The Impact of Visual Perturbations on Balance Control during Walking

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Summary statement

Visual perturbations during walking alter foot placement and body motion in humans, revealing how eye and head movements influence walking balance.

Abstract

Visual perturbations may lead to an illusory self-motion and affect balance control. We studied effects of different visual perturbations in 16 healthy young participants walking on a treadmill, by assessing foot placement and center of mass (CoM) states. Three different visual perturbations were applied: fixating on a stationary target while the background moved to the right (MB), tracking the target moving rightward over a stationary background with head rotation (MT-HR), and tracking the moving target with eye movement only (MT-EM). Deviations of foot placement, CoM and trunk orientation due to the visual perturbation were assessed. Linear models were fit to the kinematic data to predict foot placement from CoM state at mid-swing. Over the whole trial, MT-HR and MT-EM caused an increase in step width variability, CoM position variability and RMS of foot placement errors simultaneously. During visual perturbation epochs specifically, in MB, a left deviation of foot and CoM trajectories was observed from the start of the background movement. In MT-HR and MT-EM, a right deviation of foot and CoM trajectories was observed only after the target had stopped moving. Contrary to our expectations, foot placement errors did not coincide with subsequent CoM deviations in the opposite direction. An obvious change in frontal plane trunk orientation was found only in MT-HR. While all visual perturbations affected control of the CoM trajectory in the frontal plane, these effects appeared caused by effects on control of

32   heading as well. Head rotation appears to additionally disturb balance through a coupling

33   with trunk orientation.

Introduction

Balance control is a dynamic process that stabilizes the trajectory of the body's center of mass (CoM) against the destabilizing effects of gravity encountered by humans in upright postures (Bruijn and van Dieen, 2018). The main mechanism to maintain balance during walking is the selection of the appropriate location for foot placement in relation to the ongoing movement of the CoM. This control has been identified by a linear relation between the CoM state during the swing phase. This coordination of foot placement to CoM state has been found in locomotion of flies, mice, and humans (De Comite and Seethapathi, 2025 preprint), and is thought to be achieved at least in part actively (van Leeuwen, Bruijn et al. 2022). For this control, the state of the CoM is estimated from sensory information from the visual, vestibular, and proprioceptive systems (Perry et al., 2001 ; Betker et al., 2008 ; Magnani et al., 2023 ; Li et al., 2025). This information is integrated by the central nervous system (CNS), which then sends signals to alpha-motor neurons to execute muscular responses to achieve the appropriate foot placement.

The visual system plays a fundamental role in navigation and predation in animals (Barron and Srinivasan, 2006 ; Bhagavatula et al., 2011). When encountering objects of interest, animals typically fixate or track them using eye or head movements. However, such behaviors during locomotion can disrupt the use of optical information for maintaining balance. For human beings, fixating on a stationary target while the background is moving is known to perturb balance control. Previous studies have shown that such background movement can lead to an illusion of self-motion in the direction opposite to the background movement (Nakamura, 1996 ; Nakamura et al., 2016), triggering balance responses that move the CoM in the direction of the background movement. In walking, it has been found that people step in the direction of the illusory self-movement and displace their CoM in the opposite direction (Reimann et al., 2018).

Another potential visual perturbation during walking may be caused by visual tracking of moving targets. Tracking a moving target causes relative movement of the visual background on the retina, which may induce a similar illusion as described above. Tracking a moving target is usually completed by coordinated eye and head rotation movements (Gadotti et al., 2016 ; Srivastava et al., 2018 ; Yamazoe et al., 2019). Some situations, such as when a large field of view shift is needed or when a target moves too fast for visual pursuit, require concomitant head movement (Rinaudo et al., 2019). These head movements affect vestibular and neck proprioceptive information and may have possible mechanical effects on balance.

Previous literature has shown changes in the gait pattern due to visual tracking and related

head movements. Magnani et al (2020) demonstrated that yaw head motion made gait less

stable. Vallis and Patla (2004) showed that head rotation during walking coincided with a

mediolateral deviation of the CoM trajectory.

As stated above, the CoM trajectory during walking is mainly stabilized by foot placement

(Bruijn and van Dieen, 2018 ; van Leeuwen et al., 2022). However, it is not yet clear how

fixating on a stationary target over a moving background and tracking a moving target affect

control of the CoM by foot placement. For the latter condition, it has not been studied how

rotating the head and re-directing the gaze contribute to effect of visual perturbations. In the

current study, we investigated deviations in CoM trajectories and foot placement during the

aforementioned visual perturbations in walking humans. We identified the linear relation

between foot placement and preceding CoM state, in order to assess how steps taken during

the visual perturbations contributed to balance regulation. During normal walking, these foot

placement errors vary around zero. During the perturbations, however, we expected

systematic deviations from zero. We hypothesized that (1) the foot placement error will

increase and (2) people will step in the direction opposite to the background movement and in

the direction of the target movement during these visual perturbations, which will

subsequently cause displacement of the CoM in the opposite direction.

86 Methods

87 Participants

Sixteen healthy individuals (age: 23.4±3.9 years, height: 1.70±0.09 m, weight: 62.2±11.7 kg)

volunteered for this study. All participants reported themselves to be free from any

neurological or musculoskeletal disorders that could negatively affect their balance or

walking performance. All participants walked without assistive devices. Ethical approval was

obtained from the ethics committee of the Faculty of Behavioral and Movement Sciences at

Vrije Universiteit Amsterdam (VCWE-2023-170). All procedures conformed to the

Declaration of Helsinki and participants signed informed consent before participation.

95 Instruments

All measurements were conducted on a system that integrated a motion capture system

sampling at 50 samples/sec (Optotrak, Northern Digital, Waterloo ON, Canada) with an

instrumented treadmill (Motek-Forcelink, Amsterdam, Netherlands), and a data projector.

Clusters of three markers were affixed to the participant's bodies at the following locations:

the posterior surfaces of both heels, the sacrum at the level of S2, the trunk at the level of T6,

and the back of head. A screen (2.50 m* 1.56 m) was placed 1.60 m in front of the

participants with the projector behind it to present the visual perturbations. **Fig. 1A** shows the

full set-up.

Visual perturbations

A background of 12 uniformly distributed black-and-white vertical stripes (0.205 m * 1.560

m) was presented on the screen. A red target dot measuring 12 cm in diameter was positioned

at the center of the screen. The height of the red target was adjusted to be at the participant's

eye level. Participants walked under four different conditions: (a) Normal walking (NW), in

which the whole scene was stationary and participants were asked to walk normally. (b)

Moving background (MB), during this perturbation, the red target dot was fixed in the middle,

while the black-and-white background moved horizontally from the middle to the right side

corresponding to 45 degrees in 4s, stayed at the side for 8s, then it went back to the middle. In

this condition, participants were asked to keep looking at the stationary red target dot in the

middle. (c) Moving target with head rotation (MT-HR), during this perturbation, the black-

and-white background was stationary, while the red target dot moved horizontally to 45

degrees from the center to the right side in 4s and stayed at the side for 8s, then moved back

to the middle. Participants were asked to track the moving target. (d) Moving target with eye

movement (MT-EM), during this perturbation, the scene was the same as during MT-HR, but

the participants were asked to track the horizontally moving target with their eyes only while

keeping their head stationary. All conditions are illustrated in **Fig. 1B.**

Visual perturbations were triggered at right heel strikes. Approximately 14 perturbations in

total were provided in each walking trial. The first perturbation was triggered at the 20th right

heel strike. Six to eight heel strikes occurred randomly after every perturbation before a new

perturbation was provided.

Procedures

The treadmill speed was set to 1.0m/s. To enhance immersion, the lights in the lab were

turned off, and the curtains were closed. Before the actual measurement, there was a 10-

minute period during which participants were familiarized with the walking speed and all

perturbations. Subsequently, a normal walking trial was conducted, followed by the three

perturbation trials in a randomized order. Each trial lasted 5 minutes. A 5-minute seated rest

was given between trials.

Data analysis

The mediolateral CoM position was approximated as the average position of the pelvis

marker cluster. Mediolateral foot positions were represented by both heel clusters. Trunk

orientation in the frontal plane was calculated based on the trunk cluster relative to the

laboratory coordinate system. Heel strikes were determined from the maximum values of the

heel markers' position in the anteroposterior direction.

We calculated gait characteristics which reflect balance over the whole walking trial,

including step width, step width variability, step frequency, CoM position variability, trunk

orientation variability, and RMS of foot placement errors. Variability of the kinematic

variables was quantified as the standard deviation over steps (step width) or the standard

deviation averaged over phases of the time-normalized stride (CoM position and trunk

orientation). Step width was defined as the mediolateral distance between the heel positions

of both feet at heel strike. Step frequency was defined as the number of steps per minute. The

RMS of foot placement errors was defined as the RMS error between actual foot placement

and the foot placement predicted by the model described below. Variables are presented as

mean ± standard deviation. Variables that did not follow a normal distribution are presented

as median (interquartile range, IQR).

The continuous variables were low-pass filtered at 0.25Hz (2nd order bidirectional

Butterworth filter) to eliminate the fluctuations related to the stride cycle. We analysed the

time series of foot position, foot placement error, CoM position, and trunk orientation in

detail from the start of the visual perturbation to its end and divided these episodes into two

phases: moving and stationary phases (**Fig. 1B**). For all variables during the visual

perturbation epochs, we subtracted the value at the first sample of the epoch. Peak position

during each phase was selected as the maximum absolute value. We determined the average

values of these variables among subjects over perturbations. Foot placement errors in both

phases of the visual perturbation were extracted from the foot placement model described

below.

We applied a foot placement model to show step by step foot placement regulation during

visual perturbations. We used the complete time series of each trial to determine a linear

model predicting foot placement by the preceding CoM state. The model linked the variance

in mediolateral foot placement at heel strike to the variance in mediolateral CoM position and

velocity during the preceding swing phase (Wang and Srinivasan, 2014 ; Arvin et al., 2018 ;
van Leeuwen et al., 2020) as:

$$FP_i = \beta_1 * CoM_{i,\,mid-swing} + \beta_2 * vCoM_{i,\,mid-swing} + \varepsilon_i$$

with foot placement being foot placement of the leading leg (*FP*) at step *i* and

$CoM_{i,\,mid-swing}$ being the position of the CoM at mid-swing relative to the trailing foot's

position on the ground, and $vCoM_{i,\,mid-swing}$ referring to the velocity of the CoM at mid-

swing (**Fig. 1C**). β_1 and β_2 are regression coefficients and ε_i is the error for every step. The

RMS of ε over all steps was defined as the residual error in foot placement.

For each participant, we counted the number of steps from the initial right heel strike to the

end of the movement and stationary phases. We used the minimum number of steps per phase

over all participants to analyse foot placement errors. In the stationary phase, we selected the

first right step as step 1. Specifically, foot placement errors were analysed for the first seven

steps in the moving phase and the first eleven steps in the stationary phase.

Statistics

All statistical analyses were performed in Matlab (R2023a, The Mathworks Inc., Natick, MA).

For all statistics tests, we checked the assumption of normality using a Shapiro-Wilks test. To

assess the overall effects of visual perturbations on gait characteristics, we used a repeated

measures analyses of variance with Visual perturbation as a factor. For variables that did not

follow a normal distribution (i.e. CoM variability and RMS of foot placement errors), we

used a Friedman test. For the perturbation epochs, we used a one-sample *t*-test to assess if

averaged peak foot positions, peak CoM positions, peak trunk orientations, and foot

placement errors per step were significantly different from zero. For steps where the foot

placement error that didn't follow a normal distribution, we used Wilcoxon signed-rank test.

We conducted repeated measures analyses of variance with two factors (Visual perturbation

and Phase) for peak foot positions, peak CoM positions, peak trunk orientations in the

perturbation epochs (MB, MT-HR and MT-EM). If we found main effects or interaction

effects to be significant, we performed Bonferroni corrected pairwise post-hoc comparisons

to test for differences among visual perturbations for each phase (moving and stationary

phases). We calculated the effect size to provide an estimate of the magnitude of observed

effect: d (Cohen's d) for one-sample t-tests, η^2 (Eta squared) for ANOVA, W (Kendall's W)

for Friedman test, and r_{rb} (rank-biserial correlation) for Wilcoxon signed-rank test. For all

repeated measures analyses, if the assumption of sphericity was violated, the Greenhouse-

Geisser correction was be applied to adjust the degrees of freedom. For all analyses, the

significance level (p-value) was set at 0.05.

Results

Destabilizing effects of visual perturbations over the whole trial

There were no significant effects of Condition on step width and step frequency. Step width

variability was significantly affected by Visual perturbation ($F_{visual\ perturbation}$ (df = 3,45) =

10.744, $p < 0.001$, $\eta^2 = 0.417$) (**Fig. 2**). Step width variability in the NW condition (0.022 ±

0.005m) was significantly lower than in the MT-HR (0.026 ± 0.005m) and MT-EM (0.027 ±

0.005m) conditions, corresponding to 84.6% and 81.4% of the MT-HR and MT-EM values,

respectively ($p < 0.01$, $d = -0.795$; $p < 0.001$, $d = -1.079$). There was no significant difference

between MB and the other conditions.

CoM position variability was significantly affected by Visual perturbation

($\chi^2_{visual\ perturbation}$ (df = 3,45) = 30.225, $p < 0.001$, $W = 0.630$). CoM position variability in

the NW condition was significantly smaller than in the MB, MT-HR and MT-EM conditions

($p < 0.001$, $r_{rb} = -0.897$; $p < 0.001$, $r_{rb} = -1.000$; $p < 0.001$, $r_{rb} = -1.000$, respectively). CoM

position variability in NW (0.013 (0.012-0.015) m) was 68.4%, 46.4% and 41.9% of the MB

(0.019 (0.018-0.021) m), MT-HR (0.028 (0.022-0.039) m) and MT-EM (0.031 (0.025-0.034)

m) values. CoM position variability in the MB condition was significantly smaller than MT-

HR and MT-EM conditions ($p < 0.01$, $r_{rb} = -0.662$; $p = 0.012$, $r_{rb} = -0.676$), corresponding

to 67.9% and 61.3% of the MT-HR and MT-EM values. MT-HR and MT-EM were not

significantly different from each other ($p = 0.829$, $r_{rb} = -0.235$).

Trunk orientation variability was significantly affected by Visual perturbation ($F_{visual\ perturbation}$

(df = 3,45) = 31.534, $p < 0.001$, $\eta^2 = 0.678$). During NW, it was significantly smaller than

during MT-HR ($p < 0.001$, $d = -2.044$) and MT-EM ($p < 0.01$, $d = -1.044$) conditions. Trunk

orientation variability in NW (0.566 ± 0.172°) was 57.5% and 72.6% of the MT-HR (0.984 ±

0.267°) and MT-EM (0.780 ± 0.223°) values. MT-HR and MT-EM conditions also had

significantly greater trunk orientation variability than MB ($p < 0.001$, $d = 1.799$; $p < 0.01$, $d =$

0.800). Trunk orientation variability in the MB condition was not significantly different from

that in NW ($p = 0.196$, $d = 0.245$).

The RMS of foot placement errors was significantly affected by Visual perturbation

($\chi^2_{visual\ perturbation}$ (df = 3,45) = 29.775, $p < 0.001$, $W = 0.620$). It was significantly smaller in

NW (0.014 (0.013-0.016) m) than in MT-HR (0.016 (0.015-0.018) m) and MT-EM (0.015

(0.015-0.017) m), corresponding to 87.5% and 93.3% of the MT-HR and MT-EM values,

respectively ($p < 0.001$, $r_{rb} = -0.926$; $p < 0.001$, $r_{rb} = -0.971$). RMS of foot placement errors

in MT-HR was significantly greater than in MB ($p < 0.001$, $r_{rb} = 0.956$), while MB was not

significantly different from NW ($p = 0.834$, $r_{rb} = 0.221$).

Destabilizing effects during the visual perturbation

Qualitatively, foot trajectories changed during the visual perturbations (**Fig. 3**). In the MB

condition, participants placed their feet in the direction opposite to the background movement

from the start of the moving phase. A peak was reached at the beginning of the stationary

phase and then the foot trajectories tended to gradually return to the original location. In the

MT-HR condition, participants placed their feet more in the movement direction of the target

during the moving phase and continued deviating throughout the stationary phase. In the MT-

EM condition, participants placed their feet more in the direction of the target from the end of

the moving phase and continued deviating throughout the stationary phase.

Fig. 4 shows the peak foot positions averaged over perturbations during the moving and

stationary phases relative to the start of the visual perturbation for all perturbation conditions.

In MB, foot positions deviated significantly leftward in the moving phase ($p < 0.001$, $d = -$

1.663) and remained deviated to the left in the stationary phase ($p < 0.001$, $d = 1.861$). In both

MT-HR and MT-EM, foot positions were not significantly different from zero in the moving

phase (MT-HR: $p = 0.271$, $d = 0.286$; MT-EM: $p = 0.827$, $d = -0.056$). However, they

significantly deviated to the right in the stationary phase (MT-HR: $p = 0.018$, $d = 0.662$; MT-

EM: $p = 0.039$, $d = 0.565$). In MT-MR condition, during the stationary phase (0.024 ± 0.036

m), foot position deviations was 6 times larger than in the moving phase (0.006 ± 0.022 m).

In MT-EM condition, the peak foot position was greater during the stationary phase ($0.023 \pm$

0.041 m) than during the moving phase (-0.001 ± 0.021 m). We note that this effect was not

very consistent between participants.

A two-way repeated measures ANOVA showed significant effects of Visual perturbation on

averaged foot peak positions ($F_{visual\ perturbation}$ (df $= 1.390,20.854) = 17.006$, $p < 0.001$, $\eta^2 =$

0.380). Post-hoc results showed that MB was significantly different from MT-HR ($p < 0.001$,

$d = -1.392$), and MT-EM ($p < 0.01$, $d = -1.241$). Phase also had a significant effect on

averaged foot peak positions (F_{phase} (df $= 1,15) = 9.406$, $p < 0.01$, $\eta^2 = 0.055$). The interaction

between Visual perturbation and Phase ($F_{visual\ perturbation*phase}$ (df $= 2,30) = 8.869$, $p < 0.001$,

$\eta^2 = 0.053$) indicated that during the stationary phase the differences in averaged foot peak

positions between visual perturbations were larger than during the moving phase.

Qualitatively, in all conditions, the CoM appeared to follow the positions of the feet (**Fig. 5**).

In MB, significant leftward deviations occurred in the moving phase ($p < 0.001$, $d = -1.604$),

which remained significant in the stationary phase ($p < 0.001$, $d = -2.135$). In both MT-HR

and MT-EM, peak CoM positions were not significantly different from zero in the moving

phase (MT-HR: $p = 0.401$, $d = 0.216$; MT-EM: $p = 0.983$, $d = -0.005$). However, they

deviated significantly rightward in the stationary phase (MT-HR: $p = 0.026$, $d = 0.619$; MT-

EM: $p = 0.041$, $d = 0.559$). Generally, the peak CoM positions deviated leftward during MB,

whereas in MT-HR and MT-ER, they deviated to the right.

Peak CoM positions in MB were significantly ($F_{visual\ perturbation}$(df = 1.419, 21.278) = 14.918, p

< 0.001, $\eta^2 = 0.347$) smaller than in MT-HR ($p < 0.01$, $d = -1.271$) and MT-EM ($p < 0.01$, $d =$

-1.209). While there was no significant difference between MT-HR and MT-EM. A

significant effect of Phase was also observed (F_{phase}(df = 1,15) = 8.273, p = 0.012, $\eta^2 = 0.056$),

showing that the CoM deviation in the stationary phase was larger than in the moving phase

($p = 0.012$, $d = 0.470$). The interaction between Visual perturbation and Phase (F_{visual}

$_{perturbation*phase}$ (df = 2,30) = 9.061, $p < 0.001$, $\eta^2 = 0.056$) indicated that during the stationary

phase the differences in peak CoM positions between visual perturbations were larger than

during the moving phase.

Peak frontal plane trunk orientations during the moving and stationary phases are shown in

Fig. 6. In MB, trunk orientation did not significantly differ from zero in either phase (moving

phase: $p = 0.483$, $d = -0.180$; stationary phase: $p = 0.764$, $d = 0.077$). In MT-HR, the trunk

was significantly oriented leftward during both moving ($p < 0.001$, $d = -1.713$) and stationary

phases ($p < 0.001$, $d = -2.617$). In MT-EM, trunk orientation was not significantly different

from zero in the moving phase ($p = 0.133$, $d = -0.397$), while it deviated leftward in the

stationary phase ($p < 0.01$**,** $d = -0.912$).

Peak trunk orientation depended on the visual perturbation condition ($F_{visual\ perturbation}$(df =

2,30) = 24.581, $p < 0.001$, $\eta^2 = 0.559$). In MT-HR, it was significantly smaller (more leftward)

than in both MT-EM ($p < 0.001$, $d = -1.395$) and MB ($p < 0.001$, $d = -2.183$), but there was

no significant difference between MB and MT-EM ($p = 0.173$, $d = 0.789$). A significant

effect of Phase was observed as well (F_{phase}(df = 1,15) = 16.271, $p < 0.01$, $\eta^2 = 0.016$),

indicating the leftward tilt became larger during the stationary phase. The interaction between

Visual perturbation and Phase ($F_{visual\ perturbation*phase}$ (df = 2,30) = 5.944, $p < 0.01$, $\eta^2 = 0.020$)

indicated that during the stationary phase, the differences in trunk orientation between visual

perturbations were larger than in the moving phase.

The foot placement errors during the moving and stationary phases of each perturbation

condition can be seen in **Fig. 7**. In MB, leftward (negative) foot placement errors were

significant at the second ($p < 0.01$, $d = -0.929$), third ($p < 0.01$, $d = -0.867$), fourth ($p < 0.01$,

$d = -0.886$), and sixth steps ($p = 0.016$, $d = -0.679$) during the moving phase. During the

stationary phase, rightward (positive) foot placement errors were significant at the second (p

$= 0.035$, $d = 0.580$), sixth ($p < 0.01$, $d = 0.873$), and eighth ($p = 0.032$, $d = 0.593$) steps. In

MT-HR, rightward foot placement errors were significant at the fourth ($p < 0.01$, $d = 0.769$)

and seventh ($p < 0.01$, $d = 0.824$) steps during the moving phase. During the stationary phase,

rightward foot placement errors were significant at the first ($p < 0.01$, $d = 1.011$), second ($p =$

0.030, $d = 0.601$), third ($p < 0.001$, $d = 1.107$), fifth ($p < 0.01$, $d = 0.838$), sixth ($p = 0.028$, d

$= 0.610$), seventh ($p = 0.013$, $d = 0.702$), ninth ($p < 0.01$, $d = 0.806$) and tenth ($p = 0.024$, $d =$

0.629) steps. In MT-EM, a leftward foot placement error was significant in the second step (p

< 0.01, $d = -0.817$) during the moving phase. During the stationary phase, rightward foot

placement errors were significant at the second ($p = 0.021$, $r_{rb} = 0.647$), fifth ($p < 0.001$, $d =$

1.129), seventh ($p < 0.01$, $d = 0.880$), and ninth ($p = 0.037$, $d = 0.573$) steps.

308   Discussion

The visual system can be used to gather information from the environment to control balance.

However, this information can in some situations be considered as a perturbation (Logan et

al., 2010 ; Mohebbi et al., 2022). For example, on a stationary train, one may perceive to be

moving when another train slowly passes by. In this study, we applied different types of

visual perturbations to study if and how these affect balance during walking through eliciting

changes in foot placement. Our results indicated that the variability of trunk sway and foot

placement increased over the entire walking trial only when tracking a moving target, either

with head rotation (MT-HR) or with eye movement only (MT-EM). During the visual

perturbation epochs, fixating a stationary target while the background moved caused a

deviation of foot and CoM trajectories opposite to the background movement. Tracking a

moving target with head rotation or with eye movement only did not cause obvious

deviations of foot and CoM trajectories during the moving phase, but did cause deviations in

the target direction during the stationary phase.

Over the whole walking trial, a negative effect of visual perturbations on gait characteristics

was only found in MT-HR and MT-EM. In these two conditions, step width variability, CoM

position variability, trunk orientation variability, and RMS of foot placement errors were

significantly higher than in NW. This indicates that visually tracking a moving target

destabilizes walking even in healthy young participants. Unexpectedly, MB did not induce

similar changes in gait characteristics except CoM variability. Although foot and CoM

trajectories in MB deviated initially, they returned towards normal during the stationary

phase. As a result, the effect of MB may have been diluted, which may have masked the

overall impact of the perturbation on the trial.

During the visual perturbation epoch, the deviations in foot placement and CoM positions

were different across conditions as well as different phases. In the current study, we used a

0.25 Hz cutoff frequency to filter the data and a validation at 4 Hz showed consistent results

(**Fig. S1**). As expected, the deviation in foot placement during the moving phase varied

between conditions. MB caused a deviation opposite to the background movement. However,

in MT-HR and MT-EM, no obvious deviations were observed in this phase, in line with

findings from a study by Vallis and Patla (2004). This may be explained by correction based

on other information. For one, in the target tracking tasks, the CNS likely interpreted the

relative background movement as a predictable outcome of self-motion, attenuating its

perceptual salience and reducing the need for behavioral adjustments (Spering et al., 2011).

Other sources of information that might help to distinguish self-motion and external motion

may be: (1) the stationary background sensed by peripheral vision: the fixed black-and-white

vertical stripes background provided a reference, (2) proprioception: proprioceptive

information from the neck and eye extraocular muscles would indicate self-motion (Wang

and Pan, 2013 ; Blumer et al., 2024), (3) the presence of an efference copy: predictions based

on efference copy of the motor commands related to target tracking would also indicate self-

motion (Wolpert and Ghahramani, 2000). In addition, since the onset of the target movements

was unpredictable and fast, saccades may have been used during tracking instead of smooth

pursuit movements (Leigh and Kennard, 2004). While smooth pursuit eye movements appear

to disturb balance during walking, saccades were not found to do so (Thomas et al., 2017).

Saccadic eye movements may induce suppression of visual information outlasting the

duration of the saccade itself (Ibbotson and Krekelberg, 2011), which may have reduced

sensitivity to the visual perturbation.

In the stationary phases, foot placement deviations were in opposite directions for the MB

condition versus MT-HR and MT-EM conditions. In the MB condition, the deviations of the

the foot trajectories subsequently decreased (**Fig. 3**). This suggests that the stationary target

and background may have helped to correct the trajectory. The averaged peak foot placement

(**Fig. 4**) and CoM position (**Fig. 5**) were slightly larger in the stationary phase, but this may

have been caused by ongoing movement initiated during the moving phase and could be due

to a shift in peak timing caused by the low-pass filtering. In the MT-HR and MT-EM

conditions, the deviations of the foot trajectories reached significance only during the

stationary phase and increased during this phase. Obviously, accumulation of small errors

over the moving phase may have occurred, leading to significant deviations only in the

stationary phase. This finding may also reflect that heading direction was aligned with gaze

direction in this phase in all conditions. It has been proposed that head orientation or gaze

direction provides the CNS with a frame of reference, and thus a change of this reference

releases a steering synergy and affects heading direction (Hollands et al., 2002 ; Vallis and

Patla, 2004 ; Bernardin et al., 2012 ; Belmonti et al., 2013). Finally, walking with a large

head or eye rotation angle may be considered as a dual task, decreasing the control over

heading, but it is not obvious why this would lead to deviations in a specific direction.

The deviation from average CoM position and velocity at midstance could explain 80% of

variance in mediolateral foot placement (Wang and Srinivasan, 2014). We dubbed the

remaining variance "foot placement errors". Such foot placement errors could either be

caused by the control itself or by perturbations. In current study, we expected foot placement

errors during visual perturbation to point in the direction of the illusory self-motion. During

the MB perturbations, where the background moved to the right, participants indeed stepped

left of the predicted foot placement from the second to the fourth and sixth steps in the

moving phase, which would align with an illusion of a deviation in the CoM state (position or

velocity) in this phase. During the MT-HR perturbations, with a right target movement, as

expected rightward foot placement errors appeared at the 4th and 7th steps. During the MT-

EM perturbations, the second step (of the left foot) was unexpectedly placed leftwards. In the

stationary phase, significant errors were in all conditions towards the right. In MB, rightward

foot placement errors in the stationary phase coincided with the foot and CoM trajectories

returning to the origin. While in the MT-HR and MT-EM conditions, rightward foot

placement errors in the stationary phase coincided with a further rightward deviation of the

foot and CoM trajectories. These results suggest that the stationary target location determined

heading direction. In the MB condition, all sensory inputs would align with a forward

heading. In MT-HR and MT-EM conditions, sensory information was likely conflicting, with

tactile information from feet indicated a forward direction conflicting with gaze and in part

neck orientation. The walking direction appeared to follow the information from the (neck

and) head, indicating a top-down regulation.

Generally, a lateral step is associated with a force accelerating the CoM in the opposite

direction (Reimann et al., 2018). However, none of the foot placement errors was associated

with a subsequent movement of the CoM to the opposite side. Instead, in contrast with our

expectation, the foot placement deviations coincided with a CoM displacement in the same

direction (**Fig. S1**). While we expected more rightward foot placement to coincide with a

more leftward acceleration of the CoM due to a higher leftward ground reaction force and

vice versa, foot placement does not directly determine the horizontal ground reaction force

exerted during the subsequent stance phase (van Dieën et al., 2025 preprint). One may

interpret a more rightward foot placement to reflect an adaptation of the base of support to the

ongoing CoM movement, which would fit with our data. In addition, CoM accelerations

arising from the ground reaction force after foot placement may have been corrected through

ankle moments bringing the CoM in the same direction (van Leeuwen et al., 2020). Our

predictions were based on the expected role of visual information in sensing the state of the

CoM and the role of foot placement in stabilizing the CoM trajectory, in the frontal plane.

Alternatively, the conflicting findings may be attributable to the fact, already alluded to

above, that the visual tasks may affect heading estimates and that foot placement also plays a

role in control of heading.

A significant frontal trunk roll was found in MT-HR, which is consistent with previous

findings (Patla et al., 1999 ; Vallis and Patla, 2004 ; van Andel et al., 2023). Van Andel et al.

(2023) illustrated that head rotation was associated with frontal plane rotation of the trunk.

Previous studies (Patla et al., 1999 ; Vallis and Patla, 2004) proposed that this frontal trunk

roll is used as a strategy to push the CoM in the desired direction when making a turn and this

would match with our participants walking in the direction of the target. However, in our

study, trunk roll only occurred in MT-HR but not in MT-EM, where a similar deviation in

gait direction was observed. Before making a turn, people usually rotate their head in the

direction of the turn as well (Grasso et al., 1998 ; Hicheur et al., 2005 ; Dollack et al., 2019).

Therefore, we assume that the trunk roll may be a result of a mechanical coupling between

head rotation and trunk roll.

To further evaluate the plausibility of this mechanical coupling, we imposed the same visual

perturbations in the same group of participants while standing. For each condition, five

repeated standing trials were conducted. During recording, participants were instructed to

fixate on the target, or track the target either by head or eye movement and stand still for 40s.

In each trial, a visual perturbation was triggered once. The visual perturbation began around

the 10th second and lasted for 16s. The setting of the visual perturbations was the same as in

walking. The presence of trunk roll when turning the head while standing (**Fig. 8**) supports

the idea that this could result from a mechanical coupling.

Although our experiment was conducted under controlled laboratory conditions, the observed

interactions between gaze behavior and balance control likely reflect dual demands

encountered in visually complex natural environments. In such settings, moving backgrounds

and self-motion introduce visual perturbations that require integrated visual–vestibular–

proprioceptive processing to maintain stability while tracking relevant targets. Many animal

species integrate visual and other sensory inputs to support motor control, in ways that

parallel human's behaviour (Dauzere-Peres and Wystrach, 2024 ; Kodaka et al., 2004).

Evidence suggest that humans and non-human primates perceive visually induced self-motion

through similar inferential mechanisms (Kodaka et al., 2004 ; Greenlee et al., 2016). The

findings in the current study may therefore reflect general sensorimotor strategies that support

effective locomotion and spatial orientation across species.

This study has several limitations. First, we only recruited healthy young adults, and results

may be different, for example, in older adults, who have a high risk of falling (Lutz et al.,

2008). Secondly, the experiment was conducted on a treadmill. This partially constrains

walking speed and walking direction, which may have had an impact on participants'

responses to the visual perturbations. Thirdly, we did not assess foot orientation. Foot

orientation may have played a role in redirecting the CoM trajectories. Further investigations

may also consider the role of ankle moments for keeping balance during visual perturbations.

Conclusion

Our results showed that visual perturbations challenge frontal plane balance, or in other

words, the control of the CoM trajectories in this plane during walking. This was in line with

expected effects on sensory estimates of the CoM state used for the control of foot placement

in stabilizing the frontal plane CoM trajectory. Mechanical effects of head rotation,

associated with visual tracking, had an additional disturbing effect on balance. However,

effects of the gaze direction on heading appeared to affect gait simultaneously and cannot

easily be distinguished from responses related to balance control.

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Competing interests

460   The authors declare no competing or financial interests.

Data and resource availability

462   All data have been made available online. All files can be downloaded from:

463   https://doi.org/10.5281/zenodo.17289747

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Figure 1 Illustration of the experimental setup (A), visual perturbation conditions (B) and foot placement
model (C).

Figure 2 Effects of Visual perturbation conditions on step width (A), step width variability (B), step
frequency (C), CoM position variability (D), trunk orientation variability (E), and RMS of foot placement
errors (F). Variability of the kinematic variables was quantified as the standard deviation over steps (mean $\pm$
s.d., n =16). The black thick lines represent the mean value across individuals. Repeated measures analyses of
variance were used for statistical analysis. For the variables that did not follow a normal distribution including
CoM variability and RMS of foot placement errors, Friedman test was performed. Significant effects in the post-
hoc tests are indicated by asterisks (* denotes $p < 0.05$, ** denotes $p < 0.01$, *** denotes $p < 0.001$). NW:
normal walking, MB: moving background, MT-HR: moving target with head rotation, MT-EM: moving target
with eye movement. Data point represents the mean values over the time series for each individual.

Figure 3 Deviations in foot and CoM positions during visual perturbation epochs. Data represent mean
value across repeated visual perturbations and participants and the shaded area represents the between-
participants standard deviations (mean $\pm$ s.d., n =16). All the data were referenced to the first sample of the
visual perturbation epoch. From left to right: (A) MB: moving background. (B) MT-HR: moving target with
head rotation, (C) MT-EM: moving target with eye movement. The vertical dashed lines separate the different
phases: the line at 0s marks the start of the moving phase, the line at 4s marks the start of the stationary phase,
and the line at 12s marks the end of the stationary phase.

Figure 4 Averaged peak foot positions relative to the first sample of the visual perturbation epoch in the
MP (moving phase) and SP (stationary phase), respectively. We averaged the two foot positions and selected
the peak value during each phase during the visual perturbations. These peak values were then averaged across
repeated visual perturbations as the mean (n = 16). The black thick lines represent the mean value across
individuals. One-sample t-test was performed. Significant differences from zero are indicated by asterisks (*
denotes $p < 0.05$, ** denotes $p < 0.01$, *** denotes $p < 0.001$). From left to right: (A) MB: moving background;
(B) MT-HR: moving target with head rotation; (C) MT-EM: moving target with eye movement.

Figure 5 Peak CoM positions relative to the first sample of the visual perturbation epoch in the MP
(moving phase) and SP (stationary phase). We selected the peak value in each phase during visual
perturbations. These peak values were then averaged across repeated visual perturbations as the mean (n = 16).
The black thick lines represent the mean value across individuals. One-sample t-test was performed. Significant
differences from zero are indicated by asterisks (* denotes $p < 0.05$, ** denotes $p < 0.01$, *** denotes $p < 0.001$).
From left to right: (A) MB: moving background; (B) MT-HR: moving target with head rotation; (C) MT-EM:
moving target with eye movement.

Figure 6 Deviations in frontal plane trunk orientation and peak trunk orientation during visual
perturbation epochs. The panels in the first row show the deviations of trunk orientation. Data represent mean
value across repeated visual perturbations and participants and the shaded area represents the between-
participants standard deviations (mean $\pm$ s.d., n =16). The vertical dashed lines in the figures at the first row
separate the different phases: the line at 0s marks the start of the moving phase, the line at 4s marks the start of

the stationary phase, and the line at 12s marks the end of the stationary phase. The panels in second row show

the peak frontal plane trunk orientation in MP (moving phase) and SP (stationary phase), respectively. We

selected the peak value in each phase during visual perturbations. These peak values were then averaged across

repeated visual perturbations as the mean (n = 16). The black thick lines represent the mean value across

individuals. One-sample t-test was performed. Significant differences from zero are indicated by asterisks (*

denotes $p < 0.05$, ** denotes $p < 0.01$, *** denotes $p < 0.001$). From left to right: (A) MB: moving background;

(B) MT-HR: moving target with head rotation; (C) MT-EM: moving target with eye movement. All the data

were referenced to the first sample of the visual perturbation epoch.

Figure 7 Foot placement errors in moving and stationary phases after the onset of the visual perturbation

(n = 16). The black thick lines represent the mean value across individuals. One-sample t-tests were performed

for each step. For steps which did not follow a normal distribution, we used Wilcoxon signed-rank tests instead.

Steps with significant differences from zero are indicated by asterisks (* denotes $p < 0.05$, ** denotes $p < 0.01$,

*** denotes $p < 0.001$). From top to bottom: (A) MB: moving background, (B) MT-HR: moving target with

head rotation, (C) MT-EM: moving target with eye movement.

Figure 8 Frontal plane trunk orientation deviations during visual perturbation epoch in standing. Data

represent mean value across repeated visual perturbations and participants and the shaded area represents the

between-participants standard deviations (mean ± s.d., n =16). All the data were referenced to the first sample of

the visual perturbation epoch. The vertical dashed lines in the figures separate the different phases: the line at 0s

marks the start of the moving phase, the line at 4s marks the start of the stationary phase, and the line at 12s

marks the end of the stationary phase. The shaded area represents the between-participants standard deviations.

From left to right: (A) MB: moving background; (B) MT-HR: moving target with head rotation; (C) MT-EM:

moving target with eye movement.

(A)

Visual Perturbation

Screen

Marker cluster

Optotrak

Walking speed: 1.0m/s

(B)

MB

Moving Phase
Background moves

Stationary phase

MT-HR

Moving Phase
Target moves

Stationary phase

MT-EM

Moving Phase
Target moves

Stationary phase

(C)

Bottom view

Trailing leg

$\beta_1 CoM_{i,mid-swing}$

$\beta_2 vCoM_{i,mid-swing}$

ε_i

Leading leg

Side view

Mid-swing phase

(A) **(B)** **(C)** **(D)** **(E)** **(F)**

(A)   **(B)**   **(C)**