Viewpoint oscillation improves the perception of distance travelled based on optic flow

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When static observers are presented with a visual simulation of forward self-motion, they generally misestimate distance travelled relative to a previously seen distant target: It has been suggested that this finding can be accounted for by a "leaky path integration" model. In the present study, using a similar experimental procedure, this result was confirmed. It was also established that combining the translational optical flow with simulated head oscillations (similar to those during natural walking) improved the subjects' perception of the distance travelled in comparison with a purely translational flow. This improvement may be attributable to the fact that an optic flow pattern resembling that associated with walking enhances the path integration process. In a subsequent experiment, we investigated whether it was the biological or the rhythmical characteristics of the simulation that enhanced the subjects' estimates of the distance travelled. The results obtained confirm that adding rhythmic components to the optic flow pattern improved the accuracy of subjects' perception of the distance travelled. However, no significant differences between biological and rhythmical oscillations were detected. These results relate to recent studies on the effects of smooth and jittering optic flows on vection onset and strength. One possible conclusion is that oscillations may increase the global retinal motion and thus improve the vection and path integration processes. Another possibility is that the nonmonotonous pattern of retinal motion induced by oscillatory inputs may maintain optimum sensitivity to the optic flow over time and thus improve the accuracy of subjects' perception of the distance travelled.

Introduction

Humans and other animals can potentially use various sources of information to estimate the distance they have travelled. Contrary to the perception of the absolute distance, which involves depth perception mechanisms based mainly on static visual cues (Cutting & Vishton, 1995), the perception of distance travelled is based on the dynamic processing of multimodal information generated by the observer's self-motion, including dynamic visual cues (i.e., the optic flow; Gibson, 1950) and body-based information mainly provided by proprioceptive cues (Mittelstaedt & Mittelstaedt, 2001), efference copy and vestibular cues (Harris, Jenkin, & Zikovitz, 2000; Israël & Berthoz, 1989). Several studies have focused on the importance of dynamic cues in the perception of surrounding space. Loomis and Knapp (2003), for example, used procedures involving spatially guided actions in which participants looked at a target and then, when it was no longer visible, attempted to reach it using body-based cues.

During the past years, considerable interest has focused on how the visual system uses optical flow to perceive self-motion. Several authors have dealt with this topic by dissociating the optical flow from body-based cues. When optical flow occurs alone, in the absence of other sensory cues of movement, it can create an illusory sensation of self-motion, which is known as "vection" (Ash & Palmisano, 2012; Dichgans & Brandt, 1978; Palmisano, Gillam, & Blackburn, 2000). The optical flow pattern informs the viewer about the spatiotemporal relationships between himself or herself and the objects in the environment (Gibson,

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1950; Lee, 1980; Sun, Carey, & Goodale, 1992; Sun, Campos, Chan, Young, & Ellard, 2004; Warren & Hannon, 1990). It contains information about the egocentric direction of self-motion (Warren & Hannon, 1988), self-speed (Larish & Flach, 1990), and time to collision (Lee, 1976). The existence of vection phenomena therefore proves that optic flow provides us with information about our movements in the environment. Here, it was proposed to study the effects of various kinds of optic flow on subjects' perception of the distance travelled.

It has been established in several studies that insects such as honeybees are able to use optical flow to judge the distance flown (Esch & Burns, 1995; Srinivasan, Zhang, Altwein, & Tautz, 2000; Srinivasan, Zhang, Lehrer, & Collett, 1996). Humans proved to have similar abilities when presented with computer-simulated optical flow (Bremmer & Lappe, 1999; Harris et al., 2012; Lappe, Jenkin, & Harris, 2007; Redlick, Jenkin, & Harris, 2001). Specific methods have been developed to measure the perception of the distance travelled by stationary subjects exposed to an optical flow (Bremmer & Lappe, 1999; Frenz & Lappe, 2005; Redlick et al., 2001).

In the latter studies, the observer's simulated displacement in a virtual environment was induced by triggering "pure" translation of the visual scene relative to the observer's viewpoint. Zacharias and Young (1981) suggested that visually simulated self-motion at a constant speed is likely to induce the strongest sensations of vection because it will produce the least visual-vestibular conflict in stationary observers. However, contrary to the predictions of this sensory-conflict theory, adding frontal-plane jitter or oscillations to an expanding optical flow pattern was subsequently reported to enhance the vection in depth by significantly decreasing the onset latency and increasing its duration (Kim & Palmisano, 2008; Nakamura, 2013; Palmisano, Allison, & Pekin, 2008; Palmisano et al., 2000; Palmisano, Kim, & Freeman, 2012). Adding oscillatory movements resembling those that occur during normal walking to a translational optical flow has also been found to induce an illusory sensation of self-motion (vection), as well as increase its intensity and duration (Bubka & Bonato, 2010; Kim, Palmisano, & Bonato, 2012). Other authors have reported that during virtual displacement, combining the translational optical flow with simulated head oscillations (similar to those during natural walking) increases the observer's sensation of walking or running (Lécuyer, Burkhardt, Henaff, & Donikian, 2006; Terziman, Marchal, Multon, Arnaldi, & Lécuyer, 2013). The feeling of walking may increase the sense of presence in a virtual environment (Interrante, Ries, Lindquist, Keading, & Anderson, 2008). Another idea that has been put forward (although it was not actually tested) is that the feeling of walking may improve the subject's assessment of the virtually travelled distance (Terziman, Lécuyer, Hillaire, & Wiener, 2009). The question therefore arises as to whether combining a translational optical flow with simulated head oscillations is liable to affect subjects' perception of self-motion and hence their perception of the distance (virtually) travelled.

In our first experiment, it was therefore proposed to test this hypothesis directly. Stationary subjects were subjected to visually-induced virtual displacements of two kinds triggered by a global optical flow presented in an immersive environment, the Cave Automatic Virtual Environment (CAVE; Cruz-Neira, Sandin, & DeFanti, 1993). The first type of flow (called the "linear" flow) was generated by triggering a "pure" translation of the virtual environment, inducing in the observer an illusion of forward movement (at a constant speed). The second type of flow (called the "oscillatory" flow) included additional oscillations based on a model simulating the head movements that occur during walking (Cappozzo, 1981; Lécuyer et al., 2006).

Stationary observers were therefore exposed to one of the two types of optical flow, and they were asked to indicate when they thought they had reached the position of a previously seen distant target. In situations of this kind, subjects' subjective evaluation of the distance travelled is usually overestimated (i.e., they undershoot the target; Frenz & Lappe, 2005; Frenz, Lappe, Kolesnik, & Bührmann, 2007; Redlick et al., 2001). Subjects indicated that they had reached the target's position after covering only 60% of the initial target distance (Redlick et al., 2001). Lappe et al. (2007) attributed this result to the "leakage" of the process of spatial integration of optic flow into perceived self-motion, in line with the leaky integration model, according to which the path integration processes based on vestibular and proprioceptive cues contribute importantly to distance estimation (Mittelstaedt & Mittelstaedt, 2001). This model involves two main parameters: a gain factor, the proportional decrease in the current distance-to-target that occurs at every step, and a leak factor, which reduces the current distance-to-target accordingly. The parameters of this model were tentatively fitted to our experimental data (see the Methods section for a more detailed description of the model).

The main hypothesis adopted here was that an optical flow including visual properties of natural walking would improve the subjects' assessment of the distances travelled in comparison with a purely translational optical flow by enhancing the path integration processes. In other words, we tested how the properties of the optical flow may affect the parameters of the leaky path integration model.

Experiment 1

Methods

Participants

Twenty volunteers (including 10 women, mean age 28.5 ± 7 years) with normal or corrected-to-normal vision took part in these experiments. They had no vestibular antecedents or disorders liable to affect their locomotor performances. All of the participants gave their written informed consent prior to the experiments in keeping with the 1964 Helsinki Declaration, and the study was approved by the local ethics committee.

Apparatus

This experiment was conducted in a large-screen immersive display (CAVE) housed at the Mediterranean Virtual Reality Center (CRVM; http://crvm.ism.univ-amu.fr) in Marseille. It consists of a 3-m-deep, 3-m-wide, 4-m-high cubic space with three vertical screens and a horizontal screen floor. The images on the three vertical screens were back-projected, and the images on the ground were projected directly with a spatial resolution of 1.400 × 1.050 pixels and a temporal resolution of 60 Hz.

Each projection surface was illuminated by two video projectors, which were used to generate passive stereoscopic images. Each pair of projectors was equipped with colorimetric filters, and the same color filters were mounted on the three-dimensional glasses worn by the subjects. A stereo separation system (Infitec®) was used to separate the images received by the two eyes.

A tracking system (ART®) based on a set of eight cameras made it possible to measure the movements of the subjects, thus ensuring interactivity in real time with the virtual environment with which they were presented.

The entire setup was managed by a cluster of 10 PC computers equipped with professional graphic cards. This computer system is capable of synchronously generating spatially accurate stereoscopic views of virtual environments, corresponding to the subjects' real-time positions and behavior. The ICE software program (developed at the Institute of Movement Sciences) was used to prepare the environmental setup and control the experimental procedure.

The subject was standing in an "infinite" straight virtual tunnel (Figure 1), which had the same width as the CAVE setup (3 m). The subject was located 1.5 m from the side screens and 1.5 m from the front screen of the CAVE. The tunnel floor was graphically homogeneous and therefore devoid of visual marks that might be used as landmarks. Similarly, no visual marks could be taken in the tunnel because of its nonsingular random texture. The subject could see a target, a "road signal" cone of the usual size (40-cm high), placed on the tunnel floor ahead. This target was at a virtual distance of 6, 9, 12, 15, 18, or 21 m from the subject, depending on the trial (Plumert, Kearney, Cremer, & Recker, 2005; Terziman, Lécuyer, Hillaire, & Wiener, 2009).

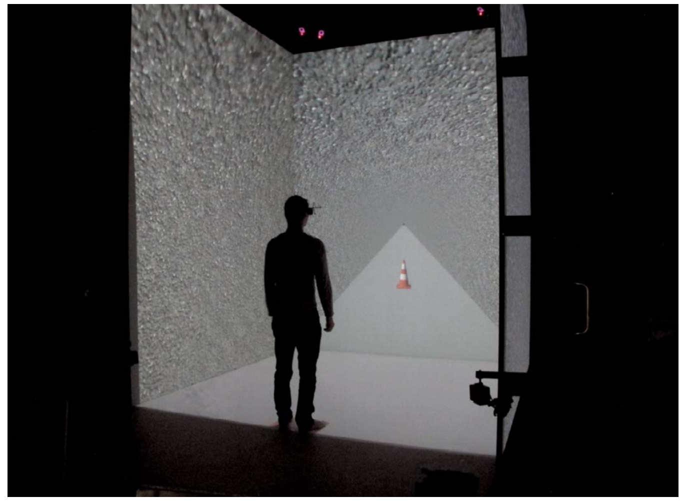

Figure 1. The experimental setup. The large screen immersive display (CAVE) at Aix-Marseille University.

Procedure

To ensure that the subjects knew the actual size of the target before the start of the experiment, we asked them to indicate with their hand how high the virtual target placed in the middle of the CAVE seemed to be. The position of this virtual target was then used as the subjects' starting point at the beginning of each trial. The subjects placed in the middle of the CAVE facing the front wall, and therefore looking at the tunnel, and holding a two-button mouse were then given the following instruction: to assess the distance to a cone (the target) after hearing a beep telling them to look straight ahead. In response to the second beep occurring 3 s after the first one, they had to trigger the trial by pressing the left button on the mouse. Pressing the button would have two simultaneous effects: The target would disappear, and the optic flow simulating the virtual displacement would start. They were asked to click again on the button when they thought they had reached the position of the previously seen target, and they were informed that this task would be repeated during several trials.

The task of assessing the distance travelled to be performed by the stationary subjects therefore consisted in indicating when they thought they had reached the previously seen position of the cone (the target). When they felt they had reached the target's initial

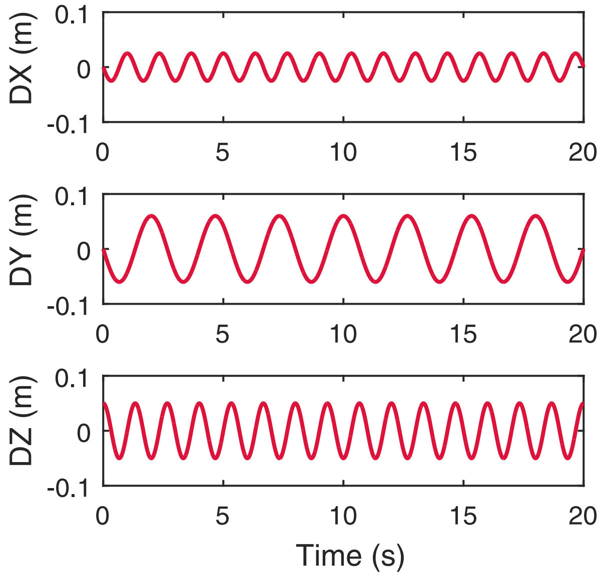

Figure 2. From top to bottom, oscillatory movements of the camera along the transverse axis (DX), the longitudinal axis (DY), and the anteroposterior axis (DZ).

position, they had to click again on the left mouse button. This second click was taken to reflect the distance virtually travelled to reach the cone. The second click also stopped the motion of the tunnel, and after an interval of 2 s, it initiated the display of the following trial. This procedure was repeated several times, varying the initial distance to the target and the modes of visual simulation used.

Ten blocks of trials, each consisting of 12 trials, were run (see the Experimental Design section). After each block, a break could be made at the subject's request. Before the actual experiment, subjects were familiarized with the procedure in two preliminary habituation trials.

Conditions of virtual simulation of self-movement: The optical flow factor

Linear: In the *linear* mode, the camera adopting the subject's viewpoint underwent a strictly linear translation at the same mean velocity as in the second condition (1.2 m.s^{-1}), as if the camera were on rails, as in a travelling shot in movie films.
Oscillatory: In the *oscillatory* mode, the virtual camera adopting the subject's point of view again underwent a linear translation in addition to periodic oscillations applied on the anteroposterior, horizontal, and longitudinal axes (Figure 2). The mean speed in the *oscillatory* mode was equal to the constant velocity in the *linear* mode (1.2 m.s^{-1}). The oscillations were based on the model presented by Lécuyer et al. (2006), modified using data by Cappozzo (1981).

The following equations were used here:

$$DX = Ax \times \cos(2\pi/T \times t)$$

$$DY = Ay \times \cos(2\pi/T \times t + \pi/2)$$

$$DZ = Az \times \cos(\pi/T \times t + \pi/2)$$

The period ($T = 2 \times L/V_0$) was expressed in terms of the step length ($L = 0.8$ m) and the speed ($V_0 =$ 1.2m.s^{-1}). The following amplitudes based on data by Cappozzo (1981) were selected: Ax (transverse) = 0.06 m; Ay (longitudinal) = 0.05 m; Az (anteroposterior) = 0.025 m.

Experimental design

The following experimental design was used here: 20 subjects were presented with 10 blocks of trials. In each block of 12 trials (six distances [6, 9, 12, 15, 18, and 21 m] × two optic flow conditions [*linear* and *oscillatory*]), the order of the trials was chosen at random. The whole experiment lasted approximately 45 min per subject. This yielded a total number of 20 × 10 × 6 × 2 or 2,400 observations and measurements of the dependent variable (the perceived distance travelled).

Data analysis

During each trial, independent variables (the subject's identity, the block number, the initial distance, and the virtual self-movement condition) and the dependent variable (the simulated distance travelled) were recorded. The simulated distance travelled was bounded by a starting signal and a stop signal. Between these two signals, the tunnel was made to advance, and the distance travelled was recorded at a sampling frequency of 60 Hz.

Subjects' estimates under the two optic flow conditions were adjusted (using Matlab® fitting functions) based on the leaky path integration model developed by Lappe et al. (2007).

According to this model, the subjects monitor the currently perceived distance $D(x)$ to the target depending on their simulated position (x) and press the button when this distance becomes zero. The instantaneous change in D with respect to x is given by

$$\frac{dD}{dx} = -\alpha D - k \quad (1)$$

where k is the gain in the sensory (visual) input ($k = 1$ in the case of an ideal observer), which will simply be called "the gain" from now on, and α represents the rate of decay of the integrator, or the "leak rate" ($\alpha = 0$ in the case of an ideal observer). The general solution to this differential equation is

$$D(x) = \left(D_0 + \frac{k}{\alpha}\right)e^{-\alpha x} - \frac{k}{\alpha} \quad (2)$$

where D_0 is the actual initial distance to the target (before the optic flow starts). From this equation, we can calculate the distance travelled (DT) at which the subjects believed they had reached the target ($D = 0$), with a given initial target distance (D_0):

$$DT = \frac{1}{\alpha}\left[\ln\left(D_0 + \frac{k}{\alpha}\right) - \ln\left(\frac{k}{\alpha}\right)\right] \quad (3)$$

Statistical analyses

Shapiro-Wilks tests were performed to check that the data were normally distributed. Once this condition had been met, statistical analyses were conducted using repeated-measures analyses of variance (rmANOVAs).

Results

When they were exposed to simulations inducing the feeling of forward movement toward a previously seen distant target, subjects indicated that they had reached the target after travelling only 90% on average of the distance to the target. The distance of travel to the previously seen target was therefore underestimated, in line with the "leaky path integration" model (Lappe et al., 2007).

An rmANOVA was conducted with STATISTICA on the simulated distance travelled at the moment when the subjects responded (the dependent variable). This analysis involved three independent variables ($\text{Block}_{10} \times \text{Distance}_6 \times \text{Optical\_flow}_2$). The results showed that the main effects involved were those of the Block factor, $F(9, 171) = 6.29$, $p < 0.001$; the Distance factor, $F(5, 95) = 674.58$, $p < 0.001$; and the Optical Flow factor, $F(1, 19) = 16.60$, $p < 0.001$. An interaction effect was also found to occur between the optical flow and distance factors, $F(5, 95) = 9.90$, $p < 0.001$.

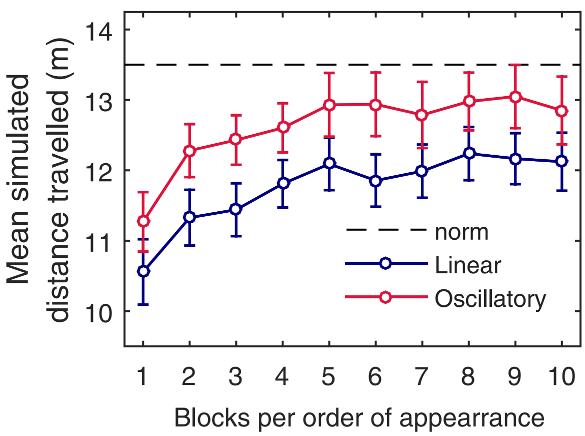

Figure 3. Mean simulated distance travelled per block of trials. Data points are means based on the performance of 20 subjects, and error bars give the standard errors of the means.

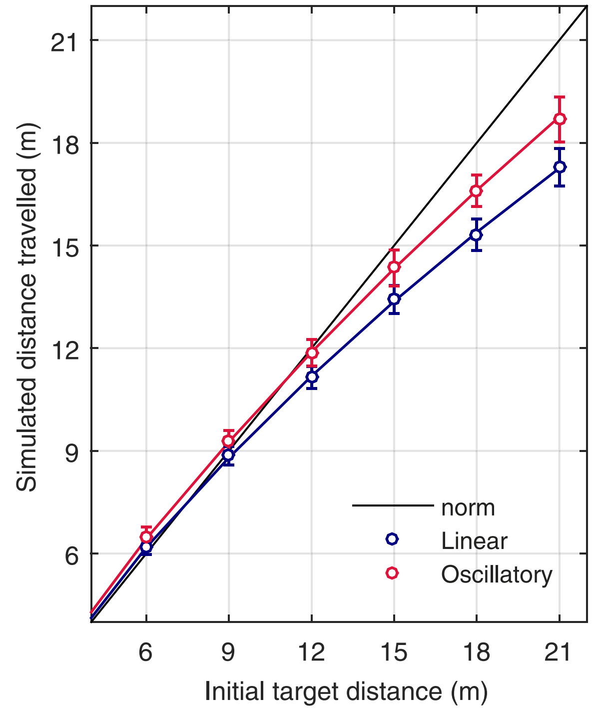

Figure 4. Simulated distance travelled depending on the initial target distance in the linear (blue) and oscillatory (red) conditions. Data points are means based on 20 subjects, and error bars give the standard errors of the means. The black line indicates the actual distances. Blue ($k = 0.89$; $\alpha = 0.04$) and red ($k = 0.86$; $\alpha = 0.03$) lines are the fits obtained by fitting average data to the leaky integration model (Lappe et al., 2007). See the Methods section for details.

The block factor effect indicates that the participants did not assess the distance travelled in the same way throughout the experiment. They tended to respond too early in the first three blocks, and their assessments tended to stabilize during the subsequent trials (Figure 3): When the analysis was restricted to the last seven blocks, the Block factor effect disappeared, $F(6, 114) = 1.22$, $p > 0.1$, whereas the effects of the Optical Flow factor, $F(1, 19) = 13.08$, $p < 0.01$; the Distance factor. $F(5, 95) = 578.51$, $p < 0.001$; and the interaction between them, $F(5, 95) = 7.87$, $p < 0.001$, persisted.

The presence of a distance effect, $F(5, 95) = 578.51$, $p < 0.001$, indicates that the participants' performance depended on the distance to be estimated. This finding suggests the existence of a positive correlation between the initial target distance and the subjects' distance travelled estimates. In addition, the degree to which the simulated distance travelled was underestimated increased with the distance to the target. Figure 4 shows the simulated distance travelled versus the distance to

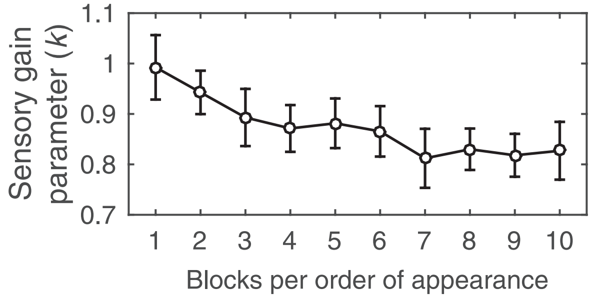

Figure 5. Mean sensory gain parameter in the leaky spatial integrator model (k) depending on the various experimental blocks. Data points are means based on 20 subjects, and error bars give the standard errors of the means.

the initially seen static target under the two optical flow conditions (*linear* and *oscillatory*). The subjects undershot the simulated distance travelled more with large distances than with short distances to the target. When the initial target was 21 m away, for example, the subjects responded after the simulated distance travelled was only 16.88 m ($SD = 4.9$) on average.

One of the main results obtained here was the presence of an optical flow mode effect, $F(1, 19) = 13.08$, $p < 0.01$. As can be seen from Figure 4, the simulated distance travelled in the *oscillatory* (red) mode tended to resemble the real distances more closely than in the *linear* (blue) condition.

Figure 4 gives the simulated distance travelled depending on the initial target distance and the optic flow conditions. The existence of an interaction between the latter two factors, $F(5, 95) = 7.87$, $p < 0.001$, means that the effect of one factor varied depending on the modalities involved in the other factor. In other words, although an overall difference was observed between the responses produced depending on the optical flow conditions, this does not mean that this was the case with all the distances tested. A Tukey's test was therefore performed to determine whether this difference was present in the case of all the initial distances. The results of this test showed the existence of significant differences between the two conditions of displacement in the case of longer distances (12, 15, 18, and 21 m) but not in that of smaller distances (6 and 9 m).

Leaky integrator model

All the subjects' responses recorded in the two optical flow conditions and with the various initial target distances were adjusted using the leaky spatial integrator model presented by Lappe et al. (2007; see Methods and Figure 4) to obtain the sensory gain (k) and the leak rate (α). The average R^2 of these fits was 0.92 ± 0.05 in the *linear* condition and 0.91 ± 0.08 in the *oscillatory* condition. An rmANOVA was performed on each of these values ($Block_{10} \times Optical\_flow_2$). In the case of the gain parameter (k), the Block factor was found to have significant effects, $F(9, 171) = 4.70$, $p < 0.001$ (Figure 5) but not the optical flow condition, $F(1, 19) = 0.44$, $p > 0.5$. The second rmANOVA showed on the contrary that the leak rate (α) did not vary between blocks, $F(9, 171) = 1.19$, $p > 0.3$, but that it varied between the optical flow conditions, $F(1, 19) = 9.96$, $p < 0.01$. The model's fit is plotted in Figure 4, and details of the relevant parameters are presented in Table 1.

	k		α	
Block	LIN	OSC	LIN	OSC
1	1.03	0.96	0.05	0.05
2	0.98	0.90	0.03	0.03
3	0.92	0.87	0.05	0.04
4	0.88	0.87	0.05	0.03
5	0.91	0.86	0.04	0.03
6	0.88	0.85	0.05	0.03
7	0.78	0.84	0.10	0.04
8	0.86	0.80	0.04	0.04
9	0.81	0.82	0.05	0.04
10	0.84	0.81	0.05	0.08
Mean	**0.89**	**0.86**	**0.05**	**0.04**

Table 1. Values of the two parameters k and α of the leaky spatial integrator model in each experimental block.

When this analysis was restricted to the last seven blocks, the effects of the block factor on the sensory gain disappeared, $F(6, 1{,}114) = 2.15$, $p > 0.05$.

Discussion

The aim of this experiment was to determine whether a visual simulation of self-motion generated by an oscillatory optic flow mimicking the visual effects of the head movements that occur during walking (the *oscillatory* condition) improved subjects' assessments of the distance travelled to a previously seen distant target, as compared with a visual simulation of forward self-motion generated by a strictly rectilinear optic flow (the *linear* condition). The results obtained suggest that this was indeed the case. In all the conditions tested, the subjects' assessments of the distance travelled to reach a previously seen distant target tended to be more accurate in the *oscillatory* than the *linear* condition. This finding suggests that the *oscillatory* optical flow improved the path integration processes in comparison with the "linear" optic flow. This effect of the optical flow depended, however, on the distance to be assessed (Figure 4): A significant difference was observed between the two optic flow conditions in the case of long distances (12, 15, 18, and 21 m) but not with shorter distances (6 and 9 m). In addition, the subjects' assessments of the distances travelled were more accurate in the *oscillatory* mode than in the *linear* mode in the case of four (12, 15, 18, and 21 m) of the six initial distances.

To support these results, we fitted our data to the leaky integrator model presented by Lappe et al. in 2007. This model involves two main parameters, the sensory gain (k) corresponding to the quality of the transformation of the optical flow into distance travelled and the rate of decay (α) corresponding to an increasing tendency to underestimate the remaining distance to the target with passing time. First, we observed that the optical flow did not affect the sensory gain parameter but that the block factor had significant effects. The latter effect is in line with the block effect observed in the case of the overall distance travelled (Figure 3) and can be taken to constitute a habituation effect. The sensory gain parameter does not seem to have been responsible for the difference between responses in the *linear* and *oscillatory* conditions, but it seems to have been responsible for increasing the perceived distance travelled between the experimental blocks. The increase in the accuracy of the subjects' responses was found to be inversely correlated with the sensory gain over the experimental blocks.

In addition, the optical flow condition was found to affect the leak rate (α), because the α values were significantly smaller in the *oscillatory* condition than in the *linear* condition. This finding suggests that the *oscillatory* optical flow gave better path integration by decreasing the loss of information over time and therefore resulted in more accurate estimates of the distance needed to reach the target. The fact that this effect was stable in all the experimental blocks suggests that the optical flow characteristics had consistent effects.

At this point, the question arises as to what exactly improved the subjects' assessments of the visually simulated distance travelled in the *oscillatory* condition. To answer this question, we focused on the following two properties: the rhythmicity and the potentially biological nature of the oscillations. In other words, we wondered whether it was the rhythmicity or the biological characteristics (such as the period, the step length, and the oscillation amplitudes) of the *oscillatory* flow that were responsible for improving the subjects' distance travelled assessments. We therefore used the same basic experimental procedure as previously used to compare the following three optical flow conditions: a *linear* condition (as previously), a *rhythmical* condition, and a *biological* condition. To enhance the distinction between the two nonlinear conditions, the *rhythmical* condition was characterized by a clearly nonbiological pattern (triangular waves), and to enhance the similarity with natural behavior, the *biological* condition was no longer based on theoretical modeling procedures as in the first experiment but on the actual recording and modelling of the head motion that occurs during natural walking.

Experiment 2

The second experiment was conducted in two phases. In the first phase, we recorded a large number of subjects' head movements while they were actually walking in a straight line at a comfortable speed. We then selected a single average individual walking pattern, which was used in the second phase.

Phase 1

Participants

Fifty-two volunteers (including 30 women, mean age 24.1 ± 3.1 years) took part in this experiment. They had no vestibular antecedents or disorders that might affect their locomotor performances. They all gave their informed consent prior to the experiment in keeping with the 1964 Helsinki Declaration, and the study was approved by the local ethics committee.

Apparatus

The participants were standing in a corridor defined by two parallel 10-m-long bands on the ground, 61 cm apart (the width of this corridor was identical to that of a GAITRite® gait analysis walkway). A target was placed at the end of this corridor, at eye height. The subjects were instructed to walk along the corridor in a natural way, while fixating the target from the beginning to the end of the walk. After reaching the target, they had to return to the starting point, and a new recording was then initiated. This procedure was repeated 20 times.

Kinematic data of the head during the walking task were recorded using the Vicon 624 system (Vicon Motion Systems, Lake Forest, CA) with five cameras operating at a frequency of 120 Hz. One spherical retroreflective marker (15 mm in diameter, placed at the nasion) was fixed to the pair of glasses worn by each subject. This made it possible to record the subjects' head translation movements with time.

Data analysis

Because the original recordings were made on distances of only up to 10 m (technical reasons), the

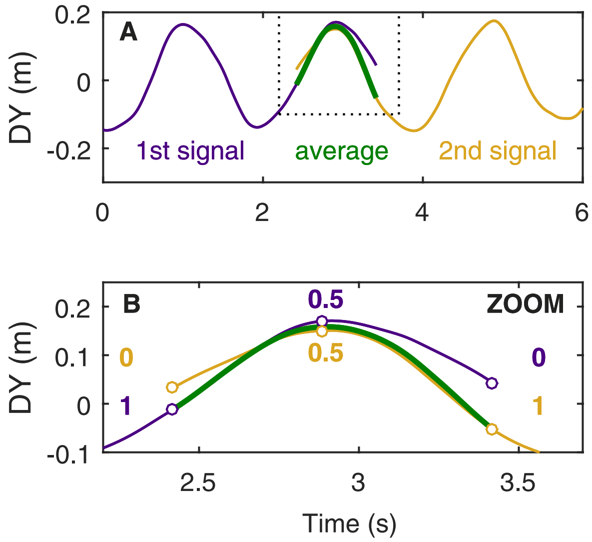

Figure 6. (A) Recordings of a selected subject's head movements on the vertical axis (DY). The green signal gives the weighted average of two signals around the last peak in the first signal (blue) and the first peak in the second signal (yellow). (B) A weight ranging linearly from 1 to 0 was assigned to the 60 data points around the last peak in the blue signal, and the inverse weight, 0 to 1, was assigned to the 60 data points around the first peak in the yellow signal.

subjects' head movement recordings were concatenated to obtain a single signal for each of them. To ensure that all the subjects were subjected to the same virtual travelling speed, we then selected the subject with the signal showing the most central kinematic characteristics (the average walking speed and step length, the average amplitudes of the lateral and vertical oscillations, and the eye height). These steps are described in greater detail below.

The processing applied to the 20 walking recordings obtained per subject consisted of extracting a "clean" signal from the raw data that accurately reflected each individual's walking pattern. To eliminate the presence of noise from the signal, we applied a conventional dual-pass Butterworth filter (order: 2, cutoff frequency: 10 Hz). We then selected the stable part of the recording because the initiation of walking affected the subjects' head movements up to the fourth step. The part of the signal occurring prior to the fourth step was then truncated.

Among the 20 clear-cut recordings obtained per subject, the nine showing the most similar average speeds were selected and combined, giving a signal that could be used to simulate long virtual displacements.

From each set of nine signals per subject, the values of the first and last peak in each signal were extracted (on the y-axis). The combination of nine signals selected was that showing the smallest sum of the differences between the value of the last peak in a signal and the first peak in the next signal.

Weighted averages were then applied around the junctions between connected signals around the last peak in the first signal and the first peak in the next signal (Figure 6). This procedure yielded individual recordings reflecting the individual characteristics of the head movements involved in each subject's usual walking pattern.

The use of a single walking pattern per subject made it possible to ensure that all the subjects moved virtually at the same speed and therefore took the same time to reach the same target. It also served to minimize the discrepancies between each subject's actual walking patterns and the selected pattern. For this purpose, some kinematic and spatial properties of each subject's walking pattern were identified: the average walking speed and step length, the average amplitudes of the lateral and vertical oscillations, and the vertical eye position. The pattern used was that having the most central features among all the recordings: the average walking speed (1.47 $m.s^{-1}$), the average step length (0.716 m), the average amplitudes of the lateral and vertical oscillations (16.3 and 22.8 mm, respectively), and the eye height (1.51 m).

Phase 2

Participants

Among the 52 participants in the first phase of the experiment, 28 (including 15 women, mean age 22.4 ± 2.8 years) with normal or corrected-to-normal vision volunteered to take part in the second phase. They had no vestibular antecedents or disorders liable to affect their locomotor performances. All the participants gave their written informed consent prior to the experiment in keeping with the 1964 Declaration of Helsinki, and the study was approved by the local ethics committee.

Apparatus

The laboratory, the virtual reality device, and the virtual scene were all identical to those used in Experiment 1.

Procedure

The procedure was practically identical to that used in Experiment 1, apart from the following three changes. First, the initial distance to the target was increased to 30 m (to be able to make comparisons with previous studies). This had one visual consequence, however, because it required making a change in the subject's position. Because the initial distances to the targets were longer than previously (6, 12, 18, 24, and 30 m), the angular size of the visual target displayed on the front screen was smaller in the case of large

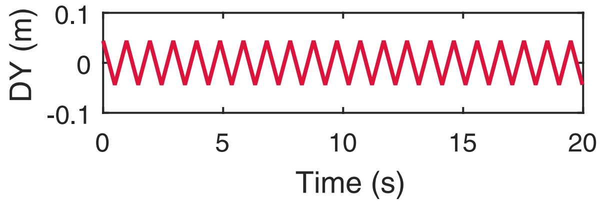

Figure 7. Oscillatory camera movements on the longitudinal axis (DY). There were no camera movements on the other axes.

distances, which made it difficult to detect. We therefore had to change the position of the subjects in the CAVE in the second experiment, where they were placed 3 m from the front screen (versus 1.5 m in Experiment 1), which increased the displayed resolution of the cone while preserving the angular size. The third change concerned the target height. Instead of being asked to assess the height of the virtual target at the beginning of the experiment, the subjects could see a physical target, the size of which exactly matched that of the virtual target.

Conditions of virtual simulation of self-movement: The optical flow factor

Biological: In the *biological* condition, subjects were exposed to a visual simulation of self-motion based directly on the actual walking pattern of an average subject (selected during Phase 1, see above). The virtual camera adopting the subject's mobile viewpoint in the scenario was subjected to a translation, to which oscillations along the anteroposterior, lateral, and vertical axes were added. The mean speed in the *biological* mode was 1.47 $m.s^{-1}$, as in the second and third conditions. These properties, translations, and oscillations were those of the head movements recorded during an actual walking task performed by a subject, which were processed as described above (in Phase 1).
Linear: The *linear* condition was the same as in Experiment 1 except that the speed was the same as in the *biological* condition (1.47 $m.s^{-1}$).
Rhythmical: In the *rhythmical* condition (Figure 7), a linear translation was imposed on the subject's viewpoint (virtual camera), combined with vertical triangular oscillations. The speed was the same as the linear forward speed component in the *biological* and *linear* conditions (1.47 $m.s^{-1}$), and the period (0.49 s) was equal to the mean period used in the *biological* condition. These oscillations differed from natural human behavior in their amplitude (which was twice that of the *biological* condition) and in their triangular shape.

Experimental design

The following experimental design was used here: 28 subjects were presented with 10 blocks of trials. In each block of 15 trials (five distances [6, 12, 18, 24, and 30 m] $\times$ three optic flow conditions [*linear*, *biological*, and *rhythmical*]), the order of the trials was chosen at random. The whole experiment lasted approximately 70 min per subject. This yielded a total number of $28 \times 10 \times 5 \times 3$ or 4,200 observations and measurements of the dependent variable (the perceived distance travelled).

Results

Experiment 2 was run using the same procedure as in Experiment 1, apart from the following four points: (a) *biological* and *rhythmical* conditions were used instead of the *oscillatory* condition, (b) the subject was placed 3 m from the frontal screen instead of 1.5 m, (c) the linear forward speed component was increased from 1.2 $m.s^{-1}$ to 1.47 $m.s^{-1}$, and (d) the initial distances to the target ranged from 6 to 30 m in 6-m steps (as compared with 6 to 21 m in 3-meter steps in Experiment 1).

Again, subjects gave their responses before reaching the position of the previously seen target. They pushed the button to indicate that they had reached the target after covering only 87% of the distance on average (approximately as in Experiment 1). Here again, there were significant differences between the effects of the optical flow conditions. Mean results are presented in Figure 8. An rmANOVA showed the existence of a main effect of the Block factor, $F(9, 243) = 5.601$, $p < 0.001$; the Distance factor, $F(4, 108) = 360.777$, $p < 0.001$; and the optical flow factor, $F(2, 54) = 16.487$, $p < 0.001$. It also showed the occurrence of an interaction between the optical flow and distance factors, $F(8, 216) = 2.761$, $p < 0.005$. A post hoc test (Tukey's HSD test) showed that the effects of the *biological* and *rhythmical* conditions differed significantly from those of the *linear* condition with longer distances (18, 24, and 30 m). This test also showed that there were no significant differences between *biological* and *rhythmical* conditions at any of the distances tested.

In line with the first experiment, subjects tended to give early responses more frequently in the first few experimental blocks, and their performances subsequently stabilized. When the analysis was restricted to the last eight blocks, no block-related effects were observed, $F(7, 189) = 1.78$, $p > 0.05$, whereas the effects of the Optic Flow factor persisted, $F(2, 54) = 170.6$, $p < 0.001$.

Leaky integrator model

Each subject's responses (in the range of initial distances tested) recorded in the three conditions of motion simulation and in the various blocks were adjusted using the leaky spatial integrator model

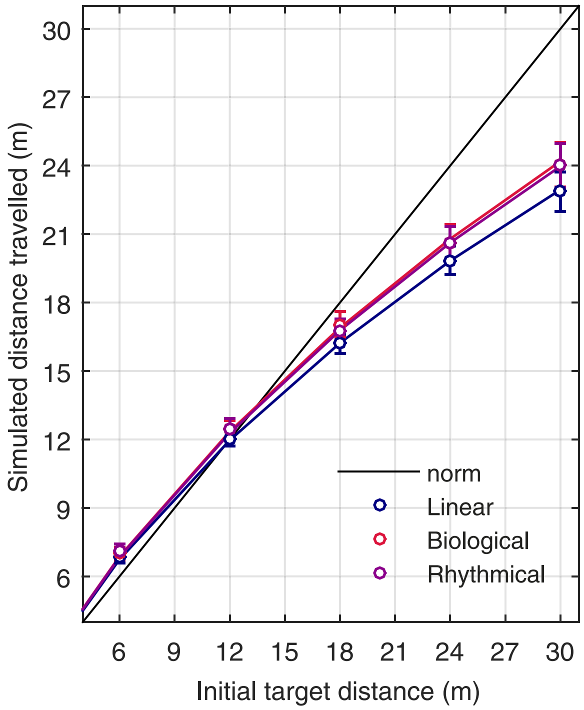

Figure 8. Distance travelled versus distance to the initially seen static target in the linear (blue), biological (red), and rhythmical (violet) conditions. Data points are means based on 28 subjects, and error bars give the standard errors of the means. The black line indicates ideal performances. Blue ($k = 0.75$; $\alpha = 0.051$), red ($k = 0.75$; $\alpha = 0.046$), and violet ($k = 0.75$; $\alpha = 0.47$) lines give the fit obtained with the leaky integration model (Lappe et al., 2007).

developed by Lappe et al. (2007) to obtain the sensory gains (k) and the leak rate (α). The average R^2 of these fits was 0.92 ± 0.05 in the *linear* condition, 0.92 ± 0.05 in the *biological* condition, and 0.91 ± 0.06 in the *rhythmical* condition. An rmANOVA was performed on each of these values ($\text{Block}_{10} \times \text{Locom}_3$). In the case of the gain parameter (k), a Block factor effect was found to occur, $F(9, 243) = 5.05$, $p < 0.001$, but the Optic Flow condition factor had no significant effects, $F(2, 54) = 2.44$, $p > 0.05$. After analyzing the last eight blocks as described above, no significant effects were observed as far as the k parameter was concerned, and therefore the average value (0.75 ± 0.20) was used for the subsequent fitting of the model. The model's fit with the mean data is plotted in Figure 8. An rmANOVA was performed on the resulting leak rate (α) in each subject and each condition. The leak rate did not vary between blocks, $F(7, 189) = 1.17$, $p > 0.05$, but it varied with the optic flow conditions, $F(2, 54) = 6.63$, $p < 0.01$ (Figure 9). A post hoc test (Tukey's HSD test) showed that the effects of the *biological* and *rhythmical* conditions differed significantly from those of the *linear* condition and that there was no difference between the effects of the *biological* and *rhythmical* conditions.

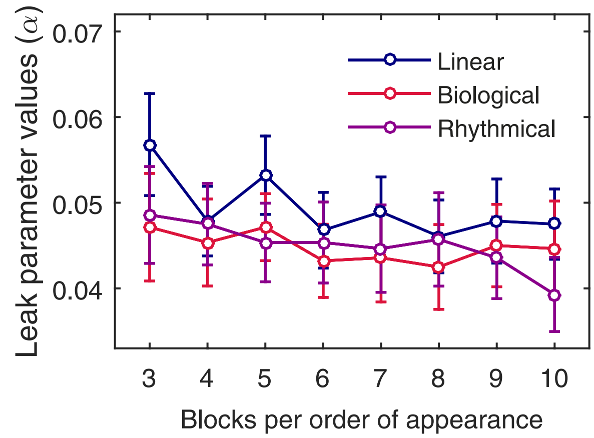

Figure 9. Mean leak parameter values (α) of the experimental blocks in the optical flow condition (the linear [blue], biological [red], and rhythmical [violet] condition). Data points are mean values based on 28 subjects, and error bars give the standard error of the means.

Discussion

The aim of Experiment 2 was to determine which oscillatory parameters (Experiment 1) generated a difference in the subjects' distance travelled assessments. Or, more specifically, it was designed to determine whether the visually induced self-motion generated by an optical flow directly based on actual recordings of subjects' head kinematics during a walking task (the *biological* condition) resulted in more accurate distance travelled assessments than a visual simulation of displacement generated by an optical flow having only a rhythmical component on the vertical axis (the *rhythmical* condition) or a visual simulation incorporating none of these properties (the *linear* condition), where only an illusion of unidirectional linear forward movement was generated at constant speed.

The results of this experiment show that the *biological* and *rhythmical* conditions yielded more accurate distance travelled assessments than the *linear* condition but that the effects of the *biological* and *rhythmical* conditions did not differ significantly (Figure 8). The subjects' perception of the distances travelled in the virtual environment tended to be closer to the truth in the *biological* and *rhythmical* condition than in the *linear* condition.

To confirm these results, we fitted our data to the leaky integrator model (Lappe et al., 2007), and once again, the optic flow condition was found to have no effect on the sensory gain parameter, contrary to the block factor (which could match with the block effect presents for distances travelled), possibly because of the occurrence of a habituation effect. Contrary to the block factor, the optic flow condition was found to affect the leak rate (α). The α values differed in the *linear* condition from those obtained in the *biological* and *rhythmical* conditions, but no difference was observed between the two latter conditions. Here again, the sensory gain parameter (k) seems to have been responsible for increasing the subjects' perception of distance travelled across the blocks, and the leak rate (α) seems to have been responsible for the differences in the subjects' distance travelled assessments between the two optical flow conditions. This finding suggests that the optical flow combined with additional oscillations around the translation axis improved the path integration process by decreasing the loss of information with time and thus gave more accurate estimates. The fact that this effect was stable across the experimental blocks suggests that it reflects a permanent effect of the optic flow.

General discussion

In these experimental studies, a virtual reality setup was used to investigate the role of the optical flow (inducing the perception of forward self-motion at a constant velocity) in the estimation of the distance travelled toward a previously seen static distant target. Observers were placed in a static position in a CAVE system so that the visual inputs were isolated from the vestibular and proprioceptive inputs. In both experiments, when the initial distances to the target were greater than 15 m, the observers underestimated the point at which they thought they had reached the target. These results are consistent with those obtained in previous studies using a similar procedure (Frenz & Lappe, 2005; Harris et al., 2012; Lappe et al., 2007; Redlick et al., 2001).

These results can be compared on the whole to the phenomenon of perceptual compression of large distances. This effect occurs in the real world (Loomis, Da Silva, Fujita, & Fukusima, 1992), as well as in virtual environments (Knapp & Loomis, 2004; Plumert et al., 2005; Thompson et al., 2003). In addition, the underestimation of distances travelled is generally more pronounced in virtual environments than under real conditions (Harris et al., 2012; Loomis & Knapp, 2003; Mohler, Thompson, & Creem-Regehr, 2006; Piryankova, De La Rosa, Kloos, Bülthoff, & Mohler, 2013).

However, this explanation does not account for the systematically differential effects of our optical flow conditions on the subjects' assessments of the distance travelled to the target. Whatever their initial distance estimates, adding oscillatory components to a translational optical flow was found to significantly increase the simulated distance travelled at which the subjects indicated that they had reached the target. In line with the studies by Lappe et al. (2007), we therefore decided to investigate how the optical flow properties are liable to affect the path integration processes (see, for example, Loomis, Klatzky, Golledge, & Philbeck, 1999) whereas subjects were passively exposed to a visual simulation of forward motion toward a previously seen target. Our working hypothesis was that observers may integrate the optic flow into a perceived displacement in order to reduce the remaining distance to the target and give their answer when this remaining distance is perceived to be is zero. First, we tested the integration model developed by Lappe et al. (2007).

In the leaky integration model, the "leaky" aspect of the integrator is due to the fact that the perceived remaining distance decreases proportionally to the remaining distance. Upon fitting our data to this model, the gain factor was found to be fairly stable between the optical flow conditions tested, but the value of the leaky parameter was systematically lower under oscillatory than the *linear* optic flow conditions. In other words, these results suggest that oscillatory optical flow stimulation favors the path integration process during simulated forward movement.

This result can be compared with those obtained in a series of experiments on vection (Bubka & Bonato, 2010; Palmisano et al., 2000; Palmisano et al., 2012) showing that adding jitter or periodic oscillations to a linear flow reduces the onset latencies, lengthens the duration of vection, and increases the vection strength. The latter authors' original explanation for this effect, in line with our initial hypothesis, was that oscillations added to a linear flow may increase the sensation of vection because it triggers visual self-motion processing and is therefore more "ecological." However, recent studies have challenged this rather simple hypothesis (Palmisano, Allison, Ash, Nakamura, & Apthorp, 2014) by showing that the ecological aspect of added oscillations did not affect the contribution of jitter to vection. Two alternative explanations have been put forward for these effects at a more basic motion perception level. First, jitter/oscillations may increase the global retinal motion and thus the sensation of vection and the path integration process. By comparing various visual simulations of displacement (involving purely radial, oscillating, and jittering optic flow) under several gaze conditions (stationary fixation, goal-directed looking, or gaze shifting), Palmisano and Kim established in 2009 that the retinal slip plays an important role in vection. These authors observed that adding jitter/oscillations to a purely translational optical flow increased the subjects' vection strength ratings, decreased the vection onsets, and increased the total duration of the vection. They also showed that vection in depth increases with the degree of retinal slip. Second, perturbations of these kinds might maintain subjects' sensitivity to retinal motion and thus reduce their motion adaptation to the linear optical flow component (Kim & Khuu, 2014; Seno, Palmisano, & Ito, 2011). In keeping with this idea, Seno et al. (2011) have reported that a radial flow with horizontal simulated viewpoint oscillation induced significantly longer vection durations and shorter motion after effects (a psychophysical index to neural adaptation) than nonoscillating radial flow. The latter hypothesis might be consistent with the reduced leakage of the perception of the remaining distance to a target observed in the present study with oscillatory optic flows.

The fact that we found no differences between the effects of *biological* and *rhythmical* optic flow seems to support the latter nonecological explanation. However, further investigations are now required because under our conditions, the oscillation frequency and the forward speed were identical in all the optical flow conditions, resulting in a biological step frequency. The possibility therefore cannot be ruled out that even the triangular-shaped oscillations (in Experiment 2) may still have had some biological characteristics. It is proposed in future studies to investigate further the effects of systematically varying the spatiotemporal characteristics of oscillatory optical flow patterns.

Conclusion

In the two studies presented here, it was established that when subjects were exposed to an optical flow simulating forward self-motion, the simulated distance travelled tended to be underestimated. In both studies, participants indicated that they had reached the target before actually reaching it. These results are consistent with those obtained in previous studies using a similar procedure (Frenz & Lappe, 2005; Harris et al., 2012; Lappe et al., 2007; Redlick et al., 2001).

In addition, it was established here that the simulated distance travelled was affected by the nature of the optical flow: Adding oscillatory movements to the translation of the environment toward the observer (in the *oscillatory*, *rhythmical*, and *biological* conditions) resulted in more accurate responses than in the purely translational condition (the *linear* condition), regardless of the subjects' perception of the absolute distance.

Keywords: perception of distance travelled, self-motion perception, optic flow, virtual reality, visual motion

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