Spatial and temporal gaze decisions during walking: role of uncertainty, task priority, and motor cost

by

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Ethics Statement

Abstract

We continuously use vision to navigate the cluttered environment in which we live. To accomplish this, we adapt the location and timing of gaze shifts to gain environmental information to achieve a behavioural goal. However, despite the growing interest in eye tracking research during natural behaviours, the factors that guide gaze behaviour to accurately navigate and interact with our environment still remain unclear. The goal of this thesis is to determine the relationship between environmental, cognitive, and biomechanical factors in the control of gaze during visually-guided walking. In the first study, I sought to understand how environmental uncertainty influences gaze behaviour to accurately perform a motor action. To test this, I used a visually-guided walking task where I manipulated the visual uncertainty associated with stepping targets. Using different task instructions to manipulate the value assigned to foot-placement accuracy, I found that environmental uncertainty increases gaze time on visual targets when having to step accurately. In the second study, I tested if motor cost, a factor that influences the way we move, is integrated into the decision of when to shift gaze to upcoming stepping targets. I found that the cost associated with redirecting foot placement onto a target modifies how gaze is allocated; when the cost to move the body increases, gaze strategies shift from one that focuses on the planning of future steps to one that prioritizes online visual control of the current action. After identifying how uncertainty, motor cost, and task priority influence gaze behaviour, in the third study, I aimed to understand how these factors interact to decide where to look when facing multiple choices for foot placement. Using a forced-choice walking paradigm, I showed that when facing a decision conflict, where two targets compete for gaze allocation, people sample the environment using different strategies that lead to differences in walking decisions. This suggests that, during walking, individuals assign a different priority to information and motor cost. Taken together, my thesis provides a novel perspective on the factors that guide gaze strategies during walking.

Keywords: Gaze; Walking; Uncertainty; Value; Cost; Decision-making

Dedication

A mi familia:
Mamá, Papá, Jesús y Rocío

To my family:
Mom, Dad, Jesús and Rocío

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List of Acronyms

ACC	Anterior Cingulate Cortex
ANCOVA	Analysis of covariance
ANOVA	Analysis of variance
BoS	Base of support
CoM	Center of mass
CWT	Control walking trials
DMS	Dynamic margin of stability
EEG	Electroencephalography
EMG	Electromyography
FEF	Frontal Eye Field
g	Gravity
HC	Heel-contact
L	Leg length
l	Distance from the chest marker to the ground
LIP	Lateral Intraparietal Area
MA	Muscle activation
SC	Superior Colliculus
SD	Standard deviation
SE	Standard error
P	Probability
PPC	Posterior Parietal Cortex
TMA	Total muscle activation
TO	Toe-off
U	Uncertainty
Vcom	Center of mass velocity
V1	Primary Visual Cortex
VOR	Vestibulo-ocular reflex
Xcom	Extrapolated center of mass
2D	Two dimensional
ω_0	Eigen (angular) frequency of the inverted pendulum

Published studies

Research contained in this thesis has been published in the following peer-reviewed journals:

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Chapter 1.

Introduction to gaze control during walking

> *"…vision evolved in animals, not to enable them to 'see' the world, but to guide their movements through it."*
>
> *(Goodale and Humphrey 1998)*

We continuously use vision to make decisions and interact with the cluttered environment in which we live. For example, in a visually guided task like walking, one of the most important roles of gaze is to sample the environment with the objective to plan and control safe foot placement, decide on our walking trajectory, and avoid hazardous terrain or obstacles.

The technological challenge to record eye movements or gaze shifts during whole body movements delayed the study of gaze control during natural tasks to the early 1990s, when Land (1994) developed a custom-made mobile eye tracker to study eye-head coordination during driving. After this, Patla and Vickers (1997) characterized gaze patterns during walking to determine how we use visual information to control locomotion. Using an obstacle negotiation task, they found that gaze is allocated in advance of an upcoming obstacle, and not during the clearance of the obstacle. They suggested that, during walking, people use gaze to acquire environmental information in advance. This strong preference for a look-ahead strategy has been replicated in multiple walking experiments (Hollands et al. 2002; Marigold and Patla 2007; Matthis et al. 2018; Pelz and Rothkopf 2007), as well as in other tasks (Hayhoe et al. 2003; Johansson et al. 2001; Land et al. 1999). For example, Land et al. (1999) instructed participants to prepare a cup of tea while wearing an eye-tracker. They found that, similar to walking, participants looked at different task-relevant objects (i.e., objects that they needed to accomplish the task) ~2 seconds before, but not during, manipulation of each object. The consistency in gaze behaviour across different tasks, unlike the variable gaze behaviour across individuals during more passive tasks (i.e., observing and describing a picture), increased the interest in studying gaze behaviour while performing natural behaviours (Tatler et al. 2011).

However, despite the growing interest in eye tracking research during natural behaviours, the factors that guide gaze sampling strategies to accurately navigate and interact with our environment still remain unclear.

The goal of this thesis is to determine the relationship between environmental, cognitive, and biomechanical factors in the control of gaze during visually-guided walking. In this introduction, I will provide a background review of gaze control of locomotion. First, I will discuss why we need to shift gaze and the neural control to perform these gaze shifts. Second, I will review the current understanding of how vision and gaze are used to control goal-directed walking. Finally, I will discuss the possible factors that may drive gaze decisions during natural behaviours and their applications to locomotion.

1.1. Neural control of gaze

The main goal of an eye movement is to orient the fovea to different areas of interest in the environment. The fovea is a small area located in the center of the macula of the retina and extends out to an angle of eccentricity of 5° (Polyak 1957). This area contains the greatest number of cones, photoreceptors that provide us with fine resolution details of a visual scene. As a result of the small foveal area, we can acquire high resolution visual information from less than 1% of the visual field at any instantaneous gaze location. Thus, to acquire detailed visual information from different regions outside of this location, we need to shift gaze and keep it still for at least 20 ms; these shifts happen two to three times every second (Land 2006; Rucci and Poletti 2016).

Small gaze shifts to reorient the line of sight are performed through fast saccadic eye movements. Saccades have a characteristic velocity waveform that linearly depends on the distance of a particular visual target from the current position of the fovea (Bahill et al. 1975). The generation of these fast eye movements involves the conjugate activity of six extraocular muscles that rotate the eyes in the orbits. These extraocular muscles are arranged in three agonist-antagonist pairs (Lateral Rectus – Medial Rectus, Superior Rectus – Inferior Rectus and Superior Oblique – Inferior Oblique) that are innervated by three cranial nerves whose nuclei are clustered in the brainstem (Kandel et al. 2013). Generation of the motor commands to drive an eye movement starts in higher cortical areas that are involved in the temporal and spatial planning of each gaze shift.

1.1.1. Cortical control of gaze shifts

The spatial and temporal planning of gaze shifts are encoded in high-level cortical regions like the frontal eye field (FEF) and the lateral intraparietal area (LIP). The FEF, located in the frontal lobe, plays an important role in spatial selective attention (Bruce and Goldberg 1985; Schall and Hanes 1993) and in the generation of voluntarily saccades through direct and indirect connections to the brainstem saccade circuitry that directly control the eye muscles (Hanes and Wurtz, 2001). Three different groups of neurons in the FEF are related to the generation of saccades: visual neurons, movement-related neurons, and visuomotor neurons. The visual neurons respond to visual stimuli in their receptive field if the stimulus is identified as a saccade target, and their activity stops before the start of the saccade. Activity of movement-related neurons is related to the decision to initiate a saccade. The firing activity of these neurons increases before the start of a saccade to a behaviourally relevant visual stimulus that falls in their receptive field. Visuomotor neurons have both visual- and movement-related characteristics

The LIP, located in the posterior parietal cortex, has reciprocal connections with FEF. During delayed memory-guided saccades, LIP neurons respond during the delay period (between target disappearance and the start of the saccade) if the visual stimulus falls in their receptive field. However, its behavioural role is not clear. One hypothesis is that neuronal responses in LIP are involved in the generation of the motor program (motor intention) to perform a saccade (Andersen and Gnadt 1989; Ipata et al. 2006; Lynch et al. 1977; Powell and Goldberg 2000). Evidence for this interpretation comes from experiments where monkeys perform a memory-guided delayed-saccade task simultaneous with another motor task (Platt and Glimcher 1999; Snyder et al. 1997). Platt and Glimcher (1999) showed that during the delay period LIP neurons responded more strongly on trials when the monkey was planning a saccade to the target than when planning a reaching movement. A second hypothesis is that LIP is involved in covert attention, or in other words, to specify how important is a stimulus to serve as the goal of a future behaviour (Colby and Goldberg 1999; Gottlieb et al. 1998). Evidence supporting this hypothesis come from experiments that show that LIP neurons responded more strongly when the saccade target is a task-relevant stimulus (Gottlieb et al. 1998, Kusonoki et al. 2000).

1.1.2. Subcortical control of gaze shifts

The eye movement plan travels from FEF and/or LIP to the brainstem where the actual motor signal is generated. The brainstem saccade generation areas are modulated by the superior colliculus (SC), a midbrain structure that plays a major role in visuomotor integration. The SC has two different functional regions: the superficial layers that receive direct input from the retina, and the oculomotor related regions located in intermediate layers (iSC). The iSC neurons are topographically organized, so that each neuron targets a specific region of the visual field. The iSC caudal region emits high-frequency bursts of activity before the onset of the saccade, inhibiting the omnipause neurons. In contrast, the iSC rostral region's activity facilitates the fixation after the eye movement by inhibiting the iSC caudal regions and exciting omnipause neurons. The generation of the motor signal to trigger a saccadic eye movement involves two different components: a pulse of activity related to the eye velocity and a step activity that drives the change in the position of the eye (Kandel et al. 2013). The signal to generate a horizontal saccade begins with a high-frequency burst of activity from the burst neurons located in the paramedian pontine reticular formation that receive inputs from higher brain areas. The burst neurons excitatory activity drives the pulse component that is sent to the extraocular motoneuron pool to activate the ipsilateral rectus muscles, driving at the same time the inhibition of the contralateral burst neurons. Burst neuron activity is modulated by the action of long-lead burst neurons and omnipause neurons. This last group of neurons tonically inhibit the burst neurons during fixations with the goal of maintaining the eye in a fixed position and must be inhibited to drive a new saccade. Excitatory burst neurons also send this velocity signal to the medial vestibular nuclei and the nucleus prepositus hypoglossi to compute the step component of the saccade. The tonic neurons in the nucleus prepositus hypoglossi act as a neural integrator to obtain a position signal from the velocity signal and prevent the return of the eye to its original position. Overall, it is clear that there is a complex circuit involved in the control of eye movements.

1.1.3. Eye-head coordination

Although small gaze shifts can be accomplished with isolated saccadic eye movements, larger gaze shifts that exceed the eye's neuromechanical limit (± 45° in the horizontal direction) need the temporal coupling of the head as well (Bizzi et al. 1972; Guitton and Volle 1987). Eye-head gaze shifts start with a high velocity eye movement followed by a slower rotation of the head in the same direction. When gaze reaches the target, the head keeps moving in the same direction, while the eyes rotate in the opposite direction in the orbit to stabilize the gaze point with a compensatory vestibulo-ocular reflex (VOR). For the VOR, the vestibular system sends a head rotation velocity signal to the eye muscles via the vestibular and oculomotor nuclei. This signal generates a reflex that counteracts for head rotation to keep the eyes stable on the region of interest. At slower velocities or when the head is stable in space, the optokinetic reflex maintains the visual scene stable on the retina by rotating the eyes in the same direction as the retinal motion.

Although the eye rotation starts before the head motion, experiments using electromyography (EMG) activity from the neck and the eye show that the neck muscle activity increases 20 ms before the eye. This indicates that the neural signal to initiate eye-head gaze shifts starts by triggering the neck muscles (Bizzi et al. 1972; Zangemeister and Stark 1981). This initial trigger could start in a subregion within the nucleus reticularis gigantocellularis that receives direct input from head-only neurons in the dSC, and whose axons project to the neck motoneurons (Quessy and Freedman 2004). The eye-head coordination to shift gaze depends on the spatial-temporal predictability of the visual target (Bizzi et al. 1972; Zangemeister and Stark 1982), the amplitude of the gaze shift (Barnes 1979; Freedman and Sparks 1997; Guitton and Volle 1987), the predisposition to move the head (Fuller 1992; Stahl 1999), and the starting position of the eyes in the orbit (Freedman 2008). The need to coordinate the head with the eyes complicates the neural control of gaze, but the brain accomplishes this feat remarkably well.

1.2. Contribution of vision and gaze to goal-directed walking

Goal-directed walking relies on the visual system to acquire environmental information. Gibson (1950) provided some of the earliest work in understanding the role of vision to control locomotion. Gibson proposed that changes in the radial pattern of optic flow, as a result of the projection of light patterns on the retina, serves to control locomotion relative to objects in the environment. The optic flow focus of expansion, which is the point in space where all optic flow vectors converge, provides an individual with direction and speed information. For example, when walking forward, the focus of expansion represents the heading direction and any changes in direction correlate with the same degree of shift of optic flow patterns. Warren et al. (2001) empirically demonstrated the importance of optic flow in the control of walking using a virtual reality environment where they manipulated the amount of optic flow cues available. In their experiment, when participants walked towards a goal location without optic flow cues, their heading error, defined as the deviation from the straighter path towards the goal location, was greater than when optic flows cues were available. When the amount of optic flow decreased, as would occur when walking in dark conditions, participants walked with constant angular error. However, in contrast to Gibson's idea, Rushton et al. (1998) found that when wearing prism goggles that distort the optical relationship with a visual target, but not the optic flow cues, people follow curved trajectories when walking towards a goal. They suggested that, instead of optic flow, we use an egocentric strategy by moving in the perceived direction of our goal. Despite their differences, both theories converge on the idea that vision plays a key role in the control of locomotion.

After Gibson's influential work, Lee (1976) introduced a control strategy theory suggesting that, from optic flow cues, the brain is able to extract an optical variable (tau) that would provide us with time-to-contact information. Time-to-contact information could have a role in the sensorimotor transformations to modify gait patterns when stepping in a particular location or avoiding an obstacle. Importantly, Marigold and Drew (2017) identified a group of posterior parietal cortex (PPC) neurons in the cat that, during an obstacle avoidance task, monitored the time and distance to contact with an obstacle. This finding provides a neural basis for the time-to-contact concept. This signal can subsequently be used to modify gait patterns or to change walking trajectories for avoiding objects and hazards.

1.2.1. Looking ahead: Gaze strategies to control locomotion

To acquire visual information to change our gait pattern we need to allocate gaze to future goal locations. Patla and Vickers (1997) supported this idea using a mobile eye tracker to monitor gaze behaviour during an obstacle clearance task. They showed that participants fixated the obstacle during the approaching phase, but not when their lead limb moved over it. This looking-ahead strategy is dynamically regulated to meet changes in the environment and to adapt our actions to the current behavioural goal. For example, when walking towards an array of vertical obstacles, gaze is used for path planning by looking at the path and obstacles during the approaching phase (Patla et al. 2007).

Interestingly, when navigating through the obstacles people usually fixated goal landmarks at the end of the path rather than on the obstacles, presumably to guide the body towards the end goal location. The anticipatory gaze shifts made before stepping over an obstacle or to a target are consistent with the notion that foveal visual information is used in a feedforward manner (in advance) to control foot placement (Patla and Vickers 2003) and/or walking trajectory (Bernardin et al. 2012; Hollands et al. 2002). The PPC may use this visual information to compute the necessary sensorimotor transformations to generate a change in walking pattern. For instance, neurons in area 5b of the cat PPC discharge 2-3 steps before stepping over an obstacle, even in situations of visual occlusion (Andujar et al. 2010; Drew and Marigold, 2015; Marigold et al. 2011). Mobile electromyography (EEG) studies in humans have similarly shown increased PPC spectral power activity during obstacle avoidance tasks (Nordin et al. 2019).

To accurately perform these visually-guided behaviours while looking ahead, environment characteristics should be kept in working memory (Lajoie et al. 2012). For example, consider the situation of hiking, where you have to step over large roots or rocks to safely place your feet. Here the ability to store information in working memory about the size, shape, and location of the obstacles facilitates acquiring information about the terrain in front of you. Visual information about an obstacle can in fact be stored for short periods of time (Lajoie et al. 2012; McVea and Pearson 2006). During walking, gaze allocation relies on this spatial memory representation (Hayhoe 2017, Hayhoe et al. 2003; Hollands and Marple-Horvat, 1996; Li et al 2018). The PPC is involved in this process by maintaining a neural representation of an obstacle relative to the current body and limb positions. Specifically, neurons in this area maintain their firing rate until the trail limb steps over the obstacle (Drew and Marigold 2015; Lajoie et al. 2010; McVea et al. 2009).

Although the use of feedforward information is dominant during goal-directed walking, this is not enough to accommodate our actions to sudden changes in the environment. Peripheral visual cues are particularly important to guide locomotion when an immediate online correction is needed. The peripheral visual field, the large area that falls outside of the fovea, is mainly formed by rod photoreceptors, which means that this area has poorer visual resolution than the central visual field. However, even when we are unable to acquire high-resolution environmental details using the peripheral visual field, peripheral cues play a major role in guiding visually-guided walking. Indeed, vision from the peripheral field is important to detect self-motion, to get online visual feedback of limb trajectory, to detect unexpected changes in the environment, and/or to monitor changes in ground terrain (Dichgans and Brandt, 1978; Marigold 2008; Turano et al. 2005). We also use peripheral visual cues to select future saccade targets (Wiecek et al. 2012). The importance of peripheral vision is highlighted in the deficits observed in patients with eye disease. For example, patients with peripheral visual deficits are unable to judge the position of distant landmarks (Rieser et al. 1992, Turano et al. 2005), and to direct gaze to relevant peripheral objects (Vargas-Martín and Peli, 2006). However, this gaze allocation deficits are less noticeable with high salient, less uncertain, stimuli (Luo et al, 2008).

1.2.2. The complex terrain problem

Gaze sampling behaviour is altered in more challenging environments. In an experiment using LCD goggles that allowed participants to control when they wanted to sample visual information, Patla et al. (1996) showed that during unobstructed walking participants only needed visual feedback for about 10% of the time. However, when participants were required to step onto irregularly spaced targets, they sampled the environment approximately 40% of the movement time. Marigold and Patla (2007) confirmed this using mobile eye tracking. They found that participants fixated closer terrain locations 40% more frequently when walking across multi-surface terrain compared to solid, uniform terrain. In fact, when navigating through complex terrain, people tend to continually allocate gaze two steps ahead to ground locations where they will eventually step (Marigold and Patla 2007; Patla and Vickers 2003). Consistent with these findings, in a naturalistic setting, Pelz and Rothkopf (2007) found that when navigating uneven dirt terrain, 62% of the time gaze was allocated to the path compared to 36% when participants walked on a paved surface.

When the need to acquire visual information increases, such as when navigating complex ground terrain, there is a tight coupling between gaze allocation and limb movement. In this situation, where we need to place our feet in a precise location, as would occur when hiking, we usually fixate the next target of footfall just before lifting the foot to swing to that target (Hollands et al. 1995; Hollands and Marple-Horvat, 2001; Laurent and Thomson, 1988). The temporal link between stepping movements and a gaze shift to a footfall location appears crucial for performing precision walking tasks, as it allows one to extract visual information about the location of a stepping target relative to the current leg and body position. Because of the consistency of this coupling, some authors suggest that once a step is initiated, visual information might not be necessary to control the trajectory of the foot. In support of this, experiments occluding vision during the swing phase when participants were instructed to accurately step onto specific targets did not find differences in foot-placement error (Hollands and Marple-Horvat, 1996; Patla et al. 1996). In contrast, Reynolds and Day (2005) found that foot-placement accuracy and foot heading trajectory was altered when visual feedback was interrupted during the swing phase. Although in this last case foot-placement error differences were small between the vision and no-vision conditions, this suggests that visual feedback during the swing phase is necessary to perform fine motor adjustments in situations that require high precision.

In situations with complex terrain, peripheral visual cues are also used to monitor the current limb trajectory and the terrain conditions. This is important to react to unexpected changes in the terrain without the need to look down while we walk. Marigold et al. (2007) showed that when people fixated a location two steps ahead, visual cues from the lower visual field were enough to detect and avoid unpredictable obstacles in their path. In addition, if the lower peripheral field is blocked, people compensate by tilting their heads down, slowing their walking speed, and decreasing their step length to walk over varied terrain (Marigold and Patla 2008). Significantly, patients with glaucoma, that are unable to use peripheral vision, have modified gaze-foot coupling during precision walking tasks that reduce foot-placement accuracy (Miller et al. 2017). Taken together, peripheral visual cues provide us with online visual information, allowing us to simultaneously use foveal vision in a feedforward manner.

In summary, studies that focused on gaze behaviour during walking show a tight linkage between gaze allocation and walking. However, most of these studies describe gaze allocation during different tasks, rather than explain which factors affect the changes in gaze allocation.

1.3. Factors orienting gaze during natural behaviours

Several theories have tried to explain the factors that guide gaze allocation. However, most experiments have used tasks where the observer had to scan a static picture. Classical psychophysical research argues that salient objects or environmental features attract gaze. However, this approach fails to incorporate the role of task and cognitive demands in natural and complex sensorimotor behaviours such as walking. More recently, neural and behavioural studies suggested that in natural behaviours, gaze is oriented to aspects of the task that are relevant to successfully accomplishing a goal, which is reflected in longer and more frequent fixations to these critical features (Ballard et al. 1995; Johansson et al 2001; Hayhoe et al. 2003; Land et al 1999; Land 1994; Marigold and Patla 2007). In addition, recent computational models suggest that a fundamental determinant to explain gaze allocation during mobility (i.e., walking, driving) is the need to reduce the uncertainty of environmental features for information gain (Sprague and Ballard 2003; Sprague et al. 2007; Sullivan et al. 2012; Tong et al. 2017). This work further suggests that the goal of gaze behaviour is to acquire information about uncertain locations to maximize task-based rewards. Understanding how we gather information from the environment through eye movements is important, as it may provide insight into human decision-making. In the following sections, I will review the behavioural and neural studies that may explain the possible factors guiding gaze allocation.

1.3.1. Salience fails to explain gaze allocation in naturalistic motor tasks

Classical attention models assume that a stimulus attracts attention and gaze automatically based on low-level visual features (such as image/object brightness), independently of the goal of the current task (Wolfe et al, 1998). For instance, an object will capture and guide attention if it differs (i.e., is salient) in some way from a series of distractors, no matter how many objects are presented (Tatler et al. 2005). This saliency could relate to a variety of characteristics, such as shape, colour, or brightness. Itti and Koch (2000) used this approach to develop a salience map model that uses low-level object features (luminance, contrast, edge orientation, contrast and color) to rank candidate regions for gaze allocation. In complex scenes, when more than one salient target candidate is presented, the different individual visual features that contribute to stimulus selection are calculated and combined to create a general salience map. In this situation, a winner-takes-all type principle guides attention such that gaze is oriented to the most salient object. At the same time, the model inhibits the return to the last fixated location to avoid attention being stuck at a single location. The feature information and the salience map are processed in a pre-attentive manner at early stages of visual processing; in particular, this processing occurs in the primary visual cortex (V1) and is conveyed to higher areas, including SC and parietal cortex (Chen et al. 2016; Li 2002). However, other authors suggest that salience maps are computed in later stages of visual processing, in higher cognitive areas, including SC, FEF, and LIP (Gottlieb et al. 1998; Thompson and Bichot 2005; White et al. 2017).

Most experiments in humans that correlate fixations with low-level visual features have used a free-viewing task in which participants have to examine a picture without any other instruction or goal. The salience model does not appear to hold during more naturalistic motor behaviours (Jovancevic-Misc et al. 2006; Jovancevic-Misic and Hayhoe 2009; Sprague et al. 2007; Turano et al. 2001). For example, during a virtual reality walking task where participants had to avoid obstacles while collecting objects, only 15% of the fixations were directed to salient background features. In contrast, the salience model predicted that more than 70% of fixations should have been directed to the background (Rothkopf et al. 2007). Collectively, this work shows that individuals mostly look to objects they have to interact with (or are task relevant). These authors argue that gaze allocation in active behaviours is not a reactive and stimulus-driven mechanism. Saliency is important and can explain part of gaze allocation, but gaze is influenced by top-down information, or task relevancy.

1.3.2. Task-relevant features and task goals orient gaze in natural behaviours

In natural behaviours, an object or a particular area of interest of a visual scene will guide gaze at a specific time if it provides critical information for future actions (Ballard et al. 1995; Johansson et al 2001; Hayhoe et al. 2003; Land et al 1999; Land 1994; Marigold and Patla 2007). Yarbus' classic experiments in scene perception already emphasized the importance of task goals on the selection of eye movement target locations. Yarbus (1967) found that, when inspecting a painting, different questions or instructions resulted in different gaze patterns. For example, if the person viewing the painting was asked to estimate the age of the people in the image, making those features task relevant for the observer, most of the fixations were directed to faces. On the other hand, if the instruction was to remember the participant's clothes, people mostly looked at the clothes. These results suggested that top-down processes, like the goal of a task, play a large role in gaze allocation.

The allocation of gaze during goal-directed behaviour has been studied in tasks such as copying arrangements of blocks (Ballard et al. 1995), making tea (Land et al. 1999), making sandwiches (Hayhoe et al. 2003), driving (Land 1994), hand washing (Peltz and Canosa 2001), object manipulation (Johansson et al 2001), and visually guided walking (Marigold and Patla 2007). The main result of these studies is that gaze is directed in advance to objects that are behaviourally relevant to successful completion of the task. For example, during a sandwich making task, eye movements are directed to task-relevant objects, such as the knife, the jelly jar, the bread, and the plate, before each item is manipulated (Hayhoe et al. 2003). Similarly, Marigold and Patla (2007) showed that during a walking task, people tend to fixate two steps ahead at locations on the ground where they will eventually step. Overall, the direction and location of gaze can be explained better by its relation to the ongoing action rather than based on the physical characteristics of the local features of a visual scene.

Task-relevant behaviours suggest some level of top-down cognitive control of gaze. In this case, instead of a feature salience map, visual information is integrated in a retinotopic attentional priority map reflecting the tendency to fixate features related to the ongoing action (Bisley and Goldberg 2010; Findlay and Walker 1999; Fecteau and Munoz 2006;). This priority map integrates high-level information from areas involved in saccade target selection, like SC (McPeek and Keller 2002), pulvinar (Robinson and Petersen, 1992), V1 (Li, 2002), visual area V4 (Mazer and Gallant 2003), LIP (Gottlieb et al.1998), and FEF (Thompson and Bichot 2005). These areas have a representation of the visual world where highly relevant locations or objects have a stronger representation. Why do task-relevant features attract attention and gaze during natural tasks? Below I offer some possibilities.

1.3.3. Reward, uncertainty, and the value of information

Rewards are important incentives that shape animal and human behaviour and one of the possible reasons why brains have evolved (Shultz 2015). Vision, among other sensory modalities, is particularly important in searching and identifying stimuli that lead to reward. Thus, is not surprising that eye movements and gaze allocation are strongly modulated by the presence of rewards. In the case of eye movements, rewarded cues produce saccades with higher peak velocities and shorter latencies (Takikawa et al. 2002). More important for the scope of this thesis, neural and behavioural studies demonstrate that extrinsic reward maximization, in the form of money/points in humans and juice in monkeys, is a fundamental determinant to explain gaze target selection (Diamond et al. 2017; Gottlieb 2012; Navalpakkam et al. 2010; Schutz et al. 2012). These studies showed that gaze decisions are biased toward locations that are associated with a higher magnitude and/or probability of acquiring a reward. This is evident during visual search experiments. For example, Failing et al. (2015) asked participants to search for a different shape (singleton target) among a series of distractors. Depending of the colour of one of the distractors, participants either received a high or a low reward after the trial. They showed that the participants looked at the distractor that signaled high reward more often and longer than the one that signaled a low reward. Reward modulation happens even when participants do not receive a reward after a reward training phase (Anderson et al. 2011). Given these behavioural results, it is not surprisingly that the neural circuitry controlling eye movements is sensitive to reward. In particular, neurons in monkey FEF, LIP, supplementary eye field, dorsolateral prefrontal cortex, and basal ganglia change their activity to both the amount of expected reward and the probability of a reward (Peck et al. 2009; Yasuda et al. 2012). In humans, certain EEG components (e.g., N2pc) are modulated by stimulus reward in visual search tasks (Eimer 1996; Kiss et al. 2009; Hickey et al. 2010; Qi et al. 2013).

During natural behaviours, however, eye movements to visual stimuli are not directly rewarded, but they do provide information. Yet, the effects of reward have almost exclusively been studied in simple decision-making or visual search tasks where animals or humans get a primary (juice/money) reward just for looking at a target. Consider the following situation: you are on a crowded street trying to find a place to eat. You fixate on objects in your way, or landmarks to locate the food establishment. In this situation, the intrinsic or subjective value that we assign to environmental stimuli that provide information to successfully perform a task may affect gaze behaviour in a similar way to classic rewards (Tong et al. 2017). Sprague and Ballard (2003) modeled this idea using reinforcement learning to explain how gaze is allocated during walking when dealing with different competing demands or goals. In the model, a walking agent learns how to solve a task based on the costs and benefits of its action. The model assigns a particular value to an eye movement based on the expected loss of information (cost of the uncertainty) if gaze is not directed to a specific location. If various locations are competing for gaze allocation, the eye is directed to the location where the agent will lose more. In other words, the eyes of the simulated agent in the model are directed to uncertain locations that are behaviourally relevant, causing it to update its internal representation of the environment. In the model, achieving a specific behavioural goal is correlated to a particular intrinsic reward. The crucial point is that eye movements serve to reduce uncertainty to minimize the loss of reward. Preliminary support for this model comes from virtual reality studies involving driving (Sullivan et al. 2012) and walking (Tong et al. 2017). In the waking task, participants walked following a line while avoiding moving floating obstacles at the same time. Participants looked longer at the obstacles when they were instructed to avoid them. The time fixating the obstacles also increased when the movement of the obstacles was unpredictable (increasing the uncertainty of the task). This suggests that fixation distribution and duration are sensitive to the uncertainty of the environment and to momentary behavioural goals.

The importance of uncertainty reduction in gaze control is supported by neurobehavioural studies using information-seeking tasks. In these tasks, humans and animals can observe cues with the only goal to update their beliefs state (or reduce uncertainty), but they do not get a reward for observing the cues. For example, Daddaoua et al. (2016) showed that, during a visual search task where the visual targets were not directly associated with a reward, macaque monkeys voluntarily searched for information when they were uncertain about the presence of an upcoming reward. They showed that this behaviour is motivated by the goal to reduce uncertainty as well as by conditioned reinforcement from positive cues. Interestingly, during an active information-seeking task, where monkeys need to perform one saccade to acquire information and a second decision saccade to get a reward, LIP neurons encode the expected information gains related to the first saccade independently of the reward (Foley et al. 2017, Horan et al 2019). Similarly, midbrain dopaminergic neurons in the monkey (usually associated with reward prediction error coding) respond strongly to highly informative cues that reduce the uncertainty about future rewards (Bromberg-Martin and Hikosaka, 2009). Crucially, animals and humans sacrifice reward for obtaining advanced information about the size of future rewards, implying that information itself is rewarding (McDevitt et al. 2016; Zentall 2016).

1.3.4. Motor cost influences behaviour and may affect gaze allocation

Several theories of motor control state that the central nervous system selects a particular motor command that minimizes the energy cost to perform a task (Todorov 2004). For example, people tend to walk at a speed that minimizes the metabolic energy cost per distance, or cost of transport (Ralston 1956; Zarrugh et al. 1974). To minimize the overall energy cost of walking, we need to redirect the center of mass (CoM) while pushing-off before the beginning of the swing phase. Recently, Mathis et al. (2011, 2013, 2015, 2017) have argued that the two-steps-ahead gaze strategy observed when navigating complex terrain allows people to acquire visual information before the end of the push-off phase, exploiting the mechanical state of the CoM to conserve energy. To test this idea, they projected stepping targets at the participant’s preferred step location (the location representing the minimum energy cost of walking) that disappeared at certain periods of the gait cycle. They showed that foot-placement errors increased when visual information from the upcoming targets appeared too early before toe-off or too late after toe-off. Because of the reduced foot-placement error when visual information arrives during the push-off phase, they argued that vision is not necessary when the leg is swinging to the next stepping target. This evidence suggests that biomechanical constraints (like the cost to step on a particular target) may influence how we use vision to control locomotion. However, there is no evidence showing a direct link between gaze allocation and cost of movement.

Importantly, the preferred foot landing, the one that minimizes the overall cost of walking, may be altered to meet changes in the environment or when avoiding an obstacle. In this case, people choose foot-placement locations that minimize the displacement from the preferred cost position (Moraes and Patla 2006; Patla et al. 1999). In such situations, there are several factors that could also constrain the selection of an alternative foothold, like the minimization of changes to the ongoing gait cycle, maintaining dynamic stability, or continuation of walking without interruption. The importance of gaze during walking is reflected by the fact that individuals fixate on their future path and step locations. However, how gaze assists in selecting a target among different alternatives during walking is still unexplored.

1.4. Outline and specific aims of this thesis

In summary, similar to other visually-guided behaviours, the location and timing of gaze shifts during walking change with the environmental characteristics and the current behavioural goal. These gaze shifts allow us to use vision in a feedforward (to plan future actions) and feedback (to track the current action) manner. However, it remains unclear as to which factors affect the spatio-temporal allocation of gaze to guide and control locomotion. *The overall goal of this thesis is to determine the relationship between environmental, cognitive, and biomechanical factors in the control of gaze decisions during visually-guided walking*. This information can then be used to define a framework to understand gaze strategies during natural behaviours. Understanding the complex interaction between task priority, uncertainty, and motor cost is essential to explain how people make decisions while navigating the world. The specific aims of this thesis are:

Aim 1 (Chapter 2): Determine how environmental uncertainty affects gaze behaviour while walking in complex environments. Research suggests that gaze is sensitive to uncertainty. This idea assumes that all eye movements made in natural behaviours can be interpreted as an action to acquire relevant information to achieve a goal (e.g., foot-placement accuracy). As such, imperfect knowledge of the environment will cause an individual to allocate gaze to uncertain features. In this first study, we test this idea and also whether this relationship is based on the subjective value that one assigns to an action.

Aim 2 (Chapter 3): Identify how motor cost affects gaze behaviour during walking. When walking through complex ground terrain people tend to allocate gaze two steps ahead. Recent evidence suggests that this gaze strategy allows us to conserve energy. If this is true, the cost to step on a particular target may influence how we use vision to control locomotion. However, there is no direct evidence showing how the cost to move our body affects gaze behaviour. In this study, we test how motor cost affects temporal gaze allocation to facilitate the planning and control of foot placement while walking in cluttered environments.

Aim 3 (Chapter 4): Identify how environmental uncertainty, subjective value, and motor cost affect gaze decisions during walking. During goal-directed motor behaviours, we often need to select a reach- or step-target location among different alternatives that can differ in their characteristics. With walking, we tend to choose stepping targets that minimize energetic cost. However, when the characteristics of the terrain in front of us become uncertain, we may be reluctant to maintain this preferred pattern. Gaze helps us to acquire environmental information to make this decision. Low uncertainty locations allow for faster information gain, and thus may drive where we direct gaze and foot placement in a continuous motor task like walking. In this study, we test for the existence of a trade-off between the cost of a step and the environmental uncertainty of the stepping target in gaze sampling and step decisions when precise foot placement is critical.

The results of this thesis provide a novel perspective on the factors that guide gaze strategies during walking, which may contribute to our understanding of other natural motor behaviours and assist in the design of clinical programs to improve mobility.

Chapter 2.

Adaptive gaze strategies to reduce environmental uncertainty during a sequential visuomotor behaviour

“It is not certain that everything is uncertain.”

(Blaise Pascal)

2.1. Abstract

People must decide where, when, and for how long to allocate gaze to perform different motor behaviours. However, the factors guiding gaze during these ongoing, natural behaviours are poorly understood. Gaze shifts help acquire information, suggesting that people should direct gaze to locations where environmental details most relevant to the task are uncertain. To explore this, human subjects stepped on a series of targets as they walked. We used different levels of target uncertainty, and through instruction, altered the importance of (or subjective value assigned to) foot-placement accuracy. Gaze time on targets increased with greater target uncertainty when precise foot placement was more important, and these longer gaze times associated with reduced foot-placement error. Gaze times as well as the gaze shifts to and from targets relative to stepping differed depending on the target’s position in the sequence and uncertainty level. Overall, we show that gaze is allocated to reduce uncertainty about target locations, and this depends on the value of this information gain for successful task performance. Furthermore, we show that the spatial-temporal pattern of gaze to resolve uncertainty changes with the evolution of the motor behaviour, indicating a flexible strategy to plan and control movement.

2.2. Introduction

To acquire environmental details necessary for performing a visually guided action, such as locating a landmark, reaching to grasp a glass, avoiding obstacles, and regulating foot placement, appropriate temporal and spatial gaze shifts are required. Consider the situation where you are hiking in the woods; you must identify hazards and obstacles, choose the route you wish to take, and step to desired locations on the ground. Here the decision where, when, and for how long to look has important implications for safety, and thus the coupling between gaze location and foot placement is critical. Although novel stimuli and image salience can capture attention and direct gaze, as supported by computer-based visual tasks and computational models (Tatler et al. 2011), recent research shows that gaze fixations during more naturalistic behaviours are highly task-relevant (Hayhoe et al. 2003; Land and Hayhoe 2001; Land et al. 1999; Marigold and Patla 2007; Rothkopf et al. 2007; Sullivan et al. 2012; Tong et al. 2017; Triesh et al. 2003). For instance, when making a sandwich, eye movements are directed to the knife, the jelly jar, the bread, and the plate before each item is manipulated (Hayhoe et al. 2003). When walking across difficult terrain, people predominantly fixate where they will eventually step (Marigold and Patla 2007). However, there is little understanding of how or why task-relevant locations are selected and prioritized, or what determines how much time a location is fixated. Consequently, a central unanswered question emerges: what factors determine how gaze is allocated in visually guided motor behaviours?

Several brain regions implicated in the control of eye movements are sensitive to reward probability (Gottlieb et al. 2014; Hikosaka et al. 2006; Kawagoe et al 1998; Platt and Glimcher 1999). For example, the discharge activity of neurons within the monkey lateral intraparietal area (LIP) varies according to the expected (juice) reward associated with an eye movement to a visual target (Platt and Glimcher 1999). With walking and other motor actions outside the lab, however, fixating a location does not usually elicit a reward. Rather, gaze shifts help the brain gather relevant details necessary for making a motor decision, such as where to place the foot. Thus, reward alone cannot explain gaze allocation during ongoing, naturalistic behaviours. Interestingly, Foley et al. (2017) recently showed that certain LIP neurons change firing rates depending on the expected gain in information needed to perform the second action in a two-step decision task, rather than for the expected reward associated with that subsequent action. This highlights the importance of immediate information gain in shaping action decisions.

Since our knowledge of the world is imperfect, our sensory feedback is noisy, and the environment changes as movement unfolds over time, this means that many environmental features relevant to an action are uncertain. This can affect the execution of movement (Maeda et al. 2017). To reduce uncertainty and make appropriate motor decisions, we continuously need to acquire new sensory information. Shifts in gaze may facilitate this process (Gottlieb 2012; Gottlieb et al. 2014). However, if gaze shifts serve to reduce uncertainty in the environment, then this likely depends on whether a target of potential interest is relevant (or important) to the task. That is, there is a high value in gaining information from that location. Indeed, the subjective value of a visual stimulus can affect the velocity of saccades (Reppert et al. 2015; Xu-Wilson et al. 2009), and the value assigned to different actions can influence action selection (Rangel et al. 2008). Sprague and colleagues (Sprague and Ballard 2003; Sprague et al. 2007) recently developed a computational model in which a value is assigned to an eye movement by taking account of the expected loss of information if gaze is not directed to a specific location. This model suggests that gaze is allocated to reduce uncertainty if it maximizes a reward associated with accomplishing the goal of the task. Preliminary support for this idea stems from virtual reality-based studies of walking (Tong et al. 2017) and driving (Sullivan et al. 2012). For example, Tong et al. (2017) found that the number of fixations to a collection of floating objects to avoid increased when their locations were made uncertain by moving them to new random positions. Gaze strategies do not always maximize information gain, though, as some studies on visual search report that people often fixate the most probable rather than the most uncertain target location when under time constraints (Ghahgheai and Verghese 2015; Verghese 2012).

In the present study, we ask how uncertainty and the value assigned to an action affects gaze when the sequence of movements associated with the motor behaviour is interdependent; in this case, the step-to-step control of foot placement during walking. We thus extend the predictions of the Sprague et al. (2003 and 2007) model to this situation. As such, we test the hypothesis that gaze is allocated to reduce uncertainty about target locations, and that this depends on the value of this gain in information for successful task performance. To accomplish this, subjects performed a visually guided walking paradigm, which required them to step onto three targets while we quantified gaze and foot placement. We used different levels of target uncertainty, and through task instruction, altered the importance of (or subjective value assigned to) foot-placement accuracy. Depending on the experiment, target uncertainties were either consistent or variable within a walking trial. The use of multiple targets and differently structured environments allowed us to also address whether target uncertainty is resolved early in the path and an estimate of the target properties maintained over the course of the sequential action, or is resolved dynamically each step in a flexible manner (Foley et al. 2017). We also determined if people gaze at all targets in advance or one step at a time, and whether these changes based on the level of uncertainty or structure of the environment. Although the Sprague et al. (2003 and 2007) model does not make predictions for these, given the strong coupling between gaze and stepping in cluttered environments (Chapman and Hollands 2006; Marigold and Patla 2007), we hypothesized that gaze is allocated to each target in sequence. We further hypothesized increased gaze times for targets early in the sequence in the consistent, but not variable, environment, particularly with greater target uncertainty. Our results show: (1) how uncertainty modulates gaze; (2) how individual gaze fixations relate to the success of the ongoing motor action; and (3) how people adapt their spatial-temporal pattern of gaze for the purposes of planning and control of movement in uncertain environments.

2.3. Methods

2.3.1. Subjects

Fourteen healthy young adults participated in this study. We excluded two subjects due to problems with the eye tracker, and thus we only analyzed data from twelve subjects (six females and six males; mean age = 24.6 ± 2.6 years). Subjects did not have any known neurological, muscular, or joint disorder that could affect their behaviour in this study but wore corrective lenses if necessary (n = 4). The Office of Research Ethics at Simon Fraser University approved the study, all experiments were performed in accordance with relevant guidelines and regulations, and subjects provided informed written consent prior to participating.

2.3.2. Experimental Paradigm

Subjects performed a visually guided walking paradigm that required them to walk across the lab at a self-selected speed and step onto three irregularly spaced targets without stopping (Fig. 2.1A). An LCD projector (Epson EX7200) displayed the targets on a black uniform mat covering the walking path. To diminish the effect of environmental references and increase target visibility, subjects walked under reduced light conditions (~0.7 lux, similar to a moonlit night). We configured the targets in MATLAB (The MathWorks, Natick, MA) with the Psychophysics Toolbox, version 3 (Brainard 1997; Kleiner et al. 2007). We created three levels of target uncertainty by varying the space constant (i.e., standard deviation) of white, two-dimensional Gaussian blobs: low (σ = 1.6 cm; diameter = 9.5 cm), medium (σ = 5.1 cm; diameter = 30.4 cm), and high (σ = 7.1 cm; diameter = 42.8 cm). Examples of these are shown in Fig. 1b. Thus, with greater standard deviation, there is more uncertainty about the centre of the target; the greater the uncertainty, the more information the subject stands to gain by resolving this uncertainty (Norwich 1993). This approach is commonly used to manipulate uncertainty of visual targets in studies of sensorimotor control and in psychophysics (Bonnen et al. 2015; Izawa and Shadmehr 2008; Solomon 2002; Tassinari et al. 2006). To confirm that target size does not affect our gaze measures, and thus ensure that any differences we see are the result of target uncertainty, we performed a pilot experiment with six subjects. In this experiment, subjects had to walk and step to the centre of three targets (of similar appearance to the low uncertainty one) in their path. On a trial-to-trial basis, we varied the target diameter; these diameters were similar to those used in the main experiments. The results clearly demonstrated no effects of target size on any of the gaze measures (see Supplementary information: Figs 2.7 and 2.8). Furthermore, target size had no effect on foot-placement error or foot-placement error variability (see Supplementary information Fig. 2.9).

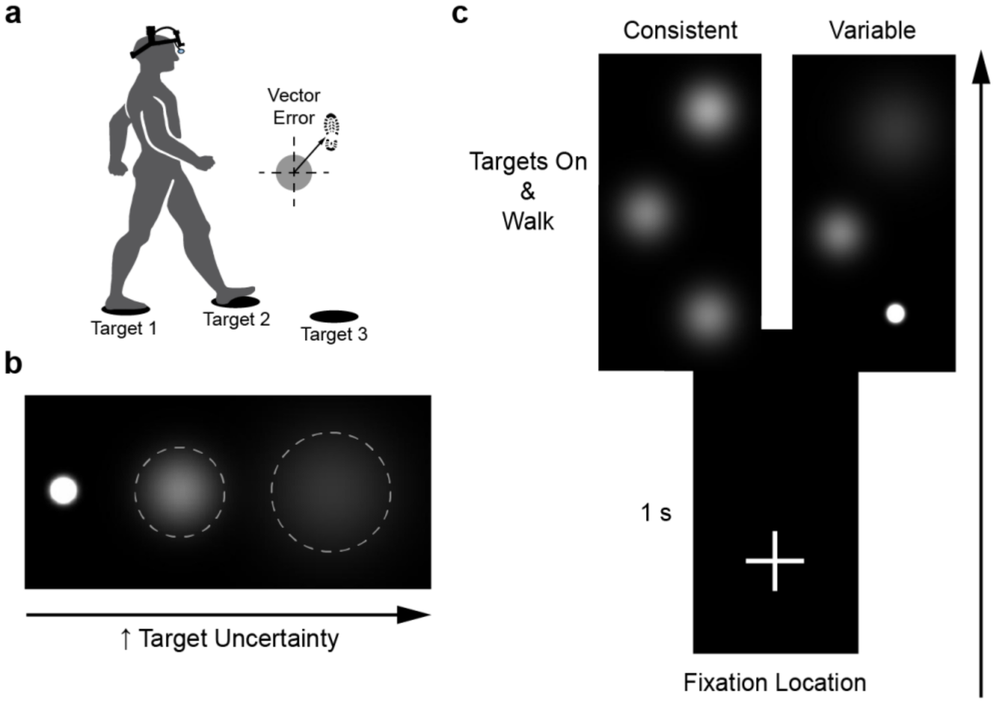

Figure 1-1. Experimental setup and procedures
(a) Visually guided walking paradigm and schematic of vector foot-placement error. (b) White two-dimensional Gaussian blob targets for each uncertainty condition. Grey dashed circles show the

approximate size of the Medium and High uncertainty targets. These circles are for illustrative purposes only and did not appear during testing. (c) Each trial started with subjects fixating a plussign on the walkway (at a distance of 50 cm with respect to the start position). After one second, we displayed all three targets at random positions and removed the fixation symbol. This signaled to the subjects to start walking. Examples of the Medium uncertainty condition for the consistent environment and one configuration of the variable environment are shown. Person illustration by Amanda Bakkum in (a) used with permission.

In the main experiments, subjects took one step before and then always stepped with a right-left-right sequence of footfalls across the three targets. We randomized the location of targets on a trial-to-trial basis using nine pre-determined configurations. The mean ± SD distances between targets in the anterior-posterior and medial-lateral directions were 68.8 ± 15.2 cm (range = 42.7 to 85.8 cm) and 27.1 ± 8.7 cm (range = 9.3 to 37.2 cm), respectively. Each trial started with a plus sign to fixate (distance of 50 cm with respect to start position). After 1 s, we displayed all three targets and removed the plus sign (Fig. 2.1c). This signalled to the subjects to start walking. We instructed subjects to terminate walking after they took one step past the third projected target. We did not provide subjects with feedback on their performance. Subjects were free to look wherever they wanted during the walking trials.

An Optotrak Certus motion capture camera (Northern Digital Inc., Waterloo, Ontario), positioned perpendicular to the walking path, recorded infrared-emitting position markers placed on the head, chest, and bilaterally on each mid-foot (second-third metatarsal head), toe (third metatarsal), and heel at a sampling frequency of 120 Hz. A high-speed mobile eye-tracker (Applied Science Laboratories: model H6-HS, Bedford, MA) mounted on the subject's head recorded (at 120 Hz) gaze position while walking using the Eye-Head integration feature synchronized with the motion capture camera. We calibrated the eye tracker using the software's standard 9-point (3-by-3 grid) calibration method at the beginning of the experiments and checked the accuracy periodically throughout testing. Based on the same calibration procedure and seven subjects not involved in this study, the spatial error of the eye tracker in the central (middle calibration point) and periphery (average of the surrounding eight calibration points) is 1.03° ± 0.55° and 1.34° ± 0.36°, respectively.

2.3.3. Experimental Protocols

Subjects performed two experiments (described below) to study differences in gaze behaviour while walking in consistent and variable environments. We counterbalanced the order across subjects. In each case, we used two tasks in separate blocks of trials that differed in the instructions provided to the subjects. In the Precision-relevant task, we instructed subjects to step with the middle of their foot to the centre of the targets as accurately as possible. In the Precision-irrelevant task, we instructed subjects to step in the targets but told them they did not have to place their foot in the centre. Task instruction served to manipulate the importance of (or subjective value assigned to) foot-placement accuracy. Specifically, the Precision-relevant task instructions increased the value of accurately stepping on the targets. We argue that this makes localizing the target centres (the relevant information) via gaze more critical. This is similar to other work using instruction as means to alter task relevance, or subjective reward of accomplishing a particular action (Sullivan et al. 2012; Tong et al. 2017). We counterbalanced the order of the Precision-relevant and Precision-irrelevant tasks across subjects in each experiment.

In the consistent environment experiment, all three targets had the same level of uncertainty for a given walking trial. However, we randomly varied the uncertainty levels (low, medium, and high) on a trial-to-trial basis. We presented each uncertainty condition in 15 trials for a total of 45 trials per instruction task (or 90 walking trials overall).

In the variable environment experiment, each of the three targets had a different level of uncertainty (low, medium, and high). We randomized the order of target uncertainty on a trial-to-trial basis. This experiment contained 20 walking trials for the Precision-relevant task and 20 walking trials for the Precision-irrelevant task (for a total of 40 trials).

2.3.4. Data and Statistical Analyses

To analyze gaze data, we first subtracted head rotation based on position markers attached to the eye tracker from gaze rotation (both in room coordinates) to extract a 3D vector of eye rotation. We then low-pass filtered this data using a 4th-order Butterworth algorithm at 15 Hz. We defined saccade onsets and offsets as the times when angular eye rotation exceeded or fell below 100 °/s for a minimum of 16 ms, respectively. Periods >66 ms between a saccade offset and a subsequent saccade onset defined gaze on a particular target or region of the ground. During walking, this means gaze is stabilized on this location but because of the vestibular-ocular reflex the eye is seldom stable in the orbit (Pelz and Rothkopf 2007; Tong et al. 2017). We used the 30 Hz video provided by a stationary camera and with the gaze location superimposed on the image to verify the presence and location of fixations and to help quantify gaze time on the targets. To assess gaze behaviour, we calculated the following measures, both normalized (i.e., divided) by total walking trial duration to control for any differences in gait speed: the total gaze time on all targets and the average gaze time on a target. Specifically, we used the total time spent looking at all three targets for a given trial in the consistent environment experiment. For the consistent and variable environment experiments, we calculated the average time spent looking at a given target in each trial. Note that for the variable environment experiment, the total gaze time on targets and average gaze time on a target are equivalent for a given trial since each of the three targets has a different level of uncertainty and are treated separately.

To determine how environmental (target) uncertainty affects gaze behaviour while walking, for the consistent experiment, we compared total gaze time on targets between uncertainty conditions and tasks using a two-way (Uncertainty x Task) ANOVA. To determine whether subjects allocate gaze to resolve the target uncertainty differently depending on the target number, in both the consistent and variable environment experiments, we compared average gaze time on a target between uncertainty conditions, tasks, and target number using three-way (Uncertainty x Task x Target) ANOVAs.

We low-pass filtered the kinematic data using a 4th-order Butterworth algorithm at 6 Hz. We calculated gait speed using the chest infrared marker as it crossed between the first and third targets. To determine heel contact on the targets, we used the local maximums of the mid-foot vertical velocity profile (O’connor et al. 2007). To determine toe-off from the targets, we used the local minimums of the anterior-posterior toe marker acceleration profile (Hreljac et al. 2000). We quantified performance by calculating the foot-placement error on each target, defined as the vector distance between the foot (mid-foot infrared marker) and the middle of the target (see Fig. 1a) when the foot’s anterior-posterior velocity and acceleration profiles stabilized to zero. We also calculated foot-placement error variability, defined as the standard deviation of foot-placement error across all three targets in the consistent environment experiment (representing within-trial variability), and the standard deviation of foot-placement error separately for each target in the variable environment experiment (representing between-trial variability since each target had a different level of uncertainty on a given trial).

To determine differences in walking motor performance, we used measures of foot-placement error and error variability as well as gait speed. To determine differences in gait speed, we performed a two-way (Condition x Task) ANOVA and a one-way (Task) ANOVA, for the consistent and variable environment experiments, respectively. We compared foot-placement error between uncertainty conditions, tasks, and target number using three-way (Uncertainty x Task x Target) ANOVAs. We also performed two-way (Uncertainty x Task) ANOVAs with foot-placement error variability. In each ANOVA, gait speed served as a covariate since we found differences between the tasks for each experiment (see Results section 2.4).

To confirm whether gaze is directed to all targets prior to stepping or each target is dealt with one at a time, we calculated the proportion of gaze shifts from target 1 to target 2 to target 3 in sequence versus not. We then subjected this to a two-way (Uncertainty x Task) ANOVA for the consistent environment experiment and a one-way (Task) ANOVA for the variable environment experiment. We also quantified two spatial-temporal measures of gaze in relation to foot-placement events (Chapman and Hollands 2006). Specifically, we calculated the time interval between the end of a saccade to a target and toe-off of the foot about to step to that same target (TO-interval), and the time difference between the onset of a saccade away from a target and heel contact on it (HC-interval). Positive TO-interval values represent gaze shifts to the target after TO, and negative values represent gaze shifts to the target before TO. For the HC-interval measure, positive values represent gaze shifts to a subsequent target after HC, and negative values represent gaze shifts away from the target before HC on it. We used separate three-way (Uncertainty x Task x Target) ANOVAs, with gait speed as a covariate, to determine differences in the mean TO-interval and HC-interval in both the consistent and variable environment experiments.

To identify a relationship between gaze behaviour and action, we performed different mixed-model ANCOVAs. For both the consistent and variable environment experiments, in one model, we used foot-placement error as the dependent variable, with average gaze time on a target as a continuous predictor variable, uncertainty condition as a categorical predictor variable, and subject as a random effect. We performed this analysis separately for each target number because of strong target number effects for each gaze and kinematic measure. In a second set of models for the consistent environment experiment, we used foot-placement error (collapsed across targets) or foot-placement error variability as the dependent variable, total gaze time on targets (summed across targets) as a continuous predictor variable, uncertainty condition as a categorical predictor variable, and subject as a random effect.

We used JMP 12 software (SAS Institute Inc., Cary, NC) with an alpha level of 0.05 for all statistical analyses. For all ANOVAs, we included subject as a random effect, and used Tukey's post hoc tests when we found significant main effects and/or interactions to determine differences between specific uncertainty conditions or target numbers.

2.4. Results

2.4.1. Effect of uncertainty on gaze time

Does target uncertainty influence gaze behaviour? Does it depend on the importance of foot-placement accuracy? We first considered whether subjects allocate a greater amount of time to more uncertain targets, quantified by the total gaze time on targets (summed across all targets and normalized to walking trial duration). As shown in Fig. 2.2a for the consistent environment, total gaze time increased from the Low to the Medium to the High uncertainty conditions in the Precision-relevant task (Uncertainty X Task interaction: $F_{2,55} = 5.4$, $p = 0.007$). In fact, total gaze time increased by 41.6% between the High and Low uncertainty conditions. In the Precision-irrelevant task, subjects spent more time looking at the targets in the High uncertainty condition than in the Low uncertainty condition. However, this represented only a 19.3% increase. We also found an increase of 35.6% and 30.1% total gaze time on targets for both the High and Medium uncertainty conditions, respectively, when the task required a high degree of precision compared to a low degree of precision.

We next considered whether the average gaze time on a target differs based on target uncertainty and importantly, whether this allocation depends on the target number in the stepping sequence and/or task instruction. Figure 2b illustrates the results of this analysis for the consistent environment. We found significant main effects of uncertainty ($F_{2,187} = 12.4$, $p < 0.0001$), target number ($F_{2,187} = 11.6$, $p < 0.0001$), and task ($F_{1,187} = 28.6$, $p < 0.0001$). Specifically, we found increased average gaze time on a target in the High and Medium uncertainty conditions versus the Low uncertainty condition. Gaze on target 1 in the High uncertainty condition, for instance, likely drove this result: average gaze time increased by 48.4% compared to the Low uncertainty condition. Subjects also showed increased average gaze time on target 1 compared to targets 2 and 3, and for the Precision-relevant versus the Precision-irrelevant task. Based on a significant Target x Task interaction ($F_{2,187} = 6.0$, $p = 0.003$), subjects had greater average gaze time on target 1 in the Precision-relevant task compared to all other targets in both tasks.

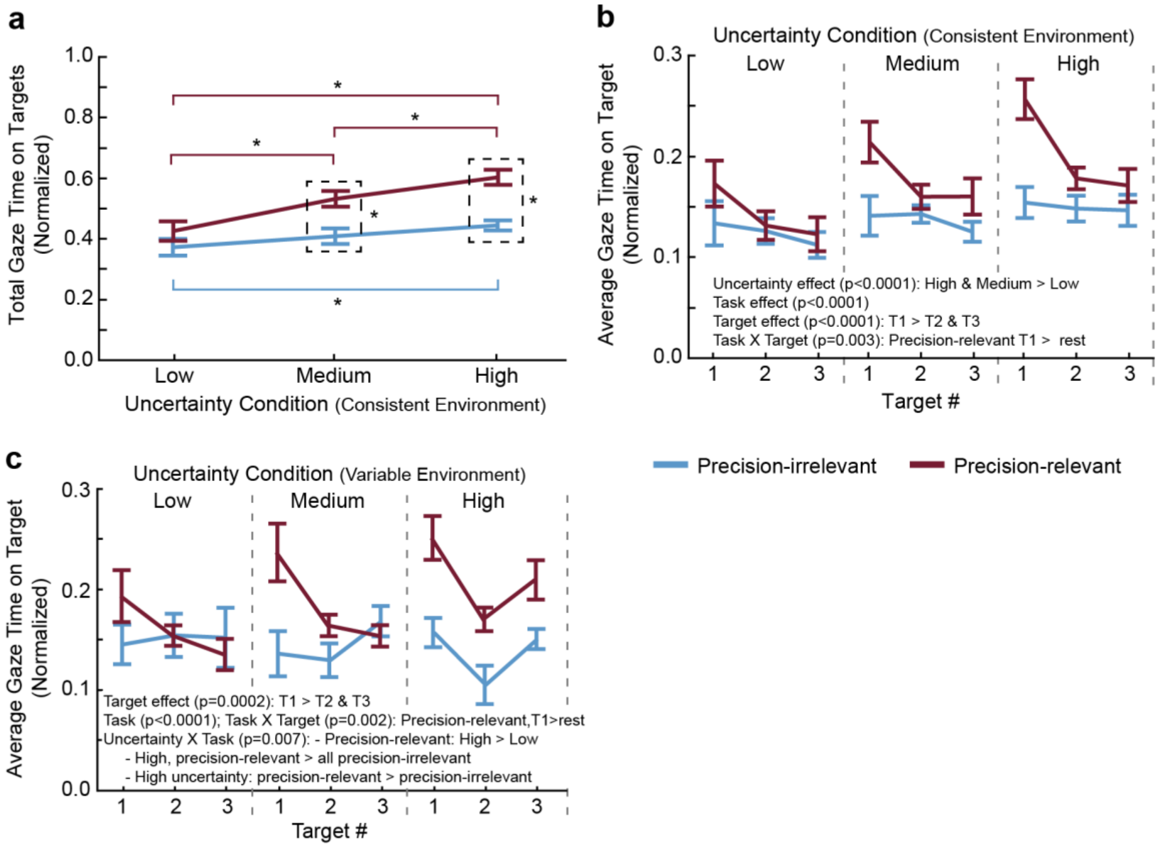

Figure 1-2. Gaze behaviour
Total gaze time on targets (a) and average gaze time on a target (b) across uncertainty conditions and tasks in the consistent environment experiment. (c) Average gaze time on a target for each uncertainty level and task in the variable environment experiment. Data are represented as mean ± SE. Gaze times are normalized (i.e., divided) by trial duration to control for differences in gait speed between trials and conditions. *Indicates that values are significantly different from each other based on post hoc tests following a significant Task X Uncertainty condition interaction ($p < 0.05$).

The terrain we encounter when walking (and the uncertainty associated with it) is often variable in nature. In our variable environment experiment, gaze time on targets depended on the task and the target uncertainty (Uncertainty X Task interaction: $F_{2,184}$ = 5.2, p = 0.007). Specifically, in the Precision-relevant task, subjects spent a greater amount of time looking at the High uncertainty target compared to the Low uncertainty target (Fig. 2c). This represented a 32.4% increase when considering target 1. Visual conspicuity (or image salience) cannot explain the increased gaze time since the Low uncertainty targets had the greatest pixel intensity. Subjects also spent more time looking at the High uncertainty target in the Precision-relevant task versus the Precision-irrelevant task. In addition, we found a Target X Task interaction ($F_{2,184}$ = 6.7, p = 0.002), such that subjects had greater gaze time on target 1 in the Precision-relevant task compared to the rest of the targets in both tasks.

Taken together, the results of the consistent and variable environment experiments suggest that uncertainty influences gaze behaviour during visually guided walking but this largely depends on the importance of (or subjective value assigned to) foot-placement accuracy. As evident in the increased gaze times to the first target in the sequence, it also appears that subjects attempt to resolve uncertainty early in the path.

2.4.2. How does target uncertainty affect motor performance?

In the consistent environment, to accommodate the different uncertainty conditions, subjects did not change their gait speed ($F_{2,55}$ = 0.9, p = 0.417). However, we found that subjects walked slower in the Precision-relevant task (1.04 ± 0.15 m/s) when compared to the Precision-irrelevant task (1.15 ± 0.13 m/s) ($F_{1,55}$ = 25.5, p < 0.0001). In the variable environment, subjects also decreased gait speed in the Precision-relevant task (1.08 ± 0.11 m/s) when compared to the Precision-irrelevant task (1.14 ± 0.12 m/s) ($F_{1,11}$ = 9.7, p = 0.010). Regardless, our gaze measures are normalized to trial duration, thereby ensuring that any minor differences in gait speed were controlled. However, we included gait speed as a covariate for the foot-placement measures.

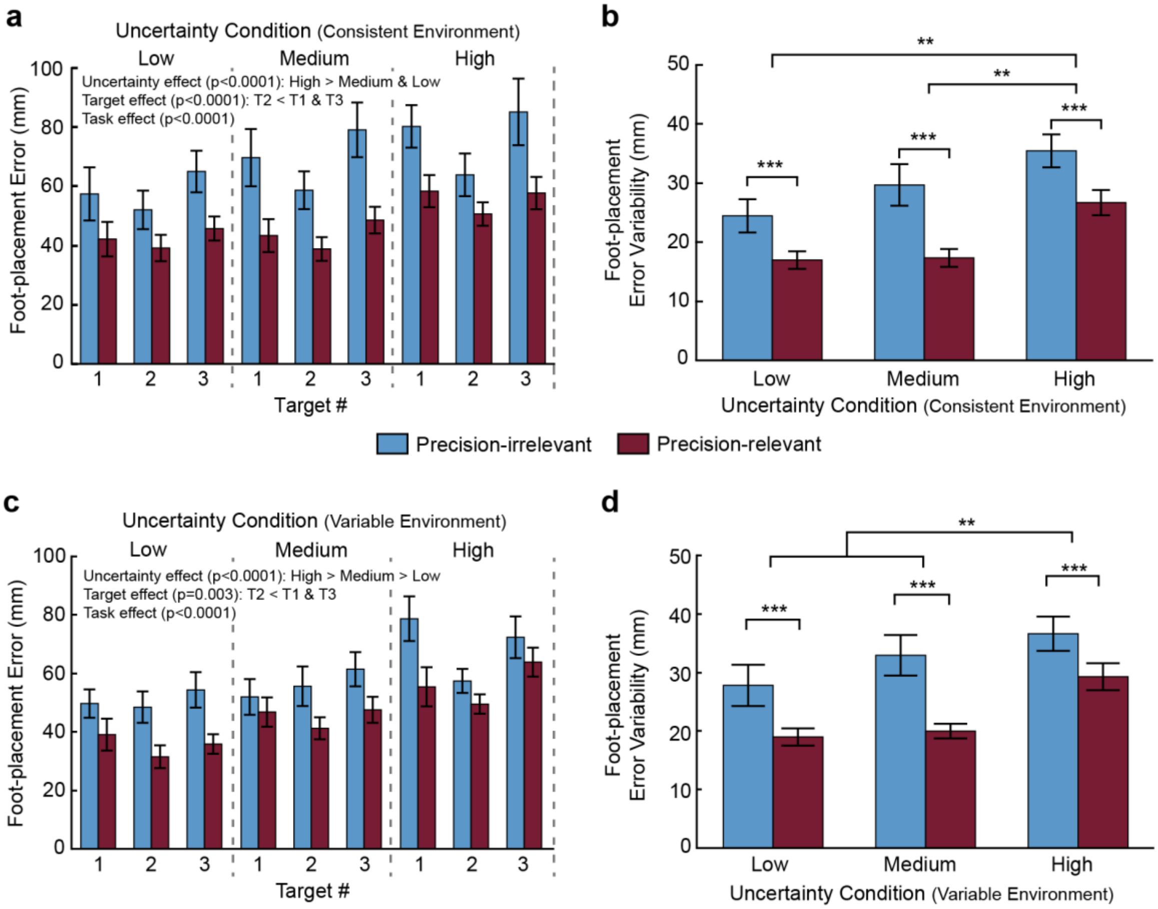

Figure 1-3. Foot-placement accuracy

Foot-placement error by target for the consistent environment (a) and variable environment (c) across uncertainty conditions and tasks is shown. Within-trial foot-placement error variability for the consistent environment (b) and between-trial foot-placement error variability for the variable environment (d) across uncertainty conditions and tasks are shown. Data are represented as mean ± SE. **Indicates uncertainty conditions are significantly different from each other (uncertainty main effect: $p < 0.05$). ***Indicates tasks are significantly different from each other (task main effect: $p < 0.05$).

We next determined if the increase in gaze allocation to more uncertain targets in the Precision-relevant task resulted in better foot-placement accuracy. Thus, we first compared foot-placement error between uncertainty conditions, task, and target number (Fig. 2.3). In the consistent environment, with low target uncertainty, subjects maintained foot-placement error around 40 mm in the Precision-relevant task. We found that subjects had significantly less foot-placement error in the Precision-relevant task compared to the Precision-irrelevant task ($F_{1,192} = 37.9$, $p < 0.0001$), as expected (Fig. 2.3a). This decrease ranged between 16.6% and 38.6% depending on the target and condition. In addition, subjects had significantly greater error in the High uncertainty condition compared to the Medium and Low uncertainty conditions ($F_{2,186} = 13.9$, $p < 0.0001$). We subsequently compared foot-placement error variability (i.e., the standard deviation of error across targets within a trial) between uncertainty conditions and tasks. Subjects had greater error variability in the High versus the Medium and Low uncertainty conditions (main effect of uncertainty: $F_{2,55} = 20.8$, $p < 0.0001$; Fig. 2.3b). We also found increased error variability in the Precision-irrelevant task compared to the Precision-relevant task ($F_{1,59} = 31.2$, $p < 0.0001$).

In the variable environment, average foot-placement error ranged between 31.5 mm with low uncertainty targets in the Precision-relevant task to 78.7 mm with high uncertainty targets in the Precision-irrelevant task (Fig. 2.3c). Greater target uncertainty resulted in increased foot-placement error (main effect of uncertainty: $F_{2,186} = 29.4$, $p < 0.0001$). Specifically, subjects had larger foot-placement error when stepping on the High uncertainty target compared with both the Medium and Low uncertainty targets, and had larger error with the Medium uncertainty targets compared to the Low uncertainty targets. Subjects also reduced foot-placement error (main effect of task: $F_{1,188} = 31.6$, $p < 0.0001$) in the Precision-relevant task compared with the Precision-irrelevant task. We found a similar result for between-trial foot-placement error variability (main effect of task: $F_{1,65} = 25.6$, $p < 0.0001$; Fig. 2.3d). In addition, subjects displayed greater between-trial error variability (main effect of uncertainty: $F_{2,55} = 10.0$, $p = 0.0002$) with High uncertainty targets compared to Medium and Low uncertainty targets.

2.4.3. The spatial-temporal allocation of gaze depends on several factors

Is gaze allocated to each target in sequence? Does this depend on target uncertainty? To address these questions, we calculated the proportion of gaze shifts to the targets in sequence. Although all three targets were presented at the same time, and all targets were visible throughout the trial, subjects chose to shift gaze in sequence, from target 1 to target 2 to target 3. This is quantified and shown in Fig. 2.4. In the consistent environment, the Medium and High uncertainty conditions showed the highest proportion of gaze shifts in this pattern, which differed significantly from the Low uncertainty condition ($F_{2,55} = 10.0$, $p = 0.0002$). The proportion of gaze shifts in this pattern was also higher in the Precision-relevant vs. Precision-irrelevant task ($F_{1,55} = 9.4$, $p = 0.003$). Regardless of condition or task, the proportion of gaze shifts in this sequence occurred over 63% of trials (with the highest proportion—over 92% of trials—for the High uncertainty condition in the

Precision-relevant task). In the variable environment, gaze shifted in sequence in over 75% of trials, with no difference between the Precision-relevant and Precision-irrelevant tasks ($F_{1,11}$ = 0.7, p = 0.427). This occurred regardless of the order of target uncertainty. Interestingly, subjects rarely re-fixated a target once shifting gaze to a new one. In fact, only 0.06 ± 0.08 re-fixations per walking trial occurred across the conditions and tasks in the consistent environment (range: 0.04 to 0.09), and only 0.05 ± 0.07 re-fixations refixations per walking trial occurred across tasks in the variable environment (range: 0.04 to 0.06).

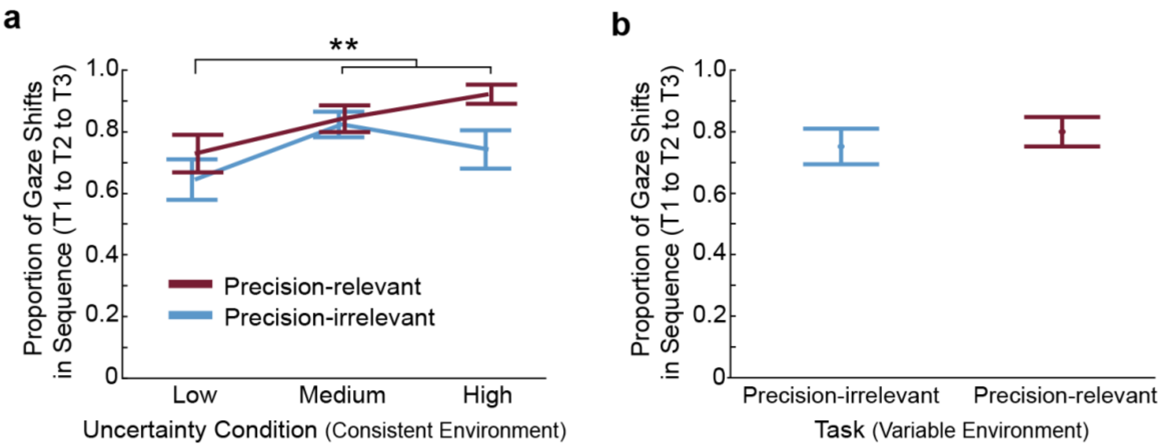

Figure 1-4. Sequence of gaze shifts
(a) Proportion of gaze shifts to sequential targets (T1 to T2 to T3) in the consistent environment with different target uncertainties. (b) Proportion of gaze shifts to sequential targets (T1 to T2 to T3) in the variable environment. **Indicates uncertainty conditions are significantly different from each other (uncertainty main effect: $p < 0.05$)

How does target uncertainty affect the spatial-temporal allocation of gaze for the purpose of planning and guiding foot placement in the precision walking paradigm? To address this, we determined the time interval between a saccade to a target and toe-off (TO) of the foot about to step to that same target (Fig. 2.5a, left panel), as well as the time interval between a saccade away from a target and heel contact (HC) on that same target (Fig. 5a, right panel).

Whereas total gaze time on a target relates to both planning and guiding foot placement, our TO-interval measure reflects primarily visuomotor planning of the upcoming step. In the majority of cases we found negative TO-intervals, indicating that gaze shifted to the target prior to initiating swing phase to step on it, and thus supporting this argument (Fig. 2.5b,c). One can also consider this as gaze leading the step. In the consistent environment (Fig. 2.5b), subjects fixated a target sooner before TO of the step towards it in the High uncertainty condition compared to the Medium and Low uncertainty conditions (uncertainty main effect: $F_{2,187} = 8.2$, $p = 0.0004$). We also found a significant Target X Task interaction ($F_{2,186} = 9.9$, $p < 0.0001$). Post hoc tests indicated that, in the Precision-relevant task, subjects fixated target 1 earlier relative to initiating the step towards it (i.e., a more negative TO-interval) compared to when encountering target 2, which in turn occurred earlier than for target 3. With high target uncertainty, the interval ranged from 608 ms for target 1 to 58 ms for target 3. In the Precision-irrelevant task, subjects shifted gaze earlier to target 1 compared to targets 2 and 3. In both tasks of the variable environment (Fig. 2.5c), subjects fixated target 1 earlier relative to initiating the step towards it compared to targets 2 and 3 (Task x Target interaction: $F_{2,184} = 8.5$, $p = 0.0003$). In contrast to the consistent environment, here we found no effect of uncertainty on TO-intervals ($F_{2,184} = 0.8$, $p = 0.445$).

Visual guidance of leg trajectory to ensure accurate foot placement in the precision walking paradigm is primarily reflected in the HC-interval measure. If we examine the consistent environment (Fig. 2.5d), we find that gaze shifted away from the stepping target ~270 ms prior to footfall on it in the Precision-irrelevant task. In the Precision-relevant task, this amount varied based on the target number in the sequence of footfalls. This is supported by a significant Task X Target interaction ($F_{2,186} = 3.6$, $p = 0.030$). Post hoc tests indicated that, in the Precision-relevant task, subjects made a saccade away from the target they were about to step on sooner when encountering target 1 (i.e., more negative HC-interval) compared to targets 2 and 3. However, uncertainty condition did not affect HC-intervals in this environment ($F_{2,186} = 0.2$, $p = 0.786$).

In the variable environment (Fig. 2.5e), we found a significant Condition X Target interaction ($F_{4,185} = 2.4$, $p = 0.049$) for the HC-interval. Specifically, in both the High and Medium uncertainty conditions, subjects maintained fixation longer on target 3 relative to stepping on it compared to target 1. In the High uncertainty condition of the Precision-relevant task, for instance, subjects shifted gaze from target 3 ~130 ms after footfall on it but shifted gaze from target 1 ~200 ms prior to footfall on it. We also found a main effect of target ($F_{2,184} = 24.3$, $p < 0.0001$), such that the HC-interval differed between all three targets, and a main effect of task ($F_{1,189} = 22.4$ $p < 0.0001$), such that subjects maintained fixation on the target they were stepping on longer when precision was more relevant.

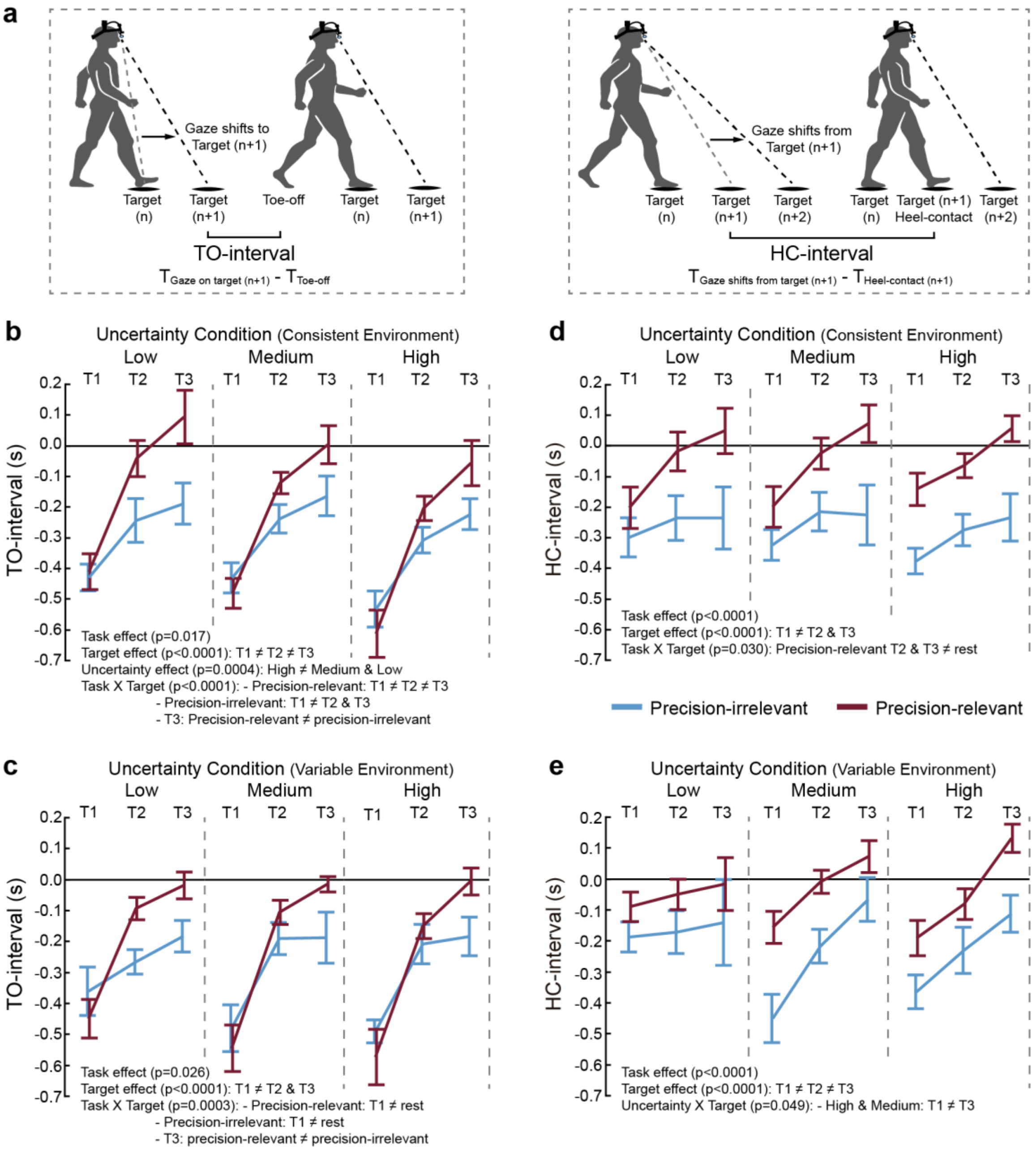

Figure 1-5. Gaze-foot spatial-temporal coupling

(a) The toe-off interval (TO-interval) is the time at which the subject fixates the target minus the time of TO for stepping on it, where negative values indicate a saccade and subsequent fixation made to the target before TO. The heel contact interval (HC-interval) is the time at which a subject saccades away from the stepping target minus the time of HC on that target, where negative values indicate a saccade away before HC on the target. Illustrated are the TO-intervals across uncertainty conditions, tasks, and target number for the consistent (b) and the variable (c) environments. Also illustrated are the HC- intervals across uncertainty conditions, tasks, and target number for the consistent (d) and the variable (e) environments. Data are represented as mean ± SE. Person illustrations by Amanda Bakkum in (a) used with permission.

Taken together, the timing of gaze shifts to and from targets dynamically changes with each step. This spatial-temporal pattern depends on both the importance of foot-placement accuracy and target uncertainty.

2.4.4. Gaze times are associated with foot-placement accuracy

To show a relationship between gaze behaviour and foot-placement accuracy in the consistent environment, we performed separate mixed model ANCOVAs. As illustrated in Fig. 2.6a, increases in average gaze time on a target associated with smaller foot-placement error with respect to target 1 ($F_{1,64}$ = 9.9, p = 0.003) and target 3 ($F_{1,59}$ = 6.4, p = 0.014), though not with target 2 ($F_{1,68}$ = 2.1, p = 0.153). The fit lines between error and gaze time for each uncertainty condition are parallel, with the High uncertainty condition significantly different than the Medium and Low conditions with respect to target 1 ($F_{2,58}$ = 12.7, $p < 0.0001$), and the High uncertainty condition different than the Low uncertainty condition with respect to target 2 ($F_{2,59}$ = 4.3, p = 0.018) and target 3 ($F_{2,60}$ = 6.0, p = 0.004). This means that the average gaze time on a target needed to reduce foot-placement error to a given value increases with target uncertainty. It also means that if subjects allocate the same average gaze time on target 1 in the Low uncertainty condition as when target 1 has high uncertainty, foot-placement error increases by 24.9 mm; the increase is 23.8 mm with respect to target 3. When we use total gaze time on targets and foot-placement error (averaged across the targets), we observed a similar relationship (Fig. 2.6b, top panel): increased total gaze time associated with reduced foot-placement error ($F_{1,67}$ = 17.0, p 0.0001). The fit lines show greater error in the High uncertainty condition compared to the Medium and Low uncertainty conditions, and greater error in the Medium uncertainty condition compared to the Low uncertainty condition ($F_{2,59}$ = 13.8, $p < 0.0001$). We also found that greater total gaze time on targets associated with larger foot-placement error variability ($F_{1,67}$ = 29.3, $p < 0.0001$; Fig. 2.6b, bottom panel). The fit lines between error variability and gaze time for each uncertainty condition are parallel, with the High uncertainty condition different than the Medium uncertainty condition, which differed from the Low uncertainty conditions ($F_{2,60}$ = 28.6, $p < 0.0001$). This means that the total gaze time on targets needed to reduce error variability to a given value increases with greater target uncertainty.

We next determined whether a relationship between gaze behaviour and foot-placement accuracy existed in the variable environment (Fig. 2.6c). Subjects spent more time looking at the targets to reduce foot-placement error with respect to target 1 ($F_{1,65}$ = 4.9, p = 0.031) and target 2 ($F_{1,58}$ = 7.2, p = 0.010). We did not find this relationship with respect to target 3 ($F_{1,63}$ = 0.0, p = 0.996). The fit lines between error and gaze time differed between the High uncertainty condition and the Medium and Low uncertainty conditions for target 1 ($F_{2,56}$ = 12.9, p < 0.0001) and target 3 ($F_{2,55}$ = 13.4, p < 0.0001), and between the High uncertainty condition and the Low uncertainty condition for target 2 ($F_{2,57}$ = 3.5, p = 0.037).

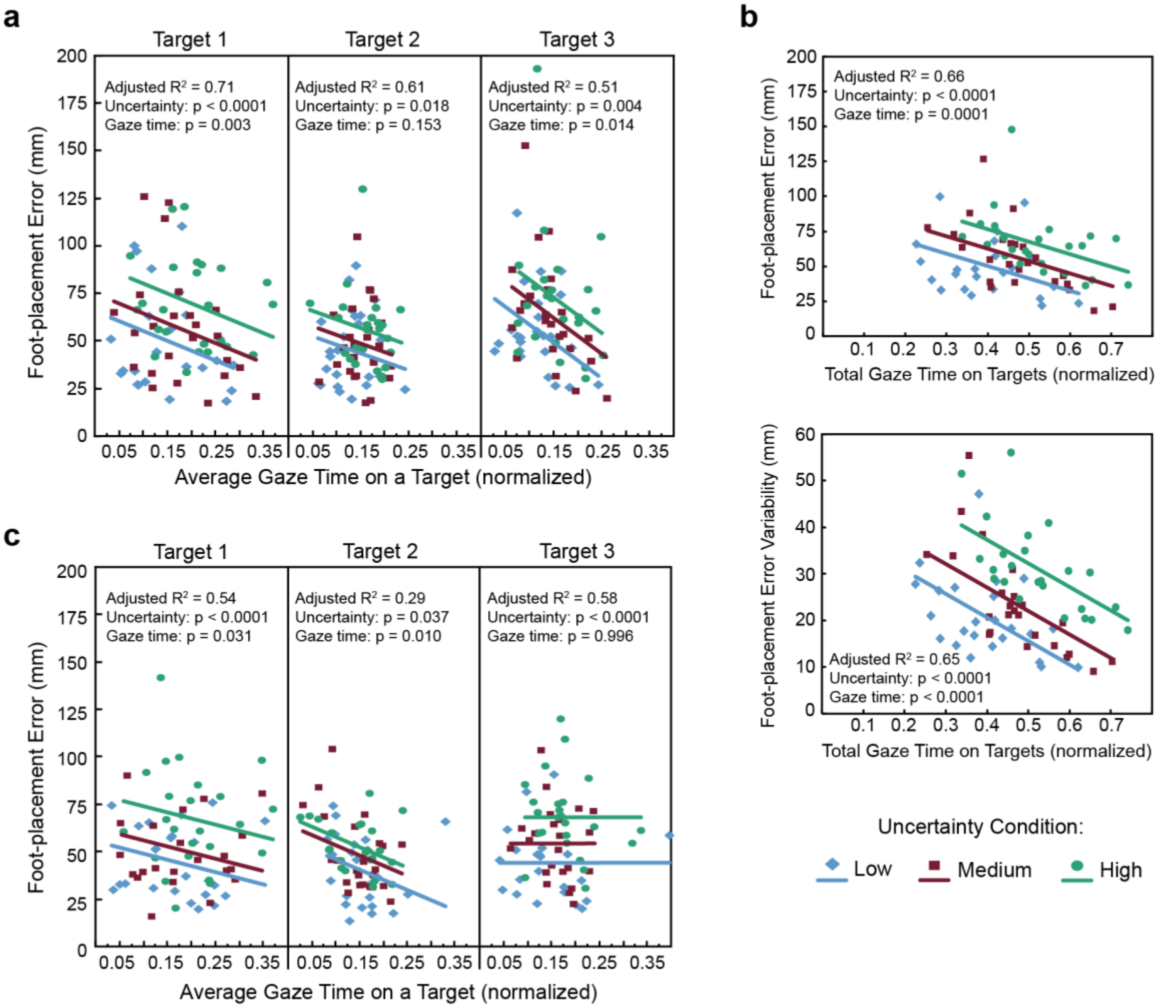

Figure 1-6. Relationship between gaze behaviour and foot-placement accuracy
(a) Scatterplots of average gaze time on a target and foot-placement error for the Low, Medium, and High uncertainty conditions in the consistent environment. (b) Scatterplots of total gaze time on targets and foot-placement error (top panel) or foot-placement error variability (bottom panel) for the Low, Medium, and High uncertainty conditions in the consistent environment. (c) Scatterplots of average gaze time on a target and foot-placement error for the Low, Medium, and High uncertainty conditions in the variable environment. Solid lines show the linear fits obtained from the ANCOVAs.

2.5. Discussion

People must select where, when, and for how long to allocate gaze to perform visually guided motor behaviours. Our findings show that environmental uncertainty affects gaze when having to step accurately during walking. Reduced foot-placement error associated with increased gaze time on targets, and this gaze allocation increased with greater uncertainty as well as when precision was more task-relevant. As such, we propose that shifts in gaze are made to reduce environmental uncertainty for the purpose of improving motor accuracy. This notion may account for a range of observations related to visually guided walking in particular, and visuomotor behaviours in general. In addition, gaze is shifted earlier to and is maintained longer on the first target in the action sequence, suggesting that people may attempt to resolve uncertainty (or acquire information) at the beginning of the path and store an estimate of the target's properties for subsequent steps. However, gaze shifts towards and away from subsequent targets occur progressively later relative to stepping on each. In fact, in the variable environment, gaze is shifted away from these latter targets after the subject has already made contact with the ground when target uncertainty is greater. We propose that uncertainty is therefore also resolved dynamically on a step-by-step basis in this situation. Taken together, our results suggest a flexibility of gaze patterns to plan and control movement.

2.5.1. What is the purpose of increasing gaze time on targets?

Gaze time on stepping targets increased with greater target uncertainty and in the precision-relevant task. This increase was not a function of slower gait speed. We propose that the increase in gaze time allows the brain to accumulate evidence of the target position/ centre to integrate this information with the state of the body and limbs for the purpose of maximizing stepping accuracy. In other words, it serves to reduce target uncertainty. This is consistent with the model of Sprague and colleagues (2003, 2007). Importantly, the data in Fig. 2.6 show a link between gaze time and accuracy. Specifically, our results suggest that to maintain an equivalent degree of foot-placement accuracy, subjects must increase gaze time on a target if that target's uncertainty is higher. In fact, if subjects adopt a similar gaze time on target 1 in both Low and High uncertainty conditions (Fig. 2.6a), foot-placement error is increased by ~25 mm in the latter. This is relatively large given that foot-placement error on targets is, on average, normally around

40 mm with no or low target uncertainty. Thus, when target uncertainty is higher, there is a cost related to foot-placement accuracy if gaze time is not increased.

Despite an increase in gaze time on targets, we found greater foot-placement error and error variability in the High uncertainty condition. With several stepping targets present in the path, there is limited time for allocating gaze to any given one. To prolong gaze time on the targets to improve foot-placement accuracy in this condition, subjects would have had to reduce gait speed. However, we found no differences between uncertainty conditions for this measure. Since changes in gait speed increase metabolic cost (Seethapathi and Srinivasan 2015), it is therefore likely that subjects choose a strategy to minimize this cost yet still maximize accuracy based on the task constraints.

Here we used different instructions to alter the importance of (or subjective value assigned to) foot-placement accuracy. Specifically, the Precision-relevant task instructions increased the value associated with accurately stepping on the targets. According to the model of Sprague and colleagues (Sprague and Ballard 2003; Sprague et al. 2007), this increases the importance of reducing target uncertainty for information gain, thus influencing gaze shifts. Furthermore, experiments in monkeys reveal that the choice of saccade target is biased to those associated with a high value for reward (Platt and Glimcher 1999; Sugrue et al. 2004). In support, we show that gaze times are longer in the Precision-relevant task compared to the Precision-irrelevant task, particularly when target uncertainty is greater. In virtual reality experiments, Sullivan et al. (2012) and Tong et al. (2017) varied task instruction as a means to manipulate the priority of two or more competing task demands, and found this affected the fixation frequency to objects and other locations. Our results extend the notion that high value stimuli influence gaze to a visually guided walking task where accurate, sequential foot placement is necessary.

We suggest that the increase in gaze time is also driven by a desire to maximize a reward associated with being accurate (Hikosaka et al. 2006; Satterthwaite et al. 2012 Sprague et al. 2007). Since we did not provide an actual reward (such as food or money), our argument requires two assumptions: accurate stepping is subjectively rewarding, and regions involved in reward processing are active in its absence. Accurate foot placement is necessary to avoid dangerous hazards in one’s path and prevent falls, thereby ensuring one safely reaches their intended destination or accomplishes a task essential to survival, such as to obtain food. This suggests that the importance of precise foot placement is likely engrained early in life. It is also worth considering that society places of a high value on accuracy; this is reflected in the large monetary rewards given to high-performance athletes. In addition, the human ventral striatum—a region involved in processing reward—is also active in the absence of an actual reward when feedback of performance in a visuomotor task is available (Lutz et al. 2012). Furthermore, the activity of this region increases following correct versus incorrect responses in a target-matching task despite no reward and no feedback (Satterthwaite et al. 2012). In the Sprague et al. (2007) model, a simulated agent walks and performs several motor behaviours, including avoiding obstacles and picking up litter. It uses a standard reinforcement learning algorithm to determine which action the agent should take for each motor behaviour given the current state of the agent and environment, with the goal of maximizing expected reward across all behaviours. Gaze is allocated based on its ability to reduce environmental uncertainty where it stands to provide the largest gain in information (or there is the greatest risk of losing a reward). Ultimately, this model argues that gaze shifts act to ensure a motor behaviour is accomplished and reward is maximized, and our results support many of its core assumptions.

2.5.2. The influence of sequential target-footfalls on gaze behaviour

The negative TO-intervals suggest that people acquire relevant information to plan gait modifications before initiating limb movement. This is similar to earlier work where subjects had to step onto non-sequential targets while walking (Chapman and Hollands 2006), and supports the idea that gaze leads or anticipates locomotor trajectory (Bernardin et al 2012; Hollands et al. 2002). These results are also consistent with recent research that demonstrates a critical phase of the gait cycle prior to toe-off during which visual feedback regarding the future footfall target is particularly important (Matthis and Fajen 2013; Matthis et al. 2015 and 2017). These authors argue that this allows the nervous system to exploit at least one determinant of the passive trajectory of the body’s centre of mass to maximize the energetic efficiency of walking across complex terrain. However, this work also suggests that people do not rely on visual feedback of the target during swing phase. In contrast, we show that subjects maintain gaze on the target well into this phase of the gait cycle, which is reflected in HC-intervals close to or greater than zero. This implies continued importance of visual feedback, which is most apparent in the higher uncertainty conditions of the Precision-relevant task. These discrepancies may relate to at least two methodological differences; we recorded gaze behaviour and used different target uncertainties, whereas Matthis and colleagues (2013, 2015, 2017) changed when and where similar targets were visible.

In the vast majority of trials in both experiments, subjects allocated gaze to each target in sequence despite the fact that all targets were visible. Importantly, how our subjects allocated gaze to identify the target position to plan and control foot placement changed over the sequence of target-footfalls. Gaze shifts happened earlier and gaze times were longer in relation to the first target compared to the others, especially with greater target uncertainty. A progressive shift towards maintaining gaze longer on later targets relative to stepping on them, particularly in the Precision-relevant task where accuracy is paramount, accompanied these changes.

Why does this sequential target effect occur? One explanation is that subjects have more time to deal with the first target due to the extra footfall before stepping on it. The same logic may explain the HC-intervals for target 3 that show subjects shifted gaze away from this target later than the others when no additional targets in the path were present. If this were the case, however, we should not see differences in gaze times on target 1 for the Precision-relevant and Precision-irrelevant tasks like we did. Nor should we have found an effect of task and uncertainty on HC-intervals. Subjects were also free to look at any target during this period of time, but we found that in the majority of trials they shifted gaze to each target in sequence as they approached them. Thus, this explanation cannot entirely account for these results.

We propose that people attempt to resolve target uncertainty early in the sequence of steps, and then use this accumulation of evidence for planning foot placement on subsequent targets. This implies that people form an internal model of the properties of the targets, with an estimate of the target centre carried forward to future targets, and hence the reduction in gaze times. The visual system is indeed capable of learning the statistical structure of the environment and objects within it (Fiser et al. 2010; Jovancevic-Misic and Hayhoe 2009; Kwon and Knill 2013). Furthermore, the brain can combine this prior estimate with new visual input based on the uncertainty of the information to guide both eye movements (Jovancevic-Misic, et al. 2009) and foot placement (Maeda et al. 2017). This strategy makes sense when target uncertainty is consistent across the environment. However, this strategy may be less efficient in a variable environment, where the uncertainty of one target does not necessarily relate to the uncertainty of subsequent targets, particularly if their uncertainty is higher. Although we found a strong target effect on gaze times similar to the consistent environment, gaze time increased again when the high uncertainty target was in the third position (Fig. 2.2c). In this case, we observed prolonged gaze on the high uncertainty target relative to footfall (Fig. 2.5e). Thus, when to shift gaze to and from a target represents another strategy—in addition to manipulating the duration of gaze—to deal with target uncertainty. Collectively, our results suggest a flexibility of gaze patterns and the ability to dynamically reduce uncertainty on a step-by-step basis. They also highlight the importance of studying complex, sequential motor behaviours typical of everyday life in addition to discrete saccade and reaching tasks, and may indicate a need for revising existing computational models of gaze behaviour for motor control (Sprague and Ballard 2003; Sprague et al. 2007).

2.5.3. Reducing environmental uncertainty may explain certain aspects of visual sampling behaviour during walking

Our results may help to explain a seemingly disparate collection of findings associated with visually guided walking over the past several decades. For instance, if subjects are given control over the amount of visual input they receive, the frequency and duration of visual sampling increases with more complex terrain (Patla et al. 1996). Furthermore, as terrain irregularity or complexity increases, people direct gaze closer to their feet (Marigold and Patla 2007; O'connor et al. 2007; T' Hart and Einhäuser 2012; Matthis et al. 2018). Although the desire to avoid tripping or falling could explain this behaviour, our data suggest that the reason relates to uncertainty in terrain characteristics, something previously proposed (Matthis et al. 2018) but not formally tested. When walking through crowds or passing through sliding doors, fixation duration and frequency to these objects increase as their motion or trajectory becomes more unpredictable (Cinelli et al. 2009; Jovancevic-Misic and Hayhoe 2009;). Additionally, people with reduced peripheral vision direct gaze to a wider area of the environment compared to normally-sighted controls (Turano et al. 2001). Finally, when the lower visual field is blocked, people pitch their head downward to a greater extent to compensate (Marigold and Patla 2008). Overall, we suggest that one can interpret each of these gaze or behavioural strategies as seeking to reduce uncertainty (or gain relevant information) about the environment to achieve a goal. Together with our results, this suggests that people can flexibly adjust their visual sampling based on task constraints.

2.6. Supplementary information: Target size does not affect gaze times

In a pilot experiment, we used targets that were similar in appearance to the low uncertainty target of the main experiments. All three targets in a given walking trial were of the same diameter. The diameters of the small, medium, and large targets were 10.5 cm, 30.5 cm, 41.5 cm, respectively. We presented these target-size conditions (5 walking trials each) in random order. Instructions to subjects matched that for the precision-relevant task in the main experiments.

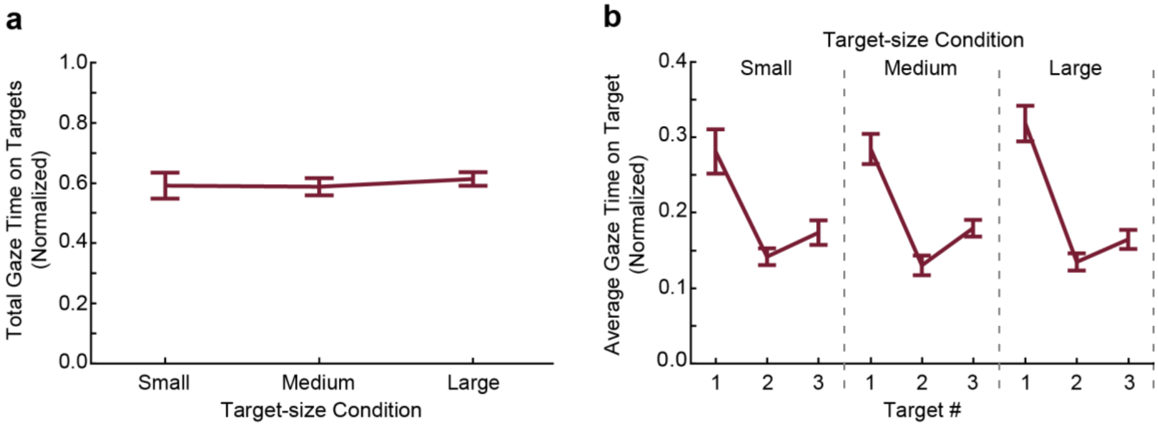

Figure 1-7. Gaze times target size experiment

(a) For total gaze times, we found no significant main effect of target size ($F_{2,10} = 0.56$, $p = 0.590$). (b) For average gaze times, we found no significant main effect of target size ($F_{2,40} = 0.23$, $p = 0.793$) or target size x target # interaction ($F_{4,40} = 0.95$, $p = 0.447$). However, we found that average gaze times to each target differed (target # main effect: $F_{2,40} = 86.8$, $p < 0.0001$), with average gaze time to target 1 greater than the other targets and average gaze time to target 3 greater than target 2. Gaze times are slightly larger in this pilot experiment compared to the main experiments due to the fact that subjects took an extra step before the first target and thus had more time to look at it.

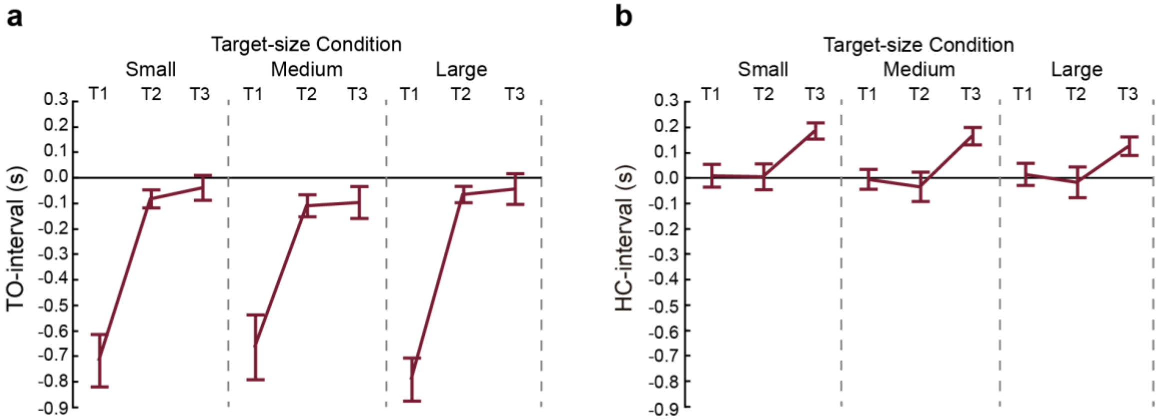

Figure 1-8. Intervals target size experiment

(a) For the TO-interval, we found no significant main effect of target size ($F_{2,41} = 0.04$, $p = 0.959$) or target size x target # interaction ($F_{4,39} = 1.01$, $p = 0.412$). However, we found that TO-intervals to each target differed (target # main effect: $F_{2,39} = 164.6$, $p < 0.0001$), where TO-interval to target 1 (T1) differed from TO-intervals to target 2 (T2) and target 3 (T3). The TO-intervals for T1 are slightly larger in this pilot experiment compared to the main experiments due to the fact that subjects took an extra step before the first target and thus had more time to look at it. (b) For the HC-interval, we found no significant main effect of target size ($F_{2,42} = 0.02$, $p = 0.979$) or target size x target # interaction ($F_{4,39} = 0.72$, $p = 0.585$). However, we found a target # main effect ($F_{2,39} = 48.3$, $p < 0.0001$), where the HC-interval to T3 differed from the HC-intervals to T2 and T1. Here we also used gait speed as a covariate.

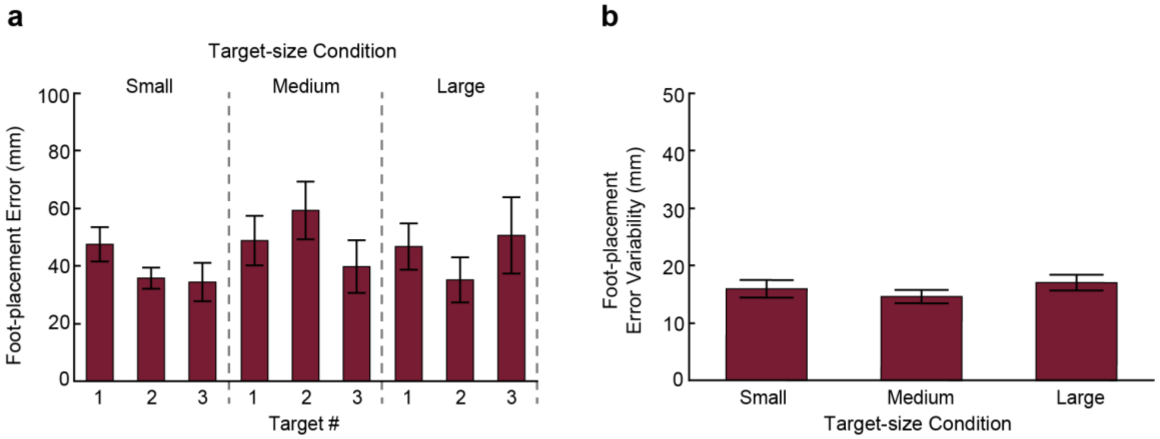

Figure 1-9. Foot-placement error and Foot-placement error variability target size experiment

(a) For foot-placement error, we found no significant main effect of target size ($F_{2,41} = 1.4$, $p = 0.257$) or target # ($F_{2,39} = 1.7$, $p = 0.196$). However, we found a significant target size x target # interaction ($F_{4,39} = 5.3$, $p = 0.002$). Tukey post hoc tests only showed greater error on target 2 in the medium target-size condition compared to error on target 2 in the large target-size condition and target 3 in the medium target-size condition. (b) For foot-placement error variability, we found no significant main effect of target size ($F_{2,11} = 1.1$, $p = 0.363$). Overall, the results suggest no consistent effect of target size on foot-placement error or error variability. Here we also used gait speed as a covariate in the analysis

2.7. Chapter contributions

Conceptualization, F. Javier Domínguez-Zamora (F.J.D.-Z). and Daniel S. Marigold (D.S.M.); Methodology, F.J.D.-Z. and D.S.M.; Investigation, F.J.D.-Z. and Shaila M. Gunn; Formal Analysis, F.J.D.-Z. and D.S.M.; Writing – Original Draft, F.J.D.-Z. and D.S.M.; Writing – Reviewing & Editing, D.S.M.

Chapter 3.

Motor cost affects the decision of when to shift gaze for guiding movement

> *‘‘Much more of the brain is devoted to movement than to language. Language is only a little thing sitting on top of this huge ocean of movement.’’*
>
> *(Oliver Sacks)*

3.1. Abstract

Frequent gait modifications are often required to navigate our world. These can involve long or wide steps, or changes in direction. People generally prefer to minimize the motor cost (or effort) of a movement, though with changes in gait, this is not always possible. The decision of when and where to shift gaze is critical for controlling motor actions, since vision informs the brain about the available choices for movement—in this case, where to step. Here we asked how motor cost influences the allocation of gaze. To address this, we had participants walk and step to the center of sequential targets on the ground. We manipulated the motor cost associated with controlling foot placement by varying the location of one target in the lateral direction on a trial-to-trial basis within environments with different numbers of targets. Costlier steps caused a switch from a gaze strategy of planning future steps to one favoring visual feedback of the current foot placement when participants had to negotiate another target immediately after. Specifically, costlier steps delayed gaze shifts away from the manipulated target. We show that this relates to the cost of moving the leg and redirecting the body’s center of mass from target-to-target. Overall, our results suggest that temporal gaze decisions are affected by motor costs associated with step-to-step demands of the environment. Moreover, they provide insight into what affects the coordination between the eyes and feet for the control of stable and accurate foot placement while walking.

3.2. Introduction

Motor decisions are affected by the cost to move the body (Gallivan et al. 2018; Morel et al. 2017; Shadmehr et al. 2016). For example, when reaching to different objects, we tend to choose the least costly trajectory (Cos et al. 2011, 2012; Huang et al. 2012; Taniai and Nishii 2015). Similarly, during walking, we usually select a step length and width that minimizes the energetic cost of foot placement and the overall walking pattern (Barton et al. 2017; Donelan et al. 2001; Moraes and Patla 2007). However, moving to minimize energetic cost is not always an option or the preferred choice in cluttered environments. Here, changes in gait are frequent. For instance, one may choose to step long or wide to avoid a spilled drink on the path. When walking in these situations, there are at least two motor costs to consider: (i) the effort (or energy) required to move the leg; and (ii) the effort involved to redirect a moving body center of mass between a changing base of support, the latter of which is dictated by the position of the two feet. This second effort is essentially the cost to maintain stability. To modify gait, though, the brain has to receive information about the environment before a limb movement can be selected. Vision serves to provide this crucial information.

Evidence suggests that vision about the environment is most critical in a specific phase of the gait cycle (Barton et al. 2017; Buckley et al. 2011; Matthis et al. 2015, 2017). The timing of this visual input is thought to ensure that one can adjust push-off force and/or change the position of the planted foot to efficiently redirect the body center of mass while stepping to precise locations (Matthis et al. 2017). When descending a sidewalk curb, visual information from the lower visual field obtained during the penultimate step affords the necessary details to position the foot relative to the edge and control the descent (Buckley et al. 2011). How does the brain make certain it gathers the visual information it needs?

The brain can direct the eyes to provide relevant information for making motor decisions. The location and timing of these gaze shifts are closely linked with ongoing motor behavior. In cluttered or other challenging environments, people usually spend most of the time fixating approximately two steps ahead (Marigold and Patla 2007; Matthis et al. 2018). When precise foot placement across sequential locations is essential, people often shift gaze to the next target location prior to lifting the foot to step to it (**Chapter 2**; Domínguez-Zamora et al. 2018; Hollands et al. 1995). These look-ahead strategies are a common aspect of most natural motor behaviors (Hayhoe et al. 2003; Johansson et al. 2001; Land et al. 1999; Land and Lee 1994; Mennie at al., 2007). However, the factors that affect the allocation of gaze in natural behavior are still unclear.

If motor cost is factored into the decision about a limb movement, and gaze informs the brain about the available choices for movement, how does the motor cost of a movement influence the allocation of gaze? To address this question, we used a precision walking paradigm that involved walking and stepping to the center of a series of sequential targets on the ground. The continuous nature of this task means there is a sequence of gaze decisions, that is, when to shift gaze to and from targets in relation to each step. We manipulated the motor cost associated with controlling foot placement by varying the location of one target in the lateral direction on a trial-to-trial basis within environments with different numbers of targets. We show that gaze shifts away from the manipulated target are delayed when the cost to move the leg is greater and the individual must redirect the body's center of mass from target-to-target due to the different constraints imposed on foot placement.

3.3. Materials and Methods

3.3.1. Participants

Ten healthy young adults participated in this study (8 females and 2 males; mean age = 26.5 ± 5.2 years; mean leg length = 95.2 ± 6.0 cm). Participants did not have any known neurological, muscular, or joint disorder that could affect their behavior in this study but wore corrective lenses if necessary (n = 1). The Office of Research Ethics at Simon Fraser University approved the study, and participants provided informed written consent prior to participating.

3.3.2. Experimental design

Participants performed a visually guided walking paradigm that required them to walk across the lab at a self-selected speed and step onto two or four white targets (9.5 cm diameter) projected on the ground without stopping. An LCD projector (Epson PowerLite 5535U; brightness of 5500 Lumens) displayed the targets on a black mat covering the walking path. To diminish the effect of environmental references and increase target visibility, participants walked under reduced light conditions (~1.2 lux surrounding the targets and ~350 lux at the center of each target). We configured the targets in MATLAB (The MathWorks, Natick, MA) with the Psychophysics Toolbox, version 3. Two Optotrak Certus motion capture cameras (Northern Digital Inc., Waterloo, Ontario), positioned perpendicular to the walking path, recorded (at 120 Hz) infrared-emitting position markers placed on the participant's head, chest, and bilaterally on each mid-foot (second-third metatarsal head), toe (third metatarsal), and heel. An electromyography (EMG) system (MA300; Motion Lab Systems, Baton Rouge, LA), synchronized via the Optotrak data acquisition unit, recorded leg muscle activity at 2,040 Hz from surface electrodes placed bilaterally over the belly of the following muscles: tibialis anterior, medial gastrocnemius, vastus lateralis, biceps femoris, and gluteus medius.

A high-speed mobile eye-tracker (Applied Science Laboratories: model H6-HS, Bedford, MA) mounted on the participant's head recorded (at 120 Hz) gaze position while walking using the Eye-Head integration feature synchronized with the motion capture system. We calibrated the eye tracker using a standard 9-point (3-by-3 grid) calibration method at the beginning of the experiments and checked the accuracy periodically throughout testing. To match experimental conditions, we positioned the nine calibration points on the floor approximately one step in front of participants. The spatial error of the eye tracker in the central (middle calibration point located on the floor) and periphery (average of the surrounding eight calibration points) is 1.03° ± 0.55° and 1.34° ± 0.36°, respectively; this is based on seven participants not involved in this study.

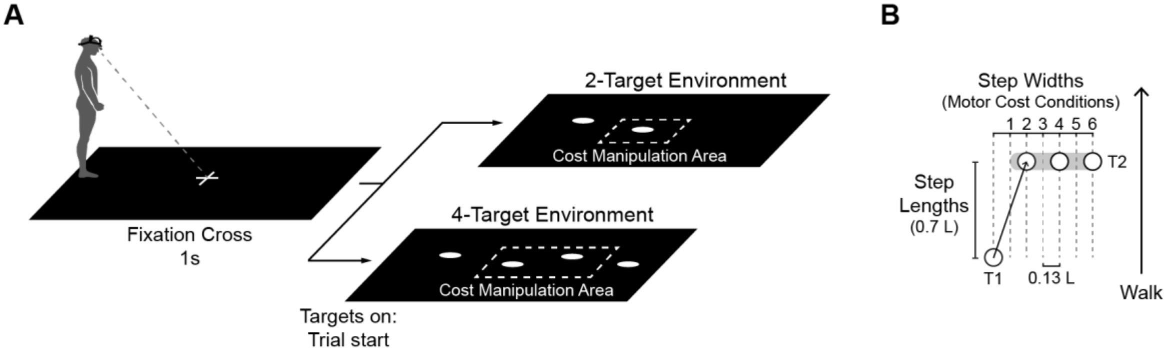

Figure 3-1. Experimental setup and procedure
Participants encountered two different environments in which they had to walk and step to the center of sequentially-positioned targets. We changed the position of the second target in the 2-target environment (top) or one of the two middle targets in the 4-target environment (bottom) on a

trial-to-trial basis. (B) We shifted the manipulated target laterally to create six different motor cost conditions. The lateral shift increased the step width by a factor 0.13 x the participant's leg length (L). We held step length constant between targets.

At the beginning of the experimental session, participants performed five trials in which we did not project targets. We used these walking (control) trials to normalize muscle activity (see below). Subsequently, participants encountered a 2-target and 4-target environment in different, counterbalanced blocks of trials (Fig. 3.1A). In each case, we instructed participants to take one step before the first target and then step with a left-right (2-target environment) or left-right-left-right (4-target environment) sequence of footfalls across the walking path. We also instructed participants to step with the middle of their foot to the center of the targets as accurately as possible and to stop walking after taking one step after the last target. We did not provide feedback on performance. Participants were free to look wherever they wanted during the walking trials. The emphasis on accuracy makes gaze more important due to the increased value of gaining relevant environmental information (Domínguez-Zamora et al. 2018). Each trial began with the participant fixating a cross located between the first and second target (2-target environment), or the second and third targets (4-target environment). After 1 s, we displayed all targets and removed the fixation cross; this signaled to the participants to start walking.

Since mechanical and metabolic cost both increase with larger step width (Donelan et al. 2001), to change the effort of moving the leg to walk forward and create six different levels of motor cost, we manipulated the step width on a trial-to-trial basis by shifting one target in the sequence laterally (Fig. 3.1B). See the Results section (and Fig. 3.2) for evidence that this affects motor cost. The step width associated with the minimum metabolic cost is presumed to be 0.13 of leg length (L), which closely aligns with the preferred step width (Donelan et al. 2001). We used this as motor cost condition 1. To create the additional five motor cost conditions, we positioned the one target laterally at 0.26, 0.39, 0.52, 0.65, or 0.78 L (Fig. 3.1B). We kept step length constant by positioning targets in the anterior-posterior direction at 0.7 L. In the 2-target environment, we only shifted the second target rightward and participants were free to step wherever they wanted after this target. In the 4-target environment, we randomly shifted the second target rightward (50% of trials) or third target leftward (50% of trials). This meant that participants had to precisely step onto at least one additional sequential target after the manipulated target. Thus, there is extra effort involved in the 4-target environment because of the greater challenge to redirect a moving body center of mass between a changing base of support, which is constrained by the additional stepping target(s). We randomly presented each motor cost condition in 10 different trials for a total of 60 trials per environment (or 120 walking trials overall).

3.3.3. Data and statistical analyses

In a preliminary analysis related to the 4-target environment, we found no significant difference between trials where participants stepped rightward (to the second target) versus leftward (to the third target) for all measures described below. Therefore, in all statistical analyses, we collapsed the data of these trials. Because gait speed varied based on environment and motor cost condition (see Results), we used it as a covariate in all analyses, except where noted.

We used kinematic data (after applying a 6 Hz low-pass Butterworth filter to it) to calculate gait speed, the timing of heel contact and toe-off events, and foot-placement accuracy. We calculated gait speed as the distance between the first and second targets (2-target environment) or the first and fourth targets (4-target environment) divided by the time it took the chest infrared marker to cross these two locations.

The local maximums of the mid-foot vertical velocity profile defined heel contact on the targets (O’Connor et al. 2007). The local minimums of the anterior-posterior toe marker acceleration profile defined toe-off from the targets (Hreljac and Marshall 2000). We quantified performance by calculating the foot-placement error on the manipulated target, defined as the vector distance between the foot (mid-foot infrared marker) and the middle of the target when the foot’s anterior-posterior velocity and acceleration profiles stabilized to zero. We also calculated foot-placement error variability, defined as the standard deviation of the manipulated target foot-placement error between trials. To determine differences in motor performance, we compared foot-placement error and foot-placement error variability between cost conditions and environments using separate two-way (Cost X Environment) ANOVAs.

We full-wave rectified and low-pass filtered (at 50 Hz with a 4th-order Butterworth algorithm) the EMG data and then separated it into two different intervals: (1) from heel contact onto the pre-manipulated target to heel contact on the manipulated target; and (2) heel contact on the manipulated target until toe-off from it. To determine differences in motor cost, we determined peak muscle activity and a total muscle activation (TMA) metric for each interval. For peak muscle activity, we determined the peak activity for each individual muscle, then normalized this value to the peak during the control walking trials. Finally, we averaged this value across all muscles.

For the TMA metric, we first calculated the muscle activation (MA) for each individual muscle:

$$MA = \left(\frac{EMG_{Area}}{EMG_{AreaCWT}}\right) \tag{3.1}$$

Where EMGArea is the area under the muscle profile during walking and stepping to targets and EMGAreaCWT is the area under the ensemble averaged profile of the control walking trials, each calculated using the trapezoid method. To account for muscle-volume differences, we used normalized volume fraction values (Handsfield et al. 2014) to calculate a weighting factor for each muscle (i), such that the sum of the weight factors equated to 1:

$$Weight\ Factor_i' = \frac{Muscle\ Volume\ Fraction_i}{\sum_{i=1}^{10} Muscle\ Volume_i} \tag{3.2}$$

Finally, we calculated the TMA, using a weighted arithmetic mean:

$$TMA = \sum_{i=1}^{10} Weight\ Factor_i' \times MA_i \tag{3.3}$$

Where *i* is each muscle analyzed. With this method, high volume muscles contribute more than low volume muscles to the total muscle activation. To determine differences in motor cost, we compared peak muscle activity and TMA between motor cost conditions and environments using separate two-way (Cost x Environment) ANOVAs.

To assess stability control (and thus quantify the need to redirect the body's CoM to step to the different targets), we used the lateral dynamic margin of stability (DMS) proposed by Hof et al. (2005). To determine the DMS, we first calculated the extrapolated center of mass (*XCoM*) based on the inverse pendulum model of walking and using the chest marker as a simplification of the CoM:

$$XCoM = CoM + \frac{V_{CoM}}{\omega_0} \tag{3.4}$$

Where *VCoM* is the *CoM* velocity and ω_0 is the eigen (angular) frequency of the inverted pendulum described by:

$$\omega_0 = \sqrt{\frac{g}{l}} \tag{3.5}$$

And where *g* represents the acceleration of gravity (9.81 ms_{-2}) and *l* is the distance from the chest marker to the ground. We calculated the DMS at heel contact and toe-off from the manipulated target as the distance between XCoM and the base of support (BoS) edge (represented by a laterally placed heel marker). For a step with the right foot on the manipulated target, we used:

$$DMS = BoS\,edge - XCoM \tag{3.6}$$

For a step with the left foot on the manipulated target, we used:

$$DMS = XCoM - BoS\,edge \tag{3.7}$$

Positive DMS values indicate a dynamically stable situation, where the XCoM is located more medial than the foot (Bruijn et al. 2013; Hof 2008). To determine differences in stability across motor cost conditions and environments, we performed two-way (Cost X Environment) ANOVAs. We did not include gait speed as a covariate for the DMS measure since it is velocity-dependent.

To analyze gaze data, we first low-pass filtered data consisting of a 3D vector of eye rotation at 15 Hz using a 4th-order Butterworth algorithm. We used this eye data to quantify gaze times. Specifically, we defined saccade onsets and offsets as the times when angular eye rotation exceeded or fell below 100 °/s for a minimum of 16 ms, respectively. Periods > 50 ms between a saccade offset and a subsequent saccade onset defined gaze on a target or region of the ground. During walking, this means gaze is stabilized on this location, but because of the vestibular-ocular reflex, the eye is rarely stable in the orbit (Pelz and Rothkopf 2007; Tong et al. 2017). We used the 30 Hz video provided by a stationary camera and with the gaze location superimposed on the image to verify the presence and location of fixations.

To assess gaze behavior, we quantified the timing of gaze shifts relative to initiating or completing a step (Domínguez-Zamora et al. 2018). We determined the time interval between the end of a saccade made to a target and toe-off of the foot about to step to the same target (TO-interval). Negative TO-interval values indicate gaze shifts to the manipulated target before toe-off, and positive values represent gaze shifts after toe-off to step to the target. In addition, we determined the time interval between the onset of a saccade away from the manipulated target and heel contact on that same target (HC-interval). In this case, positive HC-interval values represent gaze shifts to a subsequent target after HC, and negative values represent gaze shifts away from the target before HC on it. We also quantified the total gaze time looking at the manipulated target, normalized by total walking-trial duration. To determine how motor cost affects gaze behavior while walking, we compared total gaze time on the manipulated target, TO-interval, and HC-interval between motor cost conditions and environments using separate two-way (Cost X Environment) ANOVAs. As previously done (Domínguez-Zamora et al. 2018), gait speed was not included as a covariate when analyzing total gaze time since it is normalized by trial duration.

Motor cost condition affected the HC-interval (see below). Thus, to understand how the HC-interval related to our kinematic and EMG data, we first performed a linear mixed-model regression between the HC-interval (dependent variable) and foot-placement error (independent variable) for both environments. Subsequently, to determine the relative importance of the TMA and DMS (independent variables) in predicting the HC-interval (dependent variable), we entered both measures into mixed-model regressions (after converting the data of the independent variables to z-scores) for both environments. We used the DMS at heel contact on the manipulated target in combination with the TMA (calculated from heel on the pre-manipulated target to heel contact on the manipulated target) for one set of regressions. We used the DMS at toe-off from the manipulated target in combination with the TMA (calculated from heel contact on the manipulated target until toe-off from it) for the other set of regressions. In all mixed-model regressions, we used participant as a random effect.

We used JMP 13 software (SAS Institute, Cary, NC) with an alpha level of 0.05 for all statistical analyses. For all ANOVAs, we included participant as a random effect and used Tukey's post hoc tests when we found significant main effects of motor cost condition or a motor cost x environment interaction.

3.4. Results

3.4.1. Changes in step width increase motor cost

We first confirmed that changing the step width in the 2-target and 4-target environments increased motor cost. To address this, we calculated, for five bilateral leg muscles, the area under the EMG profile from heel contact before the manipulated target to heel contact on the manipulated target (or one full stride). We normalized this activity to walking trials without targets present and then summed the muscles' activity (adjusted for muscle-volume differences) to produce a total muscle activation (TMA) value. This measure quantifies the effort (or motor cost) involved to swing the leg to the target (Moraes and Patla 2006). Indeed, energy is expended for every action potential generated (Attwell and Laughlin 2001), which increases to produce more EMG activity; changes in energy consumption are related to changes in movement-related muscle activity (Gottschall and Kram 2003; Praagman et al. 2003). As shown in Fig. 3.2A, TMA increased from small to large step widths (Cost main effect: $F_{5,89} = 21.1$, $p < 0.0001$). Specifically, TMA was 25% greater for the largest step width compared to the smallest step width. However, we found no significant effect of environment (main effect: $F_{1,94} = 0.002$, $p = 0.961$; Cost x Environment: $F_{5,88} = 0.05$, $p = 0.998$). We also found a significant effect of step width for peak muscle activity (Cost main effect: $F_{5,90} = 10.0$, $p < 0.0001$) in the same direction (Fig. 3.2B). Again, we found no significant effect of environment for this measure (main effect: $F_{1,92} = 0.05$, $p = 0.822$; Cost x Environment: $F_{5,88} = 0.4$, $p = 0.879$). These results suggest that our target manipulation is an effective way to manipulate motor cost during a precision walking task.

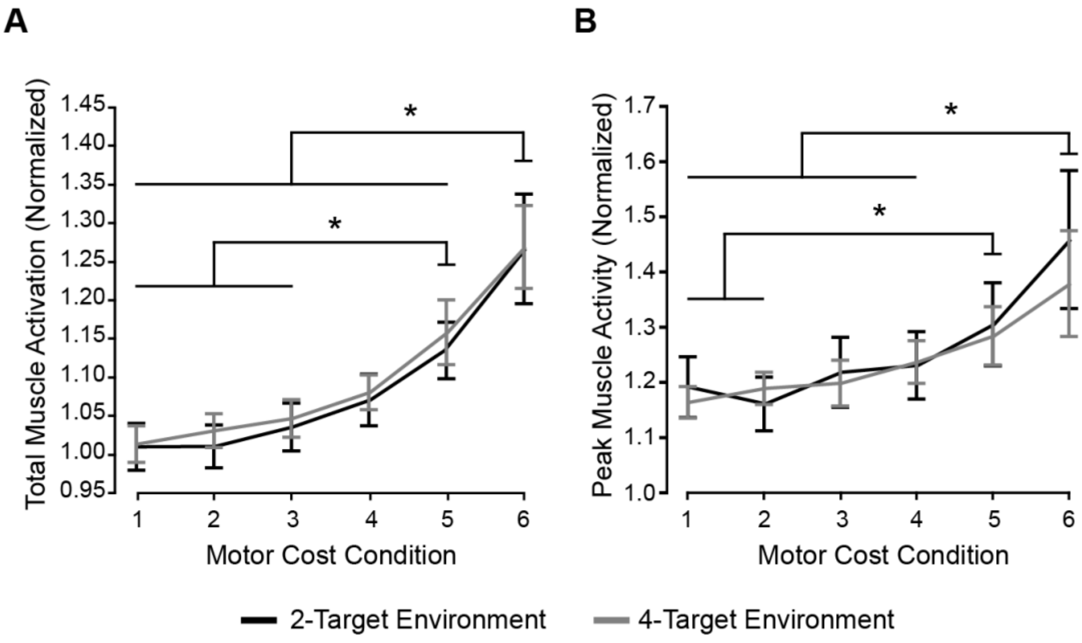

Figure 3-2. Effort involved in moving the leg forward (n = 9 participants)
(A) Total muscle activity (from five bilateral leg muscles) calculated from heel contact on the pre-manipulated target until heel contact on the manipulated target across the six motor cost conditions in the 2- and 4-target environment. Data are normalized to walking trials without targets present and adjusted for muscle-volume differences. (B) Peak muscle activity (averaged across all muscles) for the six motor cost conditions in the 2- and 4-target environment. Data are normalized to walking trials without targets present. For both measures, data are represented as mean ± SE. Asterisk indicates that values are significantly different from each other based on post hoc tests following a main effect of cost ($p < 0.05$). We excluded one participant from this analysis due to problems with the EMG system during data collection.

3.4.2. Motor cost affects decision of when to redirect gaze from current target of foot placement

Gaze is closely linked with ongoing motor behavior. As such, we considered whether the spatial-temporal patterns of gaze allocation differed across motor cost conditions. To gather information from the environment and ensure precise foot placement, the brain can decide when to shift gaze towards the upcoming target, when to shift gaze away from the current target once the foot is in contact with it, and how long to ultimately fixate the target. To address how motor cost affects these decisions, we first determined the time interval between a saccade to a target and toe-off (TO) of the foot about to step to that same target (TO-interval; Fig. 3.3A). A two-way (Cost x Environment) ANOVA on this measure revealed no main effect of cost ($F_{5,99} = 0.9$, $p = 0.471$) or environment ($F_{1,98} = 0.4$, $p = 0.529$) and no cost x environment interaction ($F_{5,96} = 0.9$, $p = 0.475$). The negative TO-intervals for all cost conditions and environments (Fig 3.3B, C) indicates that participants shifted gaze to the manipulated target prior to initiating swing phase to step on it. This is consistent with past work, showing that, when it is possible, people prioritize a look-ahead strategy to facilitate visuomotor planning of the upcoming step (Chapman and Hollands 2007; Domínguez-Zamora et al. 2018). Our results suggest that perceived motor cost does not affect the planning of this step.

We next sought to determine how motor cost affects the time interval between a saccade away from a target and heel contact (HC) on that same target (HC-interval; Fig. 3.4A). The timing of shifts in gaze relative to stepping on the target depended on both the motor cost condition and environment (Cost x Environment interaction: $F_{5,97} = 2.4$, $p = 0.043$). In the 4-target environment, participants transferred gaze away from the manipulated target they were about to step on later when encountering motor cost conditions 5 and 6 compared to motor cost conditions 1 and 2 (Fig 3.4B). This is reflected by a change from negative to positive HC-intervals. Specifically, we found that gaze shifted away from the stepping target ~127 ms prior to footfall on it in motor cost condition 1 and ~60 ms after heel contact in motor cost condition 6. In the 2-target environment, participants maintained their gaze on the target until after heel contact for all motor cost conditions (Fig 3.4B, C). These results suggest that the decision of when to redirect gaze from the stepping target is sensitive to motor cost, and that participants adapted gaze behavior to increase continued visual feedback of the leg when motor cost increased in the 4-target environment.

If gaze shifts are delayed with greater motor cost, did an increase in total gaze time on the target accompany these changes? As illustrated in Fig. 3.5, gaze time on the manipulated target was nearly twice the duration in the 2-target versus the 4-target environment (Environment: $F_{1,99} = 217.9$, $p < 0.0001$), likely because there were fewer targets to fixate. However, we found no significant differences in gaze times (normalized to trial duration) on the manipulated target across the six motor cost conditions (Cost: $F_{5,99} = 0.5$, $p = 0.775$; Cost x Environment: $F_{5,99} = 0.3$, $p = 0.893$).

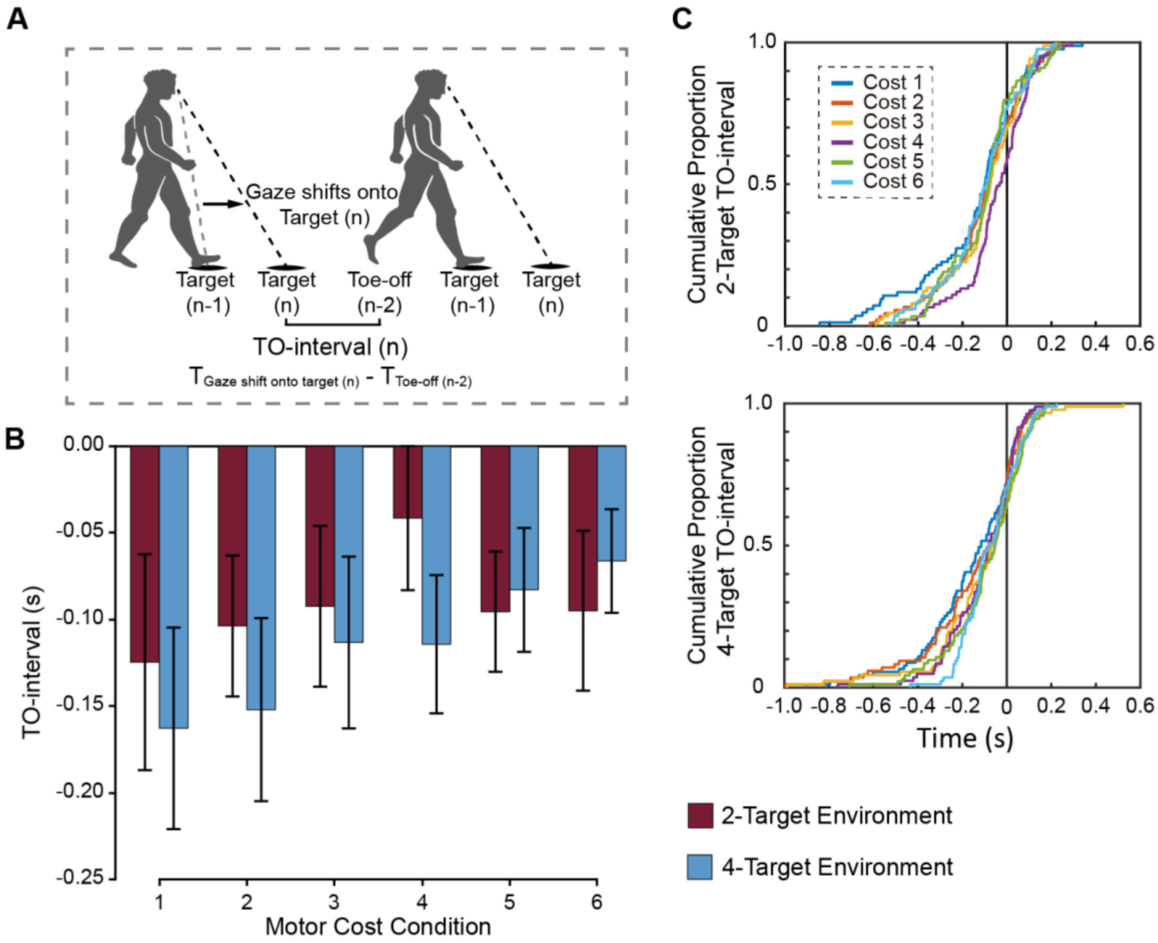

Figure 3-3. Timing of gaze shifts relative to initiating a step to the manipulated target (n = 10 participants)

(A) The toe-off interval (TO-interval) is the time at which the participant fixates the target minus TO of the foot to step on it, where negative values indicate a saccade and subsequent fixation made to the target before TO. (B) TO-intervals for the different motor cost conditions and environments. Data are represented as mean ± SE. (C) Cumulative proportion of TO-intervals for each cost condition in the 2- and 4-target environments. Each distribution combines all trials for each participant.

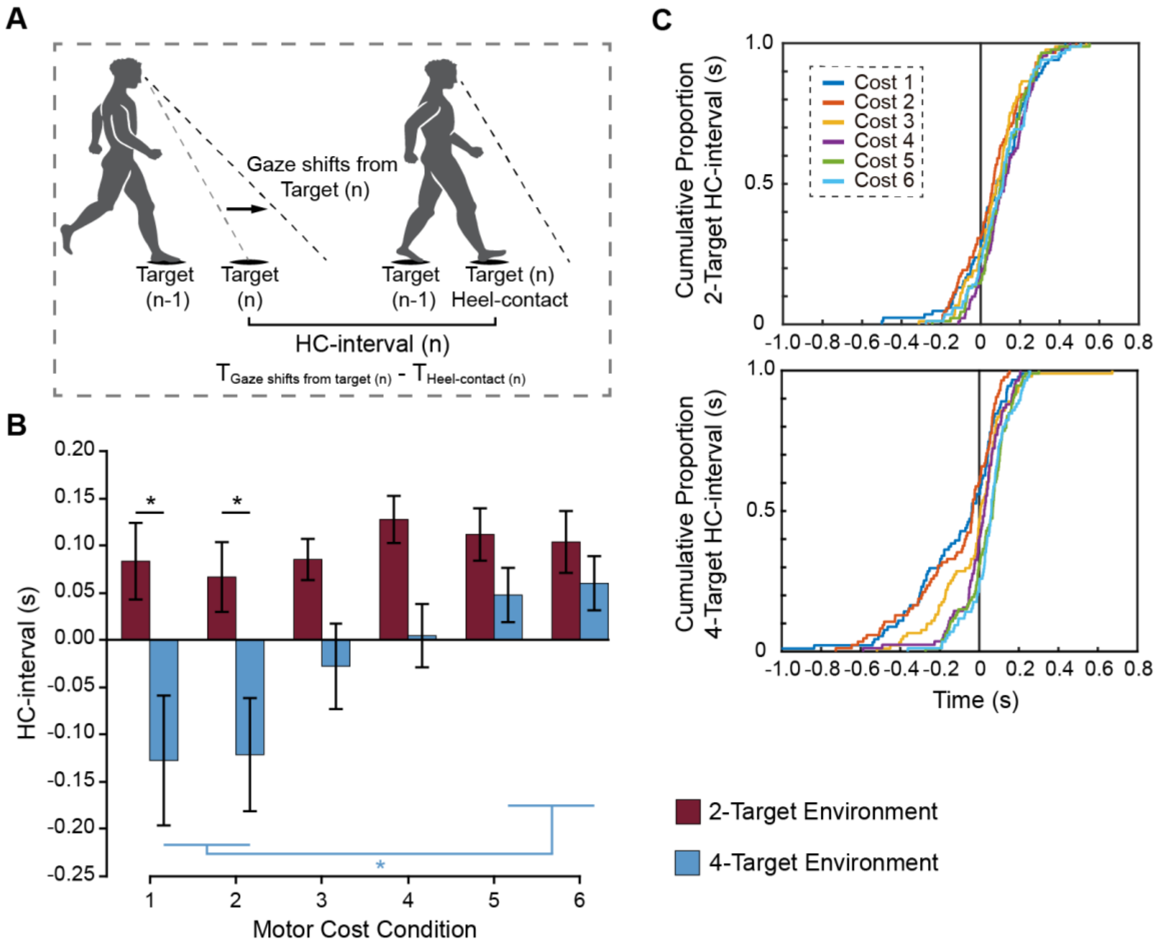

Figure 3-4. Timing of gaze shifts relative to completing a step to the manipulated
(A) The heel contact interval (HC-interval) is the time at which the participant shifts gaze away from the target relative to making HC on it, where positive values indicate that gaze is shifted away after HC. (B) HC-intervals for the different motor cost conditions and environments. Data are represented as mean ± SE. Asterisk indicates that values are significantly different from each other based on post hoc tests following a significant Cost x Environment interaction ($p < 0.05$). (C) Cumulative proportion of HC-intervals for each cost condition in the 2- and 4-target environments. Each distribution combines all trials for each participant.

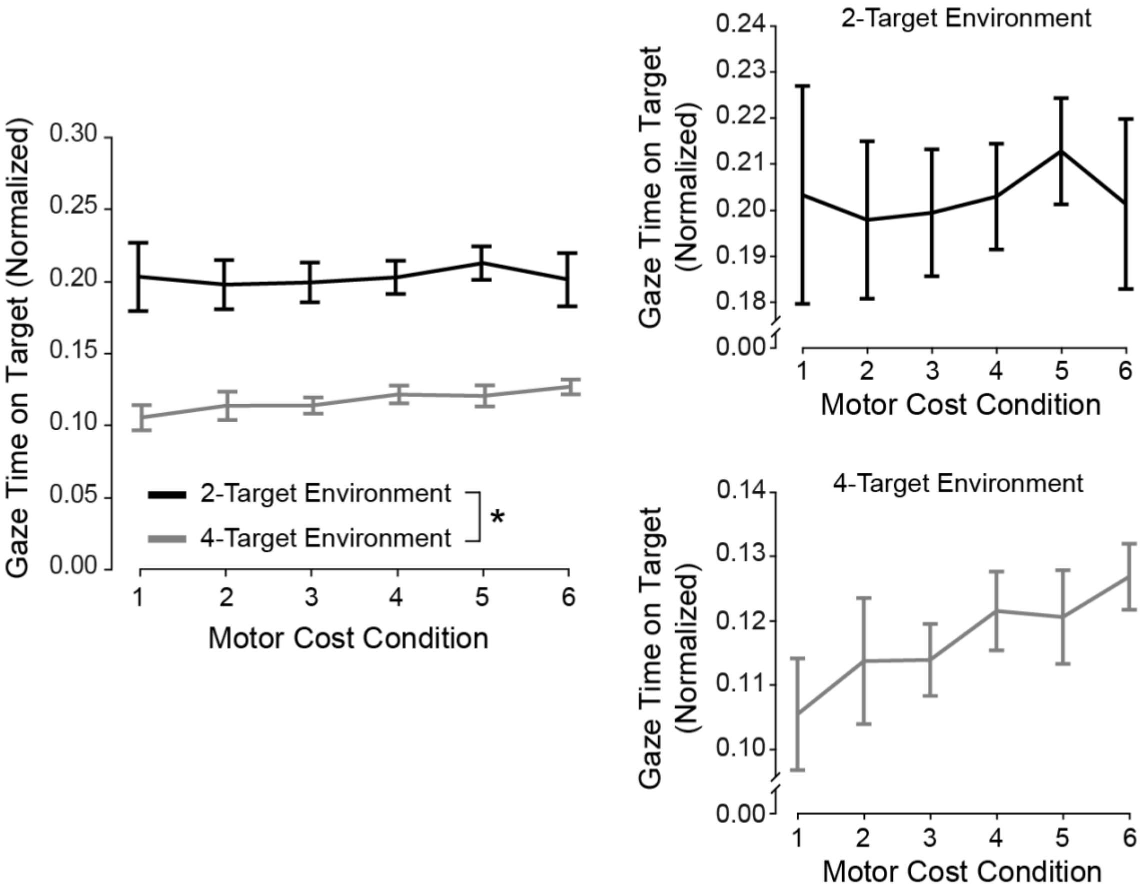

Figure 3-5. Gaze time on the manipulated target (n = 10 participants)
The left panel plots gaze times from the two environments on the same scale. The 4-target environment has more targets present and thus gaze time on the target is less ($p < 0.05$). Given this effect, the right panel provides an enlarged view for each environment. Data are normalized to trial duration and represented as mean ± SE. Asterisk indicates values are significantly different based on a main effect of environment.

3.4.3. Flexible gaze behaviour allows for similar foot placement control

To determine if changes in motor cost affected motor performance, we first quantified gait speed. A two-way (Cost X Environment) ANOVA showed that participants changed their gait speed ($F_{1,99} = 7.4$, $p = 0.008$) depending on the environment they encountered (Fig. 3.6A). Post hoc tests revealed that participants walked slower in the 2-target environment (1.18 ± 0.05 m/s) compared to the 4-target environment (1.20 ± 0.05 m/s). We found no significant interaction ($F_{5,99} = 0.4$, $p = 0.846$). However, in both environments, participants also decreased gait speed when dealing with higher motor cost targets (Cost: $F_{5,99} = 20.2$, $p < 0.0001$).

Next, we calculated foot-placement error and foot-placement error variability relative to the manipulated target. Motor cost condition did not affect foot-placement error (Cost: $F_{5,102} = 1.7$, $p = 0.143$; Cost x Environment interaction: $F_{5,99} = 0.3$, $p = 0.936$; see Fig. 3.6B). However, participants had less foot-placement error in the 4-target environment compared to the 2-target environment (Environment: $F_{1,102} = 6.9$, $p = 0.010$). Specifically, foot-placement error was 3.9 mm greater in the 2-target environment. However, this difference is relatively small given that foot-placement error on targets was, on average, 41.5 mm and 37.6 mm in the 2-target and 4-target environments, respectively. We subsequently compared foot-placement error variability (i.e., the between-trial standard deviation of foot-placement error) between cost conditions and environments (Fig. 3.6C). Participants had the same error variability in the 2-target and the 4-target environments (Environment: $F_{1,101} = 0.0001$, $p = 0.993$) and across the different motor cost conditions (Cost: $F_{5,102} = 1.6$, $p = 0.166$). We found no significant cost x environment interaction as well ($F_{5,98} = 0.7$, $p = 0.639$). Thus, the changes in gaze behavior contributed to similar foot-placement control within each environment despite differences in the cost to move the leg to the manipulated target.

Since the HC-interval varied across motor cost conditions (at least in the 4-target environment) and foot-placement error remained relatively constant, we determined whether there was a relationship between these two measures. Based on a linear mixed-model regression, however, we found no significant relationship in the 2-target environment ($R_2 = 0.85$, $p = 0.074$) or the 4-target environment ($R_2 = 0.67$, $p = 0.913$).

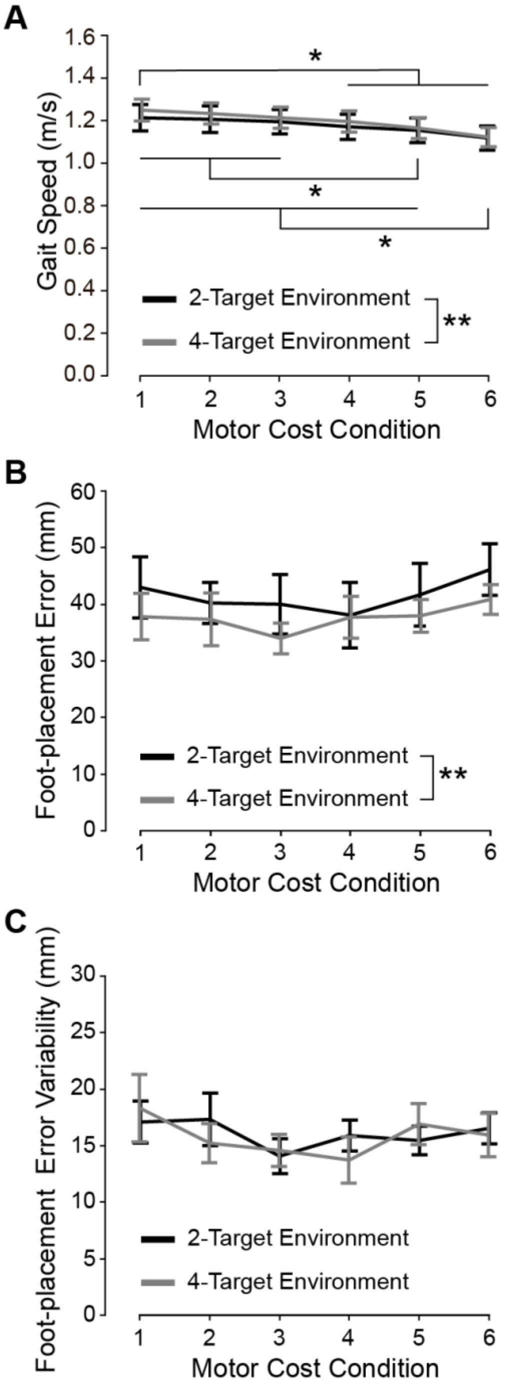

Figure 3-6. Gait speed and foot-placement accuracy on the manipulated target (n = 10 participants)

(A) Gait speed. (B) Foot-placement error based on the vector distance between the center of the manipulated target and the mid-foot in the different motor cost conditions and target-environments. (C) Foot-placement error variability based on the standard deviation of the between-trial foot-placement error. We found no statistically significant differences across motor cost conditions for either foot-placement measure. Asterisk indicates values are significantly different based on post hoc tests following a main effect of motor cost condition (*) or environment (**). Data are represented as mean ± SE.

3.4.4. The cost to control lateral stability may explain greater visual guidance for the step

Our results suggest that motor cost affects the decision of when to shift gaze away from the current stepping target (i.e., the HC-interval). However, this modulation only occurred in the 4-target environment. If the effort to swing the leg to the manipulated target is the only source of motor cost, then we would expect to see gaze differences in both environments. Is there an explanation for this finding?

Walking requires active step-by-step lateral balance control (Bauby and Kuo 2000; Bruijn and van Dieën 2018; O'Connor and Kuo 2009). This active step-by-step control would increase in the 4-target environment because of the additional step target following the manipulated one. This creates a situation where there are two large consecutive step widths in the higher motor cost conditions. Figure 3.7A illustrates the average trajectory for the trunk (represented by a chest position marker) and foot (represented by a mid-foot position marker) across three different motor cost conditions and both environments. These trajectories are from toe-off of the foot about to step on the manipulated target to toe-off from the manipulated target. Note that the shape of the trajectory for the trunk is different when comparing between the 2-target and 4-target environments. In the latter, participants maintained the trunk more medially, since they would have to redirect their body to an additional target. In the 2-target environment, the participant continues walking along a new (now laterally shifted) plane of progression since there are no additional foot-placement constraints. To quantify how this different strategy dictated by the two environments affects balance control, we calculated the medial-lateral DMS proposed by Hof et al. (2005). This measure is the distance between the base of support (based on a lateral heel position marker) and the extrapolated center of mass (see Fig. 3.7B); the extrapolated center of mass takes into account both the position and velocity of the center of mass, which we base on a position marker placed on the participant's chest. Positive DMS values indicate a dynamic stable situation, where the trunk is located more medial than the foot (Bruijn et al. 2013; Hof 2008). We chose not to include gait speed as a covariate in this analysis since the DMS already takes into account the speed of the center of mass. However, we find virtually identical results if it is included.

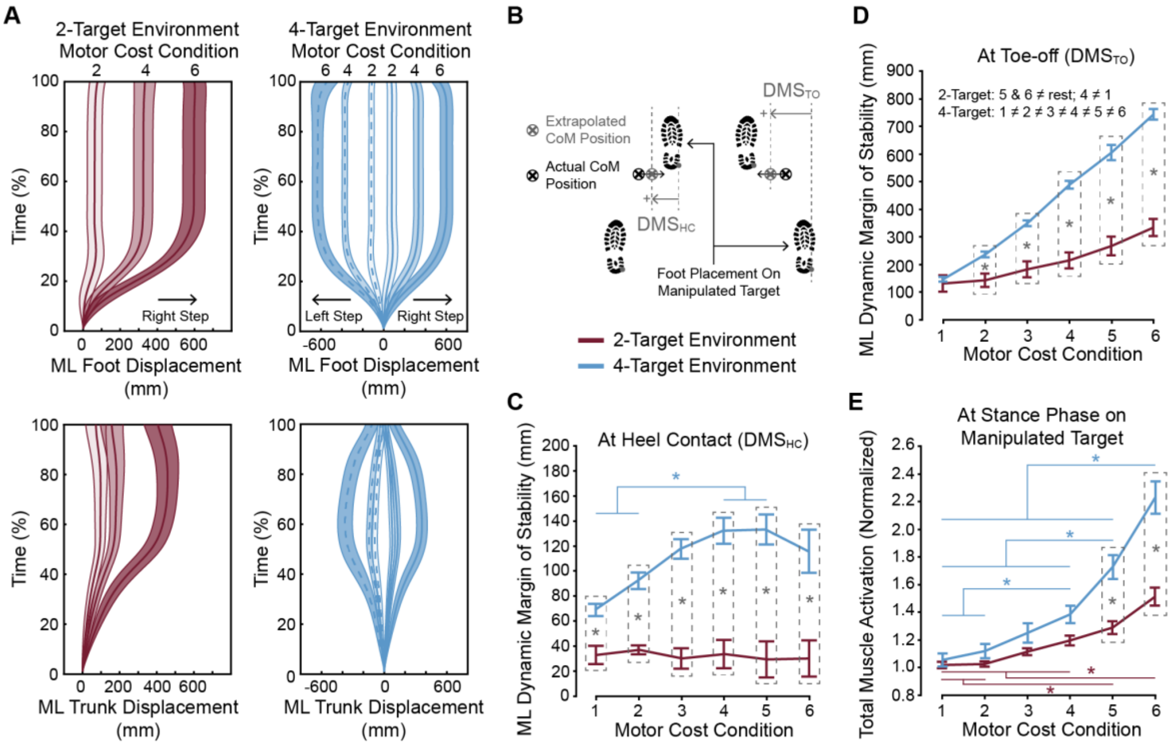

Figure 3-7. Effort involved in redirecting the body and foot (n = 10 participants)
(A) Medial-lateral (ML) trajectory of a foot and chest (or trunk) position marker for one stride. Data are time-normalized from toe-off (TO) of the foot about to step on the manipulated target to TO from the manipulated target. Only three of the six motor cost conditions are shown for simplicity. (B) Illustration showing how the dynamic margin of stability (DMS) is calculated at heel contact (HC) on, and TO from, the manipulated target. The extrapolated center of mass (CoM) takes into account the position and velocity of the body's CoM (represented by a position marker on the participant's chest). Positive values indicate that the extrapolated CoM is medial to the base of support defined by the foot. (C) The ML DMS at HC (DMS$_{HC}$) in the different environments and across motor cost conditions. (D) The ML DMS at TO (DMS$_{TO}$) in the different environments and across motor cost conditions. (E) Total muscle activity (from five bilateral leg muscles) calculated from heel contact on the manipulated target until TO from that target, normalized to walking trials without targets present and adjusted for muscle-volume differences. All data are represented as mean ± SE. Asterisk indicates that values are significantly different from each other based on post hoc tests following a significant Cost x Environment interaction ($p < 0.05$).

We first determined the value of this measure at the instance of heel contact on the manipulated target (DMS$_{HC}$) and compared it across motor cost conditions and environments using a two-way (Cost x Environment) ANOVA. We found a significant cost x environment interaction ($F_{5,99} = 6.4$, $p < 0.0001$). Post hoc tests revealed no significant differences between the DMS across the motor cost conditions in the 2-target environment (Fig. 3.7C). However, motor cost conditions 4 and 5 differed from motor cost conditions 1 and 2 in the 4-target environment. In addition, we observed larger DMS values in motor cost conditions 2 – 6 in the 4-target environment compared to all conditions in the 2-target environment.

We next determined the value of this measure at the instance of toe-off from the manipulated target (DMS_{TO}). In this case, we also found a significant interaction between cost and environment ($F_{5,99} = 45.0$, $p < 0.0001$). Post hoc tests indicated that participants chose a more stable position (greater DMS) through separation of their trunk and leg in the 4-target environment when compared with the 2-target environment (except for motor cost condition 1; Fig. 3.7D). Interestingly, the trunk-leg separation increased (greater DMS) with greater motor cost. This increase is more evident in the 4-target than in the 2-target environment.

To quantify the different effort involved in having to redirect the body towards another target in the 4-target environment, but not the 2-target environment, we calculated the TMA during stance phase (heel contact until toe-off) on the manipulated target. A two-way ANOVA (Cost X Environment) significant interaction ($F_{5,88} = 13.2$, $p < 0.0001$) showed greater TMA with the higher motor cost conditions for both environments, with greater TMA evident in the 4-target environment for motor cost conditions 5 and 6 compared to the 2-target environment (Fig. 3.7E). Taken together with the DMS measures, our results suggest that the greater active control required for redirecting the body's CoM in the 4-target environment increased the motor cost associated with the movement and contributed to the increased need for online visual feedback.

How do the DMS and TMA relate to the HC-interval across the range of motor cost conditions? To determine this, we performed mixed-model regressions for both environments. First, we used the DMS at heel contact on the manipulated target and the TMA calculated just prior to this gait event, which resulted in an overall model R_2 of 0.63 and 0.77 for the 2-target and 4-target environments, respectively. We found that the DMS significantly predicted the HC-interval in the 4-target (beta coefficient = 0.081, $p < 0.0001$), but not in the 2-target environment ($p = 0.930$). The TMA did not significantly predict the HC-interval in the 2-target environment ($p = 0.566$) or the 4-target environment (beta coefficient = 0.029, $p = 0.078$). Thus, the DMS at heel contact had a 2.8 times stronger effect on the HC-interval than the TMA. Second, we used the DMS at toe-off from the manipulated target and the TMA during stance phase on that target, which resulted in an overall model R_2 of 0.63 and 0.80 for the 2-target and 4-target environments, respectively. We found that the DMS had a significant relationship to the HC-interval in the 4-target (beta coefficient = 0.143, $p < 0.0001$), but not in the 2-target environment ($p = 0.354$). Similarly, the TMA had a significant relationship with the HC-interval in the 4-target (beta coefficient = -0.074, p = 0.015), but not in the 2-target environment (p = 0.441). In this case, the DMS at toe-off had a 1.9 times stronger relationship with the HC-interval than the TMA. In both cases, a greater DMS associated with delayed transfer of gaze away from the manipulated target.

3.5. Discussion

The cost associated with a movement is generally thought to affect how one moves (Gallivan et al. 2018; Shadmehr et al. 2016). Our findings suggest that, when precise foot placement is required to negotiate an environment, the motor cost of the step contributes to the decision of how to allocate gaze. We show that this relates to the effort of moving the leg and redirecting the body's center of mass from target-to-target due to the sequential nature of the task. Taken together, our results provide new insight into how and why gaze and leg movements are coupled together to control locomotion in cluttered environments.

Behavioral- and neurophysiological-based studies demonstrate that gaze is driven by a need to reduce environmental uncertainty and a desire to maximize reward (Domínguez-Zamora et al. 2018; Gottlieb 2018; Hayhoe 2017; Sprague et al. 2007; Tong et al. 2017). The results of recent studies suggest that cost may also influence gaze decisions. For instance, Li et al. (2016, 2018) interpreted the fact that participants initially spent longer times in an incorrect virtual room when searching for objects, and reduced head rotations and total distance travelled to find the object upon repeated exposure, as relating to a strategy to minimize the cost of moving the body and head. In addition, Matthis et al. (2018) interpreted gaze behavior when walking as possibly due to the motor cost associated with the different terrain encountered; they argued that the observed gaze strategy served to maintain energetically optimal gait. Here we systematically manipulated the cost associated with a step to a ground target. Unlike these other studies, we also quantified motor cost in our task. This included the effort to move the leg and the effort to maintain stability. Our results provide support for these previous interpretations by directly showing that motor cost is another factor that drives the allocation of gaze during naturalistic behavior.

Why did motor cost affect the decision of when to shift gaze in the 4-target but not the 2-target environment? In the 2-target environment, there are no additional foot-placement constraints after the manipulated target. Here participants step laterally and are then free to continue walking forward along this new (now shifted) direction (see Figs. 3.1, 3.7A). In all motor cost conditions in this environment gaze is transferred away from the manipulated target after the participant makes contact with it (i.e., a positive HC-interval). We have previously shown this for the last stepping target in the sequence (Domínguez-Zamora et al. 2018), and others have found this for gaze during hand movements to targets (Bowman et al. 2009).

In the 4-target environment, there are a greater number of sequential steps to make, complicating the planning and control of foot placement. There are clear differences in the HC-interval between environments for the low-cost conditions. It is possible that this stems from some form of cognitive cost in that participants had to attend to two additional targets in the path; an earlier shift of gaze away from the manipulated target may facilitate stepping to the next target. However, this potential 'cognitive cost' does not explain the shift from negative to positive HC-intervals across conditions in the 4-target environment (see Fig. 3.4). In this environment, we only manipulated one of the middle two targets on a trial-to-trial basis. We have previous found that HC-intervals for the middle targets in a sequence are negative (Domínguez-Zamora et al. 2018) and, in the present study, we found this same pattern for the low-cost conditions. A recent study (Matthis et al. 2018) argued that environments with fewer stable footholds require planning further ahead in the path. Fewer stable footholds is similar to an environment with greater constraints on foot placement (i.e., our 4-target environment). However, we did not observe this in the high-cost conditions. Our task emphasized the need for accurate foot placement, whereas the task in Matthis et al. (2018) did not, which may explain these discrepancies. If this is true, this highlights the complex interplay between the subjective value placed on the goal of the task, motor cost, terrain complexity, and path planning during walking.

To deal with a costlier step in the 4-target environment, participants delayed shifting gaze away from the current stepping target. This suggests that participants switch from a strategy of planning steps to future targets to one favoring visual feedback of the current foot placement. In the 4-target environment, there is an increase in the cost to maintain stability relative to the 2-target environment. Specifically, the higher motor cost conditions of this environment create a situation where there are two large sequential step widths (compared to just one in the 2-target environment), which requires more active control (Bauby and Kuo 2000; Bruijn and van Dieën 2018; O'Connor and Kuo 2009) and challenges stability when trying to maintain accuracy. This greater cost includes swinging the foot to the target after the manipulated one (reflected in greater muscle activity; Fig. 3.7E) and the need to redirect the body's center of mass back to the original plane of progression. This latter idea is reflected in a larger DMS, indicating the center of mass deviates further away from the foot in contact with the manipulated target (Fig. 3.7C,D), and is indirectly related to muscular effort. Greater muscle activity associated with increased step widths leads to greater signal-dependent noise in motor pathways (Harris and Wolpert 1998; Jones et al. 2002; van Beers et al. 2004), which has the potential to make steps more variable. Continued foveal-based visual feedback may serve to overcome this greater noise and inherent movement variability in the high-cost conditions, with the goal of maintaining foot-placement accuracy. This is consistent with previous research (Domínguez-Zamora et al. 2018; Chapman and Hollands 2007; Miller et al. 2018; Smid and den Otter 2013) and the fact that foot-placement error and error variability remained similar across the motor cost conditions in our experiment, though our regression analysis did not show a significant relationship between the HC-interval and foot-placement error. It is also consistent with the idea that the role of gaze is to gather critical information to complete a task (Domínguez-Zamora et al. 2018; Gottlieb 2018; Hayhoe 2017). Thus, while the purpose of gaze is to gain information necessary to compensate for greater noise to maintain foot-placement accuracy, it is the motor cost associated with stepping that drives this need in our experiment. Taken together, we propose that the greater step-to-step demands of this environment, which are most prevalent in the high-cost conditions, affect the decision of when to shift gaze to ensure stable and accurate foot placement.

Regardless of motor cost condition and environment, participants shifted gaze to the manipulated target before lifting the foot off the ground (reflected by negative TO-intervals). This look-ahead strategy (Land et al. 1999; Mennie et al. 2007) to plan future steps is compatible with the 'critical control phase' hypothesis for visually guided walking (Matthis et al. 2015, 2017). However, our finding of continued use of visual feedback during the swing phase of the step (reflected by positive HC-intervals) is not. Work on the critical control phase had targets disappear at different times and did not record gaze, which may explain the inconsistency. It is possible that participants continued to fixate the approximate step-target location even after it disappeared. Ultimately, though, the results of each of these studies highlight the importance of vision for efficient and accurate walking behavior. The delayed gaze shift may ensure visual feedback about foot placement relative to the target matches the predicted visual consequences of the intended step; others have proposed this idea for gaze-hand coordination when reaching to sequential targets (Bowman et al. 2009). This implies that the brain uses state estimation to regulate foot placement during walking (that is, it combines predicted and actual sensory feedback to form a belief about limb state or the world), a process we have recently shown to be the case (Maeda et al. 2017).

The sequential decision-making nature of our task may resemble animal foraging. Foraging behavior involves deciding whether to exploit the resources within the current patch or to explore a new patch that may be more rewarding (Stephens 2008). Leaving the current patch, though, gives rise to some level of effort or cost of time associated with traveling to the new location. If we assume that in our task gaze harvests for information at a target (or patch of ground) to obtain a reward (i.e., an accurate step), and the brain must decide when to shift gaze to the next target, can foraging theory explain aspects of our data? This theory suggests increased exploitation time, represented by gaze time, when there is more effort involved in moving to and away from a particular patch (Stephens 2008; Yoon et al. 2018). In support, a recent saccade-based foraging study found increased gaze times at the current target in situations where there was greater effort to reach that target (based on saccade ‘travel distance’), and with greater expected effort to move to the next one (Yoon et al. 2018). In the present study, we observed delayed gaze shifts with higher motor cost (which would require larger saccade and foot travel distances to the subsequent stepping target); these delayed gaze shifts are akin to leaving the current patch later. The delayed gaze shifts from the last target in the 2-target environment, even in the low-cost conditions, may simply reflect the fact that there is nothing of importance to look at ahead, so why not continue to forage with gaze on that target to maximize the intrinsic reward associated with accurate foot placement. The decision of when to shift gaze to a new location may rely, in part, on the anterior cingulate cortex (ACC) and/or frontal eye fields (FEF). For instance, during fixation, a longer travel time (reflecting more effort) results in a slower rate of rise of ACC activity to a threshold that is associated with patch-leaving decisions (Hayden et al. 2011). Furthermore, FEF neurons show suppressed activity that relates to maintaining longer fixation on a stimulus of interest (Mirpour et al. 2018). To understand this neural control in the context of walking, further research is required.

Overall, the decision of when and where to shift gaze is critical for the control of a variety of motor actions. Although the purpose of gaze is to gather information (to compensate for noise in sensorimotor pathways or uncertainty in the environment, for example), here we show that the motor cost to perform a limb-based action is factored into active visual sampling strategies when navigating the world. At a fundamental level, this provides new insight into what affects the coordination between the eyes and feet for the control of walking in cluttered environments.

3.6. Chapter contributions

F.J.D.-Z. and D.S.M. conceived and designed research; F.J.D.-Z. performed experiments; F.J.D.-Z. analyzed data; F.J.D.-Z. and D.S.M. interpreted results of experiments; F.J.D.-Z. prepared figures; F.J.D.-Z. and D.S.M. drafted manuscript; D.S.M. edited and revised manuscript; F.J.D.-Z. and D.S.M. approved final version.

Chapter 4.

Distinct gaze decisions to deal with motor cost and uncertainty during walking

> *‘‘All we have to decide is what to do with the time that is given us.’’*
>
> *(J.R.R. Tolkien)*

4.1. Abstract

When navigating through complex environments, we often need to select a step location among different alternatives. To deal with this situation, we need to decide where and for how long to allocate gaze to a particular location. These decisions are crucial to plan and control our motor actions. Here, we aimed to understand the motives driving gaze sampling decisions during walking. Specifically, we tested for the existence of a trade-off between the uncertainty of a target and the cost to step on that target in gaze sampling and step decisions. To address this, we used a precision walking paradigm that involved a decision of which of two targets to step on. To create a decision conflict where both targets compete for gaze allocation, we manipulated the visual uncertainty and motor cost associated with these step-target choices. This manipulation created situations where the most informative target (the one with lower uncertainty) was in a location that required greater energy expenditure to step onto than the other target, thus increasing the overall cost of walking. We also used different task instructions to change the subjective value that participants assign to foot-placement accuracy. We show that participants had different sampling strategies to decide where to step, and these distinct gaze behaviours led to different walking decisions. We identified a parameter (uncertainty sensitivity) to predict participant’s behaviour. For instance, participants that had greater uncertainty sensitivity sampled both targets and prioritized stepping onto highly informative locations. On the other hand, participants that had lower gaze uncertainty sensitivity only looked at one of the targets and preferred to minimize motor cost. Overall, our results suggest that when making gaze and step decisions people prioritize uncertainty and motor cost minimization differently.

4.2. Introduction

The brain must make at least two broad classes of decisions during visually guided, goal-directed movements. First, it must decide how to allocate gaze to acquire relevant information. Second, it must decide, on the basis of the visual input it receives and the goal of the task, where, when, and how to move. During walking, these decisions likely depend on the complexity of the environment, including the availability of step locations, as well as the uncertainty associated with those step locations (Fennell et al. 2015; Domínguez-Zamora et al. 2018; Domínguez-Zamora and Marigold 2019). Gaze helps us to sample the environment to evaluate which options are best to achieve our goal.

How do we use gaze to decide where to move during walking? Two main lines of work provide potential answers to this question. One approach suggests that biomechanical constraints, like the cost to maintain balance, or the cost to go from one location to another, are factored into how we use vision to guide walking (Matthis et al. 2015, 2017; Domínguez-Zamora and Marigold 2019). Indeed, the cost associated with redirecting foot placement onto a target modifies how gaze is allocated; when the cost to move the body increases, gaze strategies shift from one that focuses on the planning of future steps to one that prioritizes online visual control of the current action (Domínguez-Zamora and Marigold 2019). On the other hand, a different approach suggests that humans and animals allocate gaze with the goal of reducing uncertainty (or updating their beliefs state) about future actions (Gottlieb et al. 2014; Gottlieb 2012; Daddaoua 2016; Tong et al 2017; Domínguez-Zamora et al. 2018; Sprague and Ballard 2003; Sprague et al. 2007). In this case, we would adapt our gaze behaviour to accumulate evidence of the environment and improve the accuracy of our actions (Sprague and Ballard 2003; Sprague et al. 2007; Tong et al 2017; Domínguez-Zamora et al. 2018). While walking, these factors may compete for gaze allocation. However, which approach best describes gaze behaviour when facing multiple step choices is unclear.

In the real world, there are usually multiple choices of where to step. For instance, one may wish to step either long or wide to avoid a hazard. Research shows that people prefer to step to a location that does not deviate from the natural, ballistic motion of the leg (Barton et al. 2017) or that is based on a combination of minimizing foot displacement and maintaining both stability and forward progression (Moraes et al. 2004; Moraes and

Patla 2006). However, most studies that examine gaze behaviour during walking have focused on tasks with a single target choice that offer limited insights into the decision-making process involved in the selection of potential step locations (Hollands and Marple-Horvat 2001; Patla and Vickers 2003; Domínguez-Zamora et al. 2018; Domínguez-Zamora and Marigold 2019). Given the tight relationship between gaze and body movements, the factors driving gaze allocation may also explain motor decisions. For instance, if gaze is driven by the goal to minimize energy, we may look and step to locations that minimizes the overall cost of walking. On the other hand, if uncertainty (or information) drives our gaze decisions the brain may be reluctant to maintain the energetically optimal gait pattern and move towards more certain locations that will cause a greater energy expenditure. Consequently, understanding the factors underlying gaze decisions is essential to explain how we make motor decisions during unconstrained behaviours like walking.

In this study, we aimed to understand the motives driving gaze sampling decisions during walking. Specifically, we tested for the existence of a trade-off between the uncertainty of a target and the cost to step on that target in gaze sampling and step decisions. To address this, we used a precision walking paradigm that involved a decision between which of two targets to step on. To create a decision conflict where both targets compete for gaze allocation, we manipulated the visual uncertainty and motor cost associated with these step-target choices. This manipulation created situations where the most informative target (the one with lower uncertainty) was in a location that required greater energy expenditure to step onto than the other target, thus increasing the overall cost of walking. We used different task instructions to change the subjective value that participants assign to foot-placement accuracy. We found that participants had different gaze sampling strategies to decide where to step, and these distinct gaze behaviours led to different foot-placement decisions. Our findings go beyond previous gaze and action studies that average individual behaviour into a single theory. Instead, we show that people prioritize different factors when deciding how to sample the environment, and that this behaviour is closely related to their walking decisions.

4.3. Materials and Methods

4.3.1. Participants

Fourteen healthy young adults participated in this study (8 women and 6 men; mean age = 25.2 ± 3.7 years; mean leg length = 94.7 ± 5.9 cm). Participants did not have any known neurological, muscular, or joint disorder that could affect their behaviour in this study but wore corrective lenses if necessary (N = 2). The Office of Research Ethics at Simon Fraser University approved the study, and participants provided written informed consent before participating.

4.3.2. Experimental design and protocol

Participants performed a visually guided walking task that required them to walk across the laboratory at a self-selected speed and step onto four targets (2D Gaussian blobs) projected on the ground. An LCD projector (Epson PowerLite 5535U; brightness of 5,500 lm) displayed the white targets on a black mat covering the walking path. To diminish the effect of environmental references and increase target visibility, participants walked under reduced light conditions (~1.2 lx surrounding the targets and ~350 lx at the center of target with the lowest level of uncertainty). We configured the targets in MATLAB (The MathWorks, Natick, MA) with the Psychophysics Toolbox, version 3. Three of the “target rows” had one target present, and in either the second (50% of the trials) or third (50% of the trials) target “decision row”, participants had a choice of two targets to step on (Fig. 4.1A). In this forced-choice situation, we always positioned one of the targets at the participant’s preferred step location (Low-cost target). This equated to a step width of 0.13 of leg length (L) and a step length of 0.7 L (see Fig. 3.1B; Donelan et al. 2001). We manipulated the uncertainty level of this Low-cost target by varying the Gaussian blob’s standard deviation to create six, randomly presented uncertainty conditions (Domínguez-Zamora et al. 2018). Three of the uncertainty conditions are shown in Fig. 4.1C. We positioned the other (High-cost) target at 4x the participant’s preferred step width, a method that we have previously used to change the cost of stepping to targets while walking (Domínguez-Zamora and Marigold 2019). The High-cost and other targets in the sequence always had the lowest level of uncertainty. To reduce familiarity with the environment and avoid learning, on a trial-to-trial basis, we changed the step length (range: 0.65 - 0.75 L) in conjunction with the step width between targets—thus ensuring the same step vector—for both the low- and high-cost target; this created five different target positions.

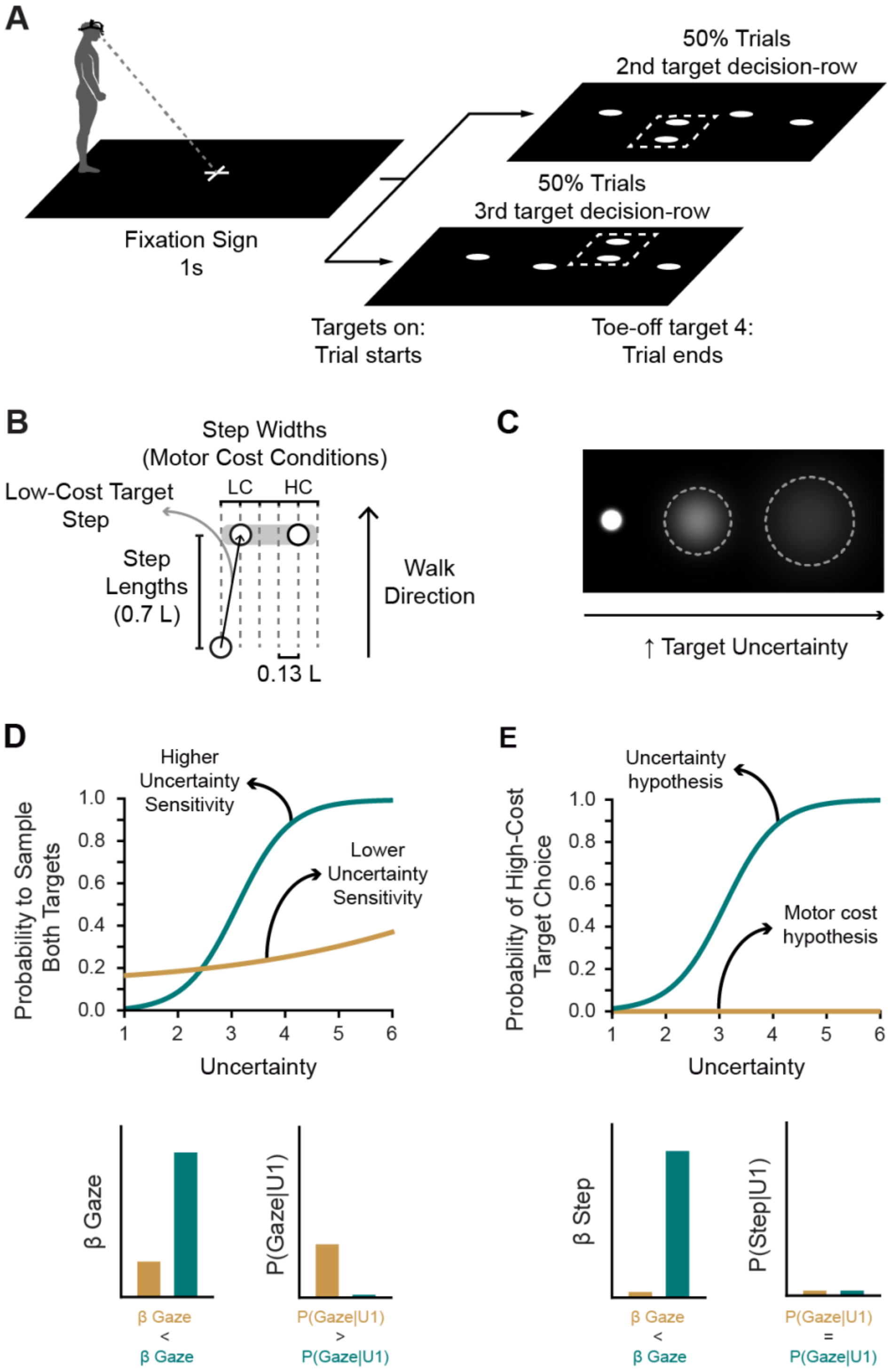

Figure 4-1. Experimental setup and hypothesis
(A) Participants (n=14) performed a visually guided walking task that required them to walk across the lab and step on four targets projected on the ground. Three of the target ‘rows’ had a single

target, and in one row (2nd or 3rd target row), participants had a choice of two targets to step on. In this forced-choice situation, we always positioned one of these step targets at the participant's preferred step location (Low-cost target). (B) To create two different levels of motor cost, we manipulated the step width by shifting the High-Cost target to 4x the preferred step width. (C) Example of targets with different uncertainty. We manipulated the uncertainty level of the Low-Cost target by varying the Gaussian blob's standard deviation to create six, randomly presented

Participants started the experiment by performing five walking trials in which we did not project targets. We used these walking (control) trials to normalize muscle activity (as described below). Subsequently, participants performed the precision walking task in two counterbalanced blocks of 60 trials that differed in the instructions provided. In the Precision-relevant task, we instructed participants to step with the middle of their foot to the centre of the targets as accurately as possible. In the Precision-irrelevant task, we instructed participants to step on the targets but informed them that they did not have to place their foot in the centre. Task instruction served to manipulate the subjective value assigned to foot-placement accuracy (**Chapter 2**; Domínguez-Zamora et al. 2018). The emphasis on accuracy makes gaze more important because of the increased value of gaining relevant environmental information.

Each precision walking trial began with the participant fixating a cross located between the second and third targets (note that the targets were not visible at this point). After 1 s, we projected all targets and removed the fixation cross; this signaled to the participants to start walking. We did not provide feedback on performance and participants were free to look wherever they wanted during the walking trials.

Two Optotrak Certus motion capture cameras (Northern Digital, Waterloo, ON, Canada), positioned perpendicular to the walking path, recorded infrared-emitting position markers placed on the participant's head and chest and bilaterally on each midfoot (second to third metatarsal head) and heel at 120 Hz. An electromyography (EMG) system (MA300; Motion Laboratory Systems, Baton Rouge, LA), synchronized using the Optotrak data acquisition unit, recorded leg muscle activity at 2,040 Hz from surface electrodes placed bilaterally over the belly of the tibialis anterior, medial gastrocnemius, vastus lateralis, biceps femoris, and gluteus medius muscles.

A high-speed mobile eye tracker (model H6-HS; Applied Science Laboratories, Bedford, MA) mounted on the participant's head and synchronized with the motion capture system recorded gaze position while walking at 120 Hz. We calibrated the eye tracker with a standard nine-point (3 x 3 grid) calibration method at the beginning of the experiments and checked the accuracy periodically throughout testing. To match experimental conditions, we positioned the nine calibration points on the floor approximately one step in front of participants. The spatial error of the eye tracker in the central (middle calibration point located on the floor) and periphery (average of the surrounding 8 calibration points) is 1.03 ± 0.55° and 1.34 ± 0.36°, respectively; this is based on seven participants not involved in this study.

4.3.3. Data and statistical analysis

To verify that the high-cost stepping target increased motor cost similar to our previous work (Domínguez-Zamora and Marigold 2019), we determined peak muscle activity and total muscle activation (TMA) during an interval between heel contact onto the target before the decision row until toe-off from the decision-row target. Prior to this analysis, we full-wave rectified and filtered the EMG data (with a zero-phase, 4th-order, 50 Hz low-pass Butterworth algorithm). For peak muscle activity, we determined the peak activity for each individual muscle and then normalized this value to the peak during the control walking trials. Finally, we averaged this value across all muscles. For the TMA metric (Domínguez-Zamora and Marigold 2019), we first determined the muscle activation (MA) for each individual muscle, which involved calculating the EMG area under the muscle profile during the precision walking trials and dividing it by the area under the ensemble-averaged profile of the control walking trials. Next, to account for muscle volume differences, we used normalized volume fraction values (Handsfield et al. 2014) to calculate a weighting factor for each muscle, such that the sum of the weight factors equated to 1. Finally, we calculated the TMA using a weighted arithmetic mean. To determine differences in motor cost, we compared peak muscle activity and TMA between motor cost conditions (High-cost versus Low-cost) with separated paired t tests.

We used kinematic data to quantify gait speed and foot-placement accuracy. Prior to this analysis, we filtered kinematic data using a zero-phase, 4th-order, 6-Hz low-pass Butterworth algorithm. We defined gait speed as the distance between the first and fourth targets divided by the time it took the chest infrared marker to cross between these two locations. We defined foot-placement error as the vector distance between the foot (midfoot infrared marker) and the middle of the target at the time point when the foot's anterior-posterior velocity and acceleration profiles stabilized to zero. We also calculated foot-placement error variability, defined as the within-trial standard deviation of the foot-placement error across all targets and between-trial standard deviation associated with stepping on a target in the decision row. We used a paired t test to determine differences in gait speed between the Precision-relevant and Precision-irrelevant tasks. In addition, we performed separate one-way ANOVAs (with gait speed as a covariate) to compare foot-placement error and foot-placement error variability on all targets in the path. We also performed this analysis for just the decision-row target between tasks (all uncertainty conditions pooled).

For each walking trial, we filtered the horizontal and vertical components of the gaze data (zero-phase, 4th-order, 12 Hz low-pass Butterworth algorithm) and then calculated the vector gaze position at each point in time. The time at which the local angular gaze velocity crossed above or below a threshold of 100 °/s for a minimum of 16 ms defined the onset and offset of gaze shifts, respectively (Domínguez-Zamora et al. 2018; Domínguez-Zamora and Marigold 2019). Periods > 50 ms between a saccade offset and a subsequent saccade onset defined gaze on a target or region of the ground. Note that while walking, gaze is rarely stable in the orbit because of the vestibulo-ocular reflex. We used the 30-Hz video of the path with crosshairs of gaze position superimposed to verify the presence and location of fixations. To assess gaze behaviour, we quantified the gaze time looking at the Low- and High-cost targets individually, the gaze time allocated to the decision-row target (the sum of gaze time on the Low-cost and High-cost targets), and the total gaze time looking at all targets on the path. We normalized all gaze measures by total walking trial duration. To determine how task instruction affects gaze behaviour while walking, we compared total gaze time between tasks using a paired t-test. To examine gaze times on the decision row, we first performed a paired t-test to compare the gaze times on the decision row (all uncertainty conditions pooled) between tasks. We also used separate two-way ANOVAs (Task x Uncertainty condition) to compare mean differences on the Low- and High-cost target gaze times. As previously done (Domínguez-Zamora et al. 2018 and Domínguez-Zamora and Marigold 2019), we did not include gait speed as a covariate when analyzing the gaze measures because they are normalized by trial duration. Finally, we used a Wilcoxon signed-rank to tests for significant differences from zero across tasks on the probability to fixate the Low-cost target first.

To model participant's choice behaviour, we fitted the individual gaze- and step-choice history with a two-parameter logit model using the fitglm function in MATLAB 2016b. For the gaze-choice model, we fitted the probability to sample both targets on the decision row. This procedure allowed us to extract the intercept (β_{0Gaze}) and slope (β_{Gaze}) of the logistic function. In this model, β_{Gaze} represents gaze uncertainty sensitivity, where higher values indicate a more variable gaze behaviour (greater tendency to sample both targets) when the uncertainty associated with the Low-cost target increases. Figure 4.1D shows hypothetical differences between both behaviours. Because the β_{0Gaze} coefficient is in the log-odds scale, we used the following equation to calculate the probability of sampling both targets:

$$P(Gaze|U) = \frac{1}{1 + e^{-(\beta_{0Gaze} + \beta_{Gaze} \times U)}} \tag{4.1}$$

P(Gaze|U) is the probability of sampling both targets in the decision row, β_{0Gaze} and β_{Gaze} are the estimated parameters, and *U* is the Low-cost target uncertainty level (1 to 6). P(gaze|U1) is the probability of sampling both Low- and High-cost targets when the uncertainty level of each was its lowest. Greater values mean a more variable gaze behaviour when there is not a decision conflict. In the subsequent analysis, we used this value, instead of the estimated β_{0Gaze}, because it is simpler to interpret. We used separate paired t tests to determine how task instruction changed the gaze-model parameters.

For the step-choice model, we fitted participant's probability to step onto the High-cost target. We used the same procedure as for the gaze model to extract the intercept (β_{0Step}) and slope (β_{Step}) of the logistic function. In this case, β_{Step} represents a participant's tendency to prioritize information or motor cost when making a step decision. Higher values indicate a greater tendency to interact with low uncertainty locations (represented by the High-cost target) when the uncertainty of the Low-cost target increases. Figure 4.1E shows hypothetical differences between the uncertainty and motor cost hypotheses. We used Eq.4.1 with the step-model parameters to calculate P(step|U1). P(step|U1) represents a participant's motor cost sensitivity, or the tendency to step onto the High-cost targets when the Low- and High-cost targets have the lowest uncertainty level. We used separate paired t tests to determine how task instruction changed the step-model parameters.

To determine the relationship between gaze and step decisions, we used separate linear mixed models with β_{Gaze} as the regressor and β_{Step} as the response variables for the Precision-relevant and Precision-irrelevant tasks. Additionally, we used separate linear mixed models with β_{Gaze} as the regressor and the gaze times on the Decision-row as the response variable.

We used Matlab 2016b (The MathWorks, Natick, MA) and JMP 14 software (SAS Institute, Cary, NC) with an alpha level of 0.05 for all statistical analyses. For all ANOVAs, we included participant as a random effect and used Tukey's post hoc tests when we found significant main effects.

4.4. Results

4.4.1. Task instructions modify walking performance

We used different task instruction to manipulate the subjective value assigned to foot-placement accuracy (Domínguez-Zamora et al 2018). To determine whether changes in task instructions affected motor performance, we compared gait speed using a paired t-test. We found that participants walked slower when performing the precision-relevant task (1.1 ± 0.1 m/s) compared to the Precision-irrelevant task (1.2 ± 0.09 m/s) ($t_{13} = 4.5$, $p = 0.0006$, 95% CI = 0.05 / 0.14).

Next, we calculated the average foot-placement error across all targets (Fig. 4.2A) and on the decision-row only (Fig. 4.2B) using separate one-way ANOVAs with gait speed as a covariate. We found that participants had greater total foot-placement error across all targets ($F_{1,17} = 16$, $p = 0.0007$) and on the decision-row target ($F_{1,17} = 17$, $p = 0.0006$) during the Precision-irrelevant task. Specifically, foot-placement error was 52.1 mm greater across all targets and 55.6 mm greater on the decision-row target during the Precision-irrelevant task. Subsequently, we compared foot-placement error variability across all targets (Fig. 4.2D) and for the decision-row target (Fig. 4.2E). In both cases, error variability was greater in the Precision-irrelevant task than in the Precision-relevant task (total foot-placement error variability: $F_{1,18} = 12.7$, $p = 0.0022$; decision-row foot-placement error variability: $F_{1,19} = 15.7$, $p = 0.0008$).

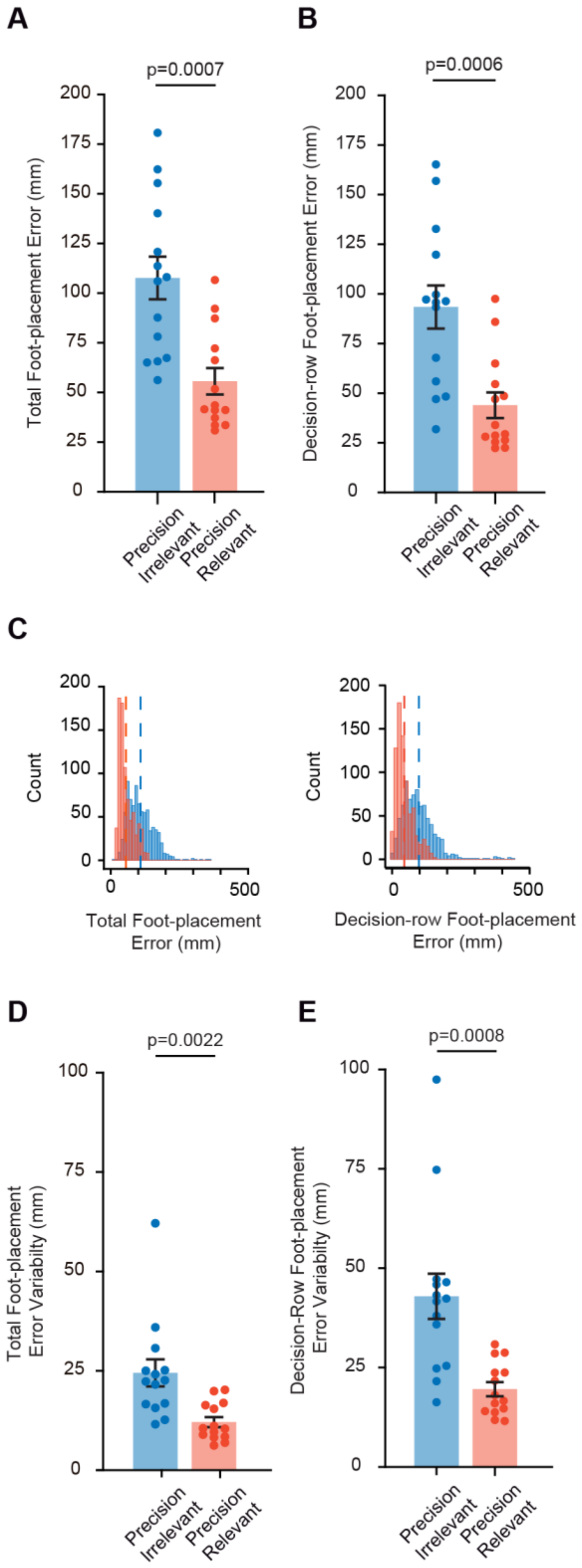

Figure 4-2. Foot-placement accuracy

(A) Foot-placement error across all target. (B) Foot-placement error on the decision-row target. (C) Distribution of foot-placement error. (D) Foot-placement error variability across all targets. (E)

Foot-placement error variability on the decision-row target. Data are normalized to walking trials without targets present. Data are represented as means ± SE, except in (C).

4.4.2. Step choices affect motor cost

Stepping on the High-cost target involves a greater cost related to swinging the leg and redirecting the body's center of mass from target to target (Domínguez-Zamora and Marigold 2019). As shown in Fig. 4.3A, TMA was 29% greater when participants stepped on the High-cost target compared to the Low-cost target ($t_{13} = 4$, p = 0.001, 95% CI = 0.13 / 0.45). We also found a significant effect of motor cost on the muscle peak activity ($t_{13} = 3.4$, p = 0.004, 95% CI = 0.1 / 0.46) (Fig. 4.3B). In this case, the muscle peak activity was 28% higher when participants stepped onto the high-cost target.

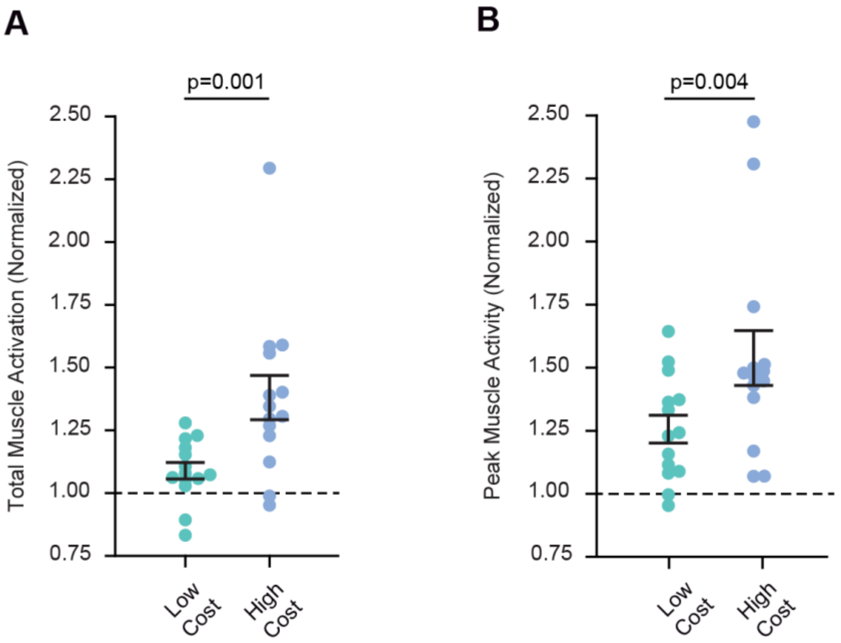

Figure 4-3. Motor cost

(A) Total muscle activity (from 5 bilateral leg muscles) calculated from heel contact on the target before the decision-row until toe-off on the decision-row target when participants choose the Low-cost versus the High-cost target. Data are normalized to walking trials without targets present and adjusted for muscle volume differences. (B) Peak muscle activity (averaged across all muscles) for the Low- and High-cost target in the decision-row. Data normalized to walking trials without targets present. For both measures, data are represented as means ± SE.

4.4.3. Task instructions and uncertainty affects gaze behaviour

Given that task instruction and step choice affect walking performance and motor cost, respectively, we asked whether task instructions and uncertainty affect gaze sampling strategies when deciding where to step. To address this, we normalized the total time looking at all stepping targets to trial duration and compared both tasks using a t test. As shown in Fig. 4.4A, and consistent with our previous work (Domínguez-Zamora et al. 2018), participants spent more time looking at all targets during the Precision-relevant when compared to the Precision-irrelevant task (total gaze time across all targets; paired t test: $t_{13} = 6.7$, $p < 0.0001$, 95% CI = 0.56 / 0.64). Specifically, the total gaze time was 14% greater during the Precision-relevant task (Total gaze time = 0.62 ± 0.05%) when compared with the Precision-irrelevant task (Total gaze time = 0.48 ± 0.08%).

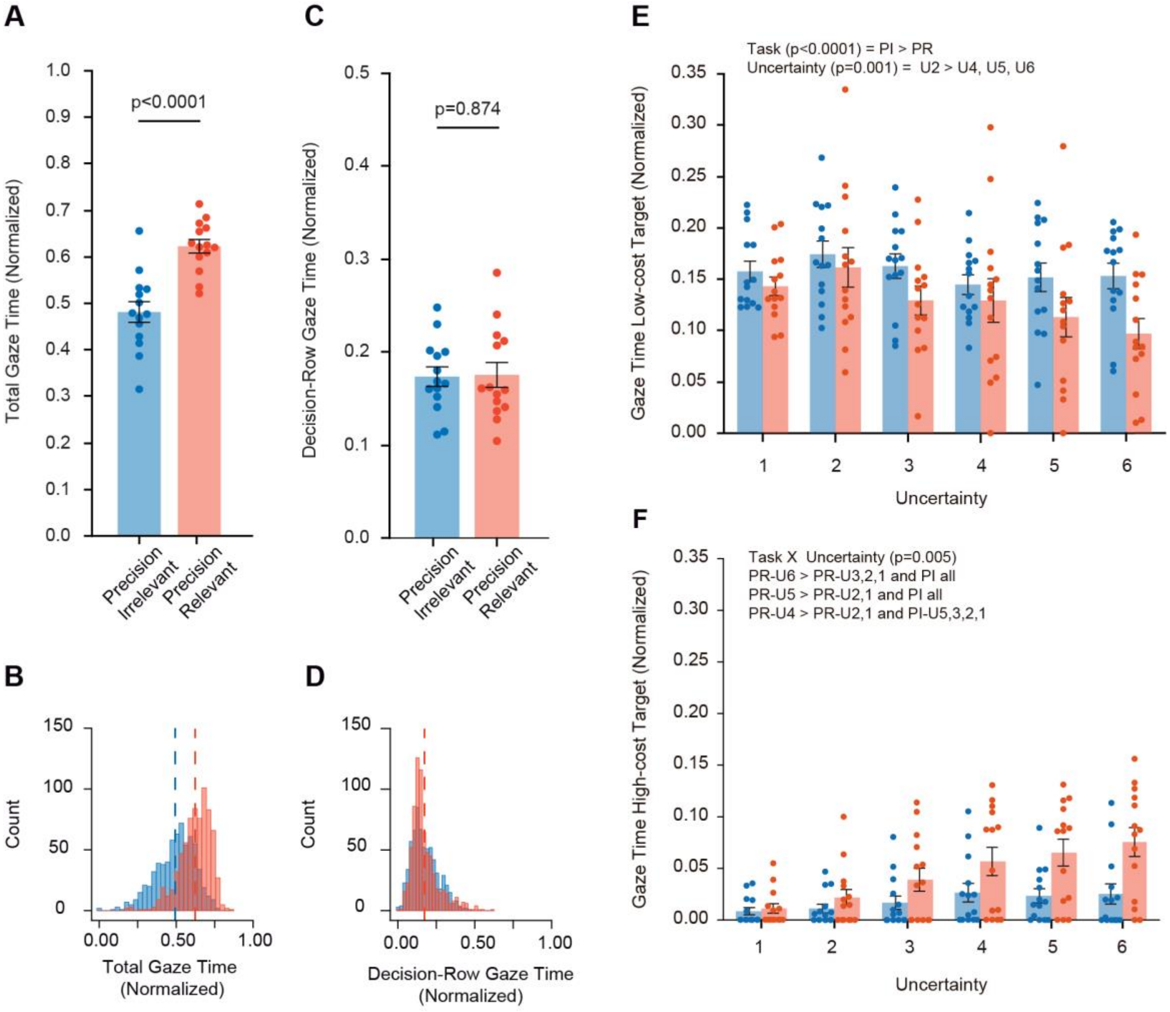

Figure 4-4. Gaze times

(A) Average total gaze time allocated to all targets for the Precision-relevant and Precision-irrelevant task. (B) Distribution of total gaze time data for all trials. (C) Average gaze times to the decision-row (summed for the Low-cost and High-cost targets) for each task instruction. (D) Distribution of decision-row gaze times data for all trials. (E) Average gaze time on the Low-cost target for each uncertainty level and task instruction. (F) Average gaze time on the High-cost target for each uncertainty level and task instruction. Data are represented as mean ± SE, except in (B) and (D). Gaze times are normalized (i.e., divided) by trial duration to control for differences in gait speed between trials and conditions.

How did participants sample the decision-row targets? To examine this question, we first summed the total gaze time allocated to the two targets on the decision-row (all uncertainty conditions pooled together). This measure provides us with one value per participant regarding the time that participants spent looking at the decision-row to make the step decision. We found no significant effect of task instructions (Fig. 4.4B; $t_{13} = 0.2$, $p = 0.874$, 95% CI = -0.02 / 0.03). In this case, gaze times were 0.18 ± 0.05% for the Precision-relevant and 0.17 ± 0.04% for the Precision-irrelevant task. The lack of differences in gaze times on the decision-row is probably a reflection of how participant's sample the individual targets to make the step decision. To examine how participants sampled the High- and Low-cost targets to make a decision when the uncertainty increases, we used separate two-way ANOVAs (task x uncertainty) to compare gaze times allocated to the Low- and High-cost targets on the decision row across task instructions and uncertainty conditions. For the Low-cost target, we found a main effect of Task ($F_{1,143} = 22.7$, $P < 0.0001$) and Uncertainty ($F_{5,143} = 4.3$, $p = 0.001$). Post hoc tests revealed that participants looked longer to the Low-cost target during the Precision-irrelevant task than when performing the Precision-relevant task. In addition, we found that participants looked longer to the Low-cost target during uncertainty condition 2 (when the Low-cost and High-cost target uncertainty differed by one level) than for uncertainty condition 4, 5, and 6. For the High-cost target gaze times, we found a significant interaction between Task and Uncertainty (Task x Uncertainty: $F_{5,143} = 3.5$, $p = 0.005$). Specifically, post hoc tests showed that participants increased their gaze times on the High-cost targets when it was associated with higher uncertainty levels (uncertainty condition 4, 5, and 6) during the Precision-relevant task. However, the large variability of gaze times across participants (see Table 4.1 for individual values) suggests that participants may have followed different gaze strategies.

This differences in gaze times between the Low- and High-cost target suggest that participants prioritize looking at the Low-cost target. To examine this, we calculated the probability to allocate the first fixation on the decision-row to the Low-cost target. We found a greater tendency to fixate the Low-cost target first during the Precision-relevant task (pair-wise Wilcoxon signed-rank test: $z = 3.3$, $p = 0.001$, 95% CI = 0.01 / 0.2; see Fig. 4.5). Importantly, participants showed a strong preference for sampling the Low-cost target first for 100% (median; IQR = 97%-100%) and 95% (median; IQR = 76%-100%) of the time during the Precision-relevant and Precision-irrelevant tasks, respectively.

Table 4-1. Gaze times decision-row

	Precision-relevant		Precision-irrelevant	
Participant	Mean	SD	Mean	SD
S1	0.16	0.07	0.14	0.09
S2	0.21	0.12	0.16	0.08
S3	0.22	0.11	0.20	0.11
S4	0.13	0.04	0.15	0.05
S5	0.16	0.06	0.16	0.05
S6	0.29	0.15	0.25	0.11
S7	0.14	0.04	0.11	0.04
S8	0.16	0.06	0.23	0.08
S9	0.24	0.11	0.20	0.08
S10	0.15	0.06	0.11	0.06
S11	0.14	0.04	0.17	0.07
S12	0.10	0.04	0.18	0.10
S13	0.15	0.04	0.20	0.08
S14	0.21	0.07	0.17	0.07

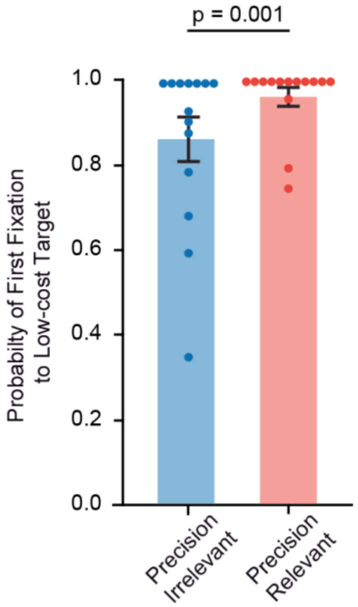

Figure 4-5. First fixation location probability
Probability to fixate the Low-cost target first for the Precision-relevant and Precision-irrelevant tasks. Data are represented as means ± SE.

4.4.4. Modelling individual differences in gaze and step choices

Previous work suggests that people make decisions motivated by different factors (KonovalovI and Krajbich 2016; Kobayashi et al. 2019). These different motives may produce different gaze patterns and considerable variability in gaze behaviour across participants. Figure 4.4 supports this notion. To quantify individual differences in gaze choices, we fitted each participant's gaze-choice behaviour with a logistic regression. To illustrate this variability, we plotted each participant's fitted choice function for the Precision-irrelevant (Fig. 4.6A) and Precision-relevant task (Fig. 4.6B). This method allowed us to use each participant's choice behaviour to extract two individual parameters that represent Gaze Uncertainty Sensitivity (βGaze) and the probability to sample both targets on the decision row when both targets had the same level of uncertainty (P(gaze|U1)). Table 2 shows the individual fitted parameters for the gaze-choice model. The subjective value that one assigns to a task may modify how one decides to sample the environment. To determine the effects of task instruction on gaze-choice behaviour, we compared the estimated parameters using separate paired t tests. We found that most participants had greater gaze uncertainty sensitivity (greater βGaze) during the Precision-relevant task than during the Precision-irrelevant task. However, we did not find differences across tasks (t_{13} = -2, p = 0.069, 95% CI = -0.58 / 0.03; see Fig. 4.6C). Furthermore, task instruction did not change participant's Pgaze|U1 (t_{13} = 0.6, p = 0.0591, 95% CI = -0.08 / 0.14; see Fig. 4.6D).

Does any relationship exist between both parameters? To test this, we performed a mixed-model linear regression to determine if participants that tend to sample both options when there is no decision conflict (the low-cost target is also the low uncertainty target) also have a more variable gaze behaviour when the uncertainty of the low-cost target increased. The linear regression analysis showed an inverse relationship between both parameters for the Precision-irrelevant task (R_2 = 0.34; β coefficient = -0.4; p = 0.017, 95% CI = -0.74 / -0.09), but not for the Precision-relevant task (R_2=0.06; β coefficient = -0.09; p = 0.202, 95% CI = -0.24 / 0.06). This indicates that the gaze parameters are independent from each other.

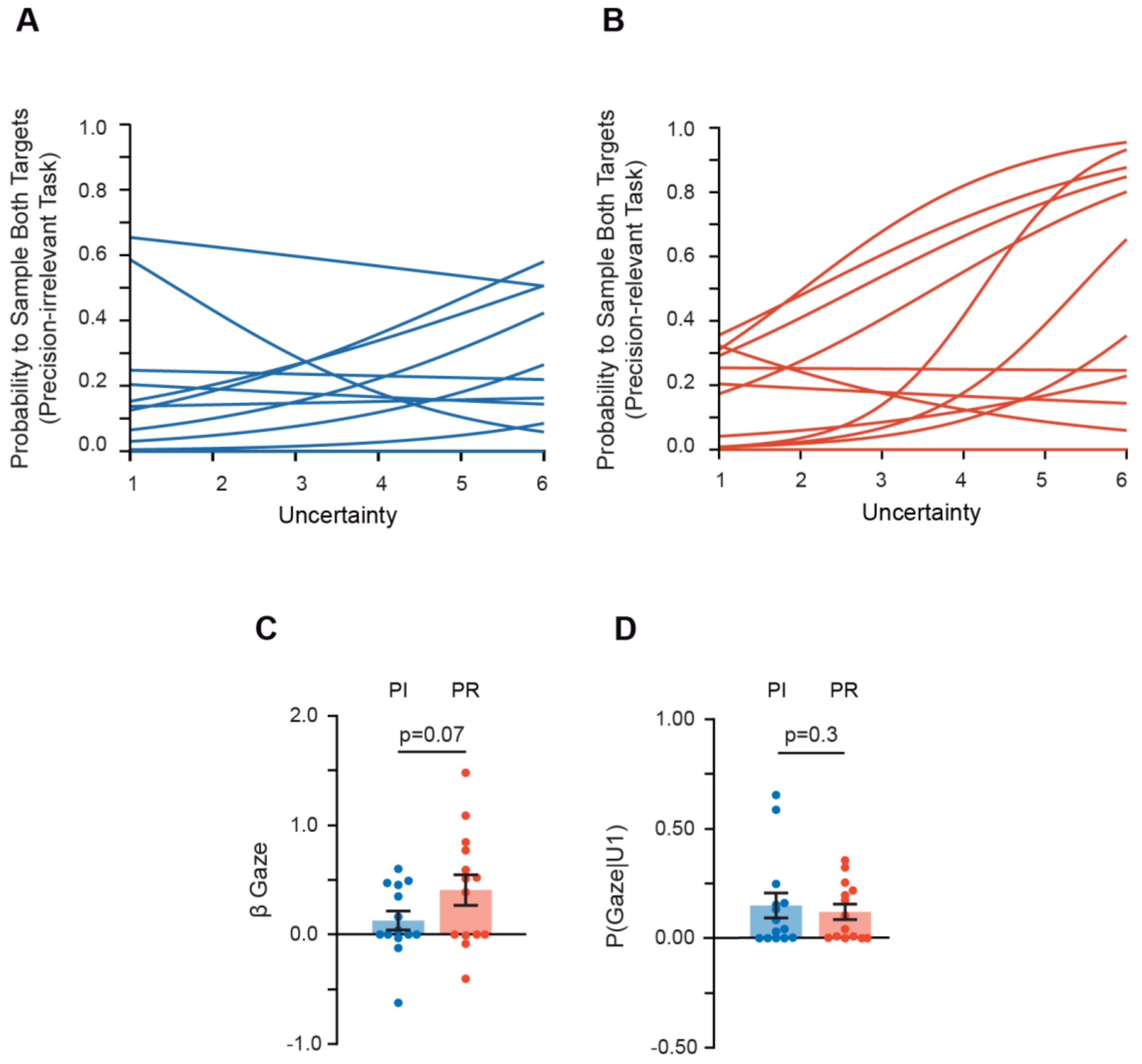

Figure 4-6. Gaze choice model

Individual choice curves for the gaze decisions during the (A) Precision-irrelevant and (B) Precision-relevant tasks. Each curve is the logistic function fit for one participant. We extracted two parameters from each individual fit. We defined βGaze (the slope of the logit regression) as Uncertainty Sensitivity (greater βGaze = greater Sensitivity) and P(Gaze|U1) as the tendency to sample both targets when both options have the same uncertainty level. (C) Uncertainty sensitivity (βGaze) for the Precision-relevant and Precision-irrelevant task. (D) P(Gaze|U1) for the Precision-relevant and Precision-irrelevant task. Data are represented as means ± SE in both (C) and (D).

Table 4-2. Gaze model parameters

	Precision-relevant							
	βGaze				β0Gaze			
Participant	Coefficient	P value	Lower CI	Upper CI	Coefficient	P value	Lower CI	Upper CI
S1	0.844	0.021	0.110	1.578	-5.668	0.003	-9.424	-1.913
S2	1.087	0.001	-0.402	1.773	-5.890	0.000	-9.257	-2.523
S3	0.511	0.032	0.028	0.994	-1.105	0.187	-2.802	0.592
S4	0.000	1.000	-1.042	1.042	-102.566	1.000	-4.068	4.068
S5	-0.008	0.964	-0.374	0.358	-1.069	0.132	-2.494	0.355
S6	0.770	0.003	-0.241	1.299	-2.338	0.016	-3.046	-0.089
S7	0.000	1.000	-0.008	0.915	-102.566	1.000	-3.555	3.555
S8	0.386	0.177	-0.188	0.961	-3.533	0.008	-6.208	-0.858
S9	1.479	0.002	0.526	2.433	-7.740	0.001	-10.027	-2.494
S10	0.591	0.002	0.206	0.976	-2.745	0.001	-3.425	-0.883
S11	-0.404	0.120	-0.928	0.119	-0.336	0.675	-1.948	1.276
S12	0.000	1.000	-1.031	1.031	-102.566	1.000	-3.171	3.171
S13	-0.084	0.682	-0.498	0.329	-1.193	0.123	-2.476	-0.078
S14	0.521	0.006	0.138	0.904	-1.929	0.011	-2.597	-0.220

	Precision-irrelevant							
	βGaze				β0Gaze			
Participant	Coefficient	P value	Lower CI	Upper CI	Coefficient	P value	Lower CI	Upper CI
S1	0.491	0.254	0.393	-1.376	-3.969	0.038	-7.907	-0.032
S2	0.000	1.000	1.677	1.677	-102.566	1.000	-6.325	6.325
S3	-0.624	0.007	-1.086	-0.163	0.973	0.170	-0.449	2.396
S4	0.000	1.000	-1.059	1.059	-102.566	1.000	-4.170	4.169
S5	-0.032	0.858	-0.390	0.326	-1.079	0.117	-2.457	0.300
S6	0.453	0.048	-0.008	0.915	-2.850	0.005	-4.009	-0.784
S7	0.000	1.000	-1.017	1.017	-102.566	1.000	-3.078	3.078
S8	-0.123	0.509	-0.499	0.253	0.760	0.308	-0.743	2.264
S9	0.600	0.448	-0.987	2.187	-6.574	0.106	-12.610	0.662
S10	0.000	1.000	-1.137	1.137	-102.566	1.000	-3.493	3.493
S11	0.348	0.087	-0.062	0.759	-2.064	0.011	-3.698	-0.430
S12	0.040	0.861	-0.422	0.503	-1.920	0.041	-3.358	-0.401
S13	0.162	0.420	-0.242	0.567	-1.817	0.033	-3.004	-0.306
S14	0.472	0.076	-0.064	1.007	-3.612	0.004	-5.146	-1.135

Table 4-3. Probability to fixate both targets when the uncertainty associated with the Low-cost target equals 1 (P(gaze|U=1))

Participant	Precision-relevant	Precision-irrelevant
S1	0.008	0.030
S2	0.008	0.000
S3	0.356	0.586
S4	0.000	0.000
S5	0.254	0.248
S6	0.173	0.083
S7	0.000	0.000
S8	0.041	0.654
S9	0.002	0.003
S10	0.104	0.000
S11	0.323	0.153
S12	0.000	0.132
S13	0.218	0.161
S14	0.197	0.042

To quantify individual differences in step choice, we fitted individual participant's step choice to a logistics function for the Precision-irrelevant (Fig. 4.7A) and Precision-relevant task (Fig. 4.7B). This allowed us to extract two individual parameters that represent motor cost sensitivity (Pstep|U1) and Motor Uncertainty Sensitivity (β_{Step}). Table 4.3 shows the individual fitted parameters for the step-choice model. Task instruction strongly modulated β_{Step} ($t_{13} = -3.6$, $p = 0.0004$, 95% CI = -1.15 / -0.28; see Fig. 4.7C). In particular, participants had greater gaze uncertainty sensitivity (greater β_{Step}) during the Precision-relevant task than during the Precision-irrelevant task. However, task instruction did not change participant's Pstep|U1 ($t_{13} = 0.6$, $p = 0.563$, 95% CI = -0.06 / 0.1; see Fig. 4.7D). A mixed-model linear regression showed no relationship between both parameters for the Precision-relevant task ($R_2 = 0.08$; β coefficient = -0.12; $p = 0.175$, 95% CI = -0.27/0.05), and the Precision-irrelevant task ($R_2 = -0.07$; β coefficient = 0.04; $p = 0.735$, 95% CI = -0.21 / 0.29). The lack of relationship between both parameters indicate that they are independent from each other.

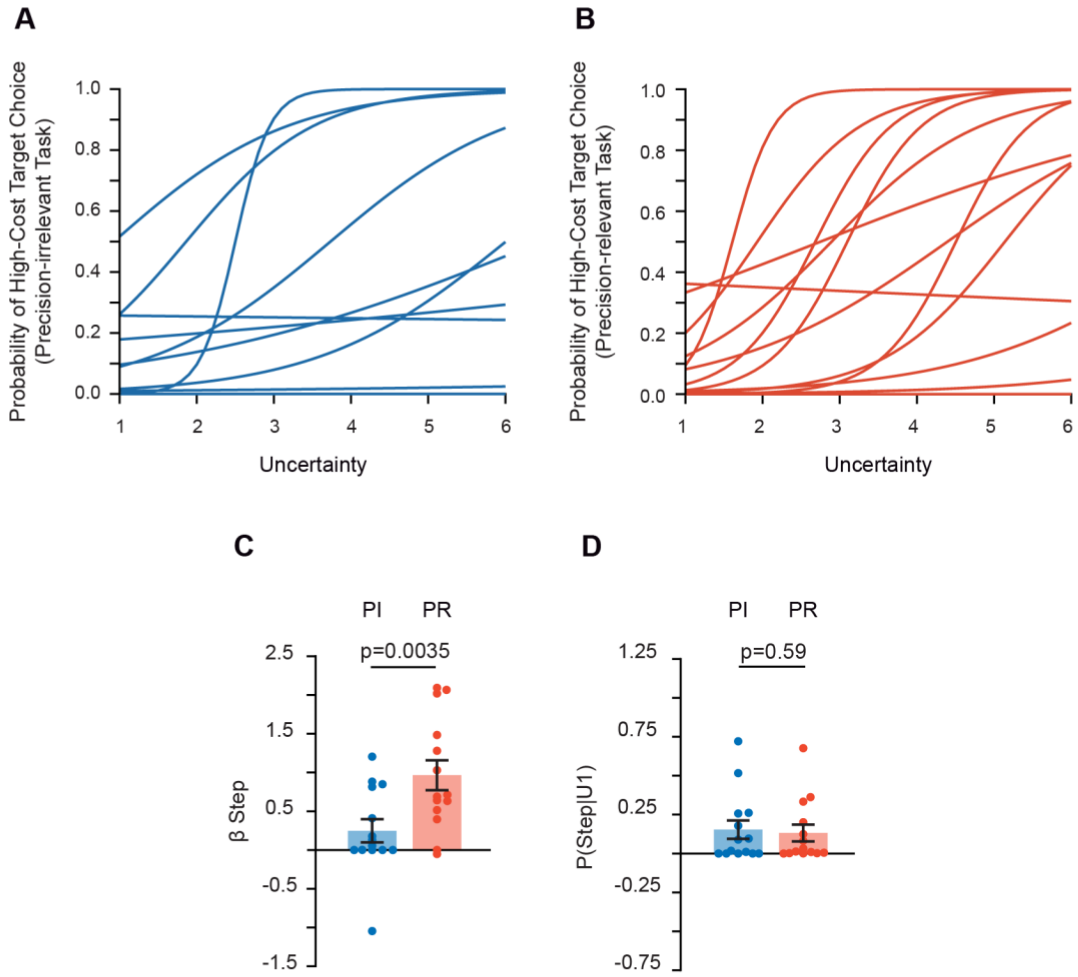

Figure 4-7. Step-choice model

Individual choice curves for the step decisions during the (A) Precision-irrelevant and (B) Precision-relevant tasks. Each curve is the logistic function fit for one participant. βStep for the Precision-relevant and Precision-irrelevant tasks. (D) P(Step|U1) for the Precision-relevant and Precision-irrelevant tasks. Data are represented as means ± SE in (C) and (D).

Table 4-4. Step model parameters

	Precision-relevant							
	βStep				β0Step			
Participant	Coefficient	P value	Lower CI	Upper CI	Coefficient	P value	Lower CI	Upper CI
S1	0.69	0.07	-0.07	1.45	-5.32	0.01	-9.18	-1.47
S2	2.09	0.00	0.97	3.22	-9.43	0.00	-14.55	-4.31
S3	1.48	0.00	0.65	2.31	-2.86	0.00	-4.84	-0.89
S4	0.64	0.43	-0.97	2.26	-6.85	0.10	-15.14	1.44
S5	-0.05	0.75	-0.37	0.27	-0.51	0.41	-1.75	0.72
S6	2.02	0.00	0.89	3.15	-5.42	0.00	-8.70	-2.14
S7	0.63	0.43	-0.98	2.24	-6.79	0.10	-15.07	1.48
S8	0.71	0.00	0.3	1.12	-3.13	0.00	-4.86	-1.40
S9	1.28	0.00	0.53	2.03	-6.58	0.00	-10.21	-2.95
S10	2.07	0.00	0.99	3.14	-6.4	0.00	-9.87	-2.93
S11	0.51	0.08	1.23	6.2	0.22	0.79	-10.32	-1.62
S12	0.00	1.00	-1.03E + 07	1.03E +07	-102.57	1.00	-3.98E + 07	-3.98E + 07
S13	0.40	0.02	0.06	0.73	-1.09	0.08	-2.34	0.16
S14	1.03	0.00	0.52	1.54	-2.98	0.00	-4.69	-1.26

	Precision-irrelevant							
	βStep				β0Step			
Participant	Coefficient	P value	Lower CI	Upper CI	Coefficient	P value	Lower CI	Upper CI
S1	0.18	0.77	-1.04	1.39	-4.74	0.07	-10.00	0.51
S2	0.00	1.00	-1.02E + 07	1.02E +07	-102.57	1.00	-3.95E + 07	3.95E +07
S3	0.88	0.01	0.24	1.52	-0.82	0.30	-2.40	0.77
S4	0.00	1.00	-1.02E + 07	1.02E +07	-102.57	1.00	-3.97E + 07	3.97E +07
S5	-1.05	0.12	-0.36	0.33	-1.05	0.12	-2.40	0.31
S6	0.85	0.00	0.41	1.29	-3.17	0.00	-4.89	-1.45
S7	0.00	1.00	-1.02E + 07	1.02E +07	-102.57	1.00	-3.95E + 07	3.95E +07
S8	1.20	0.00	0.53	1.88	-2.24	0.01	-3.96	-0.52
S9	0.00	1.00	-1.02E + 07	1.02E +07	-102.57	1.00	-3.95E + 07	3.95E +07
S10	0.00	1.00	-1.03E + 07	1.03E +07	-102.57	1.00	-3.98E + 07	3.98E +07
S11	0.05	0.79	1.60	7.34	0.90	0.22	-18.51	-3.84
S12	0.13	0.48	-0.23	0.49	-1.65	0.02	-3.13	-0.18
S13	0.41	0.04	0.02	0.80	-2.65	0.00	-4.36	-0.95
S14	0.82	0.00	0.24	1.39	-4.90	0.00	-7.72	-2.07

Table 4-5. Probability to step onto the High-cost target when the uncertainty associated with the Low-cost target equals 1 (P(step|U=1))

Participant	Precision-relevant	Precision-irrelevant
S1	0.01	0.01
S2	0.00	0.00
S3	0.20	0.52
S4	0.00	0.00
S5	0.36	0.26
S6	0.03	0.09
S7	0.00	0.00
S8	0.08	0.26
S9	0.01	0.00
S10	0.01	0.00
S11	0.68	0.72
S12	0.00	0.18
S13	0.33	0.10
S14	0.12	0.02

4.4.5. Gaze parameters explain gaze and walking behaviour

Since participants used different gaze strategies, we tested if individual gaze parameters predicted gaze times on the decision row. To test this, we performed separate mixed linear regressions for both tasks, including gaze uncertainty sensitivity (βGaze) as the regressor and gaze times on the decision row as the response variable. Interestingly, for the precision-relevant task, gaze uncertainty sensitivity predicted the amount of time that people spend looking at the decision-row (see Fig 4.8A; R_2 = 0.5, β coefficient = 0.07, p = 0.004, 95% CI = 0.03/0.1). However, they did not predict gaze times for the precision-irrelevant tasks (see Fig 4.8B; R_2 = -0.08, β coefficient = 0.007, p = 0.83, 95% CI = -0.07 / 0.08). This means that when people assign greater subjective value to information, the individual gaze parameters account for gaze variability between participants.

Do individual gaze parameters predict participant's walking behaviour? To examine this, we performed mixed-model regressions for each task using βGaze as the regressor and βStep as the response variable. This resulted in an overall model R_2 of 0.47 and -0.08 for the Precision-relevant and Precision-irrelevant tasks, respectively. We found that βGaze significantly predicted βStep in the Precision-relevant task (see Fig 4.C; β coefficient = 0.94, P = 0.0072, 95% CI = 0.3 / 1.6) but not in the Precision-irrelevant task (see Fig 4.D; β coefficient = -0.12, p = 0.814, 95% CI = -1.2 / 0.97). This implies that gaze uncertainty sensitivity predicts participant's walking behaviour. In our case, participants that had greater gaze uncertainty sensitivity preferred to step onto the low uncertainty target, prioritizing faster information gain over motor cost minimization. On the other hand, participants with lower uncertainty sensitivity prioritized minimizing motor cost over faster information gains. This highlights the importance of the subjective value that individuals assign to their actions.

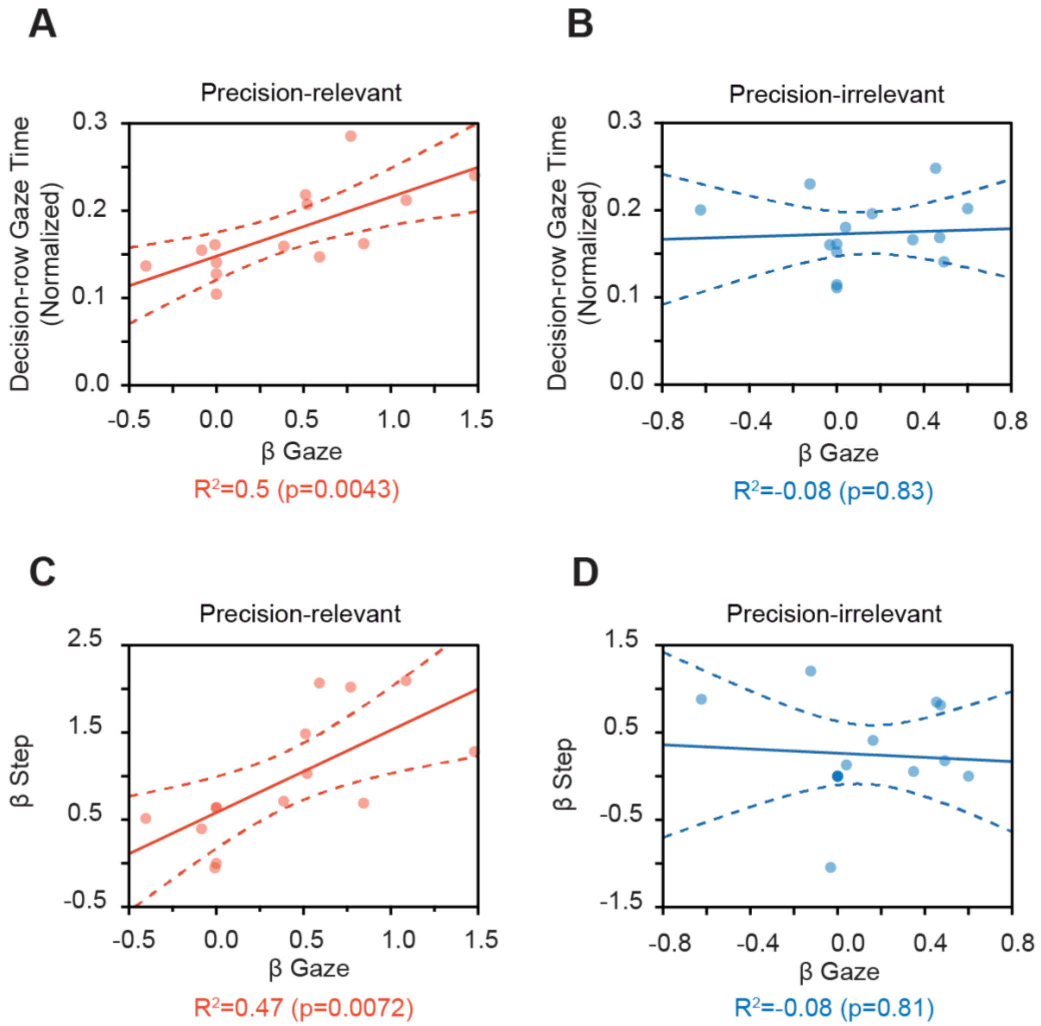

Figure 4-8. Relationship between individual gaze parameters and motor behaviour
(A) Scatterplots of the average gaze time on the decision-row targets and uncertainty sensitivity (βGaze) for the Precision-relevant task. (B) Scatterplots of the average gaze time on the decision-row targets and uncertainty sensitivity (βGaze) for the Precision-irrelevant task. (C) Scatterplots of the individual βStep and uncertainty sensitivity the Precision-relevant task. (D) Scatterplots of the individual βStep and uncertainty sensitivity the Precision-irrelevant task. Solid lines show the linear fits obtained from the mixed linear regression models and dashed lines represent the 95% confidence intervals.

4.5. Discussion

When navigating through natural environments, we often need to select a step location among different alternatives. To deal with this situation, we need to decide where to look and then where to move. Here, we aimed to understand the motives driving this gaze sampling decision. Using a forced-choice paradigm, where we manipulated the visual uncertainty and motor cost associated with the step-target choices, we show that when facing a decision conflict, participants sample the environment using different strategies. These distinct strategies lead to differences in step-location choices while walking.

There are different factors that can guide the allocation of gaze during walking. One factor is the cost to move (Patla and Vickers 2003; Matthis et al. 2015, 2017; Domínguez-Zamora and Marigold 2019). This work suggests that the gaze strategy we adopt when navigating complex terrain allows us to extract visual information about the location of a stepping target relative to the current leg and body position to exploit the mechanical state of the CoM, thus conserving energy (Patla and Vickers 2003; Matthis et al. 2017). In support, we demonstrated that the cost associated with a step to a target modified gaze allocation from a strategy that prioritized feedforward visual information to one that prioritized online visual control of the current action (Domínguez-Zamora and Marigold 2019). In the present study, we show that when facing a step decision while navigating a complex environment, participants direct the first fixation to the target associated with their energetically optimal gait pattern between 86-96% of the time (Fig. 4.5). This finding, suggests that the visuomotor system is primed to prioritize fixating on step locations that are associated with low motor cost. However, even though the first fixation is usually allocated to the Low-cost target, participants followed different sampling strategies to decide where to step. After fitting individual gaze-choice behaviour to a logit model and extracting an uncertainty sensitivity parameter (Fig. 4.6), we found that during the Precision-relevant task participants with lower uncertainty sensitivity were consistent with the idea that motor cost affects gaze. These participants tended to observe the Low-cost target (and ignore the High-cost target) even when the uncertainty associated with this target was greater than the higher cost alternative. However, the variability in gaze behaviour across participants suggests that this idea is too restrictive to fully account for gaze behaviour.

A more recent line of research suggests that humans and animals allocate gaze with the goal to reduce the uncertainty of the environment. This approach assumes that the main goal of every eye movement is to reduce the uncertainty (or update the belief state) of the environment to accurately perform a particular action (Gottlieb et al. 2014; Gottlieb 2012; Daddaoua 2016; Tong et al 2017; Domínguez-Zamora et al. 2018; Sprague and Ballard 2003; Sprague et al. 2007). We found that participants with a greater sensitivity to uncertainty allocated gaze to both targets when the uncertainty of the Low-cost target increased (Fig. 4.8C). We interpret this behaviour as a tendency to acquire as much environmental information as possible to reduce the uncertainty of the decision row. Crucially, these individuals spend more time looking at decision-row targets (Fig. 4.8A). Given that in our task the High-cost target is always associated with a lower level of uncertainty, these participants could have switched to a strategy of only sampling the High-cost target after several walking trials. However, they kept sampling both targets during the entire experiment, a strategy that may seem suboptimal. Bromberg-Martin and Hikosaka (2009 and 2011) described the neural basis of this strong preference for information, using a task were macaque monkeys could observe one of two cues that resolved 100%, 50% or 0% of the uncertainty associated with a future reward. Monkeys had a strong preference for the most informative cues, and dopaminergic neurons in the basal ganglia signaled the expected gain in information, in a similar way to primitive reward (i.e., food, water). Together, this suggests that information by itself is rewarding.

Similar to gaze decisions, we found clear differences in the step choices across participants (see Fig. 4.7). We used the individual gaze parameters to predict participant's walking behaviour, and we found a strong relationship between gaze and step decisions (Fig. 4.8). In particular, during the precision-relevant task, participants that had lower sensitivity to uncertainty tended to step onto targets associated with lower motor cost, even when this target was associated with greater uncertainty. This motor decision-making process is consistent with behavioural and computational evidence proposing that cost minimization is a major objective for human movement (Gallivan et al. 2018; Morel et al. 2017; Shadmehr et al. 2016). For example, previous walking studies show that when navigating an environment where all potential step locations have similar characteristics, one tends to choose a stepping location that minimizes the overall cost of walking (Barton et al. 2017; Donelan et al. 2001; Moraes et al. 2007). Our results extend these findings and demonstrate that some participants keep this energetically optimal pattern even when the environmental uncertainty of the preferred step location increases. However, this model does not explain every participants' walking behaviour.

Our results highlight that some participants made gaze decisions that sought to reduce the uncertainty of the environment. We found that participants with greater sensitivity to uncertainty (a greater tendency to sample both targets when the uncertainty of the preferred step location increased) preferred to step onto highly informative targets, rather than minimize the cost of their actions (see Fig.4.8). This suggests that some participants are willing to trade-off energy for interacting with highly informative locations. Crucially, previous studies showed that animals and humans prefer to sacrifice reward to acquire advance information about future outcomes. For example, Vasconcelos et al. (2015) showed that when birds make decisions between two food sources, one that offered lower probability of reward but carried immediate information about the future outcome, and another that offered higher probability of reward but only 50% chance of getting information, they prefer the option with lower probability of reward but more information. This preference for information increases when the delay between the display of the cue and the delivery of the reward increases. We show for the first time that some people are willing to sacrifice energy in order to reduce the uncertainty of their actions.

Our results are in line with recent decision-making studies proposing that people make decisions motivated by different factors (Balleine et al. 2008; Dickinson 1985, Kobayashi et al. 2019), and this difference in choice behaviour can cause distinct gaze patterns between individuals (KonovalovI and Krajbich 2016). For example, KonovalovI and Krajbich (2016) used gaze patterns to distinguish between model-based and model-free decision makers. Using a two-alternative forced-choice task, they found that model-based decision-makers based their decisions on a learned internal model (of the environment) and presented with less variable gaze behaviour. When facing a decision, these individuals usually know ahead of time which option they are going to choose and ignore all other alternatives. On the other hand, model-free decision-makers based their decisions on actions that previously led them to a reward. These individuals usually looked at all possible choices. To our knowledge, our results show for the first time that people make decisions motivated by different factors during movement.

An important observation is that individual gaze parameters predict behaviour when participants assign a greater value to accuracy during the precision-relevant task.

The key role of task priority in gaze control during natural behaviours has been a key topic in eye movement research (Tatler et al. 2011). The differences in gaze and step decisions may indicate that, in our task, people assign a different priority to information and motor cost. This requires an interaction between neural networks encoding the value of effort and information in gaze-related areas. Bromberg-Martin and Hikosaka (2011) proposed that some neurons in the lateral habenula, an epithalamus nucleus involved in the negative control of motivation, reinforce information-seeking behaviours. Inhibition of this area causes the activation of dopaminergic neurons and induces a behavioural preference for information. Interestingly, the lateral habenula receives projections from the anterior cingulate cortex (ACC) (Vadovicová 2014). The ACC is part of a network that evaluates if it is worth producing a particular effortful action for a given reward (Walton et al. 2002,2003; Botvinick et al. 2009; Kurniawan et al. 2013). These two signals, one related to information-seeking motivation and one for effortful behaviours, may interact in the lateral habenula, leading to individual behavioural differences that we describe in this study. Future research on the interaction of information and effort needs to study the neural mechanisms of this possible network.

While walking, we constantly make gaze decisions to gather the necessary environmental information to plan and guide our movements. Overall, our findings provide new insights into the motives driving these gaze sampling decisions to control locomotion in complex environments. Furthermore, our findings might help is to understand why human motor behaviour is variable across individuals, as well as the intricate relationship between gaze and action target selection

4.6. Chapter contributions

This chapter was written by me with edits from Dr. Daniel S. Marigold. Dr. Daniel S. Marigold and I conceptualized the experimental question and methodological design. I performed the experiments and analyzed the data. This work is currently being prepared for submission.

Chapter 5.

General Discussion and Conclusions

> *"Todo ser humano, si se lo propone, puede ser escultor de su propio cerebro."*
>
> *(Santiago Ramón y Cajal)*

5.1. Summary of thesis

Despite the increasing interest in studying gaze behaviour while performing natural tasks, the factors that guide gaze to accurately navigate and interact with our environment still remain unclear. This thesis provides a novel perspective on the factors that modulate the spatio-temporal allocation of gaze to guide and control locomotion. In particular, I focused my dissertation on the complex interaction between task priority, uncertainty, and motor cost in the control of gaze decisions to control accurate foot placement during visually guided walking.

When walking across complex terrain, people usually look at relevant ground locations where they will eventually step (Marigold and Patla 2007). However, there is little understanding of how or why task-relevant locations are selected and prioritized. In **Chapter 2**, I tested how uncertainty and the value assigned to an action guides gaze allocation during walking. To accomplish this, I used a psychophysical technique (gaussian blobs) to manipulate the level of uncertainty associated with visual targets. I found that, when people assign a greater value to foot-placement accuracy, uncertainty increases gaze time on the visual targets to accurately guide and control foot placement. Complex environments may also restrict the number of available foot-placement locations, causing us to step in ways that make our walking pattern more costly. In **Chapter 3**, I showed how the cost of walking is factored into the decision of when to shift gaze from a stepping target. I manipulated the cost to move the body by shifting stepping targets from the preferred gait pattern. I showed that people adapt their gaze behaviour from a feedforward to an online control strategy to deal with costly actions. These changes are strongly affected by the cost to maintain balance when we constrain the availability of foothold locations.

Once I identified how uncertainty, task priority, and motor cost affect gaze behaviour, I became interested in what motivates us to make a particular gaze decision when dealing with multiple choices that compete for gaze allocation. In **Chapter 4**, I used a two-alternative, forced-choice paradigm during a visually-guided walking task where I manipulated the motor cost and uncertainty of each stepping target. Here, I found that even when the visuomotor system can be primed to minimize cost, gaze decisions across individuals are highly variable and cannot be explained with a single theory. To explain this variable behaviour, I identified a parameter (uncertainty sensitivity) that predicts that the way we sample and interact with the environment depends on the value that we assign to information gain and motor cost minimization. These findings make it possible to define a new framework that explains how we control gaze during locomotion.

5.2. Framework for gaze control during walking

It has proved difficult to formalize models or frameworks to explain how we select where and when to look at a particular location. In recent decades, researchers have introduced several models to explain what may drive the selection of visual targets. Neurophysiological, behavioural, and computational experiments agree that gaze target selection is determined by an attentional template representing which environmental features are relevant to obtain a goal (Fecteau and Munoz 2006; Bisley and Goldberg 2010; Findlay and Walker 1999). However, the factors affecting this top-down cognitive control during natural behaviours are still unclear. I propose that, during walking, gaze is allocated to gain information about the environment to achieve some action goal that acts as an intrinsic reward. This is influenced by at least four factors: uncertainty, task priority or value of action, cost, and the motivation of the individual.

To understand how gaze is allocated, we first need to define the main behavioural goal. For example, if we go for a hike in the woods, the goal could be to safely navigate through the mountain from the trailhead to the summit. Sprague et al. (2007) suggest that we can simplify this problem with the assumption that complex behaviours are composed of independent modules or subtasks. In fact, any main behavioural goal can be divided into smaller modules of subtasks. For example, when making a cup of tea, we need to take the kettle and then go to the tap to fill it with water (Land et al. 1999). During walking, we also constantly face these momentary goals. To continue with the hiking example, to summit the mountain, we need to allocate gaze to the different signs marking the correct trail direction, avoid obstacles on the path and, the most important, decide where we are going to step until we reach our goal. Once we have selected which subtask we want to perform, we need to acquire the relevant information that would lead us to successfully accomplish our goal. To acquire this information, we need to make two kinds of decisions: first we need to decide where to look (spatial decision) and second, we need to decide for how long to allocate gaze on that particular location until we transition to the next one (temporal decision).

One of the factors affecting spatial decisions is the uncertainty associated with the environment. This uncertainty can represent the imperfect knowledge we have about the world and may arise due to the limited spatial resolution of the visual system or the inexperience with the upcoming environment or task. Sprague et al. (2007) formalize a reinforcement learning model using this idea. In their model, a particular location is selected based on the expected loss of information if gaze is not directed to a specific location. To model this idea, they used a Kalman filter that propagates a computational agent's state uncertainty of all the locations that the agent is not fixating. If various locations are competing for gaze allocation (locations have the same relevancy to perform the task), the eye is directed to the most uncertain one. After gaze is allocated to a particular location, the agent reduces the uncertainty of that location and updates its internal representation of the environment. In **Chapters** 2 and 4, we supported this model during a visually-guided walk. We showed that some people prioritize information gain when deciding where to look by spending more time looking at all possible stepping choices. We interpret this behaviour as a tendency to acquire as much information as possible to generate an accurate model of the environment that would help guide future actions. However, we extend the Sprague et al. (2007) model to identify a second factor that is also considered when making spatial gaze decisions. In **Chapter 3**, we found that motor cost affects gaze behaviour. When deciding where to look, in **Chapter 4**, we found that some people prioritize motor cost minimization over information gain. These individuals usually fixate future step locations that are close to their preferred step location (the location that minimizes the overall cost of walking). We suggest that individuals assign different priority to cost and information, and these different motivations generate the differences in spatial gaze decisions.

Once we select a particular location, for example, where to step to avoid an upcoming obstacle, we need to decide when to shift gaze to the next visual target that would help us to achieve the next subtask. In **Chapter 2**, I found that environmental uncertainty influences this temporal decision. For example, we found that people allocate greater gaze times to more uncertain locations. When we fixate a target, we reduce its uncertainty and shift gaze to the next location once we have gathered the necessary information to guide our movements. In **Chapter 3**, I show that motor cost also affects this decision. Motor cost increases the signal dependent noise on motor pathways (Harris and Wolpert 1998; Jones et al. 2002; van Beers et al. 2004). In this case, I proposed that increased online visual feedback may serve to compensate the greater signal dependent noise during more effortful actions. In addition, the complexity of the environment also plays a role in this decision. A trade-off between information (acquiring enough environmental information) and motor cost (compensate for motor noise) would dictate when to transition to the next location. We continue this cycle until we have achieved our main behavioural goal (i.e., summit the mountain) that acts as an intrinsic reward (i.e., enjoy the views).

The role of uncertainty and motor cost are often studied in isolation to formulate visual foraging and information seeking theoretical models (Kaplan and Friston 2018; Stephens 2008; Yoon et al. 2018). For example, Kaplan and Friston (2018) used a maze task that required participants to navigate from a start to a target location under uncertainty. Using an active inference model based on Markov decision processes, they showed that the resolution of uncertainty about hidden states (the uncertainty of the environment) drives visual exploratory behaviours. Additionally, in the absence of uncertainty, their model shows how novelty drives the same response as uncertainty. The concept that effort or motor cost biases gaze sampling decisions is also in line with recent foraging theories that suggest visual exploitation time on targets increases with effort (Stephens 2008; Yoon et al. 2018). These models describe the optimal within-path foraging behaviour by comparing the current rate and the effort of obtaining the reward to the average reward rate available in the environment. To maximize average reward return rate, a forager should leave the current location when the return rate in the current location drops below the average environmental reward rate. Yoon et al. (2018) used this model with a saccade task where they manipulated the effort for participants to move their eyes from one location to another. They found that the effort to reach a target and the expected effort to move to the next one delayed gaze shifts from the current target. The framework that I propose implies a novel interaction between information and motor cost to control information-seeking behaviours and suggests a need to update these models.

To fully understand the implications of this framework, it is important that future work test how it generalizes to different walking paradigms as well as to other motor tasks. In each of my experiments, participants performed a visually-guided walking task that required them to walk and step onto the center of virtually projected targets. One limitation of this approach is that it does not mimic the great amount of visual stimulation that we encounter when navigating real environments. In fact, experiments using real-world environments have contributed to ruling out some models of target selection. Land et al (1999) and Hayohe (2000) provided some of the earlier and most clear examples on how the study of everyday tasks help us in the attempt to understand how we select a particular location to look at. Using a tea and sandwich making task, they showed that the traditional saliency model did not explain how we allocate gaze during unconstrained motor tasks. They showed that gaze is tightly linked with the ongoing behaviour and that people rarely look at a salience feature that is not related to the task that they are performing. Rothkopf et al. (2007) formally tested if salience models explain gaze behaviour during walking using a virtual reality task that mimicked a real environment. They showed that in contrast with the 70% of fixations predicted by saliency models, only 15% of the fixations were directed to salient background features. On the other hand, real-world tasks can also help to prove behavioural models. However, real-environment experiments are also helpful to confirm laboratory findings. Recently, Mathis et al. (2018) linked mobile eye-tracking with motion capture to measure gaze behaviour while walking through real complex terrain. Their results confirmed laboratory work which suggested that when navigating challenging terrain people allocate their gaze two steps ahead to select a stable foot-placement location (Marigold and Patla 2007). Although we need the control of laboratory tasks to understand the principles that guide human behaviour, the advance in mobile eye-tracking and motion capture technology makes the translation of laboratory findings to real-world tasks easier than ever.

Another limitation of this framework is that participants walked at a self-selected pace without any time constraints. We included gait speed as covariate in our analyses to rule out that differences in walking speed drive the behavioural changes. However, it will be interesting to explore how time constraints modulate the factors guiding gaze. In fact, during visual search tasks under time pressure people can modify their preference for resolving uncertainty for a strategy where they select a location based on the prior probability to find the goal target (Verghese 2012, Ghahghaei and Verghese 2015). Understanding how time constraints affects gaze behaviour can shed new light into how we sample the environment during fast motor behaviours, such as running.

5.3. Application of the gaze control framework to clinical research

The gaze behaviour flexibility that we observe in each of my experiments contributes to our ability to successfully navigate our environment. Despite this vital function, gaze behaviour adaptability is rarely measured on individuals that present with mobility deficits. Although this thesis does not target any clinical populations, the findings may help to understand the principles of some behavioural changes caused by visual and neurological disorders, as well as the changes observed during aging.

Peripheral visual field loss due to glaucoma is a clear example of how a visual disorder affects motor behaviour. The peripheral visual field assists us in guiding our limbs without the need to look down, for example, when avoiding an obstacle (Marigold et al. 2007; Marigold 2008). Due to the inability to use peripheral visual cues, patients with glaucoma have greater foot-placement errors and collide with obstacles more often during walking tasks due to changes with gaze-foot coupling (Miller et al 2017; Lajoie et al 2018). In addition, these patients with peripheral visual loss are unable to judge the position of distant landmarks (Rieser et al. 1992, Turano et al. 2005) or direct gaze to relevant peripheral objects due to narrower horizontal eye-position dispersion (Vargas-Martín and Peli, 2006). However, these deficits in gaze allocation are less noticeable with highly salient stimuli (Luo et al. 2008). We can interpret these behavioural changes as the inability to acquire relevant information due to increases in uncertainty of visual feedback. If environmental uncertainty is the reason for these behavioural changes, we may design clinical interventions with the objective of training these clinical populations on how to properly sample the environment. Gunn et al. (2019) showed preliminary evidence of how a gaze training program can modify gaze patterns when older adults with glaucoma perform precision walking and obstacle navigation tasks. Using a combination of home-based and task-specific lab-based training programs, they showed that patients with glaucoma modified their gaze strategies and improved their mobility performance.

Uncertainty may also explain the differences in gaze sampling strategies that we observe between older and younger adults. In a recent study, we used an obstacle navigation task where participants needed to allocate and memorize shapes that mimic environmental landmarks (Domínguez-Zamora et al. 2019). In this task, working memory plays a key role in maintaining a visual-spatial representation of the obstacle and shape positions. In fact, working memory impacts the way we sample the environment during other walking tasks. For instance, when searching for targets in a virtual environment, the plan to fixate a particular location initially depends on memory rather than on the current visual information (Lajoie et al. 2012; McVea et al. 2006). In our study (Domínguez-Zamora et al. 2019), to maintain the same level of performance, older adults looked more often and longer to the shapes than younger adults. We interpret these findings as the need to update the environmental representation kept in working memory due to a faster decay of working memory as we age. This faster decay creates environmental uncertainty and increases the need to re-fixate environmental features to update the previously stored information.

The gaze control framework that I propose may also help to understand the behavioural changes that are present in some neurological disorders. For example, when turning or circumventing an obstacle, patients with Parkinson's disease delay gaze shifts from the current location (Pereira et al. 2019) resulting in a lack of anticipatory gaze shifts to plan body trajectories (Ambati et al. 2016). Crucially, motor pathways in Parkinson patients have lateralized increased signal-dependent noise associated with action potential timing (higher on the most affected side) during force production (Salimpour et al. 2015). I suggest in **Chapter 3**, that the increased signal-dependent noise when performing costly steps delays gaze shifts from the current stepping target. The delay increased the amount of online limb control to compensate for the motor noise. This observation may explain Parkinson's patients gaze behaviour during some walking tasks. This is an important consideration for the design of rehabilitation programs that use visual cues to promote gait in Parkinson's disease and other neurological conditions like Huntington's disease.

5.4. Future directions

This thesis highlights the factors that mediate gaze behaviour during walking. However, a key question arises: Do these factors affect the way we learn how to allocate gaze? To answer this question, we first need to understand how gaze behaviour is learned. When humans walk, the brain needs to balance the need to acquire new information (uncertainty sensitivity) with a particular behavioural goal. To solve this problem, people learn new priorities for gaze allocation by learning the dynamic properties of the natural world. This learned information is used to perform predictive saccades to future environmental cues in the absence of sensory information to avoid hazards or ensure walking efficiency. For example, when walking in a corridor with other pedestrians, people are able to adapt their gaze allocation strategy, looking sooner and longer to pedestrians that represent a danger (Jovancevic-Misic et al. 2009). People show the same behaviour in passive free viewing experiments and when performing other complex tasks, such as table tennis (Land and Furneaux 1997; Diaz et al. 2013) or squash (Hayhoe et al. 2012). Sailer et al. (2005) demonstrated how this visuomotor learning process occurs through three different stages: 1) An exploratory stage characterized by a noisy feedback gaze strategy to monitor our movements while learning the dynamics of the new task or environment; 2) A skill acquisition stage, where gaze starts shifting to a feedforward strategy, fixating future goal locations, and where task performance improves quickly; and 3) A skill refinement stage, characterized by a stable feedforward gaze strategy where peripheral vision provides enough online information to control the current action. The reduction of uncertainty through a learning process can explain these changes in gaze behaviour.

This learning process can also alter gaze allocation during effortful actions. Do people adapt their gaze behaviour to a new cost landscape to prioritize acquiring future information? In **Chapter 3**, we specifically randomized the presentation of each motor cost condition in different trials to avoid learning. We showed that participants prioritized an online control gaze strategy when interacting with locations associated with greater motor cost. However, maintaining this strategy may not be optimal. During walking, looking ahead (two-steps-ahead strategy) allows us to extract visual information about the location of a stepping target relative to the current leg and body position and conserve energy (Matthis et al. 2017; Patla et al. 1996). It will be interesting to design experiments where participants can learn and adapt their movements to a given cost condition to see if people are able to shift to a more optimal gaze strategy. Additionally, I manipulated motor cost by shifting environmental foot-placement locations from the preferred step location. To fully understand the role of motor cost in gaze behaviour, it is important to test how other forms of cost, like changing the cost of swinging the leg or the cost to maintain balance by perturbing the position of the CoM, affect gaze allocation.

Finally, it will be important to determine where the information and motor cost integration processes occur within the brain. In **Chapter 4**, I show that people incorporate both information value and motor cost into their gaze decisions. A candidate neural structure that could play a role in this integration is the ACC. ACC plays a key role in evaluating if it is worth producing an action requiring high effort (Walton et al. 2002, 2003; Botvinick et al. 2009; Kurniawan et al. 2013). Some have recently proposed that ACC might also signal when it is necessary to resolve an information gap when facing a cognitive conflict (Gruber and Ranganath 2019). However, characterizing the role of this area during walking is a complex issue that will require the combination of functional neuroimaging experiments during highly controlled saccade tasks with walking experiments using eye-tracking and mobile EEG. In recent years, the advance in mobile EEG technology, that allowed the replication of key animal electrophysiological studies in humans (Nordin et al 2019), has made the possibility to characterize the neural correlates of decision-making during walking a more realistic endeavor.

5.5. Concluding remarks

To conclude, characterizing the factors that dictate how we gather environmental information through eye movements is essential to understanding human decision-making. This thesis advances our understanding of the factors that modulate the tight relationship between gaze and body movements during walking. Using these findings, in combination with previous research, I have developed a novel framework to explain the complex interaction between uncertainty, task priority, and motor cost in guiding spatial and temporal gaze decisions during walking. In the future, this framework can motivate the development of more accurate theoretical information-seeking models. Furthermore, the framework that I propose can be useful to understand the behavioural changes that we observe in clinical populations affected by visual and neurological disorders and advance the design of clinical programs seeking to improve mobility.

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