RESEARCH ARTICLE | *Control of Movement*

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

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Domínguez-Zamora FJ, Marigold DS. Motor cost affects the decision of when to shift gaze for guiding movement. *J Neurophysiol* 122: 378–388, 2019. First published May 29, 2019; doi:10.1152/ jn.00027.2019.—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, although 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.

NEW & NOTEWORTHY Changes in gait allow us to navigate our world. For instance, one may step long or wide to avoid a spilled drink. The brain can direct gaze to gather relevant information for making these types of motor decisions; however, the factors affecting gaze allocation in natural behaviors are poorly understood. We show how the motor cost associated with a step influences the decision of when to redirect gaze to ensure accurate foot placement while walking.

cost; decision making; gaze; locomotion; vision

INTRODUCTION

Motor decisions are affected by the cost of moving 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 minimize the

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energetic cost of foot placement and the overall walking pattern (Barton et al. 2017; Donelan et al. 2001; Moraes et al. 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: *1*) the effort (or energy) required to move the leg and *2*) the effort involved in redirecting a moving body center of mass (CoM) between a changing base of support (BoS), the latter of which is dictated by the position of the two feet. This second effort is essentially the cost of maintaining 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 CoM 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 before lifting the foot to step to it (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 CoM from target to target because of the different constraints imposed on foot placement.

MATERIALS AND METHODS

Participants. Ten healthy young adults participated in this study (8 women and 2 men; mean age = 26.5 ± 5.2 yr; 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 written informed consent before participating.

Experimental design. Participants performed a visually guided walking paradigm that required them to walk across the laboratory 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 5,500 lm) 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 lx surrounding the targets and ~350 lx 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, Waterloo, ON, Canada), positioned perpendicular to the walking path, recorded (at 120 Hz) infrared-emitting position markers placed on the participant's head and chest and bilaterally on each midfoot (second to third metatarsal head), toe (third metatarsal), and heel. An electromyography (EMG) system (MA300; Motion Laboratory 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 (model H6-HS; Applied Science Laboratories, 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 with a standard nine-point (3 × 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.

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 two-target and a four-target environment in different, counterbalanced blocks of trials (Fig. 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 because of 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 targets (2-target environment) or between 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. 1B). See RESULTS (and Fig. 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. 1B). We kept step length constant by positioning targets in the anterior-posterior direction at 0.7 L. In the two-target environment, we only shifted the second target rightward, and participants were free to step wherever they wanted after this target. In the four-target environment, we randomly shifted the second target rightward (50% of trials) or the 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 four-target environment because of the greater challenge to redirect a moving body CoM
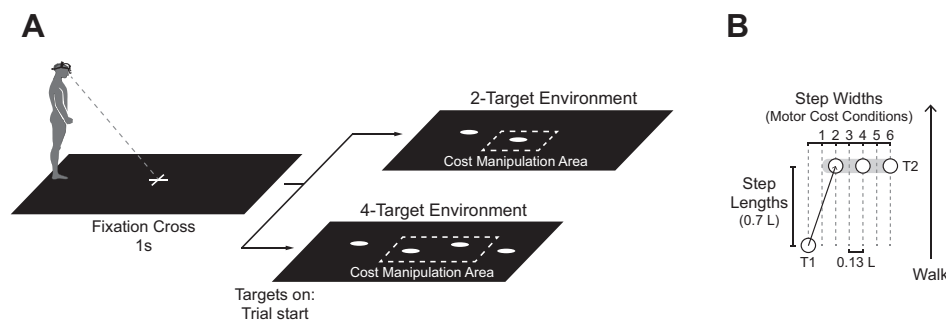

Fig. 1. Experimental setup and procedure. *A*: participants encountered 2 different environments in which they had to walk and step to the center of sequentially positioned targets. We changed the position of the second target in the 2-target environment (*top*) or 1 of the 2 middle targets in the 4-target environment (*bottom*) on a trial-to-trial basis. *B*: we shifted the manipulated target laterally to create 6 different motor cost conditions. The lateral shift increased the step width by a factor of 0.13 × the participant's leg length (*L*). We held step length constant between targets. The illustration shown is for the 2-target environment, where T1 represents *target 1* and T2 represents *target 2* (i.e., the manipulated target).

A

B

Fig. 2. Effort involved in moving the leg forward ($n = 9$ participants). *A*: total muscle activity (from 5 bilateral leg muscles) calculated from heel contact on the premanipulated target until heel contact on the manipulated target across the 6 motor cost conditions in the 2- and 4-target environments. 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 6 motor cost conditions in the 2- and 4-target environments. Data are normalized to walking trials without targets present. For both measures, data are represented as means ± SE. *Values are significantly different from each other based on post hoc tests after a main effect of cost ($P < 0.05$). We excluded 1 participant from this analysis because of problems with the EMG system during data collection.

—— 2-Target Environment   —— 4-Target Environment
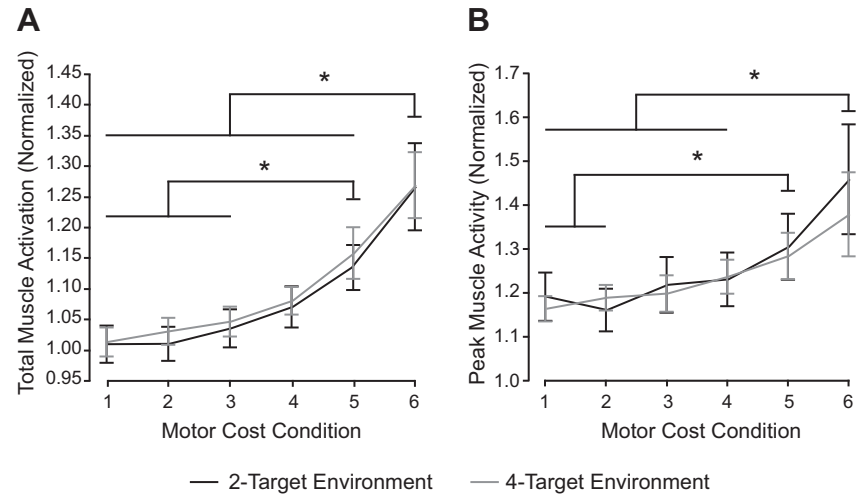
between a changing BoS, which is constrained by the additional stepping target(s). We randomly presented each motor cost condition in 10 different trials, for a total of 60 trials per environment (or 120 walking trials overall).

Data and statistical analyses. In a preliminary analysis related to the four-target environment, we found no significant difference between trials in which 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 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 between 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 maxima of the midfoot vertical velocity profile defined heel contact on the targets (O'Connor et al. 2007). The local minima 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 (midfoot 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 with separate two-way (cost × 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 them into two different intervals: *1*) from heel contact onto the premanipulated target to heel contact on the manipulated target and *2*) from 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 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, we first calculated the muscle activation (MA) for each individual muscle:

$$MA = \left(\frac{EMG_{Area}}{EMG_{AreaCWT}} \right) \qquad (1)$$

where EMG_{Area} is the area under the muscle profile during walking and stepping to targets and $EMG_{AreaCWT}$ is the area under the ensemble-averaged profile of the control walking trials, each calculated with 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:

$$Weight\ Factor_i' = \frac{Muscle\ Volume\ Fraction_i}{\sum_{i=1}^{10} Muscle\ Volume_i} \qquad (2)$$

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

$$TMA = \sum_{i=1}^{10} Weight\ Factor_i' \times MA_i \qquad (3)$$

where i is each muscle analyzed. With this method, high-volume muscles contribute more than low-volume muscles to TMA. To determine differences in motor cost, we compared peak muscle activity and TMA between motor cost conditions and environments with separate two-way (cost × 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:

$$XCoM = CoM + \frac{V_{CoM}}{\omega_0} \qquad (4)$$

where V_{CoM} is the CoM velocity and ω_0 is the eigen (angular) frequency of the inverted pendulum described by

$$\omega_0 = \sqrt{\frac{g}{l}} \qquad (5)$$

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 BoS edge (represented by a laterally placed heel marker). For a step with the right foot on the manipulated target, we used

$$DMS = BoS\ edge - XCoM \qquad (6)$$

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

$$DMS = XCoM - BoS\ edge \qquad (7)$$

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 × environment) ANOVAs. We did not include gait speed as a covariate for the DMS measure because it is velocity dependent.

To analyze gaze data, we first low-pass filtered data consisting of a three-dimensional vector of eye rotation at 15 Hz using a 4th-order Butterworth algorithm. We used these 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 that gaze is stabilized on this location, but because of the vestibuloocular 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 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 heel contact, and negative values represent gaze shifts away from the target before heel contact 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 × environment) ANOVAs. As previously done (Domínguez-Zamora et al. 2018), gait speed was not included as a covariate when analyzing total gaze time, because 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 premanipulated 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 α 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 × environment interaction.

RESULTS

Changes in step width increase motor cost. We first confirmed that changing the step width in the two-target and four-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 1 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 TMA value. This measure quantifies the effort (or motor cost) involved in swinging 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. 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 with the smallest step width. However, we found no significant effect of environment (main effect: $F_{1,94} = 0.002$, $P = 0.961$; cost × 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. 2B). Again, we found no significant effect of environment for this measure (main effect: $F_{1,92} = 0.05$, $P = 0.822$; cost × 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.

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 toward 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 of the foot about to step to that same target (TO-interval; Fig. 3A). A two-way (cost × 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 × environment interaction ($F_{5,96} = 0.9$, $P = 0.475$). The negative TO-intervals for all cost conditions and environments (Fig. 3, B and C) indicates that participants shifted gaze to the manipulated target before 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 on that same target (HC-interval; Fig. 4A). The timing of shifts in gaze relative to stepping on the target depended on both the motor cost condition and environment (cost × environment
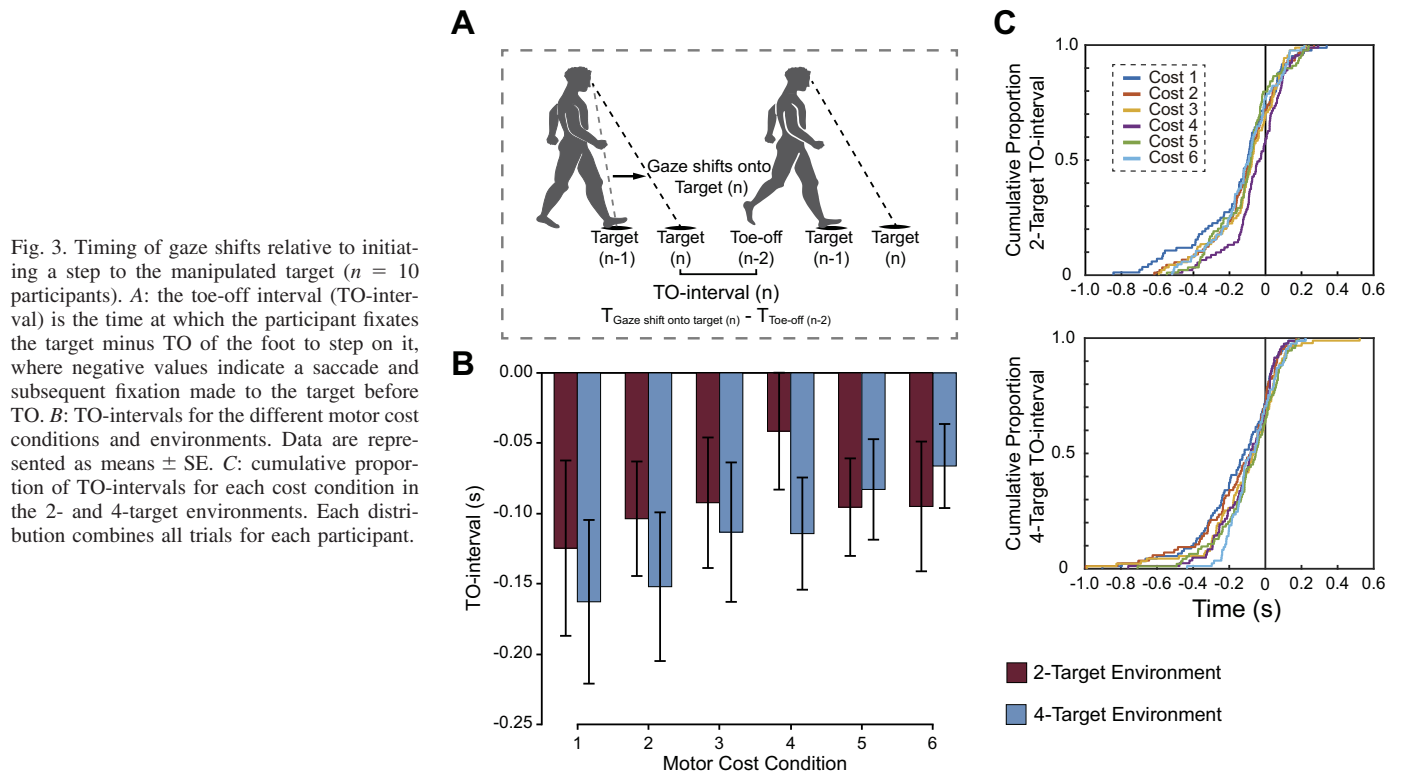
Fig. 3. Timing of gaze shifts relative to initiating a step to the manipulated target ($n = 10$ participants). *A*: the toe-off interval (TO-interval) is the time at which the participant fixates the target minus TO of the foot to step on it, where negative values indicate a saccade and subsequent fixation made to the target before TO. *B*: TO-intervals for the different motor cost conditions and environments. Data are represented as means ± 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.

interaction: $F_{5,97} = 2.4$, $P = 0.043$). In the four-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 with *motor cost conditions 1* and *2* (Fig. 4*B*). 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 before footfall on it in *motor cost condition 1* and ~60 ms after heel contact in *motor cost condition 6*. In the two-target environment, participants maintained their gaze on the target until after heel contact for all motor cost conditions (Fig. 4, *B* and *C*). These results suggest that the decision of when to redirect gaze
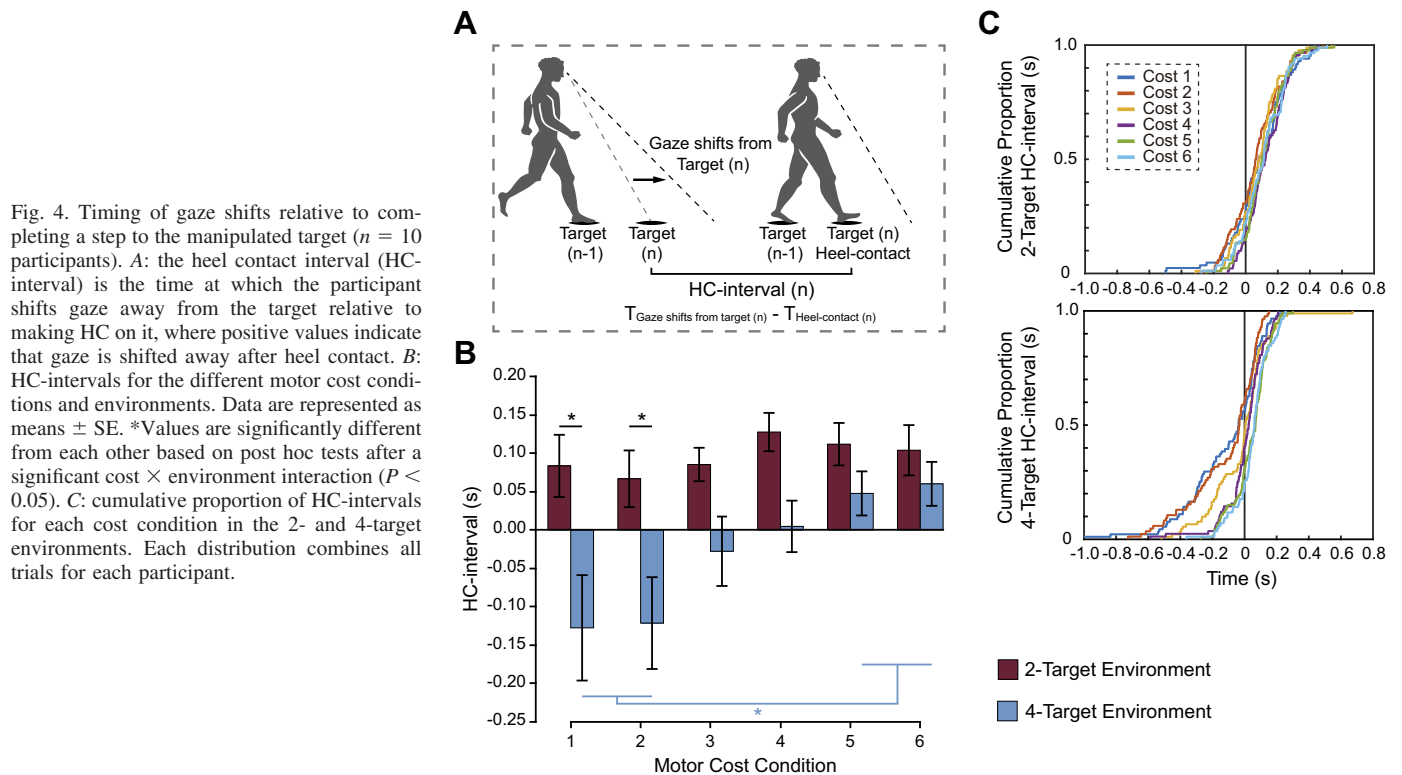

Fig. 4. Timing of gaze shifts relative to completing a step to the manipulated target ($n = 10$ participants). *A*: the heel contact interval (HC-interval) is the time at which the participant shifts gaze away from the target relative to making HC on it, where positive values indicate that gaze is shifted away after heel contact. *B*: HC-intervals for the different motor cost conditions and environments. Data are represented as means ± SE. *Values are significantly different from each other based on post hoc tests after a significant cost × 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.
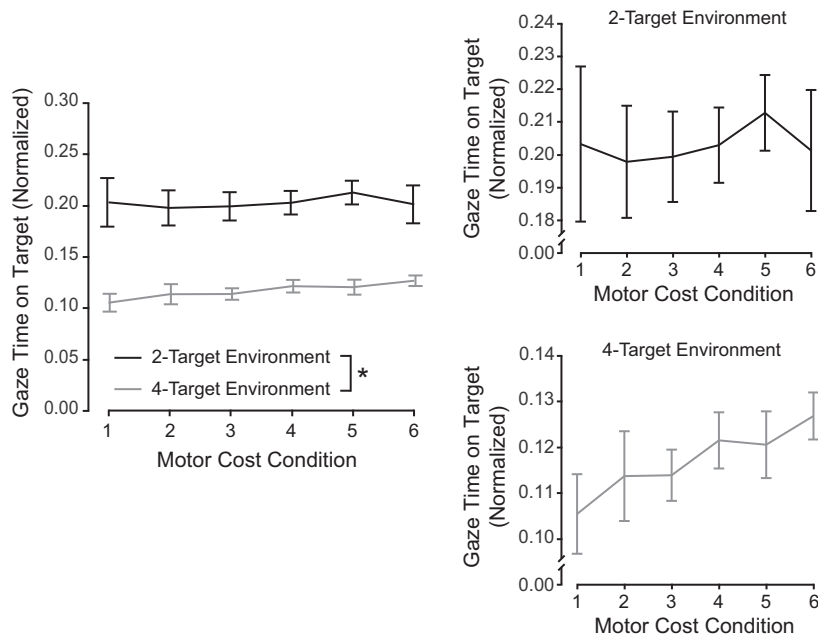
Fig. 5. Gaze time on the manipulated target ($n = 10$ participants). *Left*: gaze times from the 2 environments on the same scale. The 4-target environment has more targets present, and thus gaze time on the target is less ($P < 0.05$). *Right*: given this effect, an enlarged view for each environment. Data are normalized to trial duration and represented as means ± SE. *Values are significantly different based on a main effect of environment.

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 four-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. 5, gaze time on the manipulated target was nearly twice the duration in the two-target versus the four-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 × environment: $F_{5,99} = 0.3$, $P = 0.893$).

Flexible gaze behavior allows for similar foot placement control. To determine whether changes in motor cost affected motor performance, we first quantified gait speed. A two-way (cost × environment) ANOVA showed that participants changed their gait speed ($F_{1,99} = 7.4$, $P = 0.008$) depending on the environment they encountered (Fig. 6A). Post hoc tests revealed that participants walked slower in the two-target environment (1.18 ± 0.05 m/s) compared with the four-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 × environment interaction: $F_{5,99} = 0.3$, $P = 0.936$; see Fig. 6B). However, participants had less foot placement error in the four-target environment compared with the two-target environment (environment: $F_{1,102} = 6.9$, $P = 0.010$). Specifically, foot placement error was 3.9 mm greater in the two-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 two-target and four-target environments, respectively. We sub-

sequently compared foot placement error variability (i.e., the between-trial standard deviation of foot placement error) between cost conditions and environments (Fig. 6C). Participants had the same error variability in the two-target and four-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 × environment interaction either ($F_{5,98} = 0.7$, $P = 0.639$). Thus the changes in gaze behavior contributed to similar foot placement control within each environment despite differences in the cost of moving 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. With a linear mixed-model regression, however, we found no significant relationship in the two-target environment ($R^2 = 0.85$, $P = 0.074$) or the four-target environment ($R^2 = 0.67$, $P = 0.913$).

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 four-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 four-target environment because of the additional step target following the manipulated one. This creates a situation in which there are two large consecutive step widths in the higher-motor-cost conditions. Figure 7A illustrates the average trajectory for the trunk (represented by a chest position marker) and foot (represented by a midfoot 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.
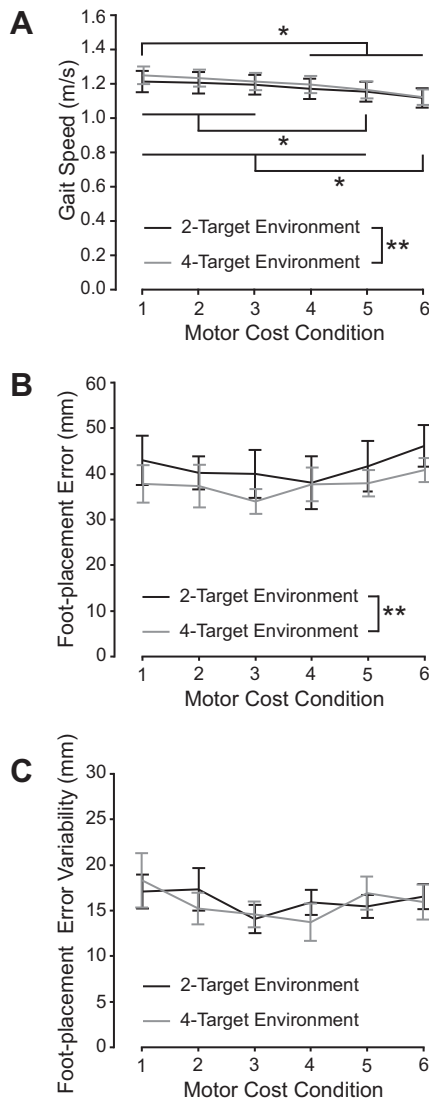
Fig. 6. Gait speed and foot-placement accuracy on the manipulated target ($n = 10$ participants). *A*: gait speed. *B*: foot placement error based on the vector distance between the center of the manipulated target and the midfoot in the different motor cost conditions and target environments. *C*: foot 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. Significantly different values based on post hoc tests: after a main effect of motor cost condition (*) or environment (**). Data are represented as means ± SE.

Note that the shape of the trajectory for the trunk is different when comparing between the two-target and four-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 two-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 BoS (based on a lateral heel position marker) and the XCoM (see Fig. 7*B*); the XCoM takes into account both the position and velocity of the CoM, 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 CoM. However, we find virtually identical results if it is included.

We first determined the value of this measure at the instance of heel contact on the manipulated target and compared it across motor cost conditions and environments with a two-way (cost × environment) ANOVA. We found a significant cost × 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 two-target environment (Fig. 7*C*). However, *motor cost conditions 4* and *5* differed from *motor cost conditions 1* and *2* in the four-target environment. In addition, we observed larger DMS values in *motor cost conditions 2–6* in the four-target environment compared with all conditions in the two-target environment.

We next determined the value of this measure at the instance of toe-off from the manipulated target. 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 four-target environment compared with the two-target environment (except for *motor cost condition 1*; Fig. 7*D*). Interestingly, the trunk-leg separation increased (greater DMS) with greater motor cost. This increase is more evident in the four-target than the two-target environment.

To quantify the different effort involved in having to redirect the body toward another target in the four-target environment, but not the two-target environment, we calculated the TMA during stance phase (heel contact until toe-off) on the manipulated target. A two-way ANOVA (cost × 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 four-target environment for *motor cost conditions 5* and *6* compared with the two-target environment (Fig. 7*E*). Taken together with the DMS measures, our results suggest that the greater active control required for redirecting the body's CoM in the four-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 before this gait event, which resulted in an overall model R^2 of 0.63 and 0.77 for the two-target and four-target environments, respectively. We found that the DMS significantly predicted the HC-interval in the four-target (β coefficient = 0.081, $P < 0.0001$) but not the two-target ($P = 0.930$) environment. The TMA did not significantly predict the HC-interval in the two-target environment ($P = 0.566$) or the four-target environment (β 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 two-target and four-target environments, respectively. We
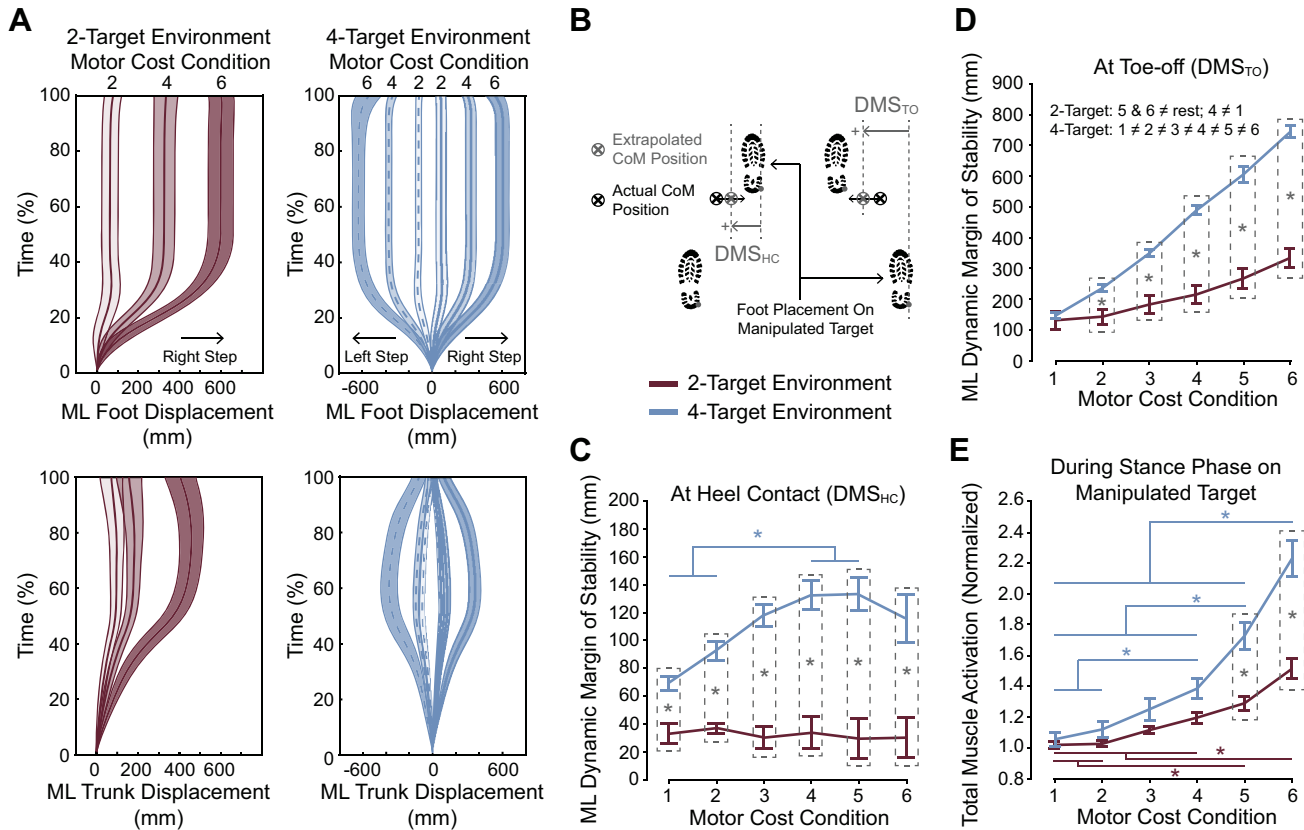
Fig. 7. Effort involved in redirecting the body and foot ($n = 10$ participants). *A*: medial-lateral (ML) trajectory of a foot and chest (or trunk) position marker for 1 stride. Data are time-normalized from toe-off (TO) of the foot about to step on the manipulated target to TO from the manipulated target. Only 3 of the 6 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 5 bilateral leg muscles) calculated from HC 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 means ± SE. *Values are significantly different from each other based on post hoc tests after a significant cost × environment interaction ($P < 0.05$).

found that the DMS had a significant relationship to the HC-interval in the four-target (β coefficient $= 0.143$, $P < 0.0001$) but not the two-target ($P = 0.354$) environment. Similarly, the TMA had a significant relationship with the HC-interval in the four-target (β coefficient $= -0.074$, $P = 0.015$) but not the two-target ($P = 0.441$) environment. 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.

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 CoM 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 neurophysiology-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 traveled 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 four-target but not the two-target environment? In the two-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 Fig. 1, Fig. 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 four-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 four-target environment (see Fig. 4). In this environment, we only manipulated one of the middle two targets on a trial-to-trial basis. We have previously 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 four-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 four-target environment, there is an increase in the cost to maintain stability relative to the two-target environment. Specifically, the higher-motor-cost conditions of this environment create a situation in which there are two large sequential step widths (compared with just 1 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. 7E) and the need to redirect the body's CoM back to the original plane of progression. This latter idea is reflected in a larger DMS, indicating that the CoM deviates further away from the foot in contact with the manipulated target (Fig. 7, C and 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 fovea-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 (Chapman and Hollands 2007; Domínguez-Zamora et al. 2018; 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, although 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, although 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. In light of these findings, 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 that 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 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 of this, 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 two-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 and/or frontal eye fields. For instance, during fixation, a longer travel time (reflecting more effort) results in a slower rate of rise of anterior cingulate cortex activity to a threshold that is associated with patch-leaving decisions (Hayden et al. 2011). Furthermore, frontal eye field 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 of performing 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.

DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR 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 of manuscript.

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