The Impact of Visual Perturbations on Balance Control during Walking

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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 foot placement residual error 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 heading as well. Head rotation appears to additionally disturb balance through a coupling with trunk orientation.

Keywords: visual perturbations, foot placement, stability, locomotion

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), 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). This information is integrated by the central nervous system (CNS), which then sends signals to alfa-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., 2018b).

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, to understand how steps during the visual
perturbations contribute to balance regulation. During normal walking, these foot placement
errors vary around zero. During the perturbations, systematic deviations from zero were
expected. 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.

80 Methods

81 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.

89 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. **Figure 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 **Figure 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 foot placement residual error. 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 foot placement residual error was defined
as the RMS of the foot placement error based on the model described below.
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 (**Figure 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:

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

with foot placement of the leading leg (FP) at step i and position of the CoM at mid-swing

($CoM_{i,\,mid-swing}$) with respect to the location of the trailing leg's foot that is on the ground

(the stance foot), $vCoM_{i,\,mid-swing}$ referring to the velocity of the CoM at mid-swing. 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 foot placement residual error),

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 ($F_{\text{visual perturbation}}$ (df = 3,45) =

10.744, p < 0.001, η^2 = 0.417) (**Figure 2**). Step width variability in the NW condition was

significantly smaller than in the MT-HR and MT-EM conditions (p < 0.01, d = -0.795; p <

0.001, d = -1.079, respectively). There was no significant difference between MB and the

other conditions.

CoM position variability was significantly affected by Visual perturbation

($\chi^2_{\text{visual perturbation}}$ (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 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). 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 ($F_{\text{visual perturbation}}$

(df = 3,45) = 31.534, p < 0.001, η^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. 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).

Foot placement residual error was significantly affected by Visual perturbation

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

NW than in MT-HR (p < 0.001, r_{rb} = -0.926) and MT-EM (p < 0.001, r_{rb} = -0.971). Foot

placement residual error 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).

214 Destabilizing effects during the visual perturbation

Qualitatively, foot trajectories changed during the visual perturbations (**Figure 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.

Figure 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: $p = 0.039$, $d = 0.565$). 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 ($F_{\text{visual perturbation}}$ (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 ($F_{\text{visual perturbation*phase}}$ (df = 2,30) = 8.869, $p < 0.001$, η^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 (**Figure**

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 ($F_{\text{visual perturbation}}$(df = 1.419, 21.278) = 14.918, p

< 0.001, η^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, η^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}

$_{\text{perturbation*phase}}$ (df = 2,30) = 9.061, p < 0.001, η^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

Figure 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 ($F_{\text{visual perturbation}}$(df =

2,30) = 24.581, p < 0.001, η^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, η^2 =

0.016), indicating the leftward tilt became larger during the stationary phase. The interaction

between Visual perturbation and Phase ($F_{\text{visual perturbation*phase}}$ (df = 2,30) = 5.944, p < 0.01, η^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 **Figure 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.

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 foot placement residual error 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.

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 (**Figure 3**). This suggests that the stationary

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

placement (**Figure 4**) and CoM position (**Figure 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., 2018a). 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 (Figure S1). Possibly, the CoM trajectory was adjusted immediately after foot

placement 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, both in

the frontal plane. 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 test this idea, 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. **Figure 8** shows that a trunk roll is also present when turning the head while

standing, supporting 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

The authors declare no competing or financial interests.

Data availability

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

ARVIN, M., HOOZEMANS, M. J. M., PIJNAPPELS, M., DUYSENS, J., VERSCHUEREN, S. M. & VAN DIEEN, J. H. 2018. Where to Step? Contributions of Stance Leg Muscle Spindle Afference to Planning of Mediolateral Foot Placement for Balance Control in Young and Old Adults. *Front Physiol,* 9**,** 1134.

BARRON, A. & SRINIVASAN, M. V. 2006. Visual regulation of ground speed and headwind compensation in freely flying honey bees (Apis mellifera L.). *J Exp Biol,* 209**,** 978-84.

BELMONTI, V., CIONI, G. & BERTHOZ, A. 2013. Development of anticipatory orienting strategies and trajectory formation in goal-oriented locomotion. *Exp Brain Res,* 227**,** 131-47.

BERNARDIN, D., KADONE, H., BENNEQUIN, D., SUGAR, T., ZAOUI, M. & BERTHOZ, A. 2012. Gaze anticipation during human locomotion. *Exp Brain Res,* 223**,** 65-78.

BETKER, A. L., MOUSSAVI, Z. M. K. & SZTURM, T. 2008. Ambulatory Center of Mass Prediction Using Body Accelerations and Center of Foot Pressure. *IEEE Trans Biomed Eng,* 55**,** 2491-2498.

BHAGAVATULA, P. S., CLAUDIANOS, C., IBBOTSON, M. R. & SRINIVASAN, M. V. 2011. Optic flow cues guide flight in birds. *Curr Biol,* 21**,** 1794-9.

BLUMER, R., CARRERO-ROJAS, G., CALVO, P. M., STREICHER, J., DE LA CRUZ, R. R. & PASTOR, A. M. 2024. Proprioceptors in extraocular muscles. *Exp Physiol,* 109**,** 17-26.

BRUIJN, S. M. & VAN DIEEN, J. H. 2018. Control of human gait stability through foot placement. *J R Soc Interface,* 15.

DAUZERE-PERES, O. & WYSTRACH, A. 2024. Ants integrate proprioception as well as visual context and efference copies to make robust predictions. *Nat Commun,* 15**,** 10205.

DE COMITE, A. & SEETHAPATHI, N. 2025. Foot placement control underlies stable locomotion across species. *bioRxiv***,** 2024.09.10.612345.

DOLLACK, F., PERUSQUIA-HERNANDEZ, M., KADONE, H. & SUZUKI, K. 2019. Head Anticipation During Locomotion With Auditory Instruction in the Presence and Absence of Visual Input. *Front Hum Neurosci,* 13**,** 293.

GADOTTI, I. C., ELBAUM, L., JUNG, Y., GARBALOSA, V., KORNBLUTH, S., DA COSTA, B., MAITRA, K. & BRUNT, D. 2016. Evaluation of eye, head and trunk coordination during target tracking tasks. *Ergonomics,* 59**,** 1420-1427.

GRASSO, R., PREVOST, P., IVANENKO, Y. P. & BERTHOZ, A. 1998. Eye-head coordination for the steering of locomotion in humans: an anticipatory synergy. *Neurosci Lett,* 253**,** 115-8.

GREENLEE, MARK W., FRANK, SEBASTIAN M., KALIUZHNA, M., BLANKE, O., BREMMER, F., CHURAN, J., CUTURI, L. F., MACNEILAGE, PAUL R. & SMITH, ANDREW T. 2016. Multisensory Integration in Self Motion Perception. *Multisensory Research,* 29**,** 525-556.

HICHEUR, H., VIEILLEDENT, S. & BERTHOZ, A. 2005. Head motion in humans alternating between straight and curved walking path: combination of stabilizing and anticipatory orienting mechanisms. *Neurosci Lett,* 383**,** 87-92.

HOLLANDS, M. A., PATLA, A. E. & VICKERS, J. N. 2002. "Look where you're going!": gaze
behaviour associated with maintaining and changing the direction of
locomotion. *Exp Brain Res,* 143**,** 221-30.
IBBOTSON, M. & KREKELBERG, B. 2011. Visual perception and saccadic eye
movements. *Curr Opin Neurobiol,* 21**,** 553-8.
KODAKA, Y., MIURA, K., SUEHIRO, K., TAKEMURA, A. & KAWANO, K. 2004. Ocular
tracking of moving targets: effects of perturbing the background. *J Neurophysiol,*
91**,** 2474-83.
LEIGH, R. J. & KENNARD, C. 2004. Using saccades as a research tool in the clinical
neurosciences. *Brain,* 127**,** 460-77.
LOGAN, D., KIEMEL, T., DOMINICI, N., CAPPELLINI, G., IVANENKO, Y., LACQUANITI, F.
& JEKA, J. J. 2010. The many roles of vision during walking. *Exp Brain Res,* 206**,**
337-50.
LUTZ, W., SANDERSON, W. & SCHERBOV, S. 2008. The coming acceleration of global
population ageing. *Nature,* 451**,** 716-9.
MAGNANI, R. M., BRUIJN, S. M., VAN DIEEN, J. H. & VIEIRA, M. F. 2020. Head orientation
and gait stability in young adults, dancers and older adults. *Gait Posture,* 80**,** 68-
73.
MAGNANI, R. M., VAN DIEËN, J. H. & BRUIJN, S. M. 2023. Effects of vestibular
stimulation on gait stability when walking at different step widths. *Exp Brain Res,*
241**,** 49-58.
MOHEBBI, A., AMIRI, P. & KEARNEY, R. E. 2022. Identification of human balance control
responses to visual inputs using virtual reality. *J Neurophysiol,* 127**,** 1159-1170.
NAKAMURA, S. 1996. Effects of background stimulation upon eye-movement
information. *Percept Mot Skills,* 82**,** 627-35.
NAKAMURA, S., PALMISANO, S. & KIM, J. 2016. Relative Visual Oscillation Can
Facilitate Visually Induced Self-Motion Perception. *Iperception,* 7**,**
2041669516661903.
PATLA, A. E., ADKIN, A. & BALLARD, T. 1999. Online steering: coordination and control
of body center of mass, head and body reorientation. *Exp Brain Res,* 129**,** 629-
34.
PERRY, S. D., SANTOS, L. C. & PATLA, A. E. 2001. Contribution of vision and cutaneous
sensation to the control of centre of mass (COM) during gait termination. *Brain*
Res, 913**,** 27-34.
REIMANN, H., FETTROW, T. & JEKA, J. J. 2018a. Strategies for the control of balance
during locomotion. *Kinesiology Review,* 7**,** 18-25.
REIMANN, H., FETTROW, T., THOMPSON, E. D. & JEKA, J. J. 2018b. Neural Control of
Balance During Walking. *Front Physiol,* 9**,** 1271.
RINAUDO, C. N., SCHUBERT, M. C., FIGTREE, W. V. C., TODD, C. J. & MIGLIACCIO, A. A.
2019. Human vestibulo-ocular reflex adaptation is frequency selective. *J*
Neurophysiol, 122**,** 984-993.
SPERING, M., SCHUTZ, A. C., BRAUN, D. I. & GEGENFURTNER, K. R. 2011. Keep your
eyes on the ball: smooth pursuit eye movements enhance prediction of visual
motion. *J Neurophysiol,* 105**,** 1756-67.
SRIVASTAVA, A., AHMAD, O. F., PACIA, C. P., HALLETT, M. & LUNGU, C. 2018. The
Relationship between Saccades and Locomotion. *J Mov Disord,* 11**,** 93-106.

THOMAS, N. M., DEWHURST, S., BAMPOURAS, T. M., DONOVAN, T., MACALUSO, A. &
VANNOZZI, G. 2017. Smooth pursuits decrease balance control during
locomotion in young and older healthy females. *Exp Brain Res,* 235**,** 2661-2668.
VALLIS, L. A. & PATLA, A. E. 2004. Expected and unexpected head yaw movements
result in different modifications of gait and whole body coordination strategies.
Exp Brain Res, 157**,** 94-110.
VAN ANDEL, S., SCHMIDT, A. R. & FEDEROLF, P. A. 2023. Distinct coordination patterns
integrate exploratory head movements with whole-body movement patterns
during walking. *Sci Rep,* 13**,** 1235.
VAN LEEUWEN, A. M., BRUIJN, S. M. & VAN DIEEN, J. H. 2022. Mechanisms that
stabilize human walking. *Braz J Mot Behav,* 16**,** 326-351.
VAN LEEUWEN, A. M., VAN DIEEN, J. H., DAFFERTSHOFER, A. & BRUIJN, S. M. 2020.
Active foot placement control ensures stable gait: Effect of constraints on foot
placement and ankle moments. *PLoS One,* 15**,** e0242215.
WANG, J. & PAN, Y. 2013. Eye proprioception may provide real time eye position
information. *Neurol Sci,* 34**,** 281-6.
WANG, Y. & SRINIVASAN, M. 2014. Stepping in the direction of the fall: the next foot
placement can be predicted from current upper body state in steady-state
walking. *Biol Lett,* 10.
WOLPERT, D. M. & GHAHRAMANI, Z. 2000. Computational principles of movement
neuroscience. *Nat Neurosci,* 3 Suppl**,** 1212-7.
YAMAZOE, H., MITSUGAMI, I., OKADA, T. & YAGI, Y. 2019. Analysis of head and chest
movements that correspond to gaze directions during walking. *Exp Brain Res,*
237**,** 3047-3058.
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Figure 1 Illustration of the experimental setup (A) and visual perturbation conditions (B).

Figure 2 Effects of Visual perturbation conditions on step width, step width variability, step frequency, CoM position

variability, and trunk orientation variability. Variability of the kinematic variables was quantified as the standard deviation

over steps. 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 foot

placement residual error, 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 ± 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: MB: moving background; MT-HR: moving target with head rotation; 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: MB: moving background; MT-HR: moving target

with head rotation; MT-EM: moving target with eye movement.

Figure 6 Frontal plane peak trunk orientation during visual perturbation epochs. From left to right: MB: moving

background. MT-HR: moving target with head rotation. MT-EM: moving target with eye movement. All the data were

referenced to the first sample of the visual perturbation epoch. 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 ± 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).

Significant differences from zero are indicated by an asterisk.

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:

MB: moving background, MT-HR: moving target with head rotation, MT-EM: moving target with eye movement.

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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 column: MB: moving background. MT-HR:
moving target with head rotation. MT-EM: moving target with eye movement.

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