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No Evidence That Frontal Optical Flow Affects Perceived Locomotor Speed and Locomotor Biomechanics When Running on a Treadmill

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Abstract: We investigated how the presentation and the manipulation of an optical flow while running on a treadmill affect perceived locomotor speed (Experiment 1) and gait parameters (Experiment 2). In Experiment 1, 12 healthy participants were instructed to run at an imposed speed and to focus on their sensorimotor sensations to be able to reproduce this running speed later. After a pause, they had to retrieve the reference locomotor speed by manipulating the treadmill speed while being presented with different optical flow conditions, namely no optical flow or a matching/slower/faster optical flow. In Experiment 2, 20 healthy participants ran at a previously self-selected constant speed while being presented with different optical flow conditions (see Experiment 1). The results did not show any effect of the presence and manipulation of the optical flow either on perceived locomotor speed or on the biomechanics of treadmill running. Specifically, the ability to retrieve the reference locomotor speed was similar for all optical flow conditions. Manipulating the speed of the optical flow did not affect the spatiotemporal gait parameters and also failed to affect the treadmill running accommodation process. Nevertheless, the virtual reality conditions affected the heart rate of the participants but without affecting perceived effort.

Keywords: virtual reality; visual speed perception; treadmill running; self-motion perception; optical flow; locomotion; biomechanics

1. Introduction

Human locomotion is controlled through a complex sensorial integration of different types of information, in particular about the relative motion between the body and the surrounding environment [1]. Visual, vestibular, proprioceptive, and auditory information is integrated by the central nervous system, allowing the generation of the perception of motion [2]. Though walking is influenced by different factors [3], the main contribution derives from visual, vestibular and proprioceptive signals. Using static cues, object-motion cues and optical flow cues, the visual system allows us to discriminate self-motion from movement of objects of the environment [4]. Vestibular cues provide motion data about changes of velocity or direction-based data about accelerations [5]. Lastly, the proprioceptive system uses joint- and muscle-related information to provide feedback about the status of the whole musculoskeletal system, which greatly contributes to the perception and control of motion during active movements [3]. Speed perception, goal-directed movements, navigation, and collision avoidance all rely on the congruency and integration of the signals provided by these different sensory systems.

Visual information plays an important role in motion perception. In particular, optical flow information is used to estimate direction [6], egocentric speed [7], and time-to-collision [8], and it heavily contributes to heading perception [9–11]. The absolute travelled distance can also be calculated by integrating this information [12,13]. However, when visual cues are in conflict with other sensory information about self-motion, visual information not always constitutes the "dominant" source of information [4,14]. In fact, when walking at constant speed, people tend to weight the information deriving from proprioceptive cues higher than visual cues [15–17]. Nevertheless, visual input seems to have a great impact on self-motion perception while walking, and studies have shown how the manipulation of the optical flow affects visuomotor recalibration [11,15,17–19]. In particular, it was found that if optical flow is manipulated to create sensory conflicts when walking, the locomotor speed decreases as the optical flow speed increases [15,20], suggesting a response to the relative weightings assigned to different sensory cues, in this case proprioceptive and visual cues [15]. Some studies have also shown that the manipulation of optical flow can significantly influence locomotor patterns [15,17,21,22].

All above-mentioned studies were performed with walking participants and, to our knowledge, the influence of optical flow on self-motion perception and on locomotor patterns has never been investigated with running individuals. Yet, locomotor patterns are modulated differently in walking and running [23–25], with automated spinal programs allowing path integration in running, while walking is more dependent on visual control [24]. For this reason, one might wonder whether the results obtained with walking individuals can be generalized to running individuals.

Here we investigated how the presence and manipulation of a virtual optical flow influences the control of locomotion while running on a treadmill. In Experiment 1, we tested how the presence and manipulation of a virtual optical flow influences self-motion speed perception. Specifically, participants were instructed to retrieve a previously presented reference running speed while being exposed to different optical flow conditions. In Experiment 2, we investigated how the presence and manipulation of an artificial optical flow influences gait parameters while treadmill running at a self-selected constant speed with different optical flow conditions.

2. Experiment 1

2.1. Introduction

In this experiment, we tested if the perception of self-motion speed is influenced by the presence and the manipulation of an optical flow. For walking, studies have shown that movement influences the perception of the optical flow speed in virtual environments [26], and that the rate of optical flow has a modulating effect on walking speed, with an inverse linear relationship between optical flow and walking velocity [15]. Optical flow has also been shown to affect stride length, cadence, and velocity [17]. All these results suggest an internal calibration between locomotion and visual perception. Here we investigated if participants were able to retrieve a previously experienced running speed in different optical flow conditions while running on a treadmill.

2.2. Methods

2.2.1. Participants

12 healthy participants (4 female, 8 male) with a mean age of 25.0 (±1.2 SD) participated in this study. They were unaware of the purpose of the study, were moderately trained to trained, had normal

or corrected-to-normal vision, and none had a history of cardiovascular disease. All participants gave their informed and written consent prior to the inclusion in the study. This study was performed in accordance with the ethical standards specified by the 1964 Declaration of Helsinki and approved by the Ethics Committee of the University of Fribourg.

2.2.2. Experimental Setup

Participants ran on a HP Cosmos Mercury treadmill with a running surface of 150 × 50 cm. The treadmill was positioned in front of a 4.30 × 2.70 m screen at a distance of 1.7 m, leading to an effective field of view of 90°. To simulate optic flow, a virtual environment was projected onto the screen using a Barco F50 WUXGA projector with a 1920 × 1200 pixels resolution. The VR scene for which judgements were made and that was subsequently manipulated was created using Unity and depicted a neutral open-air hallway presented at constant-velocity motion (Figure 1). Rich optical flow information was provided by a granular texture on the floor and by the random pattern on the walls, without giving any landmarks or usable spatial information. The room was darkened during the experiment, with the display screen was the only source of light. While running, participants wore a soundproof headset (Hearing Protection type Pamir—Swiss Army).

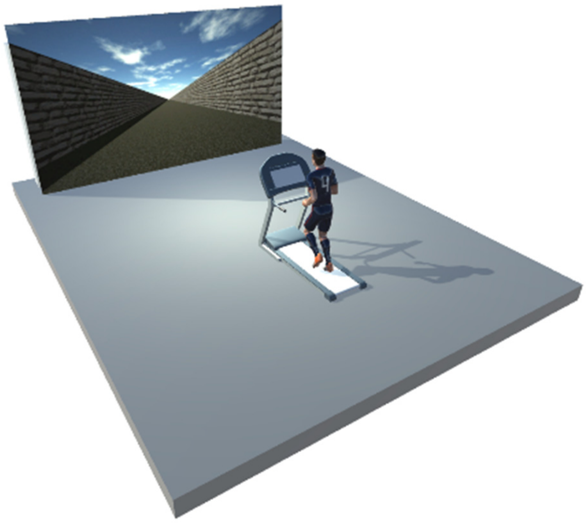

Figure 1. Experimental setup.

2.2.3. Procedure

Prior to the running task, the participants filled out a custom-made questionnaire about their sports activity.

Before starting the actual test, participants familiarized themselves with treadmill running and experimental trials were initiated when the participant felt comfortable. Every single trial would start with the participant running at constant speed. Participants were instructed to gaze at the fixation cross, that was positioned straight ahead and was visible for the whole duration of the test.

For the running task, participants were asked to run at 10 km/h for 2 min in front of the black screen focusing on the sensations perceived while running. The participants wore a soundproof headset to prevent them from using the sound of the treadmill as an information about the running speed. The treadmill display was covered so that participants did not have any feedback on their actual running speed. After 2 min of running at 10 km/h, the participants were asked to pause for 1 min. After this short pause, they started running at 7 km/h and had to manipulate the treadmill speed until they found a running speed that they perceived as matching the reference speed of 10 km/h.

This task was proposed in four different blocks in which the participants were asked to regulate the speed of the treadmill to match the previous speed while being presented with:

- No optical flow (noOF)
- An optical flow matching the treadmill speed (matchOF)
- A faster optical flow (+5 km/h) (fastOF)
- A slower optical flow (−5 km/h) (slowOF).

The order of presentation of the conditions was randomly selected. Note that the fixation cross was positioned so that it corresponded to the focus of expansion of the visual scene in the conditions with optical flow.

The treadmill speed perceived by participants as matching the reference speed and the time necessary to define this speed were recorded at the end of each block.

In between blocks, participants were asked to walk for about 2 min.

2.3. Results

For each condition, data distribution was assessed using the Shapiro–Wilk test (please refer to Supplementary Materials S1-T1 for the data). We then compared the selected running speed to the reference running speed using in each case either a *t*-test when data was normally distributed or a Wilcoxon signed rank test. For all four tests, the alpha level was corrected for multiple comparisons using Bonferroni correction (i.e., 0.05/4 = 0.0125). For all conditions, the selected running speed was not significantly different from the reference running speed after correction.

We then tested whether the selected running speed was different based on the optical flow condition. Since data was not normally distributed, a Friedman rank sum test for repeated measures was used. No differences were found for the selected running speed in the four conditions $\left[\chi^2(3) = 3.1,\ p = 0.3765\right]$ (see Figure 2). Because we did not find any significant difference between the means (i.e., we could not reject H0), we also computed the Bayes factor. The Bayes factor was 0.37, a value which can be interpreted as an 'anecdotal' evidence in favour of H0 [27].

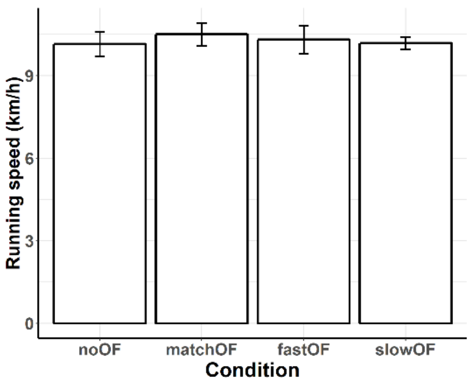

Figure 2. Running speed selected as matching the reference running speed in different optical flow conditions. The bars represent the means and the error bars the 95% confidence interval of those means.

Lastly, we tested whether the duration of the selection phase was different based on the optical flow condition. Data was not normally distributed, so a Friedman rank sum test for repeated measures was used. Here again, we did not find any significant difference between optical flow conditions regarding the duration of the running phase $\left[\chi^2(3) = 1.084,\ p = 0.7809\right]$ (see Figure 3). As for the previous analysis, we computed the Bayes factor, which was 0.11, thereby constituting a moderate to strong evidence in favour of H0 [27].

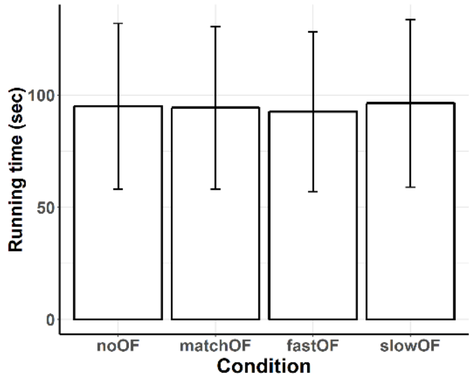

Figure 3. Task duration. Time needed for the participants to retrieve the running speed they perceived as matching the previously experienced reference running speed. The bars represent the means and the error bars the 95% confidence interval of those means.

2.4. Discussion

Participants running on a treadmill were asked to match their running speed to a previously experienced reference running speed while being presented with different optical flow conditions. For all optical flow conditions, participants selected a running speed that did not differ significantly from the reference speed, and there was no difference in the selected speed between the four optical flow conditions. Also, the duration of the selection task did not differ significantly between the four optical flow conditions.

Previous studies with walking participants showed an influence of the optical flow rate on the control of locomotor speed [15,17,28], suggesting an internal calibration between locomotion and visual perception. Here, the adaptation of running speed to the presented optical flow speed was not possible, as the treadmill was not self-driven, but should have influenced the ability to retrieve the reference running speed due to the disruption of this internal calibration. Our results show that this is not the case for running individuals. Moreover, for walking individuals, previous studies suggested the presence of a predetermined expectation of the visual effect that should be associated with a certain walking speed [26]. This should also have led to expecting an influence on the ability to retrieve an imposed speed in the different optical flow conditions. It seems that visual incongruences do not have the same influence on running speed control as they do on walking speed control, possibly due to the higher automatization of running compared to walking as well as to the fact that it requires less cortical control [25,29].

Note that our results might be consistent with a statistically optimal integration model [30], which predicts that sensory information from multiple sources is weighted according to the estimation of the reliability of each sensory source. In our task, because running at the reference speed was performed without optical flow, participants might have given more weight to proprioceptive information than to visual information also in the second part of the running task.

3. Experiment 2

3.1. Introduction

In this experiment, we tested if treadmill running is influenced by the presence and the manipulation of an optical flow. Studies show that the manipulation of the optical flow has a destabilizing effect on postural stability [31–34], and a significant influence on locomotor patterns when walking [15,17,21,22]. The results regarding modifications of gait parameters and their variability as an effect of a virtual optical flow are contradicting, suggesting a great influence of the specific setup, the walking mode (i.e., fixed speed vs. self-paced treadmill) and the time to adapt to the new environment. Specifically, some studies found a lower stride length, with an increased step width [35,36], an increased walking speed variability, and an increased step width variability [15,36,37]. On the other hand, other authors found a stabilizing effect on locomotion patterns [38]. Here we investigated if the presence and manipulation of an optical flow could influence spatiotemporal gait parameters during treadmill running.

3.2. Methods

3.2.1. Participants

20 healthy participants (13 female, 7 male) with a mean age of 25.4 (±2.7 SD) participated in this study. They were unaware of the purpose of the study, were moderately trained to trained, had normal or corrected-to-normal vision and none had a history of cardiovascular disease. All participants gave their informed and written consent prior to the inclusion in the study. This study was performed in accordance with the ethical standards specified by the 1964 Declaration of Helsinki and approved by the Ethics Committee of the University of Fribourg.

3.2.2. Experimental Setup

The experimental setup was the same as in Experiment 1, except for the position of the treadmill, which was at a distance of 2.5 m from the screen, leading to an effective field of view of 70°.

While running, participants' heart rate (HR) was constantly monitored (Polar Team2 System, Polar Electro Oy—Kempele, Finland). Moreover, the NaturalPoint Optitrack system (NaturalPoint, Inc. DBA OptiTrack—Corvallis, OR, USA) with 16 OptiTrack cameras (Prime 17W model) was used to monitor the position of the markers that were used for the estimation of the spatiotemporal gait parameters.

3.2.3. Procedure

As in Experiment 1, prior to the running task, the participants filled out a custom-made questionnaire about their sports activity. For this experiment, also the short version of the International Physical Activity Questionnaire (IPAQ—French version) was used.

At the beginning of the experiment and prior to the testing phase, the participants spent 4 min familiarizing themselves with treadmill running. During this phase, they were instructed to "select an exercise intensity that you prefer and can be sustained for 20 min" [39,40]. The selected running speed was then used for the subsequent testing phase. To ensure that the participant's speed selection was solely based on perception, the speed display on the treadmill was covered so that it was only visible to the investigator. Self-selected running speed was used to reduce inter-individual differences, because fitness level and running experience have an influence on the parameters measured for this study.

The first part of the experiment allowed us to assess the visual speed perceived as matching the chosen running speed for each participant. Participants were presented with the visual scene while running at their preferred running speed. They were instructed to estimate if the optical flow was slower or faster than the actual running speed. Four consecutive tests were proposed in a random order using a one up–one down staircase method [41,42]. The optical flow started two times at a higher speed than the actual treadmill speed (+4 km/h) and two times at a lower speed (−4 km/h). The order of starting speed was randomized. The speed of the visual scene was adjusted according to the one up–one down staircase method, with an increase/decrease of the visual speed of 0.5 km/h until the first inversion of the participant's response, followed by steps of 0.3 km/h. This allowed us to determine the perceptual threshold that indicated the visual speed perceived as matching the actual running speed, i.e., the point of subjective equality (PSE). Prior to the task, participants were familiarized with the experimental setting and task using a training program. The single trials started with the participant running at the previously chosen speed. The visual scene was presented for 2 s before the participants were challenged with a black screen presenting the question "up or down", thus asking them to decide if they wanted to increase (i.e., up) or decrease (i.e., down) the speed of the visual scene. For each trial, participants gave their response while continuing their treadmill run by pressing a switch put on top of a light custom-made plastic cylinder (115 × 30 mm, 15 g) they were holding in each hand. The responses (i.e., left for up and right for down) were sent to the computer via Bluetooth and directly integrated into the staircase test. Once the participant pressed the chosen button, the graphics returned to the visual scene of the following trial (see Figure 4). Each staircase ended when 15 inversions of the responses were reached and the participants were free to take a pause before starting the subsequent test.

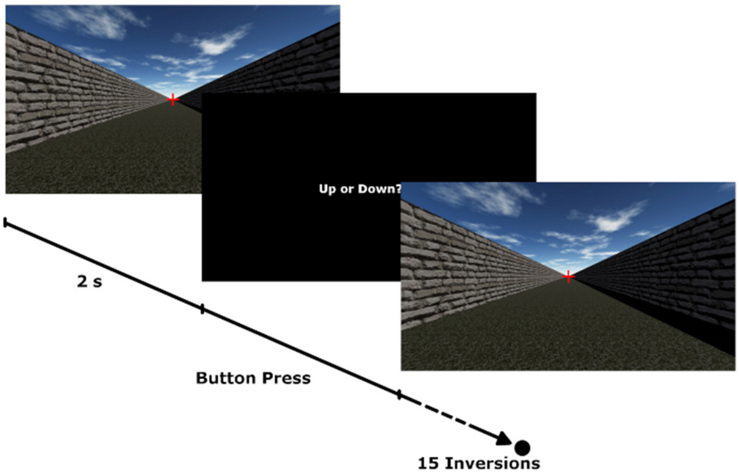

Figure 4. Experimental design.

The second part of the experiment consisted of 4 different blocks in which the participants were asked to run at constant speed for 3 min and 30 s while being presented with different optical flow conditions. The reference value for the optical flow speed was personalized for each participant using the PSE found with the staircase test. The four conditions were:

- no optical flow (noOF)
- matching optical flow with a visual speed corresponding to the PSE (matchOF)
- faster optical flow with a visual speed that was 40% higher than the PSE (fastOF)
- slower optical flow with a visual speed that was 40% lower than the PSE (slowOF).

The order of conditions was randomly assigned. At the end of each block, the participants took a 2-min pause before starting the next block.

For all the parts involving the presentation of a visual speed, the participants were instructed to gaze at the fixation cross that was visible in all conditions.

At the end of the running phase, the participants estimated their perceived exertion using the Borg RPE Scale (6 to 20 scale), with values ranging from 'no exertion at all' to 'maximal exertion'.

3.2.4. Spatiotemporal Parameter Analysis

For the spatiotemporal gait parameter estimation, the information derived from the OptiTrack system was used. The participants were equipped with two reflective markers, one positioned on each heel. The data analysis was performed on steady gait by removing the first and the last 15 s of each block.

The different gait parameters were estimated using the heel marker trajectory and were averaged for each block, as described in Dubois and Bresciani [43]. Table 1 shows which spatiotemporal gait parameters were estimated and how they were calculated.

Table 1. Gait parameters and their method of estimation.

Spatiotemporal Parameters	Estimation
Step duration (s)	The duration between the local minima of the left and right heel
Step length (m)	Treadmill speed (m/s) × Step duration (s)
Step frequency (steps/s)	1/step duration
Step width (cm)	The distance on the x-axis between the left and right heel

For analysis, these values were averaged both for the whole duration of the block as also for each minute of each block.

3.3. Results

We first compared the perceived visual speed with the actual running speed using a paired *t*-test, as both running and perceived visual speed were normally distributed (please refer to Supplementary Materials S1-T2 for the data.) This allowed us to determine how visual speed was estimated compared to the actual running speed, i.e., treadmill speed. Participants set visual speed significantly higher than the actual treadmill speed ($t(19) = -4.8743$, $p < 0.001$). Figure 5 shows the difference between running speed and perceived visual speed.

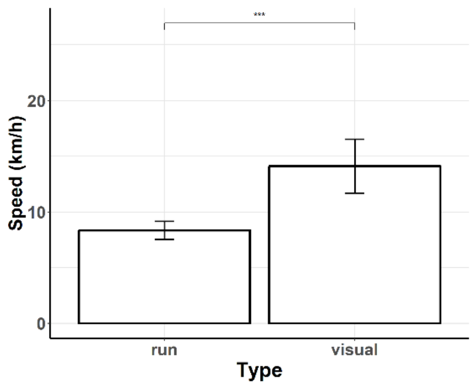

Figure 5. Visual speed underestimation. Speed of the visual scene that was perceived as matching running/treadmill speed. The bars represent the means and the error bars the 95% confidence interval of those means.

We then tested whether the presentation and manipulation of the optical flow affected spatiotemporal parameters in treadmill running using a 4 × 3 (Condition[noOF, matchOF, fastOF, slowOF]*minute[1,2,3]) mixed analysis of variance (ANOVA). The results showed no main effect of the condition for all the spatiotemporal parameters, i.e., step length, step duration, step frequency, and step width. Even if there was no influence of the condition, the results showed a significant effect of the minute of the acquisition. There was no interaction between the main factors. Table 2 reports all the results.

Table 2. Results of the 4 x3 mixed ANOVA. Significant difference: * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

Variable	Condition	Minute	Interaction
Step length	$F(3,57) = 1.695$, $p = 0.178$	$F(2,38) = 10.000$, $p < 0.001$ ***	$F(6,114) = 1.423$, $p = 0.212$
Step duration	$F(3,57) = 1.747$, $p = 0.168$	$F(2,38) = 10.085$, $p < 0.001$ ***	$F(6,114) = 1.357$, $p = 0.238$
Step frequency	$F(3,57) = 1.977$, $p = 0.128$	$F(2,38) = 9.492$, $p < 0.001$ ***	$F(6,114) = 1.534$, $p = 0.173$
Step width	$F(3,57) = 1.011$, $p = 0.395$	$F(2,38) = 11.514$, $p < 0.001$ ***	$F(6,114) = 0.255$, $p = 0.956$

A Tukey's post-hoc test indicated that the difference was significant when comparing minute 1 to minute 3 for step duration ($p < 0.05$), step frequency ($p < 0.05$) and step width ($p < 0.01$), while there was only a tendency for step length ($p = 0.061$).

For the HR, since a plateau was observed in all participants, the mean value was calculated as average of 30 s once the plateau was reached. A repeated-measures ANOVA showed a significant difference for mean HR [F(3,57) = 5.7465, $p < 0.01$], while the starting HR did not differ between conditions $\left[\chi^2(3) = 0.6528, p = 0.8842\right]$. A Tukey's post-hoc test indicated a significant difference between the noOF and the VR conditions (noOF-matchOF: $p < 0.01$, noOF-fastOF: $p < 0.05$, noOF-slowOF: $p < 0.001$) as shown in Figure 6.

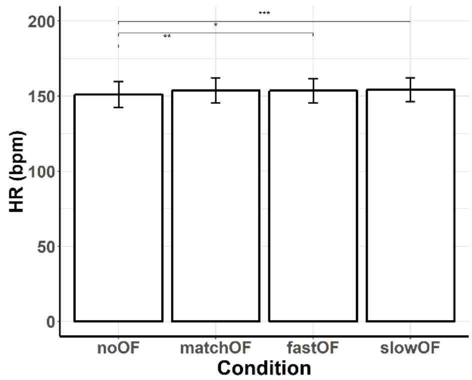

Figure 6. Mean heart rate. The bars represent the means and the error bars the 95% confidence interval of those means.

Last, a repeated-measures ANOVA performed on perceived effort values (as measured with the Borg RPE scale) showed no difference between the different OF conditions $\left[\chi^2(3) = 2.4296,\ p = 0.4882\right]$.

3.4. Discussion

First, participants running on a treadmill while being presented with a moving virtual scene were asked to match the visual speed of the VR scene to their actual running speed. Participants set visual speed significantly higher than the actual running speed, i.e., treadmill speed. In other words, the visual scene had to move significantly faster than the treadmill speed for the two speeds to be perceived as equivalent, indicating and underestimation of visual speed relative to treadmill speed. Then, spatiotemporal gait parameters and HR were measured with participants running on a treadmill at their preferred running speed while being presented with different optical flow conditions. At the end of each condition, perceived effort was recorded. We did not observe any significant difference between optical flow conditions regarding the spatiotemporal gait parameters. However, we observed an effect of the time (i.e., minute) of acquisition. In addition, the HR was significantly different in the noOF condition than in the VR conditions, while there was no difference between conditions regarding perceived effort.

Our results confirm the general tendency to underestimate visual speed relative to locomotor speed in virtual environments, both when walking [18,44–46] and running [47–49]. Compared to previous work with running participants, our results show that visual speed underestimation relative to running speed also occurs with participants running at their preferred running speed. Specifically, previous work was always based on imposed running speeds [47–49], which were not necessarily in the range of preferred speeds of all participants. Here, every participant selected his/her running speed, reducing a possible influence of fatigue. This likely also reduced the attentional demand and fear of falling off of the treadmill [50] thanks to an increased felt safety compared to an imposed running speed.

Previous studies on walking showed that the manipulation of the optical flow can significantly affect locomotor patterns [15,17,21,22]. In particular, optical flow can modulate parameters known to be reflective of gait instability, such as step width, step length, stride cycle, and stride velocity variability [51,52]. Our results show that this influence on locomotor patterns cannot be extended to individuals running on a treadmill. In fact, none of the spatiotemporal gait parameters (i.e., step length, step duration, step frequency, and step width) was significantly affected by the optical flow condition. This suggests that when running at a self-selected speed, the presence and manipulation of the optical flow has no stabilizing or destabilizing effect. The difference between our results and those previously reported with walking participants could be linked to the fact that running seems to be characterized by a higher automatization and a lower cortical control compared to walking [25,29]. The observed effect of the minute of acquisition could be linked to treadmill running accommodation, which can be different from individual to individual [53]. Moreover, our results show that the presence and manipulation of the optical flow does not influence this accommodation process, since no difference was found between the four optical flow conditions.

Even if there was no significant effect of the optical flow conditions on spatiotemporal running parameters, VR seems to influence HR. Specifically, we found significant differences between the noOF and the VR conditions. Because the order of presentation of the conditions was randomized, exercise intensity was the same for each subject in all conditions, and starting HR did not differ between blocks. Therefore, the observed difference should not be linked to the running task per se. The higher HR values in the VR conditions may therefore be linked to an emotional activation, HR being a possible indicator of excitement [54]. This would also explain the absence of difference in perceived effort as measured with the Borg RPE Scale, even with the higher HR values in the VR conditions. In fact, even if there was no significant difference, there was a slight tendency toward lower RPE values for the VR conditions compared to the noOF condition. This could confirm the results of previous studies that suggest that VR exercise equipment could act as a distraction from the exercise intensity [55,56].

4. General Discussion

The control of locomotion by the central nervous system relies on the integration of sensory information provided by different systems such as the visual, vestibular, proprioceptive, and auditory systems. When the information provided by one of these sensory inputs is considered as less reliable or is in conflict with other cues, the central nervous system tends to weight sensory information taking into account its estimated reliability. Our results suggest that when running in a treadmill-mediated virtual environment, participants tend to provide a higher weight to proprioceptive information than to visual information. Specifically, the presence and manipulation of a simulated optical flow did not affect the ability of participants to retrieve a 'proprioceptive' reference speed previously experienced. In addition, optical flow did not affect the spatiotemporal gait parameters known to be indicators of gait stability.

The results of Experiment 2 confirm that the speed of an artificial optical flow is underestimated relative to treadmill speed when running in treadmill-mediated virtual environments. In particular, our results show that this relative underestimation applies not only to situations in which the running speed is imposed, as shown in previous studies [47–49], but also to situations in which participants are allowed to run at their preferred running speed. Specifically, in our study, the participants were free to select their running speed for the tests. This likely increased their feeling of safety compared to tests performed at an imposed running speed. It also likely lowered the influence of fatigue and the fear of falling off of the treadmill [50]. This means that the visual underestimation previously reported with participants running in virtual environments still applies at running speeds for which past experience from practice could have been used for recalibration [57,58]. This could be linked to treadmill running in itself, since it has been shown to influence speed perception. In fact, treadmill running has been shown to be perceived as faster compared to the same overground running speed [59–62]. It has also been shown to influence the capacity to discriminate actual running speed due to differences in kinetics and kinematics compared to overground running [53,63]. Another factor that could have influenced the results is the specific experimental setup. In fact, studies suggest that visual speed is perceived more accurately as peripheral flow increases [44,49,64–66]. Moreover, a 3D stereoscopic environment would have been more immersive than the simple 2D on the projection screen and studies show that 3D environments induce a stronger sense of presence during spatial navigation tasks [67]. Nevertheless, here we used a 2D setup since more immersive 3D virtual reality situations inducing a strong sense of presence have been shown to have a greater capability of inducing postural instability compared to 2D VR situations [68] presenting also a greater possibility that participants might have experienced VR induced symptoms and effects [69].

Though our study confirms the tendency to misperceive the speed of a simulated optical flow when running in treadmill-mediated virtual environments, it shows that this misperception might not have an influence on the control of treadmill running itself. This result suggests that the findings of previous studies that reported an influence of the optical flow rate on the control of locomotor speed might not apply when running on a treadmill. This difference between previous results and ours could result from a higher automatization of running compared to walking, with the former requiring less cortical control [25,29]. This would in turn lead to a reduced influence of visual incongruences on the control of running speed. This would be in line with the results of Jahn et al. [24,70], who found larger gait deviations with vestibular and visual stimulation during walking compared to running. Those results can probably be attributed to a suppression of sensory signals during unhindered running in order to avoid potential disturbances of the optimized spinal program controlling running motor pattern [71,72]. In fact, studies have shown that locomotion without disturbances or obstacles is more independent of cortical control, the latter being mainly required when exact foot placement is needed, or when the system must react to external perturbations, notably by changing muscle activity to modify limb trajectories to step over obstacles [73]. This would also explain the lower impact of visual incongruences on balance and locomotor patterns while treadmill running, as shown in Experiment 2. Our results contradict previous studies on walking, which showed an influence of an artificial optical flow on postural stability [31–34] and on locomotor patterns. In particular, Pailhous et al. [17] found that when walking overground, stride length decreases in presence of an artificial optical flow. Prokop et al. [15] found that when walking on a treadmill at constant speed, stride-cycle variability increases and the optical flow significantly modulates walking velocity. Hollman et al. [36] found that when walking at pre-determined speeds on a treadmill in VR, step width increases and step length decreases, whereas the variability of stride velocity and step width increases. All these parameters are known to characterize gait instability [51,52], suggesting that the presence of VR during treadmill locomotion may lead to a more instable gait. In fact, a shorter step length and an increased step width are associated with a more conservative gait pattern, often adopted in case of instability or fear of falling. Other studies show that this influence on locomotor patterns extends also to the walk–run and run–walk transition, leading to changes in the transition speed based on the speed of the optical flow [38,74]. Our results show that this influence on locomotor patterns cannot be extended to running individuals, and that for running at a self-selected speed, the presence and manipulation of the optical flow has no stabilizing or destabilizing effect. This could also be due to the fact that when visual cues are in conflict with other sensory information about self-motion, which is the case when manipulating optical flow speed without having the possibility to vary locomotor speed, visual information ceases to be dominant compared to other types of information [4,14]. In fact, studies show that when participants are asked to walk at a constant speed, they tend to weight information from proprioceptive cues higher than cues derived from the visual system [15–17].

Our results also indicate that the simulated optical flow does not influence the process of accommodation to treadmill running, because no differences were found between the four optical flow conditions. This accommodation process has been shown to vary between individuals [53]. Healthy adults devoid of experience with treadmill running can familiarize themselves with the task after 6 min in a single session, and angular kinematics as well as spatiotemporal parameters are highly reliable after 2 min [75]. White et al. [76] found that there was no significant difference in vertical force after 30 s of treadmill running. The differences we found between minute 1 and 3 could be linked to the new accommodation required after each pause in between the blocks. This would be in line with the fact that previous studies have shown that minimal amounts of treadmill training are necessary before full accommodation to treadmill locomotion [77].

Surprisingly, our results suggest that the presentation of an artificial optical flow can influence HR. Specifically, the results of Experiment 2 show a significant difference between the HR monitored in the noOF condition and the HR monitored in the VR conditions. Because the HR is an indicator of excitement [54], the observed results could be linked to an emotional activation, which would also explain the absence of difference between the four optical flow conditions regarding perceived effort. This excitement could be due to the novelty of the virtual scene and to some sense of presence deriving from the optical flow compared to the traditional treadmill-running settings, which are often considered as boring [78]. This would be in line with previous studies showing that VR can act as a distraction from exercise intensity, favoring a dissociation of the attentional focus [55,56], and improving some of the mood benefits of physical exercise [79]. If confirmed, this effect could be exploited to increase engagement and adherence to physical activity, notably in the context of health and disease prevention.

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