Gait behavioral and neuromuscular characterization in response to increasing working memory load while walking under optic flow perturbations in young adults

Authors
Valentin Lana[1], Julien Frère[2], Vincent Cabibel[1], Tristan Réguème[1], Nicolas Lefèvre[3], Leslie M. Decker[1,3,*]

Affiliations
[1] Normandie Univ, UNICAEN, INSERM, COMETE, GIP Cyceron, Caen, France.
[2] Univ. Grenoble Alpes, CNRS, Grenoble INP, GIPSA-Lab, Grenoble, France.
[3] Normandie Univ, UNICAEN, CIREVE, Caen, France.

***Corresponding author:**
Leslie Marion DECKER
UMR-S 1075, INSERM / Université de Caen Normandie
COMETE – Mobilités : Vieillissement, Pathologie, Santé
Pôle des Formations et de Recherche en Santé
2, Rue des Rochambelles, 14032 Caen Cedex 5
Electronic address: leslie.decker@unicaen.fr
Phone: +33 (0)6 70 40 58 44
Fax: +33 (0)2 31 56 82 19

Highlights:

- Cognitive performance was preserved during DTW regardless of optic flow condition.
- ML POF under DTW increased subjective mental workload.
- Young adults counteracted ML POF by adopting an effortful gait control strategy.
- DTW led them to prioritize gait control in the ML direction over AP direction.
- Concurrent WM load attenuated ML POF effect on step velocity variability.

Abstract:
The precise role of cognitive control on optic flow processing during locomotion has rarely been investigated. Therefore, this study aimed to determine whether coping with unreliable visual inputs during walking requires attentional resources. Twenty-four healthy young adults walked on an instrumented treadmill in a virtual environment under two optic flow conditions: normal (NOF) and perturbed (POF, continuous mediolateral pseudo-random oscillations). Each condition was performed under single-task and dual-task conditions of increasing difficulty (1-, 2-, 3-back). In all conditions, subjective mental workload was estimated (raw NASA-TLX). For kinematic variables, mean, standard deviation, statistical persistence and step-to-step error correction were computed from gait time series in mediolateral and anteroposterior directions. For EMG variables of *soleus* and *gluteus medius*, the full width at half maximum and the variance ratio were calculated. Performance on N-back tasks was assessed using mean reaction time and d-prime. Cognitive performance was not affected by simultaneous walking in any optic flow condition. Gait variability was altered under POF compared to NOF, so that young adults sought to counteract those perturbations by adopting an effortful gait control strategy, independently of concurrent working memory (WM) load. Increasing WM load led changes first at the neuromuscular level, then at the behavioral level, with a prioritization of gait control in the mediolateral direction. Interestingly, dual-tasking lowered the effects of POF but in the anteroposterior direction only. These findings and their theoretical implications provide valuable insight into the complex interaction effects of cognitive and visual constraints on gait control during treadmill walking.

Keywords: Gait; lateral balance; muscle activity; variability; nonlinear dynamics; executive function.

Abbreviations:

1-back task (1b)
2-back task (2b)
3-back task (3b)
Analysis of variance (ANOVA)
Central nervous system (CNS)
d-prime (d')
Detrended fluctuations analysis (DFA)
DFA alpha scaling exponent (α)
Dual-task cognitive performance (DTC)
Dual-task walking (DTW)
False alarm (FA)
Full width at half maximum (FWHM)
Gluteus medius (Gmed)
Interdisciplinary center for virtual reality (CIREVE)
Lateral body position (z_B)
Linear correlation (R^2)
Mediolateral (ML)
Raw NASA task load index (Raw NASA-TLX)
Normal optic flow (NOF)
Perturbed optic flow (POF)
Preferred Walking Speed (PWS)
Reaction time (RT)
Single-task cognitive performance (STC)
Single-task walking (STW)
Slope of least-squares regression line (M)
Soleus (Sol)
Standard deviation (SD, σ)
Step velocity (V)
Step width (W)
Surface electromyography (EMG)
Variance ratio (VR)
Working memory (WM)

1. Introduction

Walking is usually considered to be a simple and automatic behavior relying on the central pattern generators, present in the spinal cord (Brown, 1911; Takakusaki, 2017). However, walking in the complex environments of everyday life requires the brain to continuously adapt to external sensory inputs such as obstacles or irregular surfaces (Kuhman et al., 2021) and to internal cognitively demanding tasks (Malcolm et al., 2018). To this end, human locomotion relies on a widespread cerebral network consisting of cortical sensorimotor areas controlling gait initiation (Takakusaki, 2013, 2017) and subcortical structures such as basal ganglia ensuring gait regulation (Grillner et al., 2008; Hamacher et al., 2015). These mechanisms allow the control of the multiple joints and muscle groups in order to cope with the associated large degrees of freedom (Bernstein, 1967).

As a way to better understand how the brain controls gait under unstable conditions, mediolateral (ML) perturbations (mechanical or visual) are of particular interest. Human walking is indeed more variable and unstable in the ML direction (Bauby and Kuo, 2000), in particular step width and ML foot placement (O'Connor and Kuo, 2009; Bruijn and van Dieën, 2018; Dingwell and Cusumano, 2019). Recently, Dingwell and Cusumano (2019) proposed a ML multi-objective control model of normal human gait and demonstrated that step width and, in a lesser extent, ML displacement of the center of mass were primarily controlled to regulate walking. These results were latter experimentally confirmed under mechanically or visually perturbed walking (Kazanski et al., 2020, 2022; Render et al., 2021). In this context, step width and ML displacement of the center of mass were more variable but also more tightly regulated when walking under continuous lateral oscillations of the visual field, and even more when walking under continuous lateral oscillations of the support surface, in comparison with no perturbation (Kazanski et al., 2020). Interestingly, no differences were found between healthy young and older adults, demonstrating that healthy ageing did not alter step-to-step ML regulation during perturbed walking. Since age-related cognitive decline reduces the adaptability under dual-task walking in older people (Beauchet et al., 2003; Al-Yahya et al., 2011; Mirelman et al., 2012), the likely effect of cognitive load on step-by-step ML regulation during perturbed walking remains an open question.

Francis et al. (2015) reported small effects of concurrent cognitive task on mean and variability of step width and step length compared to the effects of optic flow perturbations. Under dual-task conditions, the attentional cost associated with regulation of gait relies on many factors, including the type and complexity of the two tasks (Al-Yahya et al., 2011). For example, cognitive tasks involving both working memory and information processing or attention have been shown

to have greater impact on gait (*e.g.* changes in variability of step width and stride time) than those involving inhibition or visuospatial cognition, especially during perturbed walking (Kao and Pierro, 2022). For instance, tasks that involved interfering factors at the external level (*e.g.* Go/No-go task, choice reaction time task) have less impact on gait than those that involved interfering factors at the internal level (*e.g.* mental arithmetic task; n-back task, PASAT). This result is due to the competition between the cognitive functions involved in both locomotor and cognitive tasks which interfered with the self-organizing dynamics of the motor system (Lindenberger et al., 2000; Lövdén et al., 2008; Verrel et al., 2009). Using an incremental cognitive load protocol with young adults, a decrease in the antipersistence of the fluctuations of step velocity have been demonstrated (Decker et al., 2013) while Verrel et al. (2009) observed an increase in the regularity of walking. In contrast, in older adults, Verrel et al. (2009) found an increase in the regularity of walking at a low difficulty level because an easy cognitive task would allow the system to easily perform the motor task in an automated fashion (Wulf and Prinz, 2001; Beilock et al., 2004). However, they observed a decrease at higher difficulty levels that would result from a cross-domain resource competition. Hence, this inversed U-shaped relationship would occur when participants reached their attentional capacity limit (Huxhold et al., 2006; Van Snellenberg et al., 2014). Malcolm et al. (2018) also showed that young participants exhibited a decrease in the variability of step width and standard deviation of the head position in both anteroposterior (AP) and ML directions under dual-task conditions. The authors interpreted this finding as reduced effect of the perturbed optic flow with the addition of a concurrent cognitive task. Similarly, Pechtl et al. (2020) found an increase of errors in a visual reaction time task when participants were exposed to optic flow perturbations during treadmill walking as compared to similar task performed in the auditory modality. This allowed to confirm that the sensory modality of the concurrent task matters. Indeed, a cognitive task presented in the auditory modality may reduce the ability to process visual information (Wickens, 2002; Redfern et al., 2017; Brockhoff et al., 2022), due to the allocation of attentional resources towards another sensory (auditory) modality. In turn, this phenomenon could decrease the influence of ML optic flow perturbations on gait stability (*e.g.* standard deviation of the head position, Malcolm et al., 2018).

Every movement, including gait, are initiated and controlled by the activation of one or more muscle groups. At this level, Acuña et al. (2019) showed that antagonist leg muscle coactivation is more sensitive to the effects of optic flow perturbations than those of concurrent cognitive load. In general, dual-task walking reduces muscle activity (Fraser et al., 2007) and the cortical contribution to this activation (Clark et al., 2013). In some cases, it also prevents the development of adaptation strategies during perturbed walking under single-task condition

(Wellinghoff et al., 2014). In addition, the activation and power generated by the hip abductor (*gluteus medius*) and ankle plantar flexors (*soleus* and *gastrocnemius*) strongly contribute to the control of frontal plane balance and of the foot placement in both AP and ML directions during walking (Neptune and McGowan, 2016; Roelker et al., 2019). An increased *gluteus medius* activity is predictive of a more lateral foot placement (Rankin et al., 2014) and has been associated with an increased step width (Kubinski et al., 2015). These results have been confirmed by Stokes et al. (2017) during walking under optic flow perturbations. By using perturbations of the support surface during walking (*i.e.* slippery floor or beam and uneven surface or platform displacements, respectively), Martino et al. (2015) and Santuz et al. (2020) observed an increased muscle activation duration of the lower limbs, which have been interpreted as a compensatory mechanism implemented by the central nervous system (CNS) under increased postural threat. To our knowledge, no study has assessed the extent to which the availability of attentional resources modulates this compensatory mechanism.

Based on the theoretical and computational framework of a ML multi-objective control model of human gait (Dingwell and Cusumano, 2019), the present study aimed to determine the attentional cost associated with gait control under ML optic flow perturbations at both the kinematic and muscular levels in young adults. We hypothesized that cognitive-locomotor dual-tasking would lower the effects of ML optic flow perturbations on neuromuscular and kinematic gait parameters due to the redirection of attentional resources towards the sensory (auditory) modality in which the concurrent task to walking is presented, and that this phenomenon would be more pronounced when the cognitive (working memory) load increases.

2. Materials and methods

2.1. Participants

Twenty-four healthy young adults (21.67 ± 2.28 years; 12 men and 12 women) took part in this study. Prior to the experiment, participants were interviewed regarding their health history. Exclusion criteria were: (1) any lower limb injury within the last six months, (2) pain, functional limitations or any discomfort that may affect walking, (3) history of vestibular, neurological or musculoskeletal disorders, (4) body mass index of 30 or higher, (5) sedentary lifestyle, (6) any medication altering the cognitive or physical abilities. The physical activity level was assessed by an adapted version of the question 1 of the Modifiable Activity Questionnaire (Vuillemin et al., 2000). The lower limb laterality was determined by the leg used to kick a ball (van Melick et al., 2017). All participants gave their written informed consent prior to the experiment. The study

was approved by an Ethics Committee (IRB00012476-2020-30-11-76) and conducted with respect to the principles of the Declaration of Helsinki regarding human experimentation.

2.2. Experimental procedures

The experiment was conducted in the immersive room (dimensions: 4.80 × 9.60 × 3 m) of the Interdisciplinary Centre for Virtual Reality (CIREVE) at the University of Caen Normandie. The training session started with a familiarization of the participants to the 2 × 0.5 m walking treadmill (M-Gait, Motekforce Link, The Netherlands) followed by the determination of their preferred walking speed (PWS) according to the method of Jordan et al. (2007). Briefly, each participant started at a relatively low speed (*e.g.* 0.6 $m.s^{-1}$) which was progressively increased by 0.05 $m.s^{-1}$ increments until the participant reported being at his/her PWS. Then, walking speed was further increased by approximately 0.42 $m.s^{-1}$ and decreased in 0.05 $m.s^{-1}$ decrements until the participant reported once again being at his/her PWS. The procedure was repeated until the ascending and descending speeds reported by the participant were close (difference below 0.1 $m.s^{-1}$). Afterwards, the participants were familiarized with the auditory N-back task with three levels of working memory (WM) load (*i.e.* 1-back, 2-back, and 3-back). Each familiarization trial lasted at least 1 minute.

The testing session was composed of three blocks performed in a randomized order: (1) three N-back conditions in a seated position (*i.e.* single-task cognitive performance, STC), (2) walking under normal optic flow (NOF) conditions, and (3) walking under perturbed (oscillating) optic flow conditions (POF) in the ML direction. In the latter two blocks, the walking tasks were performed under both single-task (STW) and dual-task (DTW) conditions (*i.e.* responding to the N-back tasks). Participants were asked to walk naturally while looking straight ahead. The treadmill speed was adjusted to their PWS. The blocks (2) and (3) began and ended with a STW condition while the three DTW conditions were performed in a randomized order between the two STW conditions (Schaefer et al., 2015). Under dual-task conditions, no task priority instructions were given (Schaefer et al., 2015). Each condition lasted 3 minutes. Hence, a total of thirteen experimental conditions were performed (Figure 1).

At the end of each condition, participants were asked to complete the NASA task load index (NASA-TLX), a subjective multidimensional assessment questionnaire of perceived workload, on a digital tablet (Hart and Staveland, 1988; French version: Cegarra and Morgado, 2009). In this questionnaire, three subscales relate to the demands imposed on the participant (*i.e.* physical, mental and temporal demands), and three others to the interaction of the participant with the task (*i.e.* effort, frustration, performance).

2.2.1. Manipulation of the optic flow

Participants were asked to walk in a virtual environment composed of a street in ancient Rome in which white statues of 2.4 m height were spaced every 3 meters to increase motion parallax (Bardy et al., 1996; Salinas et al., 2017; Figure 2). In all conditions, the velocity of the OF in the AP direction was congruent with the treadmill belt velocity. During the perturbed OF conditions, the visual field oscillated in the ML direction. The perturbation consisted of a pseudo-random sum of four sinusoids with an amplitude of 0.25 m that has previously been used in the literature (McAndrew et al., 2011; Kazanski et al., 2020):

$$D(t) = 0.25.[1.0 \sin(0.16.2\tau t) + 0.8 \sin(0.21.2\tau t) + 1.4 \sin(0.24.2\tau t) + 0.5 \sin(0.49.2\tau t)]$$

where D(t) is the lateral translation distance (m).

2.2.2. Manipulation of the working memory load

The WM load was parametrically manipulated through three levels of an auditory N-back task. This task consists of a continuous sequence of auditory stimuli, presented one-by-one, in which the participant must determine if the currently presented stimulus is the same as the stimulus presented N trials before. Thus, the factor 'N' (number of items stored in WM) allows increasing the task difficulty and thus the WM load (Grissmann et al., 2017). Using noise-cancelling headphones, participants easily and distinctly heard the letters "E - A - I - O - R - T" pronounced in French and were asked to answer "Yes" when the letter heard was the same as the one presented N trials earlier (*i.e.* 1-back, 2-back, 3-back). Responses were recorded using a microphone. The letters were presented with an inter-stimulus interval of 1800 to 2200 ms (2000 ± 10%) to prevent the influence of rhythm on walking (Schaefer et al., 2015), and a stimulus presentation duration of 500 ms. Each sequence consisted of one third of targets (*i.e.* 90 stimuli for which the participant had to answer "Yes"; Owen et al., 2005) as well as 9 (10%), 13 (14.4%) and 16 (17.8%) lures for the 1-back, 2-back and 3-back, respectively (Szmalec et al., 2011). Each condition lasted 3 minutes.

2.2.3. Kinematic recording

The participants were equipped with 4-mm diameter retroreflective markers, fixed to specific anatomical landmarks on the body, on top of fitted clothing (Vaughan et al., 1999). The model used for marker placement was an adaption of the Plug-in Gait full-body model (Davis et al.,

1991): only the head, trunk and lower limb markers were used for a total of 27 markers. The three-dimensional (3D) marker positions were collected at 200 Hz using 12 infrared cameras (Vero 2.2, Vicon Motion Systems Ltd., Oxford, United Kingdom). The origin of the reference frame was at the treadmill's center. Any gap in the raw motion capture data were filled using Vicon Nexus software, (version 2.8.1, Oxford Metrics, Oxford, United Kingdom). The 3D marker trajectories were then imported into MATLAB® R2020a (The MathWorks Inc., Natick, Massachusetts, USA) for further analyses.

2.2.4. Electromyographic recording

Once the skin prepared (*i.e.* shaving, light abrasion, cleaning with alcohol solution), surface electromyographic electrodes (EMG Trigno Snap Lead Sensors, Delsys, Inc., Natick, Massachusetts, USA) were placed on the *soleus* (Sol) and *gluteus medius* (Gmed) muscles of the dominant lower limb (conversion A/D, 1000 Hz, 10 V). Electrodes were placed longitudinally with respect to the arrangement of muscle fibers (De Luca, 1997) and located according to the recommendations from Surface EMG for Non-Invasive Assessment of Muscles (SENIAM; Hermens et al., 2000).

2.3. Data analysis

All data collected can be downloaded at Dryad (https://doi.org/10.5061/dryad.bnzs7h4ds).

2.3.1. Subjective mental workload

In all conditions, subjective mental workload was estimated based on the Raw NASA task load index (Raw NASA-TLX, with a maximum possible score of 100 points), that is the sum of the scores of the six subscales (Hart, 2006).

2.3.2. Cognitive task performance

Mean reaction time for target trials (RT, in second) and d-prime (d', a.u.) were used to assess performance on N-back tasks (Pelegrina et al., 2015; Kumar et al., 2021; Michail et al., 2021). The d' is the difference between the Z-score obtained from hit rate, Z_{Hit}, and that obtained from false alarms (FA) rate, Z_{FA} ($d' = Z_{Hit} - Z_{FA}$; Haatveit et al., 2010). The higher the hit rate and the lower the FA, the better the participant's ability to discriminate target and non-target letters. In the present experiment, a d' of 4.5 indicates 100% correct responses and no false alarms.

2.3.3. Gait kinematics

The kinematic data was low-pass filtered using a fourth-order zero-phase Butterworth filter with a cut-off frequency of 6 Hz. Heel strikes were computed from the heel marker trajectory using

the algorithm of Zeni et al. (2008). Then, step velocity (V), step width (W) and lateral body position (z_B, which corresponds to the distance between the center of the treadmill and the midpoint between the two feet) were extracted, as previously done (Dingwell and Cusumano, 2019; Kazanski et al., 2020). The mean (steadiness), standard deviation (variability) and statistical persistence/anti-persistence of the time series (complexity) of these parameters were then computed. To quantify how stepping fluctuations were regulated from one step to another, the Detrended Fluctuations Analysis (DFA) scaling exponent (α), which assesses the presence and strength of statistical persistence or anti-persistence in the investigated time series, was used (Peng et al., 1993; Hausdorff et al., 1997; Damouras et al., 2010; Dingwell et al., 2010). An $\alpha < 0.5$ suggests that the time series contains anti-persistent correlations, *i.e.* subsequent deviations are more likely to be in the opposite direction, consistent with a tightly controlled process. An $\alpha = 0.5$ indicates uncorrelated deviations that are attributed to noise. An $\alpha \approx 0.5$ is typically exhibited by variables that are more tightly regulated. An $\alpha >> 0.5$ (*i.e.* strong persistence) is typically exhibited by variables that are less tightly regulated (Dingwell and Cusumano, 2010, 2019; Kazanski et al., 2020). Given the length of our time series (290 steps), the scaling exponent (α) was computed following the recommendations of Phinyomark et al. (2020). Also, we performed a direct control analysis of step-to-step corrections to complete the DFA (Dingwell and Cusumano, 2015). For $q \in \{V, W, z_B\}$, participants trying to maintain a constant average value, $\bar{q}$, on the treadmill exhibit deviations away from $\bar{q}$ on any given step, $q'_n = q_n - \bar{q}$. Each such deviation is corrected on the subsequent step with a corresponding change in the opposite direction, $\Delta q_{n+1} = q_{n+1} - q_n$. From plots of Δq_{n+1}vs. q'_n, we computed (using least-squares regression) linear slopes and strength of correlation (R^2). Parameters tightly controlled would be corrected quickly, yielding slopes (M) close to -1 and higher R^2 (Dingwell and Cusumano, 2019; Kazanski et al., 2020).

2.3.4. EMG analysis of gait

The raw EMG signals were band-pass filtered using a fourth-order zero-phase IIR Butterworth filter with cut-off frequencies of 50 and 450 Hz, then rectified and smoothed using a fourth-order low-pass zero-phase IIR Butterworth filter with a cut-off frequency of 10 Hz (Martino et al., 2015). After subtracting the minimum, the muscle activation profiles were normalized in amplitude to the average peak activation of the selected gait cycles (*i.e.* n= 80). Lastly, each gait cycle was time-normalized to 200 points by a spline interpolation. In order to assess neuromuscular intra-individual variability (*i.e.* inter-cycle variability within each condition), the variance ratio (VR) was computed for the *soleus* and *gluteus medius* (Hershler and Milner, 1978; Kadaba et al., 1985). The full width at half maximum (FWHM) was used to characterize

differences in the duration of muscle activation (Cappellini et al., 2006; Martino et al., 2015). Specifically, cycle-by-cycle, this parameter determines the number of points (percentage of cycle) exceeding half of the maximum activation of each cycle. Then, the values obtained for each of the cycles were averaged to have one value of FWHM per condition (Santuz et al., 2020). We excluded data of 4 participants from EMG analyses because of the poor quality of the signal (*i.e.* movement-related artefacts). Therefore, EMG data from 20 right-handed participants were retained (21.80 ± 2.42 years old; BMI: 21.60 ± 2.65 kg.m^2; 10 men and 10 women).

2.4. Statistical analysis

A linear mixed-model analysis (including a random intercept for each participant) was performed to compare the effect of *Task* (1-back, 2-back, 3-back) and *Cognitive condition* (STC, DTC-NOF, DTC-POF) on cognitive performance (*i.e.* d' and RT) and subjective mental workload (*i.e.* raw NASA-TLX score) dependent variables. When main effects were significant, relevant pairwise comparisons were conducted using estimated marginal means with the Tukey adjustment.

The performance achieved during the second STW conditions (*i.e.* performed at the end of the walking blocks) were not considered in the analysis after having observed and statistically confirmed a disengagement or relaxation of the participants during these conditions (Fig. S1, *Supplementary materials*). Thus, linear mixed models (including a random intercept for each participant) were constructed accordingly to compare the effect of *Optic flow* (NOF, POF) and *Walking condition* (STW, DTW-1b, DTW-2b, DTW-3-b) on kinematic (*i.e.* mean, standard deviation, α, M and R^2 for V, W, z_B) and EMG (*i.e.* VR and FWHM for *soleus* and *gluteus medius*) dependent variables. When main effects were significant, relevant pairwise comparisons were conducted using estimated marginal means with the Tukey adjustment.

Linear mixed-models were fitted using the lme4 package (Bates et al., 2015) and tested based on the likelihood ratio tests (LRT) using the lmerTest package (Kuznetsova et al., 2017). For kinematic variables, given that the residuals are often not normally distributed (Kazanski et al., 2020), which was verified in our samples, parameters were estimated using the pbkrtest package by computing 5000 parametric bootstraps (Halekoh and Højsgaard, 2014). Post-hoc comparison tests were performed using the emmeans package (v1.7.5). The significance threshold was set to 0.05. Effect sizes were also examined and reported for post-hoc comparison tests using Cohen's d ($d < 0.2$, $0.5 < d < 0.8$ and $d > 0.8$, indicating weak, moderate and large effects, respectively). All the statistical analyses were conducted using R 4.0.5 (R Core Team, 2022).

3. Results

A summary of the statistical output is reported in Supplementary materials (Tables S1-S6).

3.1. Cognitive performance and subjective mental workload

A significant main effect of *Task* was found for d' (LRT > 100, $p < 0.001$) and RT (LRT > 100, $p < 0.001$). Post-hoc tests revealed a decrease of d' (Figure 3A) and an increase of RT (Figure 3B) with increasing WM load. Precisely, for both dependent variables, 3-back performance was lower than 1-back ($p < 0.001$, $d = 4.910$) and 2-back ($p < 0.001$, $d = 2.890$) performances, and 2-back performance was also lower than 1-back performance ($p < 0.001$, $d = 2.020$). Significant main effects of *Task* (LRT > 100, $p < 0.001$) and *Cognitive condition* (LRT = 25.58, $p < 0.001$) were found for the raw NASA-TLX score. Post-hoc tests revealed an increase in subjective mental workload i) with increasing WM load ($p < 0.001$, $d > -1.730$ for all levels), and ii) in DTC-POF condition compared to STC ($p < 0.001$, $d = 0.811$) and DTC-NOF conditions ($p < 0.001$, $d = -0.628$) (Figure 3C, Table S1).

3.2. Gait kinematics

3.2.1. Gait steadiness

A significant main effect of *Walking condition* was found for mean V (LRT = 12.21, $p < 0.001$). Post-hoc tests revealed a decrease of mean V in DTW-1b compared to STW conditions ($p < 0.01$, $d = 0.772$). A significant main effect of *Optic flow* was found for mean W (LRT = 54.61, $p < 0.001$) and mean Z_B (LRT = 4.573, $p = 0.036$). Post-hoc tests revealed an increase in mean W ($p < 0.001$, $d = -1.290$) and a decrease in mean Z_B ($p = 0.040$, $d = 0.334$) in POF compared to NOF conditions (Figure 4A; Table S4).

3.2.2. Gait variability (SD: standard deviation)

A significant main effect of *Optic flow* was found for standard deviation (SD) of W (LRT > 100, $p < 0.001$) and SD of z_B (LRT > 100, $p < 0.001$). Post-hoc tests revealed increased SD values in POF compared to NOF conditions ($p < 0.001$, $d > -2$). The effect of POF on SD of V was reduced in DTW compared to STW conditions (LRT = 10.99, $p = 0.016$). Post-hoc tests revealed decreased SD values between POF-DTW-1b and POF-STW ($p = 0.022$ $d = -1.281$), between POF-DTW-2b and POF-STW ($p = 0.006$, $d = -1.196$), and between POF-DTW-3b and POF-STW ($p < 0.001$, $d = -1.537$; Figure 4B; Table S4).

3.2.3. Gait complexity (α: alpha exponent, M: least-squares regression linear slopes, R^2: strength of correlation)

Significant main effects of *Optic flow* (LRT = 5.998, $p = 0.017$) and *Walking condition* (LRT = 9.109, $p = 0.033$) were found for α of V. Post-hoc tests revealed an increase in anti-persistence of V in

POF compared to NOF conditions ($p < 0.001$, $d = 0.384$) and a decrease in anti-persistence of V in DTW-3b compared to DTW-1b conditions ($p = 0.016$, $d = -0.672$). A significant main effect of *Walking condition* was found for α of W (LRT = 10.18, $p = 0.015$). Post-hoc tests revealed a decrease in persistence of W in DTW-2b compared to STW conditions ($p = 0.015$, $d = -0.681$). A significant main effect of *Optic flow* was found for α of z_B (LRT > 100, $p < 0.001$). Post-hoc tests revealed a decrease in persistence of z_B in POF compared to NOF conditions ($p < 0.001$, $d = 2.110$; Figure 4C; Table S4). Additionally, W and Z_B exhibited more negative slopes (LRT = 49.82, $p < 0.001$ and LRT = 57.65, $p < 0.001$, respectively) and increased R^2 values (LRT = 49.46, $p < 0.001$ and LRT = 57.69, $p < 0.001$, respectively) in POF compared to NOF conditions (all $p < 0.001$ and $d > -1.170$; Figure 5; Table S5).

3.3. Gait EMG

The VR of the *soleus* and *gluteus medius* muscles were influenced by *Optic flow* (LRT = 49.97, $p < 0.001$; LRT = 69.07, $p < 0.001$, respectively) and *Walking condition* (LRT = 22.23, $p < 0.001$; LRT = 26.07, $p < 0.001$, respectively). Post-hoc tests revealed increased VR values in POF compared to NOF conditions for the *soleus* muscle ($p < 0001$, $d = -1.170$) and the *gluteus medius* muscle ($p < 0.001$, $d = -1.460$), and decreased VR values in DTW compared to STW conditions for the *soleus* muscle ($p < 0.005$ and $d < -0.773$ for all comparisons) and the *gluteus medius* muscle ($p < 0.001$ and $d < -0.887$ for all comparisons). A significant main effect of *Walking condition* on FWHM was found for the *soleus* muscle (LRT = 10.02, $p = 0.023$). Post-hoc tests revealed higher FWHM values in DTW-1b ($p = 0.044$, $d = 0.592$) and DTW-2b ($p = 0.030$, $d = 0.624$) conditions compared to STW condition (Figure 6; Table S6).

4. Discussion

The aim of the present study was to determine the attentional cost associated with gait control under ML optic flow perturbations in healthy young adults. As prerequisite, our results confirmed that gait control was altered under ML POF compared to NOF, both at the behavioral (kinematic) and neuromuscular (EMG) levels, and that young adults sought to counteract those perturbations by adopting an effortful gait control strategy. Furthermore, those effects were independent of concurrent WM load. But interestingly, increasing WM load led changes first at the neuromuscular level, then at the behavioral level, with a prioritization of gait control in the ML direction over the AP direction. Our hypothesis, according to which dual-tasking would lower the effects of ML optic flow perturbations on gait control, was partly supported since this effect was only found at the behavioral level in the anteroposterior direction.

With regard to cognitive performance, as expected, cognitive performance decreased (greater TR and lower d'; Pelegrina et al., 2015; Lamichhane et al., 2020) and subjective mental workload increased (greater raw NASA-TLX score; Sadeghian et al., 2021) with increasing WM load thus validating our incremental dual-task paradigm (3-back > 2-back > 1-back) under both single-task and dual-task conditions. In addition, participants reported a higher subjective mental workload under POF compared to both NOF and sitting (STC) conditions. However, similarly to Pechtl et al. (2020), cognitive performance did not differ between sitting and walking conditions, indicating that participants sustained their cognitive engagement regardless of the context. Conversely, this is in contrast to what was observed by Kao and Pierro (2022) who found dual-task effects on cognitive performance under perturbed walking (*i.e.* continuous treadmill platform sways). The lack of interference of concurrent WM load on cognitive performance could be due to the perturbation modality, visual *vs.* mechanical, which involves different mechanisms, and thus probably does not require the same demand in terms of attentional resources (Kazanski et al., 2020; Rafiee and Kiemel, 2020). Hence, it is likely that the complexification of the locomotor task, through the use of visual perturbations, does not represent a sufficiently large threat to healthy young adults, in contrast to mechanical perturbations, so that they are able to maintain their engagement in concurrent cognitive task performance.

The effects of ML POF on gait control were observed at both the behavioral and neuromuscular levels. In line with previous studies, variability in mediolateral (z_B, W) and anteroposterior (V) kinematic parameters increased under ML POF (Kazanski et al., 2020; Osaba et al., 2020; Selgrade et al., 2020; Dingwell et al., 2021; Song et al., 2022). This increased variability was also visible at the neuromuscular level as evidenced by the increased variance ratio for both the *gluteus medius* and *soleus* muscles. To our knowledge, this is the first demonstration in the literature. This finding is complementary to that of Stokes et al. (2017), who observed that an increase in lateral foot placement magnitude positively correlated with that of *gluteus medius* muscle activation in response to ML POF. On the other hand, contrary to what was expected, no change was observed in the FWHM of both muscles under ML POF. This discrepancy may stem from the types of perturbation: mechanical perturbations, as investigated in other studies (Martino et al., 2015; Santuz et al., 2020), might generate larger neuromuscular modulation compared to visual perturbations. To compensate for the increased gait variability under ML POF, young adults made changes on other aspects of gait control, notably in terms of steadiness and complexity. As for gait steadiness, young adults walked with wider steps under ML POF (Beurskens et al., 2014; Kao and Pierro, 2022). This control strategy is likely a beneficial adaptation counteracting the increased step-to-step variability induced by ML POF in order to

maintain gait balance (Kazanski et al., 2020). As for gait complexity, as previously reported in the literature, young adults tightened their ML stepping regulation under ML POF, by increasing step-to-step corrections of both lateral body position and step width (control slopes closer to -1.0) and by decreasing persistence of fluctuations in lateral body position while maintaining that of step width (Kazanski et al., 2020; Render et al., 2021). Furthermore, as in previous studies, raw values showed stronger corrections for step width than for lateral body position across all conditions (Dingwell and Cusumano, 2019; Kazanski et al., 2020). Overall, these findings agree with multi-objective control simulations (Dingwell and Cusumano., 2019), according to which the young adult increases the control to enact greater corrections for deviations in both step width and lateral body position in order to maintain a central position on the treadmill. Lastly, fluctuations in step velocity exhibited an increase in antipersistence under ML POF ($\alpha < 0.5$). This increase in antipersistence, associated with a tighter control in the mediolateral direction (z_B, W), suggests over-correction typical of less optimal regulation (Dingwell et al., 2010; Decker et al., 2012, 2013). Collectively, these findings provide further evidence that young adults counteracted ML POF by adopting an effortful gait control strategy.

The effects of concurrent WM tasks on gait control were observed first at the neuromuscular level and then at the behavioral level. Precisely, at the neuromuscular level, the widened activation time (FWHM) of the *soleus* muscle suggests that young adults stiffened the control of their gait when faced with a simultaneous WM task, likely in order to make treadmill walking more stable and safer, as previously suggested (Martino et al., 2015). This occurred from the first level of difficulty of the concurrent WM load (*i.e.* DTW-1b) which mainly involves an external focus of attention but relatively few executive resources. Given the decreased variability under dual-task walking, the observed neuromuscular adaptation supports the fact that concurrent WM load led to a more rigid gait control in order to improve walking stability and balance (Verrel et al., 2009; Kao and Pierro, 2022) and thus release attentional resources towards the concurrent cognitive task. This more rigid gait pattern under dual-task conditions is proving to be effective as evidenced by the absence of changes on gait stationarity (*i.e.* mean values of kinematic parameters). Hence, the gait pattern is more sensitive to visual than cognitive perturbations (Francis et al., 2015; Acuña et al., 2019). With increasing difficulty of the simultaneous WM task (*i.e.* DTW-2b and DTW-3b), fluctuations in step width became more tightly regulated from STW to DTW-2b condition. This tighter regulation was certainly enabled through the involvement of executive functioning (Decker et al., 2012, 2013). Taken together, the decreased persistence of fluctuations in step width and the widened activation time of the *soleus* muscle are consistent with the adoption of a more rigid walking pattern. Accordingly, the search for greater stability

comes at the expense of flexibility and adaptability of gait. Conversely, fluctuations in step velocity became less tightly regulated from DTW-1b to DTW-3b; in other words, young adults had no longer sufficient executive resources to rapidly correct speed deviations on subsequent steps in AP direction. This was also found in our previous study, in which cognitive load was manipulated using a dichotic listening paradigm (Decker et al., 2013). Collectively, these findings provide further evidence that executive functions are involved in regulation of gait task-relevant parameters and that, under increasing concurrent WM load, young adults prioritize gait control in the ML direction (*i.e.* tighter control) over the AP direction (*i.e.* looser control). Actually, it is likely that, under high concurrent WM load (*i.e*. DTW-3b), young adults no longer have sufficient executive resources, so that control of walking in the AP direction is neglected. Such a strategy enables most effective use of executive resources, assuming that walking has passive dynamic stability in the AP direction but instability in the ML direction (Bauby and Kuo, 2000; O'Connor and Kuo, 2009).

Our assumption according to which concurrent WM load would lessen the negative effects of ML POF on gait control was partially confirmed since it was observed for step velocity variability only. This raises the question of why an interaction effect was found for this variable specifically. A likely explanation is that the ML visual constraint (*i.e.* POF) increased step velocity variability by interfering with the AP mechanical constraint (*i.e.* treadmill moving at a constant speed). Young adults, by directing their attentional resources to the concurrent auditory task, may have paid less attention to visual information from the virtual environment, thus mitigating the impact of ML POF on gait control. The absence of an interaction effect for all ML variables may seem counterintuitive but could be explained by the fact that changes in gait control in the ML direction are so robust that they remain unaffected by concurrent WM load. Besides, from a methodological point of view, the use of a conservative statistical method (i.e. linear mixed-effects model with bootstrapping) may have limited interaction effects in our analyses compared with other studies (Kazanski et al., 2020; Malcolm et al., 2018).

A few methodological issues must be considered when interpreting the results of this study. First, STW conditions were systematically performed before the DTW ones; indeed, STW conditions performed after the DTW ones were not included in the main analyses for the reasons mentioned in the *Supplementary material S1*. However, substantial initial familiarization to treadmill walking had taken place beforehand to limit any possible learning effect. Second, treadmill walking was carried out at a fixed speed (although self-selected by the participant). The differences between fixed-speed treadmill walking and overground walking (*i.e.* everyday walking) have been extensively studied and highlighted in many studies (*e.g.* Dingwell et al.,

2001; Wrightson et al., 2020). For example, some studies have observed a decrease in variability of several kinematic parameters during treadmill walking compared to overground walking (Hollman et al., 2016; Wrightson and Smeeton, 2017). This phenomenon has not prevented to observe the impact of visual and cognitive constraints on gait variability. Furthermore, the use of fixed-speed treadmill walking was intended to explore the impact of experimental constraints on variables known to be regulated by the locomotor system, *i.e.* variables that allow the (implicit) goal of the locomotor task ("do not step off the AP and ML limits of the treadmill") to be satisfied.

To conclude, this study has provided insights into gait control strategies when faced to visual and cognitive constraints, applied separately or jointly. Concurrent WM task led to a more rigid gait control, especially in the ML direction, in order to enable stable locomotion. Precisely, the increase in concurrent WM load resulted in tighter control in the ML direction and looser control in the AP direction. This control strategy proves to be effective as it allows the young adult to maintain their cognitive performance. ML POF increased gait variability both at the behavioral and neuromuscular levels. Adding a concurrent WM task lessened the negative effects of ML POF in the AP direction (*i.e.* step velocity variability), but not in the ML direction, probably because gait control is prioritized in the latter direction. Lastly, cognitive performance was preserved under DTW, regardless of optic flow condition, suggesting that the complexification of the locomotor task, through the use of ML POF, does not represent a sufficiently large threat to healthy young adults, in contrast to other perturbations (*e.g.* mechanical). Together, these findings pave the way for new strategies to identify balance deficits that may lead to an increased likelihood of falling in older adults or patients with central or peripheral deficits.

Acknowledgements: L.M.D., J.F., V.L. designed the whole study; N.L. conceived the virtual environment; L.M.D., J.F., V.L. conceived the data analysis plan; V.C., V.L., T.R. collected the data; V.C., V.L. analyzed the data; L.M.D., J.F., V.L. interpreted the results; L.M.D., J.F., V.L. wrote-up the manuscript, L.M.D. obtained research grants from the University of Caen Normandy, the European Union and the Normandy Region as part of the ERDF 2014-2020 operational program. All authors read and approved the final version of the manuscript before submission.

Declarations of interest: None.

Funding: This work was funded by the National Agency for Research and Technology (ANRT) through a CIFRE doctoral fellowship awarded to Valentin Lana and the partnership between the NOVATEX MEDICAL company and the COMETE and GIPSA-Lab laboratories (CIFRE N°2018/0478).

References

Acuña SA, Francis CA, Franz JR, Thelen DG (2019) The effects of cognitive load and optical flow on antagonist leg muscle coactivation during walking for young and older adults. J Electromyogr Kinesiol 44:8–14.

Al-Yahya E, Dawes H, Smith L, Dennis A, Howells K, Cockburn J (2011) Cognitive motor interference while walking: A systematic review and meta-analysis. Neurosci Biobehav Rev 35:715–728.

Bardy BG, Warren WH, Kay BA (1996) Motion parallax is used to control postural sway during walking. Exp Brain Res 111:271–282.

Bates D, Mächler M, Bolker B, Walker S (2015) Fitting Linear Mixed-Effects Models Using **lme4**. J Stat Softw 67 Available at: http://www.jstatsoft.org/v67/i01/ [Accessed September 14, 2022].

Bauby CE, Kuo AD (2000) Active control of lateral balance in human walking. J Biomech 33:1433–1440.

Beauchet O, Kressig RW, Najafi E, Aminian K, Dubost V, Mourey F (2003) Age-Related decline of gait control under a dual-task Condition. J Am Geriatr Soc 51:1187–1188.

Beilock SL, Bertenthal BI, McCoy AM, Carr TH (2004) Haste does not always make waste: Expertise, direction of attention, and speed versus accuracy in performing sensorimotor skills. Psychon Bull Rev 11:373–379.

Bernstein NA (1967) The co-ordination and regulation of movements. Oxford; New York: Pergamon Press. Available at: http://books.google.com/books?id=F9dqAAAAMAAJ [Accessed February 13, 2022].

Beurskens R, Wilken JM, Dingwell JB (2014) Dynamic stability of individuals with transtibial amputation walking in destabilizing environments. J Biomech 47:1675–1681.

Brown TG (1911) The Intrinsic Factors in the Act of Progression in the Mammal. Proc R Soc Lond Ser B Contain Pap Biol Character 84:308–319.

Bruijn SM, van Dieën JH (2018) Control of human gait stability through foot placement. J R Soc Interface 15:20170816.

Cappellini G, Ivanenko YP, Poppele RE, Lacquaniti F (2006) Motor Patterns in Human Walking and Running. J Neurophysiol 95:3426–3437.

Cegarra J, Morgado N (2009) Étude des propriétés de la version francophone du NASA-TLX. :6.

Clark DJ, Kautz SA, Bauer AR, Chen Y-T, Christou EA (2013) Synchronous EMG Activity in the Piper Frequency Band Reveals the Corticospinal Demand of Walking Tasks. Ann Biomed Eng 41:1778–1786.

Damouras S, Chang MD, Sejdić E, Chau T (2010) An empirical examination of detrended fluctuation analysis for gait data. Gait Posture 31:336–340.

De Luca CJ (1997) The Use of Surface Electromyography in Biomechanics. J Appl Biomech 13:135–163.

Decker LM, Cignetti F, Potter JF, Studenski SA, Stergiou N (2012) Use of Motor Abundance in Young and Older Adults during Dual-Task Treadmill Walking Kline AE, ed. PLoS ONE 7:e41306.

Decker LM, Cignetti F, Stergiou N (2013) Executive function orchestrates regulation of task-relevant gait fluctuations. Gait Posture 38:537–540.

Dingwell JB, Cusumano JP (2015) Identifying Stride-To-Stride Control Strategies in Human Treadmill Walking van Beers RJ, ed. PLOS ONE 10:e0124879.

Dingwell JB, Cusumano JP (2019) Humans use multi-objective control to regulate lateral foot placement when walking Haith AM, ed. PLOS Comput Biol 15:e1006850.

Dingwell JB, Cusumano JP, Cavanagh PR, Sternad D (2001) Local Dynamic Stability Versus Kinematic Variability of Continuous Overground and Treadmill Walking. J Biomech Eng 123:27–32.

Dingwell JB, Cusumano JP, Rylander JH, Wilken JM (2021) How persons with transtibial amputation regulate lateral stepping while walking in laterally destabilizing environments. Gait Posture 83:88–95.

Dingwell JB, John J, Cusumano JP (2010) Do Humans Optimally Exploit Redundancy to Control Step Variability in Walking? Diedrichsen J, ed. PLoS Comput Biol 6:e1000856.

Francis CA, Franz JR, O'Connor SM, Thelen DG (2015) Gait variability in healthy old adults is more affected by a visual perturbation than by a cognitive or narrow step placement demand. Gait Posture 42:380–385.

Fraser SA, Li KZH, DeMont RG, Penhune VB (2007) Effects of Balance Status and Age on Muscle Activation While Walking Under Divided Attention. J Gerontol Ser B 62:P171–P178.

Grillner S, Wallén P, Saitoh K, Kozlov A, Robertson B (2008) Neural bases of goal-directed locomotion in vertebrates—An overview. Brain Res Rev 57:2–12.

Grissmann S, Faller J, Scharinger C, Spüler M, Gerjets P (2017) Electroencephalography Based Analysis of Working Memory Load and Affective Valence in an N-back Task with Emotional Stimuli. Front Hum Neurosci 11:616.

Haatveit BC, Sundet K, Hugdahl K, Ueland T, Melle I, Andreassen OA (2010) The validity of *d* prime as a working memory index: Results from the "Bergen *n* -back task." J Clin Exp Neuropsychol 32:871–880.

Halekoh U, Højsgaard S (2014) A Kenward-Roger Approximation and Parametric Bootstrap Methods for Tests in Linear Mixed Models - The *R* Package **pbkrtest**. J Stat Softw 59 Available at: http://www.jstatsoft.org/v59/i09/ [Accessed September 14, 2022].

Hamacher D, Herold F, Wiegel P, Hamacher D, Schega L (2015) Brain activity during walking: A systematic review. Neurosci Biobehav Rev 57:310–327.

Hart SG (2006) Nasa-Task Load Index (NASA-TLX); 20 Years Later. Proc Hum Factors Ergon Soc Annu Meet 50:904–908.

Hart SG, Staveland LE (1988) Development of NASA-TLX (Task Load Index): Results of Empirical and Theoretical Research. In: Advances in Psychology, pp 139–183. Elsevier. Available at: https://linkinghub.elsevier.com/retrieve/pii/S0166411508623869 [Accessed October 1, 2020].

Hausdorff JM, Mitchell SL, Firtion R, Peng CK, Cudkowicz ME, Wei JY, Goldberger AL (1997) Altered fractal dynamics of gait: reduced stride-interval correlations with aging and Huntington's disease. J Appl Physiol 82:262–269.

Hermens HJ, Freriks B, Disselhorst-Klug C, Rau G (2000) Development of recommendations for SEMG sensors and sensor placement procedures. J Electromyogr Kinesiol 10:361–374.

Hershler C, Milner M (1978) An Optimality Criterion for Processing Electromyographic (EMG) Signals Relating to Human Locomotion. IEEE Trans Biomed Eng BME-25:413–420.

Hollman JH, Watkins MK, Imhoff AC, Braun CE, Akervik KA, Ness DK (2016) A comparison of variability in spatiotemporal gait parameters between treadmill and overground walking conditions. Gait Posture 43:204–209.

Huxhold O, Li S-C, Schmiedek F, Lindenberger U (2006) Dual-tasking postural control: Aging and the effects of cognitive demand in conjunction with focus of attention. Brain Res Bull 69:294–305.

Jordan K, Challis JH, Newell KM (2007) Walking speed influences on gait cycle variability. Gait Posture 26:128–134.

Kadaba MP, Wootten ME, Gainey J, Cochran GVB (1985) Repeatability of phasic muscle activity: Performance of surface and intramuscular wire electrodes in gait analysis. J Orthop Res 3:350–359.

Kao P-C, Pierro MA (2022) Motor adaptation to cognitive challenges and walking perturbations in healthy young adults. Gait Posture 92:167–175.

Kazanski ME, Cusumano JP, Dingwell JB (2020) How healthy older adults regulate lateral foot placement while walking in laterally destabilizing environments. J Biomech 104:109714.

Kazanski ME, Cusumano JP, Dingwell JB (2022) Rethinking margin of stability: Incorporating step-to-step regulation to resolve the paradox. J Biomech 144:111334.

Kubinski SN, McQueen CA, Sittloh KA, Dean JC (2015) Walking with wider steps increases stance phase gluteus medius activity. Gait Posture 41:130–135.

Kuhman D, Hurt CP, Reed WR, Rosenblatt NJ, Visscher K, Walker H (n.d.) GAIT ADAPTABILITY WITH HEALTHY AGING AND PARKINSON'S DISEASE. :24.

Kumar V, Nichenmetla S, Chhabra H, Sreeraj VS, Rao NP, Kesavan M, Varambally S, Venkatasubramanian G, Gangadhar BN (2021) Prefrontal cortex activation during working memory task in schizophrenia: A fNIRS study. Asian J Psychiatry 56:102507.

Kuznetsova A, Brockhoff PB, Christensen RHB (2017) **lmerTest** Package: Tests in Linear Mixed Effects Models. J Stat Softw 82 Available at: http://www.jstatsoft.org/v82/i13/ [Accessed September 14, 2022].

Lamichhane B, Westbrook A, Cole MW, Braver TS (2020) Exploring brain-behavior relationships in the N-back task. NeuroImage 212:116683.

Lindenberger U, Marsiske M, Baltes PB (2000) Memorizing While Walking: Increase in Dual-Task Costs From Young Adulthood to Old Age. :20.

Lövdén M, Schaefer S, Pohlmeyer AE, Lindenberger U (2008) Walking Variability and Working-Memory Load in Aging: A Dual-Process Account Relating Cognitive Control to Motor Control Performance. J Gerontol Ser B 63:P121–P128.

Malcolm BR, Foxe JJ, Butler JS, Molholm S, De Sanctis P (2018) Cognitive load reduces the effects of optic flow on gait and electrocortical dynamics during treadmill walking. J Neurophysiol 120:2246–2259.

Martino G, Ivanenko YP, d'Avella A, Serrao M, Ranavolo A, Draicchio F, Cappellini G, Casali C, Lacquaniti F (2015) Neuromuscular adjustments of gait associated with unstable conditions. J Neurophysiol 114:2867–2882.

McAndrew PM, Wilken JM, Dingwell JB (2011) Dynamic stability of human walking in visually and mechanically destabilizing environments. J Biomech 44:644–649.

Michail G, Senkowski D, Niedeggen M, Keil J (2021) Memory Load Alters Perception-Related Neural Oscillations during Multisensory Integration. J Neurosci 41:1505–1515.

Mirelman A, Herman T, Brozgol M, Dorfman M, Sprecher E, Schweiger A, Giladi N, Hausdorff JM (2012) Executive Function and Falls in Older Adults: New Findings from a Five-Year Prospective Study Link Fall Risk to Cognition Laks J, ed. PLoS ONE 7:e40297.

Neptune RR, McGowan CP (2016) Muscle contributions to frontal plane angular momentum during walking. J Biomech 49:2975–2981.

O'Connor SM, Kuo AD (2009) Direction-Dependent Control of Balance During Walking and Standing. J Neurophysiol 102:1411–1419.

Osaba MY, Martelli D, Prado A, Agrawal SK, Lalwani AK (2020) Age-related differences in gait adaptations during overground walking with and without visual perturbations using a virtual reality headset. Sci Rep 10:15376.

Owen AM, McMillan KM, Laird AR, Bullmore E (2005) N-back working memory paradigm: A meta-analysis of normative functional neuroimaging studies. Hum Brain Mapp 25:46–59.

Pechtl KS, Jennings JR, Redfern MS (2020) Optic flow and attention alter locomotion differently in the young and old. Gait Posture 76:1–6.

Pelegrina S, Lechuga MT, García-Madruga JA, Elosúa MR, Macizo P, Carreiras M, Fuentes LJ, Bajo MT (2015) Normative data on the n-back task for children and young adolescents. Front Psychol 6 Available at: http://journal.frontiersin.org/Article/10.3389/fpsyg.2015.01544/abstract [Accessed October 1, 2020].

Peng C-K, Mietus J, Hausdorff JM, Havlin S, Stanley HE, Goldberger AL (1993) Long-range anticorrelations and non-Gaussian behavior of the heartbeat. Phys Rev Lett 70:1343–1346.

Phinyomark A, Larracy R, Scheme E (2020) Fractal Analysis of Human Gait Variability via Stride Interval Time Series. Front Physiol 11:333.

R Core Team (2022) R: A language and environment for statistical computing. Available at: https://www.R-project.org/.

Rafiee S, Kiemel T (2020) Multiple strategies to correct errors in foot placement and control speed in human walking. Exp Brain Res 238:2947–2963.

Rankin BL, Buffo SK, Dean JC (2014) A neuromechanical strategy for mediolateral foot placement in walking humans. J Neurophysiol 112:374–383.

Redfern MS, Chambers AJ, Jennings JR, Furman JM (2017) Sensory and motoric influences on attention dynamics during standing balance recovery in young and older adults. Exp Brain Res 235:2523–2531.

Render AC, Kazanski ME, Cusumano JP, Dingwell JB (2021) Walking humans trade off different task goals to regulate lateral stepping. J Biomech 119:110314.

Roelker SA, Kautz SA, Neptune RR (2019) Muscle contributions to mediolateral and anteroposterior foot placement during walking. J Biomech 95:109310.

Roerdink M, Daffertshofer A, Marmelat V, Beek PJ (2015) How to Sync to the Beat of a Persistent Fractal Metronome without Falling Off the Treadmill? Haddad JM, ed. PLOS ONE 10:e0134148.

Sadeghian M, Yazdanirad S, Mousavi SM, Jafari MJ, Khavanin A, Khodakarim S, Jafarpishe AS (2021) Effect of tonal noise and task difficulty on electroencephalography and cognitive performance. Int J Occup Saf Ergon:1–9.

Santuz A, Brüll L, Ekizos A, Schroll A, Eckardt N, Kibele A, Schwenk M, Arampatzis A (2020) Neuromotor Dynamics of Human Locomotion in Challenging Settings. iScience 23:100796.

Schaefer S, Jagenow D, Verrel J, Lindenberger U (2015) The influence of cognitive load and walking speed on gait regularity in children and young adults. Gait Posture 41:258–262.

Selgrade BP, Meyer D, Sosnoff JJ, Franz JR (2020) Can optical flow perturbations detect walking balance impairment in people with multiple sclerosis? Sakakibara M, ed. PLOS ONE 15:e0230202.

Song K, Franz JR, Wikstrom EA (2022) Optical flow balance perturbations alter gait kinematics and variability in chronic ankle instability patients. Gait Posture 92:271–276.

Stokes HE, Thompson JD, Franz JR (2017) The Neuromuscular Origins of Kinematic Variability during Perturbed Walking. Sci Rep 7:808.

Szmalec A, Verbruggen F, Vandierendonck A, Kemps E (2011) Control of interference during working memory updating. J Exp Psychol Hum Percept Perform 37:137–151.

Takakusaki K (2013) Neurophysiology of gait: From the spinal cord to the frontal lobe: Neurophysiology of Gait. Mov Disord 28:1483–1491.

Takakusaki K (2017) Functional Neuroanatomy for Posture and Gait Control. J Mov Disord 10:1–17.

Terrier P, Dériaz O (2013) Non-linear dynamics of human locomotion: effects of rhythmic auditory cueing on local dynamic stability. Front Physiol 4 Available at: http://journal.frontiersin.org/article/10.3389/fphys.2013.00230/abstract [Accessed February 15, 2022].

van Melick N, Meddeler BM, Hoogeboom TJ, Nijhuis-van der Sanden MWG, van Cingel REH (2017) How to determine leg dominance: The agreement between self-reported and observed performance in healthy adults Macaluso A, ed. PLOS ONE 12:e0189876.

Van Snellenberg JX, Slifstein M, Read C, Weber J, Thompson JL, Wager TD, Shohamy D, Abi-Dargham A, Smith EE (2014) Dynamic shifts in brain network activation during supracapacity working memory task performance. Hum Brain Mapp 36:1245–1264.

Vaughan CL, Vaughan CL, Vaughan CL, Vaughan CL (1999) GaitCD. Howard Place, Western Cape, South Africa: Kiboho Publishers. Available at: https://archive.org/details/dynamicsofhumang0000unse [Accessed February 15, 2022].

Verrel J, Lövdén M, Schellenbach M, Schaefer S, Lindenberger U (2009) Interacting effects of cognitive load and adult age on the regularity of whole-body motion during treadmill walking. Psychol Aging 24:75–81.

Vuillemin A, Oppert J-M, Guillemin F, Essermeant L, Fontvieille A-M, Galan P, Kriska AM, Hercberg S (2000) Self-administered questionnaire compared with interview to assess past-year physical activity: Med Sci Sports Exerc 32:1119–1124.

Wellinghoff MA, Bunchman AM, Dean JC (2014) Gradual mechanics-dependent adaptation of medial gastrocnemius activity during human walking. J Neurophysiol 111:1120–1131.

Wickens CD (2002) Multiple resources and performance prediction. Theor Issues Ergon Sci 3:159–177.

Wrightson JG, Ross EZ, Smeeton NJ (2016) The Effect of Cognitive-Task Type and Walking Speed on Dual-Task Gait in Healthy Adults. Motor Control 20:109–121.

Wrightson JG, Schäfer L, Smeeton NJ (2020) Dual-task prioritization during overground and treadmill walking in healthy adults. Gait Posture 75:109–114.

Wrightson JG, Smeeton NJ (2017) Walking modality, but not task difficulty, influences the control of dual-task walking. Gait Posture 58:136–138.

Wulf G, Prinz W (2001) Directing attention to movement effects enhances learning: a review. Psychon Bull Rev 8:648–660.

Zeni JA, Richards JG, Higginson JS (2008) Two simple methods for determining gait events during treadmill and overground walking using kinematic data. Gait Posture 27:710–714.

Figure Captions

Figure 1. Experimental procedures. A training session was first performed, consisting of: 1) a 10-minute familiarization period with treadmill walking (10 minutes), 2) the determination of the participant's preferred walking speed (PWS) on treadmill according to the method of Jordan et al. (2007), and 3) a 1-minute familiarization trial with each of the three auditory N-back tasks (*i.e.* 1-back, 2-back, and 3-back). Afterwards, three experimental blocks were performed in a randomized order. In the latter two blocks, participants began and ended with a single-task walking (STW) condition (*i.e.* free walking) while the three dual-task walking (DTW) conditions were performed in a randomized order between the two STW conditions. The experimental conditions lasted 3 minutes. Empty circles correspond to the familiarization trials while solid circles correspond to the experimental conditions.

Figure 2. Experimental setup. Photograph of the M-Gait system used in the study (Motekforce Link, Amsterdam, Netherlands). The participant, equipped with 27 retroreflective markers (4-mm diameter) placed on specific anatomical landmarks according to an adaptation of the Plug-in-Gait full-body model (Vicon Motion Systems Ltd.) and surface electromyographic electrodes (EMG Trigno Snap Lead Sensors, Delsys Inc.) placed on the *soleus* and *gluteus medius* muscles of the dominant lower limb, is walking on a dual-belt instrumented treadmill in the virtual environment.

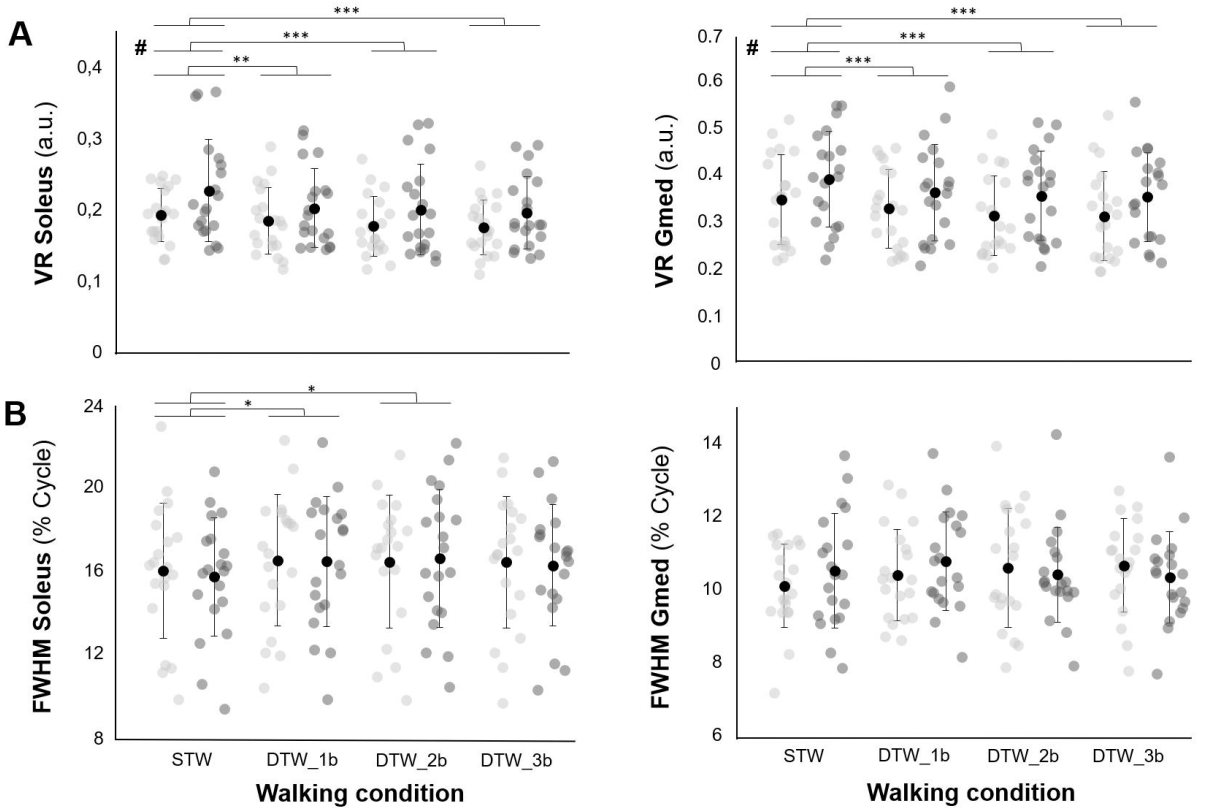
Figure 3. Cognitive performance: A) d-prime (d', a.u.), B) mean reaction time for target trials (RT, in second), and C) raw NASA task load index (Raw NASA-TLX, the maximum score is 100), for the three N-back tasks, *i.e.* 1-back, 2-back, 3-back, performed under three cognitive conditions, *i.e.* single-task cognitive performance in a seated position (STC, very light grey circles), dual-task cognitive performance while walking with normal optic flow (DTC-NOF, light grey circles) and perturbed optic flow (DTC-POF, dark grey circles). Black dots represent the mean and the error bars correspond to the standard deviations. *: Significant differences between the three task loads (* if $p < .05$; ** if $p < .01$ and *** if $p < .001$). #: significant differences between DTC-POF and the other conditions (STC and DTC-NOF).

Figure 4. A) Mean, B) Standard deviation (σ), and C) DFA scaling exponent (α) of step velocity (V, left), step width (W, middle) and lateral body position (z_B, right), for the four walking conditions: single-task walking (STW) and dual-task walking (DTW), *i.e.* walking while concurrently responding to auditory 1-back (DTW-1b), 2-back (DTW-2b), and 3-back (DTW-3b), performed under two optic flow conditions, *i.e.* normal optic flow (NOF, light grey circles) and perturbed optic flow (POF, dark grey circles). Black dots represent the mean and the error bars correspond

to the standard deviations. *: Significant differences between the four conditions (* if $p < .05$; ** if $p < .01$ and *** if $p < .001$). #: significant differences between normal optic flow and perturbed optic flow.

Figure 5. A) Slopes of least-squares fits (M) for $(V)'_n$ vs $\Delta(V)_{n+1}$, $(W)'_n$ vs $\Delta(W)_{n+1}$, $(z_B)'_n$ vs $\Delta(z_B)_{n+1}$ for all conditions (see legend of Figure 4 for details). B) Strength of correlation (R^2) of these least-squares fits $(V)'_n$ vs $\Delta(V)_{n+1}$, $(W)'_n$ vs $\Delta(W)_{n+1}$, $(z_B)'_n$ vs $\Delta(z_B)_{n+1}$ for all conditions.

Figure 6. A) Variance ratio (VR, a.u.) of *soleus* and *gluteus medius* and B) Full width at half maximum (FWHM, % cycle) of *soleus* and *gluteus medius* for all conditions (see legend of Figure 4 for details).


A
B
VR Soleus (a.u.)
VR Gmed (a.u.)
FWHM Soleus (% Cycle)
FWHM Gmed (% Cycle)
#
***
**
*
STW
DTW_1b
DTW_2b
DTW_3b
Walking condition

Training session

- ○ 10-min treadmill walking (PWS determination)
- ○ 1-min STC-1b
- ○ 1-min STC-2b
- ○ 1-min STC-3b

Block 1
N-back task - seated

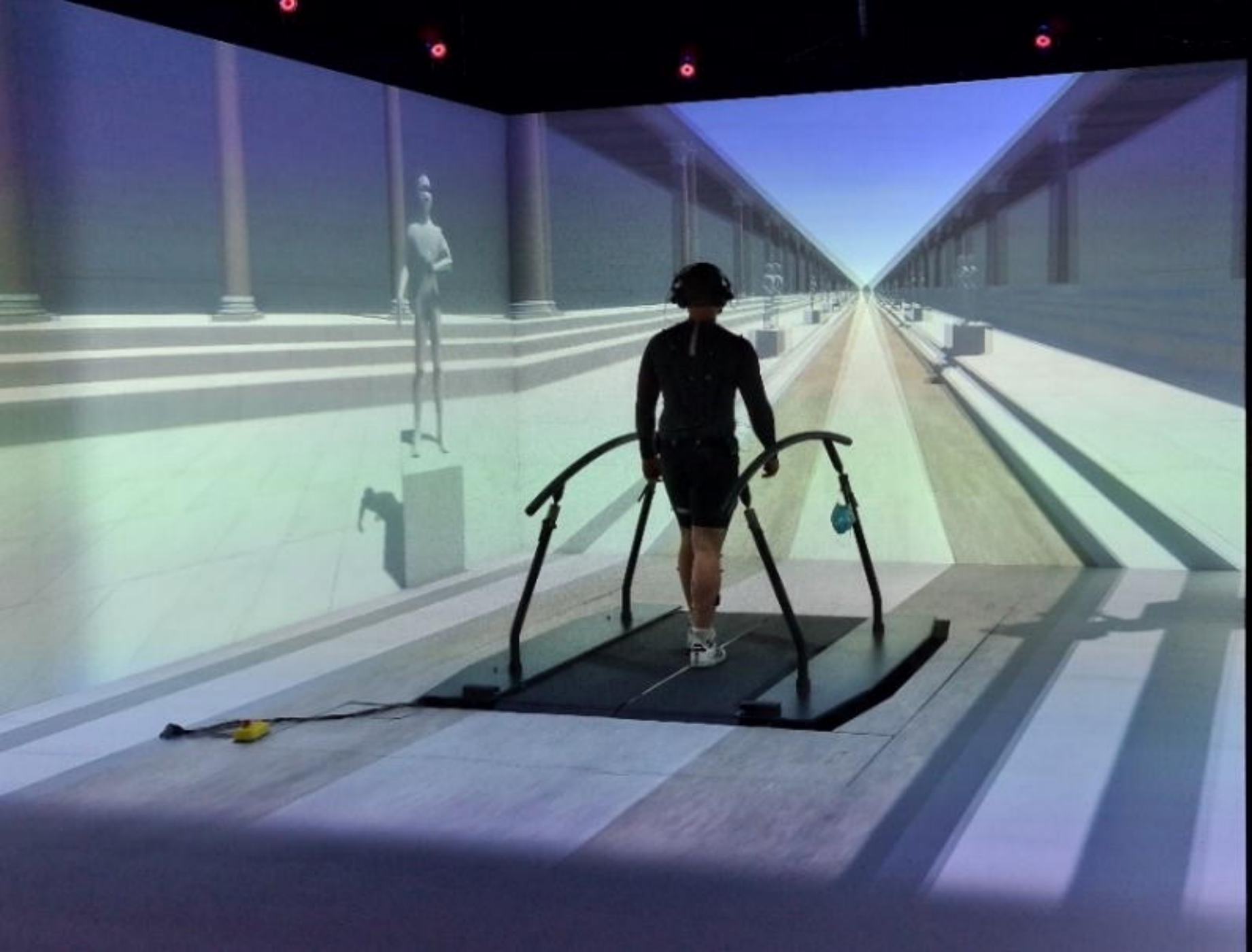
- • 3-min STC-1b
- • 3-min STC-2b
- • 3-min STC-3b

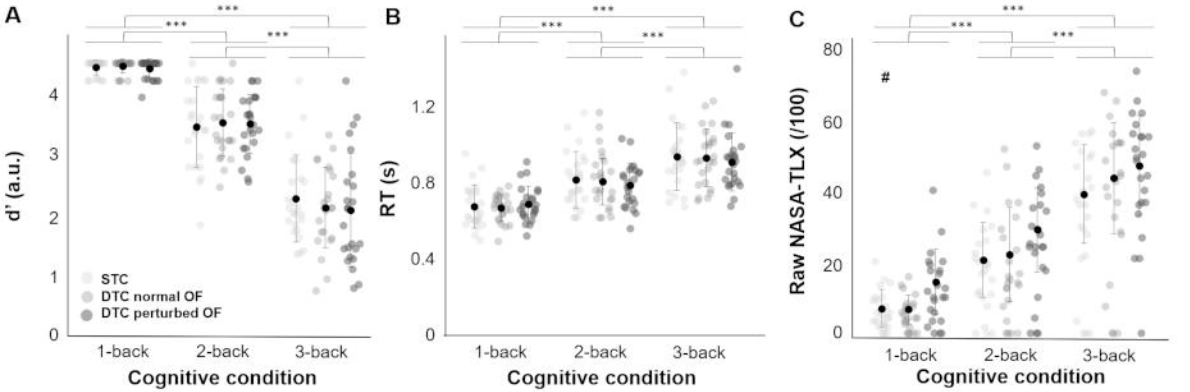
Block 2
Walking - NOF

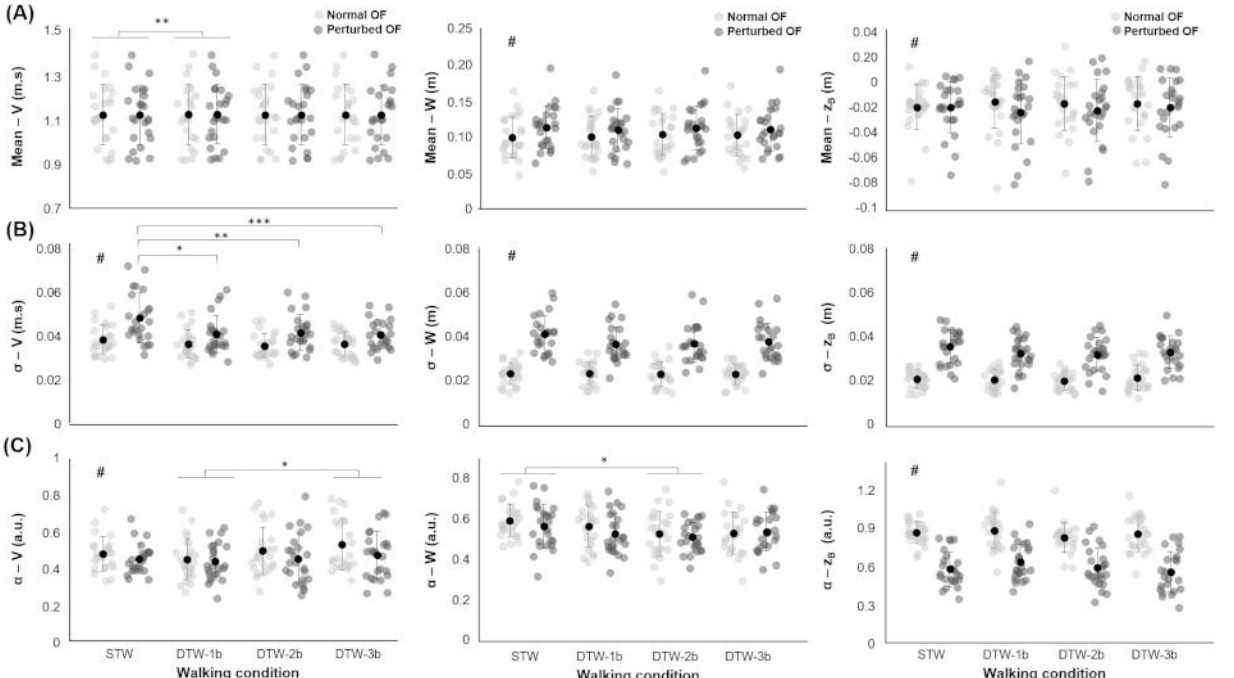
- ○ 3-min STW (familiarization)
- ○ 3-min STW (first trial)
- • 3-min DTW-1b
- • 3-min DTW-2b
- • 3-min DTW-3b
- ○ 3-min STW (second trial)

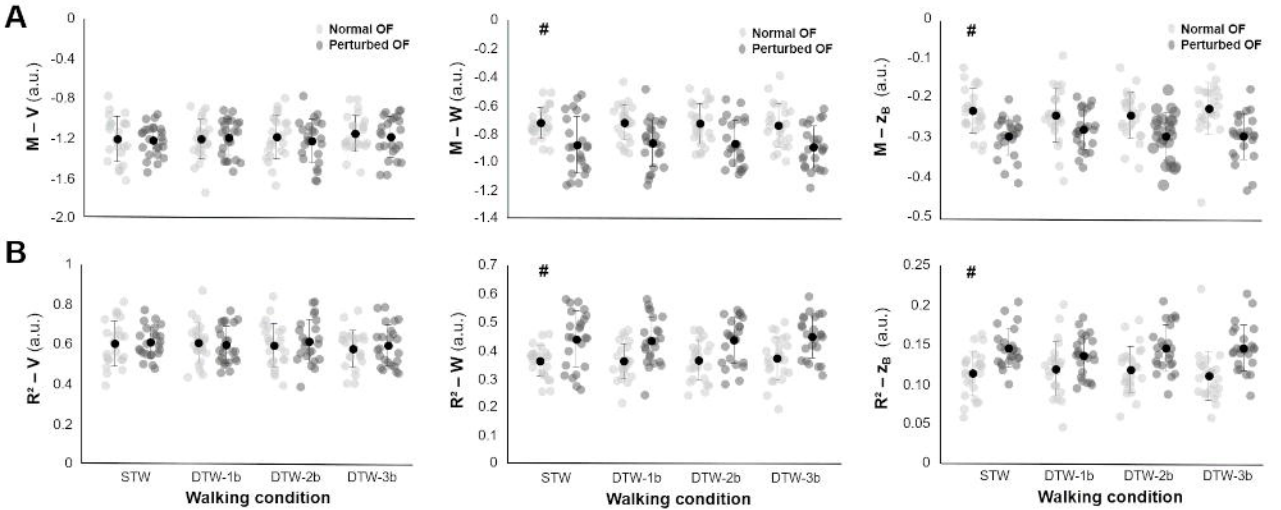
Block 3
Walking - POF

- ○ 3-min STW (familiarization)
- ○ 3-min STW (first trial)
- • 3-min DTW-1b
- • 3-min DTW-2b
- • 3-min DTW-3b
- ○ 3-min STW (second trial)




A
B
C
***
#
d' (a.u.)
RT (s)
Raw NASA-TLX (/100)
STC
DTC normal OF
DTC perturbed OF
1-back
2-back
3-back
Cognitive condition


(A)
(B)
(C)
Normal OF
Perturbed OF
Mean – V (m.s)
Mean – W (m)
Mean – z_B (m)
σ – V (m.s)
σ – W (m)
σ – z_B (m)
α – V (a.u.)
α – W (a.u.)
α – z_B (a.u.)
STW
DTW-1b
DTW-2b
DTW-3b
Walking condition


A
B
Normal OF
Perturbed OF
#
M – V (a.u.)
M – W (a.u.)
M – z_B (a.u.)
R^2 – V (a.u.)
R^2 – W (a.u.)
R^2 – z_B (a.u.)
STW
DTW-1b
DTW-2b
DTW-3b
Walking condition