in mean angles between the groups (all $T^2(1,15) < 1.4$, $p > 0.1$) or between steps with and without vision (all $T^2(2,8) < 9.3$, $p > 0.5$).

6.4.4.2 Randomisation tests

The distributions returned by the randomisation tests resembled those in Figure 5.6B and Figure 5.6C of Chapter 5. A significant p value was returned in the vast majority of the randomisation tests, both for HC and SCA6 subjects (HC: 75/80, 84%; SCA6: 48/64, 75%). However, relatively fewer randomisation tests reached significance in SCA6 than HCs (group: U = 17.5, p = 0.043). There was no effect of vision on the randomisation test significance in either HCs or SCA6 (vision (ON v OFF): 39/40 v 36/40, Z = 1.7, p = 0.083; 24/32 v 24/32, Z = 0.0, p > 0.99, respectively). Significant randomisation tests were also split equally across step directions in SCA6

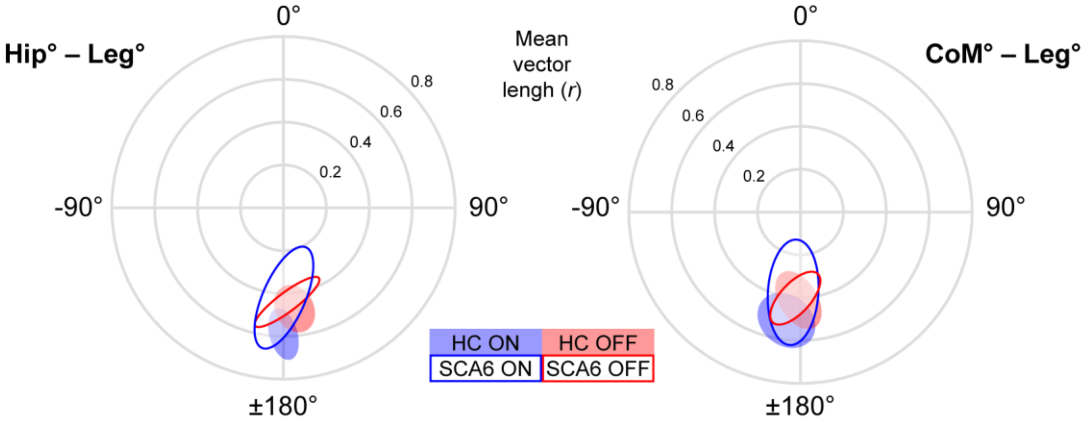

Figure 6.5. Co-variation of body and leg movements. Angular difference between the foot-relative-to-hip (leg) and either the hip (*left*) or centre of mass (CoM; *right*) vectors. Ellipses are 95% Hotelling's ellipses of the group mean either with vision ON (blue) or OFF (red).

(T1 v T3: 24/32 v 24/32, $Z = 0.6$, $p = 0.564$) and HCs (38/40 v 37/40, $Z = 0.4$, $p = 0.891$) and step side (left v right: SCA6: 24/32 v 24/32, $Z = 0.6$, $p = 0.564$).

6.5 Discussion

This chapter aimed to investigate the effect of cerebellar dysfunction on the coordination of a step. As expected, foot placement error was increased in subjects with cerebellar dysfunction (SCA6). It was asked whether this originated from increased body and leg movement error or dyscoordination between the body and leg movements. The results suggest that both are true.

6.5.1 Increased body and leg movement variability contributes to increased foot placement error in SCA6

The increased error in foot placement observed in SCA6 could have originated from several sources. One source could have been that the body movement, leg movement or both body and leg movements were more variable, without an impaired coordination between the two. It appears that increased body and leg movement variance was at least partly the origin of the increased foot placement error. This was because both the body (hip) and leg (foot-relative-to-hip) were more variable in SCA6 than HC at the end of the step. It would therefore be expected for the foot to land in a more variable location, even if SCA6 subjects displayed the same level of coordination and error correction as HC.

A potential confound in this interpretation is that the SCA6 subjects started each step from a more variable location than HC. The reasons for this were two-fold: firstly, decreased ability to return to the same starting location consistently and secondly, impaired postural control during quiet stance. Prior to a step, subjects stood quietly for approximately 1.5 seconds with their feet 15 cm apart. The starting position was chalk-marked and considerable effort was made to ensure that SCA6 subjects returned to the same location to begin each step. However, several subjects struggled to comply with this and needed to repeatedly shuffle their feet into the chalk-marks to obtain an adequate starting foot position. As a result, their starting feet position was more variable. The location of the hip before the step was also more variable in SCA6 subjects. This was likely due to impaired postural control during quiet stance. Prior to the beginning of the experiment each subject completed two thirty-second trials of quiet stance with their feet together and eyes closed to ascertain their stance instability. The results showed that the variability of the CoP velocity below the subjects' feet was significantly greater in SCA6 than HC, reflecting greater stance instability in SCA6. Whilst this was not a direct measure of body sway (such as C7 location) the results clearly showed that stance instability was increased in SCA6, which agrees with previous studies of stance instability in SCA6 (Bunn *et al.*, 2013). It has previously been shown that SCA6 subjects display greater stance instability than HC with stance widths ranging 0-32 cm (Bunn *et al.*, 2013), which encompasses the stance width used prior to each step in the present experiment. It seems that this instability in SCA6 translated to increased variability of the body position prior to the step. It is unclear how increased starting variability of the body or foot translated to variability at the end of the step, or whether they interacted.

6.5.2 Dyscoordination of the body and leg in SCA6 stepping

Another source of the increased error in foot placement in SCA6 could have been dyscoordination between the body and leg movements used during a step. Several lines of evidence suggested this was a major influence on the increased foot placement error in SCA6.

Firstly, in HC subjects the variability of the foot was less than that of the leg. This showed, like as seen in Chapter 5, that foot placement error was vastly reduced below the level expected had the body and leg not been organised to reduce foot placement error. HC subjects therefore demonstrated tight coordination for a reduction in foot placement error. However this was not the case in SCA6, where there was no difference in variability between the leg and foot. This suggested that foot placement error was not reduced to the same extent as HC. Secondly, SCA6 foot placement variable error was disproportionately increased over the course of the step. The foot began the step in a variable location and this variability was increased by the time the foot landed in both SCA6 and HC (Figure 6.4C). However, the increase in variability over the step was larger in SCA6 than that of HC. The increase in variability of the body over the step did not show the same trend and was no different between groups. As such, the increased variable error in the foot was not due to increased variability of the body during the step alone, but must have originated from imprecise coordination.

A lack of coordination implies that the movement of the body and leg would be independent of one another. In effect, randomly coupling the body and leg movement used within a step, as in the randomisation tests, caused the body and leg to become independent. A non-significant randomisation test would signify that the observed coupling between the body and the leg was no better than random and that the variance in the body and leg was essentially independent. The proportion of significant randomisation tests was decreased in SCA6 in comparison to HC. This showed that the body and leg movements used by SCA6 subjects were more likely to be independent of one another and that their organisation was less precise.

6.5.3 Coordination of the body and leg in SCA6 stepping

Despite the seeming dyscoordination between the body and leg in SCA6, several key points should be noted. Firstly, the variability of the foot was not greater than that of the body and leg. If the movement of the body and leg were independent then a much greater variance in foot placement would have been expected than that observed. The fact that foot placement variability was not increased above and beyond body and leg variability shows that the body and leg were in some way dependent and coordinated. Secondly, the vast majority (75%) of SCA6 randomisation tests were significant, indicating that, more often than not, the body and leg were dependent and organised to reduce foot placement variable error. Thirdly, there was a systematic relationship between the orientation of the body and leg variability (Figure 6.5). As shown previously in Chapter 5, the body and leg vectors used in a step were oppositely directed, which was also the case in HC. As shown in Chapter 5, this was true whether the hip or whole-body CoM was used as a marker of body location. Together, this shows that whilst the coordination between the body and leg was less precise in SCA6, there was still considerable and demonstrable coordination in their movement.

6.5.4 Possible contributors to cerebellar gait ataxia?

The question posed by this chapter was whether features of ataxic stepping could be explained by deficits in the movement of the body, leg or the coordination between the body and leg movements during a step. In other words: what are the contributing mechanisms of cerebellar ataxic gait? As has been discussed, increased movement variability and impaired coordination both seem to influence the performance of a step in SCA6. This suggests that deficits in each of the throw of the body, the movement of the leg to catch the body and the coordination between the throw and catch contribute to cerebellar ataxic gait. Alternative but related mechanisms have been proposed by other groups to explain cerebellar ataxic gait.

Morton and Bastian (2003) have proposed that cerebellar gait results from deficits in balance control, which loosely relates to the throw of the body, rather than deficits in coordinated movement of the stepping-leg to catch the body. To investigate the relative contributions of deficits in balance and coordinated leg-movements to cerebellar gait, the authors asked individuals with and without cerebellar dysfunction to perform a balance task (lateral weight shifting, similar to the movement produced prior to a step) and a leg-movement task (a goal-directed step with the weight supported to quantify coordinated leg-movement deficits in the absence of balance constraints). Cerebellar patients were then grouped as either having a balance deficit, a coordinated leg-movement deficit, or both a balance and a coordinated leg-movement deficit based on their performance in the two tasks relative to HC. It was found that individuals with predominantly balance-related deficits differed from HC in several measures of gait performance (such as step length, step length variability and the peak hip, knee and ankle joint angles) whereas individuals with predominantly leg-movement related deficits generally did not differ from HC, except for a measure of intra-limb coordination. Morton and Bastian (2003) therefore suggested that deficits in balance were more closely related to cerebellar gait ataxia than coordinated leg-movement deficits.

Conversely, Ilg *et al.* (2007) have demonstrated that the variability in the intra-joint coordination of the stepping-leg movement is increased in individuals with cerebellar degeneration compared to HC, suggesting that coordinated leg-movement deficits also contribute to cerebellar ataxic gait. Moreover, measures of temporal variability were found to correlate with clinical ratings of deficits in limb control and intra-limb coordination during goal-directed movements, whereas spatial measures (such as step width and lateral sway during gait) were found to correlate with clinical ratings of balance deficits, suggesting that coordinated leg-movement deficits influence cerebellar gait independently of balance deficits. Cerebellar gait was also compared to gaits of other populations with balance deficits (Parkinson’s disease and peripheral vestibular failure). Whilst abnormalities in balance-related gait measures and spatial gait variability was seen in each of cerebellar, Parkinsonian and vestibulopathic gait, increased temporal variability of intra-joint coordination in the stepping-leg was only found in cerebellar gait. This further emphasised that stepping-leg coordination is impaired in cerebellar gait and acts independently of balance deficits, suggesting that both balance and coordination deficits contribute to cerebellar ataxic gait (Ilg & Timmann, 2013).

The present results also suggest that both balance and coordination deficits contribute to cerebellar ataxic gait. However, I suggest that deficits in motor execution offer a simple explanation of these deficits and consequently SCA6 stepping behaviour and cerebellar ataxic gait. Day *et al.* (1998) have proposed that cerebellar dysfunction causes movements to be executed with greater error. In the case of a step, greater error could mean that the movement of the body (or leg) was moved further in one direction than planned. Over repeated steps to the same location this would result in increased variability at the end of the step, which was seen in SCA6 steps. To compensate for error in, for example, the movement of the body, a corrective movement of the leg would need to be made in the opposite direction to that of the body movement error. However, Day *et al.* (1998) also suggest that such corrective movements are themselves executed with greater error in cerebellar dysfunction, leading to an accumulation of error. In SCA6, corrective movements could on average have been directed appropriately but also contained error, resulting in imprecise coordination of the body and leg and increased foot placement error. Additionally, greater error in movement execution in cerebellar dysfunction would explain how the body and leg were still relatively coordinated in SCA6, but not as precisely as in HC.

6.5.5 Limitations

There are some important limitations to note with this experiment. Firstly, due to the scarcity of patients with SCA6, the sample size analysed here is relatively small. This was compounded by two SCA6 patients being excluded from the analysis. The first of these subjects was excluded due to an inability to step to the target without losing balance. This subject had the greatest SARA score of all SCA6 subjects. Interestingly, this subject was able to walk, albeit clumsily, without losing balance but would immediate lose balance when a constraint was imposed on foot placement location, as with the step in the experiment here. The remaining subjects had relatively low SARA scores. Due to the low number of subjects and small range of SARA score ratings, the relationship between the measures analysed here and clinical ratings of disease severity was not examined. It remains to be seen whether the measures of coordination described here scale with disease severity.

A homogeneous population with cerebellar degeneration was used here, which effectively offered a pure cerebellar lesion group with which to compare the fully functioning human brain. However, all lesion studies are limited in their ability to infer function from behavioural deficits. Jonas and Kording (2017) recently explored this by asking whether a neuroscientist could understand a well understood circuitry (a microprocessor) using the same techniques used to attempt to understand the brain. The authors could lesion a part of the microprocessor and observe the change in behaviour it elicited in two computer games: Space Invaders and Donkey Kong. They demonstrated that lesioning one site could stop Space Invaders working whereas lesioning another led to Donkey Kong failing. It could therefore be falsely concluded that different sites on the microprocessor controlled each game. In the same way, it could be concluded that because damage to the cerebellum (as in SCA6) leads to impaired coordination that the cerebellum must control coordination of movement. Rather, it can only be inferred that the cerebellum contributes in some way to the coordination of movement. Moreover, whilst SCA6 offers a relatively pure form of cerebellar degeneration, it does not rule out the possibility that, over the course of time, other structures are able to compensate for this impairment and for function to be partly regained. For example, even individuals born without a cerebellum are capable of learning to walk, albeit unsteadily (Yu *et al.*, 2015).

No consistent effect of vision was found on stepping performance in either HC or SCA6. This is in contrast to a study of goal-directed reaching in individuals with cerebellar dysfunction. Day *et al.* (1998) instructed healthy controls and individuals with various degenerative cerebellar conditions to reach as accurately as possible to visual targets. It was found that, like here, end-point error was increased in cerebellar dysfunction but that, unlike here, end-point error was further increased in cerebellar degeneration when visual feedback was denied during the movement. This discrepancy could have resulted from differences in the task (reaching versus stepping), the cerebellar patients (a heterogeneous group versus a homogenous group here) or simply a lack of statistical power to detect this difference here. In addition, the lack of effect of vision here could have been due to the target being relatively small and lacking any distinct edges with which to guide the foot. It is also possible that proprioceptive or vestibular feedback were able to compensate and guide movement when visual feedback was denied during the step.

6.6 Conclusion

This chapter shows that SCA6 subjects step with greater foot placement error than HC. The increase in foot placement error can partly be explained by greater body and leg movement error. The remainder of the foot placement error can be explained by greater imprecision in the coordination between the body and the leg in SCA6 subjects. However, both the increased variability of movement and impaired coordination seen in SCA6 subjects could be due to enhanced movement execution error. Therefore, it remains to be seen whether ataxia results from impaired coordination in cerebellar dysfunction.

7 Chapter 7: General Discussion

7.1 Summary of findings

This thesis studied the control and coordination of a human step. A series of experiments were conducted in individuals with either normal neurological function or degeneration of the cerebellum. In each experiment, a subject was required to translate their body from a stationary starting position to a new location by stepping as accurately as possible to a visually-presented target placed on the floor ahead of them. Chapters 3 and 4 were designed to investigate how the motion of the body is controlled during a step, whereas Chapters 5 and 6 investigated the coordination between the body and leg movements during a step.

Chapters 3 and 4 demonstrated that the movement of the body prior to a step is modulated by the future location of the foot. This pre-step movement provided the body with an initial velocity and position relative to the stance foot at the instant the stepping foot lifted from the ground. These initial conditions were coupled to the intended step location. In Chapter 3, it was demonstrated that the pre-step movement is adjusted after an unexpected change in step target location such that the body's initial conditions are more suitable for the new intended step than had the pre-step movement not changed. The control of these initial conditions therefore seemed important to the brain. Chapter 4 demonstrated that the movement of the body during a step is largely determined by the body's initial conditions but that mid-step ankle torques are also used to control the motion of the body. As such, the body initiates a gravity-driven fall along a trajectory defined by its initial conditions during the step and mid-step torques modify the body's path. These mid-step torques seemed particularly important in controlling forwards body motion.

Chapters 5 and 6 then investigated the coordination between the body and leg movements during a step. Chapter 5 demonstrated that in healthy, young subjects the body and leg are organised to reduce foot placement error. The body and leg are tightly coupled such that error in the movement of one is compensated in the other to preserve foot placement accuracy. This coordination did not seem greatly dependent on vision as it was preserved when visual feedback was denied during the step. Chapter 6 demonstrated that individuals with a genetically determined and pure form of cerebellar dysfunction (spino-cerebellar ataxia type 6; SCA6) step with greater foot placement error and that both the body and leg movements used during a step are more variable than healthy controls. Although coordination in SCA6 seemed impaired, the body and leg were still organised to reduce foot placement error. It is postulated that, although the mechanism for coordination is intact in SCA6, the impaired coordination and increased movement error both result from deficits in motor execution caused by cerebellar degeneration.

7.2 The throw-and-catch model revisited

The concept of the throw-and-catch model of human gait was outlined in the General Introduction and Chapter 3. The experiments in this thesis directly tested some of its predictions. One of the major predictions of the throw-and-catch model is that the pre-step movement is coupled to the intended step location. This prediction was verified in the experiments in Chapters 3 and 4 in steps to various locations both when the step target changed location unexpectedly and when the step location did not change. The throw-and-catch model also predicts that the body undertakes a gravity-driven fall along a trajectory determined by the throw of the body into the step. Chapter 4 set out to directly test this prediction by modelling the body as a truncated cone which was free to fall under gravity during the step. The model was given the same initial conditions as the body at the instant the foot lifted and allowed to fall for the same time as the observed step's duration. As had been shown previously (Lyon & Day, 1997), the results demonstrated that the initial conditions were a strong predictor of medio-lateral body motion during the step. However, the initial conditions were not as strong a predictor of forwards body motion. This indicated that the forwards motion of the body during a step is not entirely ballistic. When mid-step torques were added to the model it could predict forwards body motion with reasonable accuracy, demonstrating that the body's motion is modified during the step.

7.3 Limitations

7.3.1 Sample size

In each experiment the number of subjects used was relatively low (a maximum of n = 16 in a single group). This is a common theme in many biomechanical studies due to the time consuming and expensive nature of the research. In Chapter 6 this was also due to the rarity of individuals with SCA6, coupled with the stringent inclusion criteria necessary. Individuals who are more severely affected by SCA6 than the people in this thesis are often unable to walk unassisted and sometimes require the use of a wheelchair. Clearly individuals like this were unable to participate in the experiments here. In an ideal world, power calculations would have been performed to estimate the required number of SCA6 subjects with which to test. However, this was not possible as no suitable data of SCA6 stepping was present at the time the experiment was performed. One potential way of boosting sample size would have been to included other patients with cerebellar dysfunction, for example other SCA types. This was not an attractive option due to the group heterogeneity and potential mix of cerebellar and extra-cerebellar damage. Instead only SCA6, a pure form of cerebellar damage, was studied. Additionally, a large number of trials were performed by each subject. For example, a total of 240 steps were performed by each participant during the experiment in Chapter 5 and 120 per subject in Chapter 6. It is therefore hoped that the mean value of each measure of stepping performance contains minimal noise for each subject.

7.3.2 Target light shape

The step targets were 2.5 cm diameter circles that were placed in various locations on the floor in front of the subject. In all experiments, the subject was instructed to step to the location of this target as accurately as possible. In Chapters 5 and 6 vision was occluded during the step and it was found that the denial of visual feedback tended to increase foot placement error, but that this increase was small. It is possible that if the step target had been larger, for example shaped-like the foot or a rectangle of similar size to the foot, then the effect of visual occlusion would have been larger. However, this would have resulted in foot placement error decreasing when visual feedback was available as opposed to an increase in error when visual feedback was denied. Consequently, the assertion that visual feedback is not of critical importance in the coordination of a step still holds. In Chapters 3 and 4, the accuracy of the foot was not of critical importance to the questions posed and thus the shape of the target had little importance.

7.4 Further study

7.4.1 Does a single step relate to gait?

Presumably the performance of a goal-directed single step, like that observed in this thesis, relates to the performance of a step during gait. However, it remains to be seen to what extent this is true. It is therefore unclear how well the current data generalises. To answer this, the analyses outlined in this thesis could be applied to data from gait and its initiation. A direct comparison between the first step of gait initiation and the single step performed in this thesis may be the most appropriate test given that both start from a stationary location with the feet side-by-side. The analysis conducted in Chapter 4 would be of particular interest here. In Chapter 4 it was demonstrated that mid-step torques applied about the ankle joint act to modify the motion of the body during a step and that these mid-step torques seem to effect forwards more than medio-lateral body motion. It would be interesting to see if this was also true of the first step in gait initiation. If so, it would suggest that mid-step modification of body motion is an important control strategy in a variety of steps. If not, it would suggest that the mid-step modifications seen here were specific to the task of a single goal-directed step.

7.4.2 Do step duration and speed influence the control of body motion?

Speed-accuracy trade-offs have been demonstrated in the performance of a goal-directed step (Reynolds & Day, 2005b), which implies that movement speed influences the control and coordination of a step. When stepping to initiate gait with increasing speed, the forwards momentum given to the body by the pre-step movement is enhanced (Breniere & Do, 1986; Breniere *et al.*, 1987; Brunt *et al.*, 1999). This speed-dependent change in the body's initial conditions will alter the trajectory of the body during the step. The speed, and thereby duration, of a step could have important consequences for the control of body motion during a step. For example, when taking a slower step, the body is falling under gravity for a longer duration. Presumably this means that the initial conditions need to be modified according to the duration of the step as well as the step's location. Such a relationship has been suggested by experiments involving stepping over an obstacle; however, these experiments have not constrained the stepping foot's location at the end of the step (Zettel *et al.*, 2002a, b; Yiou *et al.*, 2016). Subsequently, it is unclear whether step duration directly impacts the initial conditions of the body.

Additionally, the duration and speed of a step could influence the control strategy used during the step. For example, it is conceivable that the importance of mid-step modifications would be reduced during faster steps due to there being less time for them to alter body motion. If this were true it may be expected that the body's initial conditions would completely determine the motion of the body during a fast step. Likewise, mid-step modifications could be of more importance in slower steps, which could even lead to the initial conditions being controlled less precisely than in faster steps. To investigate this, the experiment in Chapter 4 could be repeated with the time from foot-lift to foot-land being dictated to the subject to manipulate step duration.

7.4.3 The role of sensory feedback in the coordination of a step

Vision did not seem of major importance to the coordination of a step in Chapter 5 and 6. Presumably other sources of sensory information were able to update movement and correct for errors. One potentially useful source of sensory information is from the vestibular system. The vestibular system provides the brain with information about the linear and rotational acceleration of the head and contributes to the sense where the body is in space (Day & Fitzpatrick, 2005). Online vestibular information has been consistently shown to be of use in correcting arm and body movements (Bresciani *et al.*, 2002a; Bresciani *et al.*, 2002b; Bresciani *et al.*, 2002c; Day & Reynolds, 2005; Smith & Reynolds, 2017). Perturbation of vestibular afferents has been shown to alter the path of walking (Fitzpatrick *et al.*, 1999; Bent *et al.*, 2000; Jahn *et al.*, 2000; Bent *et al.*, 2002; Deshpande & Patla, 2007) but similar effects on a single step have so far been elusive. This is perhaps due to the previous experiments not studying a goal-directed step. Galvanic vestibular stimulation (GVS) offers a non-invasive technique to perturb vestibular afferents and create an illusion of whole-body rotation in the roll plane (Fitzpatrick & Day, 2004; Day & Fitzpatrick, 2005). If vestibular information is used online to update a goal-directed step, it would be expected that perturbation of vestibular afferents by GVS would elicit an alteration in the placement of the foot. For example, if GVS gave the illusion that the whole-body was falling further to the right than reality, a leftward correction of the leg would be expected to compensate for this perceived error. The foot would consequently end the step further leftward than normal. This could be answered by repeating the experiment in Chapter 5 with the vestibular system being perturbed during randomly selected steps. To avoid any visuo-vestibular interactions and to increase the strength of the perceptual deviation of the body, vision would be occluded during all steps.

7.5 Conclusions

This thesis studied the control and coordination of a human step. It was asked how the body and leg move during a step. It is concluded that the body is thrown into the step with initial conditions that allow the body to fall along a desired trajectory. Mid-step torques then modify the motion of the body during the step. At the same time, the foot swings towards its intended target. The body and leg movements used within a step are tightly coupled to land the foot accurately on its target.

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9 Appendices

9.1 Force offset Matlab code

The following is Matlab code used to remove small drifts in force plate recordings. Its use is outlined in Chapter 2.4.

```
% FORCE OFFSET ALGORITHM % Matlab 2015a; Requires Image Processing Toolbox.
%
% Potential times the foot has been lifted from the force plate are estimated based
% based on when Z force is below a set threshold and the rate of X and Y force is
% small. The foot is considered off the force plate during the longest period that
% the above conditions are satisfied. The force offset is the median force over this
% period.
% Input variables:
%
% Force - n x 3 matrix containing force plate recordings where n is the number of
% samples. Column 1 contains X (medio-lateral) force, column 2 contains Y (antero-
% posterior) force and column 3 contains Z (vertical) force.
%
% Output variables:
%
% offset - 1 x 3 vector containing X (Col 1), Y (Col 2), and Z (Col 3) force offsets.

aboveThreshold = (abs(diff(Force) < 0.02); % is absolute rate of force above or below
threshold (= 0.02 N/ms)? Returns n x 3 (x,y,z) matrix of logicals: 1 = yes; 0 = no.
thresh = min(Force(:,3)) + abs((min(Force(:,3))*2)); % threshold that Z force must be
under for foot off - min z force + 2 x minimum.
aboveThreshold(:,4) = (Force(:,3) < thresh); % is Z force below minimum Z force
threshold? 1 = yes; 0 = no.
logic = sum(aboveThreshold,2) == 4; % sum each row (x+y+z). When row = 4 x, y and z
all satisfy condition and z is below force threshold. Returns logical array.
spans = bwlabel(logic);   %identify contiguous ones
spanLength = regionprops(spans, 'area'); spanLength = [ spanLength.Area]; %length of
each span
maxspan = find(spanLength == max(spanLength)); % find index of longest span.
footoff_ind = find(ismember(spans, maxspan)); % index of longest span (foot is off
force plate).
offset = median(Force(footoff_ind,:),1); % median of x, y and z force whilst foot off
force plate.
```