From Embodiment of a Point-Light Display in Virtual Reality to Perception of One's Own Movements

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Abstract

Humans can recognize living organisms and understand their actions solely on the basis of a small animated set of well-positioned points of light, i.e. by recognizing biological motion. Our aim was to determine whether this type of recognition and integration also occurs during the perception of one's own movements. The participants (60 females) were immersed with a virtual reality headset in a virtual environment, either dark or illuminated, in which they could see a humanoid avatar from a first-person perspective. The avatar's forearms were either realistic or represented by three points of light. Embodiment was successfully achieved through a one-minute period during which either the realistic or point-light avatar's forearms faithfully reproduced voluntary flexion-extension movements. Then, the "virtual mirror paradigm" was used to evoke kinaesthetic illusions. In this paradigm, a passive flexion-extension of the participant's left arm was coupled with the movements of the avatar's forearms. This combined visuo-proprioceptive stimulation, was compared with unimodal stimulation (either visual or proprioceptive stimulation only). We found that combined visuo-proprioceptive stimulation with realistic avatars evoked more vivid kinaesthetic illusions of a moving right forearm than unimodal stimulations, regardless of whether the virtual environment was dark or illuminated. Kinaesthetic illusions also occurred with point-light avatars, albeit less frequently and a little less intense, and only when the visual environment was optimal for slow motion detection of the point-light display (lit environment). We conclude that kinaesthesia does not require visual access to an elaborate representation of a body segment. Access to biological movement can be sufficient.

Key words: kinaesthesia, biological motion, virtual reality, embodiment

Introduction

Motion representation from visual cues

The visual perception of movement does not require precise spatial resolution (Johansson 1973). Light dots situated at key-points of a moving body suffice for recognition of biological motion as a whole, but also for estimation of physical properties of manipulated object and for higher–order classification up to identification of the agent performing the action (for a review, see Troje 2012). The weight of an object being lifted (Runeson and Frykholm 1981), the distance to which it may be thrown (Munzert et al., 2010), the agent's gender (Mather & Murdoch, 1994) and the agent's identity (Wellerdiek, Leyrer, Volkova, Chang, & Mohler, 2013) all become, so-to-say, visible through such point light-animation.

Visual signals are also of great relevance for the movement perception of oneself (i.e., kinaesthesia), in association with other motor (Gandevia et al., 2006, Metral et al., 2013), proprioceptive (Proske & Gandevia, 2018, Rothwell et al., 1982; Teasdale et al., 1993) or tactile ones (Blanchard et al., 2011, Chancel et al., 2016). Our objective here was therefore to test whether a small amount of visual information about one's own body, can provide a large amount of information for the perception of one's own movement in the same way as it does for the perception of external objects. Perception of one's own movement can be derived from visual motion signals that originate from body segments whose visual appearance is markedly degraded. In a recent study, Chancel et al (2016) manipulated the visual appearance of the participant's arms via the mirror paradigm. Seeing the reflection of one moving hand in a mirror positioned along the midline axis (separating the left and right sides) gives the appearance of symmetrical bimanual movements; it therefore induces illusory movements in the other (static) arm hidden behind the mirror (Altschuler et al., 1999; Guerraz et al., 2012, Tsuge et al., 2012, Metral et al., 2013; 2015). Chancel et al. (2016) showed that kinaesthetic mirror illusion can even be induced when a high proportion (up to 84%) of "mirror pixels" reflecting the arm were masked. Thus, for kinaesthesia, relevant visual cues can be extracted from a degraded image of a body segment. However, it should be noted that the overall shape of the arm was still recognizable with the remaining (16%) pixels. Would the mirror illusion persist without any information about the limb shape? Virtual reality offers an easy way to answer this question by manipulating the body's visual appearance.

Body representations of the self

The body representation's boundaries are rather flexible, and can stretch to include avatars but also other objects such as prostheses up to rubber body segments. For instance, synchronous stroking of both the real body and a virtual body (Slater et al., 2010) displayed from a first-person perspective through a head-mounted-display (HMD) typically induces self-attribution of the virtual body; the latter is then perceived as being the source of the visuo-tactile signals. Self-attribution of a virtual body is even more intense when the visual stimulation is synchronized with motor commands (Sanchez-Vives et al. 2010; Romano et al., 2015; Kalckert and Ehrsson 2012; Peck et al., 2013; Maselli and Slater 2013).

Kinesthesia needs not to be supported by the true picture of the body segment in play; it can rely on the movement expressed by the equivalent segment of an avatar (Metral and Guerraz 2019; Giroux et al., 2018). In the experiment described by Giroux et al. (2018), embodiment of the avatar was achieved through visuo-motor synchronization, the participant playing at moving an avatar's forearms she saw tightly following her own voluntary movements. Next, the right arm remaining static, her left forearm was passively moved while she saw both, left and right, moving in her avatar. As in the real mirror paradigm (see Guerraz et al., 2012, Tsuge et al., 2012, Metral et al., 2013; 2015), the feeling that both her own (real) limbs were moving was thus induced by this virtual mirror setup. Visual information on motion from the embodied avatar therefore contributes to kinaesthesia, even though the avatar's visual appearance leaves no doubt that the body is false. If a small amount of visual information about one's body is sufficient for the perception of one's own movement, visual motion cues from a point-light animation of an avatar's forearms should induce similar kinaesthetic mirror-like virtual illusions.

Self-motion perception from a point-light animation

In the present study, a 3-D virtual body was displayed from a first-person perspective through an HMD. The virtual forearms were either realistic or limited to three points located on the hand, mid-forearm, and elbow of each arm without any overt visual connection between them (Figure 1). Because the mirror illusion and its virtual counterpart are not purely visual, virtual displacement of the avatar's forearms (viewed through the HMD) was combined with passive displacement of the participant's left forearm by the use of a motorized manipulandum.

Indeed, for each arm, the movement perception (Izumizaki et al 2010; Chancel et al., 2016; 2017) benefits from bilateral integration of proprioceptive signals. This explains why, in the specific context of the mirror paradigm, contralateral proprioceptive signals enhance illusory kinaesthetic perception (see Giroux et al., 2018, Chancel et al., 2016). Here, the kinaesthetic illusions were evoked by combining the virtual displacement of the avatar's forearms (visual signal) and the passive displacement of the participant's left forearm (proprioceptive signal). This "bimodal" condition seemed optimal to highlight the potential use of visual motion cues from a point-light animation for kinaesthesia. To investigate this bimodal superiority, the bimodal condition was compared to unimodal visual and proprioceptive conditions.

In a first experiment, the avatar (either realistic or point-light versions) was viewed in a totally dark background and was thus the only visible object in the virtual environment. In a second experiment, the avatars were presented in front of a textured illuminated background. The purpose of this background was to facilitate visual detection of the forearm's motion. Indeed, the threshold for perceiving a relative motion between two objects in the environment is lower than that for perceiving the displacement of a single object (Abadi et al., 1999; Guerraz et al., 2000, Snowden 1992). In brief, our main hypothesis was that kinaesthetic illusions can be induced with visual motion cues from a point-light animation. As secondary assumptions, we expected that the bimodal conditions, either with realistic or point-light avatars, would elicit more intense illusions than each unimodal condition separately.

METHOD

Participants

Since the avatar used here was female, only female participants were included in the experiment. As reported in previous studies, some individuals do not experience kinaesthetic illusions in the mirror paradigm (Chancel et al., 2016; 2017; Guerraz et al., 2012; Metral et al., 2015) or in its virtual reality adaptation (Giroux et al., 2018). Hence, we screened the participants in a preliminary test: the virtual kinaesthetic illusion was evaluated in six trials during which displacement of both the avatar's (realistic) forearms in an illuminated virtual environment was combined with passive displacement of the participant's left forearm only (see Giroux et al., 2018). For each experiment we ran a power analysis with $\alpha = 0.05$ and $1-\beta=0.80$ for within-subject comparison (RStudio software, RStudio Team, 2016). The effect size expected in the dark environment was based on Chancel et al.'s (2016) study of the impact of mirror reflection degradation on the kinaesthetic illusion (a subjective speed rating). The effect size was d = 1.09 (n = 16). Given the frequent overestimation of effect sizes in the literature (Open Science Collaboration, 2015), we chose to base our study on half of this value, i.e. d = 0.545 leading to a required sample size of n = 29. The effect size expected in the illuminated environment was based on the comparison between the bimodal and the proprioceptive conditions for the point-light avatar in the dark environment. The effect size was d = 0.57 yielding a required sample size of n = 26.

Thirty-eight and thirty-four healthy adult females volunteered to take part in the first and second experiment respectively. Of these, thirty experienced the virtual mirror illusion in the screening test of each experiment and were therefore included (first experiment: mean ± standard deviation (SD) age: 19.73 ± 2.53; second experiment: 20.37 ± 5.24). None of them took part to both experiments. All but one of the participants were right-handed (Edinburgh Inventory Test; Oldfield, 1971). None of the participant reported visual, motor or somatosensory impairments. Before the experiment, they declared in writing, their free choice to participate and to leave during the essays. The study met all requirements of the 1964 Declaration of Helsinki and was approved by the university's ethical board for research and teaching (C.E.R.E.U.S, Savoie Mont Blanc University, Chambéry, France).

Material

The HMD (Oculus Rift; Oculus VR, Irvine, CA, US) immersed the participant in a virtual room. The position and the orientation of the head was tracked online, and reported in the virtual world with perspective correction. The HMD supra-aural 3D spatial audio headphones masked outer sound interference with a continuous white noise. The virtual environment and actions were programmed with Unity software (Unity Technologies, San Francisco, CA, USA). Hardware comprised an MSI Geforce GTX 980 Gaming 4G graphics card (Micro-Star International, Taipei, Taiwan) and an Intel Core i7–4790K processor (Intel Corporation, Santa Clara, CA, USA). The participant was immersed in a virtual environment in which she could see the avatar (a female sitting as the participant, with her elbows positioned on a virtual table) from a first-person perspective. The virtual environment could be dark (so that the participant could only see the avatar, in a first experiment) or illuminated (so that the participant could see both the avatar and the environment, representing a room with black and white chequered walls and a table, in a second experiment). The avatar's forearms consisted of either realistic forearms or three red spheres located instead of the hand, mid-forearm, and elbow of each arm (Fig. 1). Spheres (3D) were used instead of dots (2D) because virtual reality was 3D. The red colour was chosen so that spheres were always visible wherever they appeared in the black and white background when visible. The other parts of the body were always realistically displayed since only the avatar's forearms could move and point-light displays can only be interpreted when in motion (Johansson, 1973; Kozlowski & Cutting, 1977).

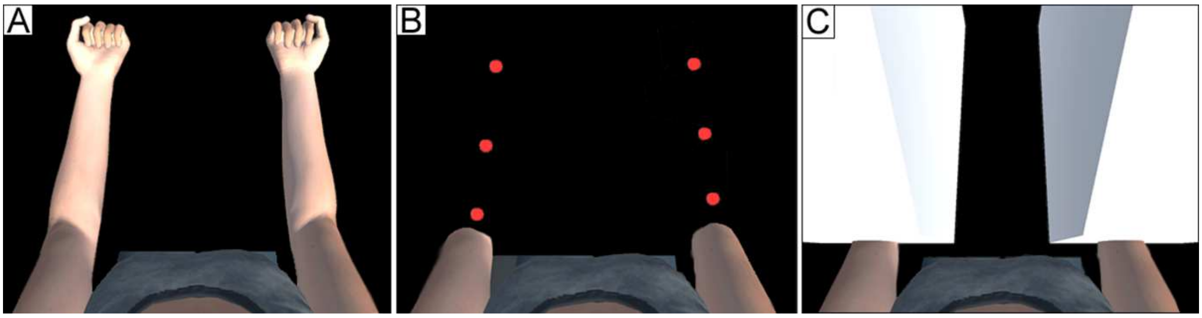

Figure 1. The virtual reality setup. The panels show the participant's view (i.e. a first-person perspective) when the avatar's forearms were either (A) visible and realistic, (B) visible and represented as points of light, or (C) masked by virtual white boxes.

Displacements of the avatar's forearms could be driven in real time by the displacements of the participant's forearms, as detected by an electromagnetic motion capture system (Liberty™, Polhemus, Colchester, VT, US) at a sampling frequency of 240 Hz. In order to avoid wrist movements, participants wore splints on each hand on which the sensors were positioned. The participant sat at a table with the forearms placed forwards, parallel to the sagittal plan. During the experimental trials in both experiments (but not during the embodiment phases), the participant's two forearms were held by a manipulandum aligned with the shoulder. Each manipulandum consisted of a wooden arm (on which the participant positioned her forearm) and a handgrip at the end of the wooden arm. The right manipulandum was static, whereas the left manipulandum was fitted with a low-noise synchronous DC motor (24 V, Maxon with planetary reductor 1296:1, Maxon Motor AG, Sachseln, Switzerland) that could flex or extend (via a remote control) the participant's left forearm from the initial starting position with an angular amplitude of 30°, a constant angular speed of 3.8°/s (duration of 8 s). The participant's left forearm was positioned on the manipulandum so that the latter's rotational axis coincided with that of the elbow joint.

Procedure:

The avatar embodiment phase

Wearing the virtual reality HMD, the participant sat with her elbows on the table and was asked to actively flex and extend both arms at a natural speed and amplitude by alternating phase and antiphase movements for one minute. During this embodiment phase, the avatars faithfully reproduced the participant's real movements. Such an embodiment phase of 60s was performed once with the realistic forearms (prior to the three blocks of trials with realistic forearms) and once with the point-light forearms (prior to the three blocks of trials with point-light forearms). After this initial embodiment phase, the participant filled out a brief embodiment questionnaire (in French) containing nine relevant items (1, 2, 3, 6, 7, 8, 9, 14, and 15 see Appendix B) translated from Gonzalez-Franco and Peck (2018). The latter questionnaire contains a set of assertions about various sub-components of embodiment, and each item is scored on a seven-point Likert scale. The items used in the present study specifically tested body ownership (i.e. the feeling that the avatar's body is one's own), agency and motor control (i.e. the feeling that one can control the avatar's body as one's own), and body location (i.e. the feeling that one's own body is located in the same place as the avatar's body). The *embodiment score* ranged from -3 (no embodiment of the avatar) to +3 (strong embodiment) and comprised three embodiment subscores for *Body ownership, Agency,* and *Body Location*. In the present study, we considered that the avatar was embodied when the embodiment score was greater than zero. Additional 30s embodiment periods were performed before each following block of trials (see Fig. 2).

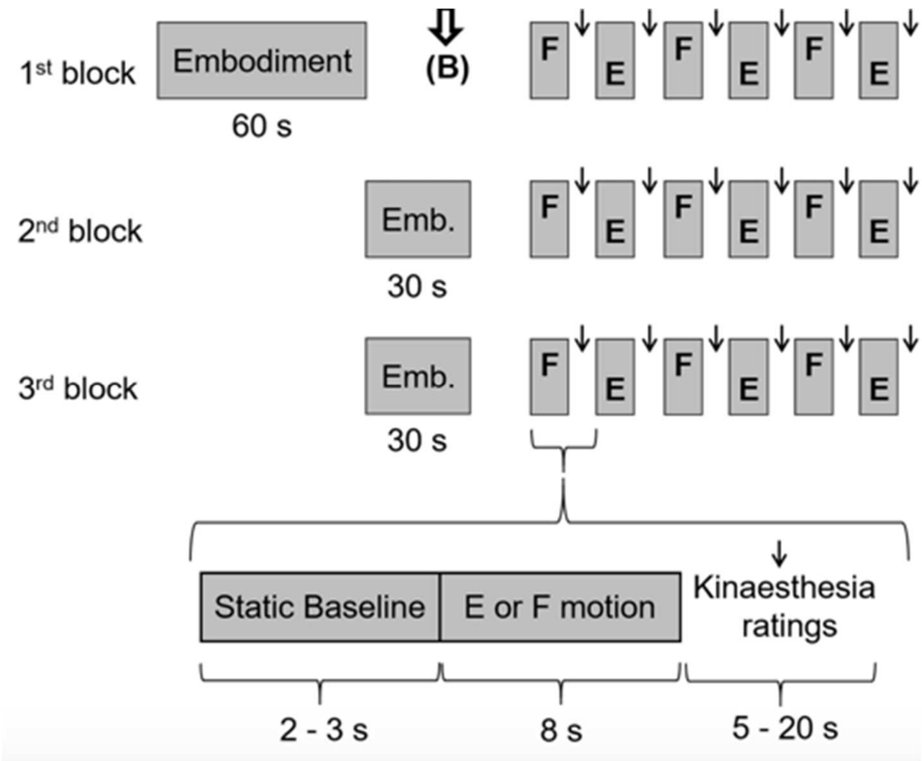

Figure 2. Experimental session. Each participant carried out two sessions of three randomised blocks (Bimodal, Visual, Proprioceptive), one session with realistic avatars and the other one with point-light avatars. A block comprised six trials (alternating flexions F and extensions E). Kinaesthesia was rated (arrows) after each trial. Each block was preceded by an embodiment phase. The first embodiment phase lasted 60s and was followed by an embodiment rating (B). These two sessions were performed in either a dark (first experiment) or an illuminated background (second experiment).

Experimental phase with induction of the kinaesthetic illusion

After the initial 60s embodiment phase had been completed and rated, the participant's forearms were positioned on the manipulanda for the first block of trials. The right arm remained static and was maintained at an angle of 30° to the horizontal plane. The left arm was positioned at an angle of either 15° or 45° to the horizontal plane, before each block of six trials (Fig. 2). Participants were told 1) not to resist passive displacements of their left forearm, 2) to focus their attention looking at their right forearm, as controlled by the investigator on a monitor reporting the participant's sight of the scene. A trial started with an introduction of 2-3 second without forearm movement (neither real nor virtual); then the real and/or virtual arms moved for eight more seconds (Fig. 2).

Kinaesthesia ratings

The illusory feeling of the right forearm movement was rated verbally after each trial. The speed of the right forearm felt movement was compared with that of the left forearm on an integer scale ranging from 0 in the absence of feeling, to 10 for a right forearm felt moving at the same speed as the left one. The direction of this illusory movement was labelled as similar or opposite to that of the left forearm (the actual left forearm or its avatar). Inverse illusions (illusions in the opposite direction) were quoted as negative speed values. Thus, the speed values can vary from -10 to 10. The participant was also required to estimate the beginning and the end of the illusory displacement with respect to the start of the trial, with both estimates thus varying from 0 s to 8 s (e.g., "started three seconds after the beginning of the trial" and "ended seven seconds after the beginning of the trial"). Once these different parameters had been rated, the next trial began.

Three sensory modality conditions were tested during each session: a "bimodal" condition, a "visual" condition, and a "proprioceptive" condition, each during one block.

- In the "bimodal" (both visual and proprioceptive) condition, both (avatar) forearms were seen in movement, while the participant's left forearm (alone) was passively displaced (left proprioception). This condition replicates the physical mirror paradigm in which one can see both arms moving while only one is actually displaced.
- In the "visual" (unimodal) condition, both (avatar) forearms were seen in movement, while none of the real ones really moved (vision only).
- In the "proprioceptive**"** (unimodal) condition, the avatar's forearms were masked by two virtual boxes, while the participant's left forearm (alone) was passively displaced (Fig. 1)

In the dark virtual environment, the virtual boxes were still visible.

Displacements were driven in flexion or extension at 3.8°/s for 8 s (from either 15° to 45° or from 45° to 15°, relative to the horizontal plane). After a block was completed, the participants removed their arms from the manipulanda so that they could move them freely and experience a new 30s phase of embodiment.

Procedure for the experiment in the dark environment.

The experiment consisted in six blocks of six trials, three successive blocks with the realistic avatar's forearms (corresponding to each of the three sensory modality conditions in a random order) in one session and another session of three blocks with the point-light avatar's forearms, in a counterbalanced order between participants. Each of the six experimental conditions (3 sensory modality * 2 avatars) was tested in a separate block alternating three flexions and three extensions, giving a total of 36 flexion or extension trials (Fig. 2). The direction of the first movement (i.e. flexion or extension) was the same for the three blocks of trials with one type of avatar and reversed with the other avatar. This was also counterbalanced between participants.

***Procedure for the experiment in the illuminated environment*.**

The procedure was similar to that of the first experiment except that the virtual environment was illuminated (Fig. 3).

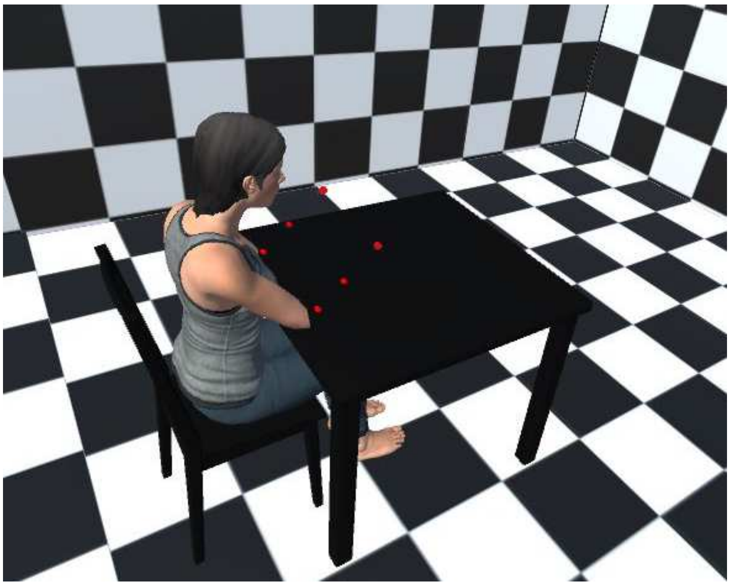

Figure 3. Representation of the illuminated virtual environment in the second experiment.

STATISTICS

Statistical analyses were performed on the duration of the illusory movement (time interval between the beginning and end of the kinaesthetic illusion, expressed in seconds from 0 to 8) and its speed (from -10 to 10). Since the normality assumption required to run frequentist parametric analyses was not systematically achieved under our experimental conditions (Shapiro-Wilk: $p<.05$), the data were subjected to Bayesian statistics (Kruschke 2010). Analysis of variance and pairwise comparisons t-tests were assessed with Bayesian equivalent tests.

Statistical analysis was performed using JASP software (JASP Team 2018, https://jasp-stats.org/)(See also Wagenmakers et al., 2018). Statistical evidence was reported using Bayes factors (BFs), BF_{10} for paired sample comparisons as well as for correlation analysis and BF_{incl} for ANOVAs denoting the level of evidence of the alternate hypothesis (non-signed difference), and the inclusion of a specific parameter in a model (ANOVA) respectively. The cut-off values defined by Jeffreys (1998) were used to interpret BFs. The kinaesthetic illusion's duration and speed were assessed in a 3 x 2 within-subject, repeated-measure analysis of variance (ANOVA) [Sensory modality (''Bimodal", "Proprioceptive" and "Visual") x Type of avatar (''realistic" versus "point-light'')] for the first experiment and the second experiment. A non-parametric Wilcoxon signed rank test was used to assess responses from the "embodiment" questionnaire as recommended (Gonzalez-Franco and Peck, 2018).

RESULTS

Experiment in the dark environment:

Embodiment phase

Based on the score for the 9 items (1-3, 6-9, 14-15) from the Gonzalez-Franco and Peck (2018) embodiment questionnaire, all but one of the 30 participants embodied the realistic avatar (median (*me)*=1.74) and the point-light avatar (*me*=1.88). In a Wilcoxon signed-rank test, the difference between these two avatar conditions was not significant (z=-0.12, p=.90). This was also true for each subcomponent of the embodiment score (Body Ownership: z = -1.25, p=.21; Agency: z = -0.72, p=.47 and Location: z = 1.67, p=.09).

Occurrence of the kinaesthetic illusion

When the avatar was realistic, the kinaesthetic illusion occurred in 82% of the bimodal trials, 37% of the visual unimodal trials, and 38% of the proprioceptive unimodal trials. With the point-light avatar, the kinaesthetic illusion occurred in 60% of the bimodal trials, 30% of the visual unimodal trials, and 40% of the proprioceptive unimodal trials. It should be noted that whatever the sensory modality, the great majority of the kinaesthetic illusions were in the same direction as the avatar's displacements. However, the illusion occurred in the opposite direction in a few trials (<5%). All trials were considered in further analyses.

The duration of the kinaesthetic illusion (in seconds)

The Bayesian repeated measures ANOVA showed extreme evidence for an effect (H1; BF_{incl}= $7.8e^{+10}$) of the sensory modality on the duration of the kinaesthetic illusion with a mean $\pm$ SD duration longer in the bimodal condition (4.6 $\pm$ 2.4) than in the two unimodal conditions (proprioception: 2.2 $\pm$ 2.1; vision: 1.76 $\pm$ 2.0). This was confirmed by Bayesian repeated sample t-tests that revealed extreme evidence for a longer duration of the illusion in the bimodal condition as compared to the two unimodal conditions (bimodal vs proprioception: BF_{10}= 21309; bimodal vs vision: BF_{10}= 21829) when the two types of avatars were pooled. In contrast, there is moderate evidence for an absence of difference (H0) between the two unimodal conditions (BF_{10}= 0.284).

The Bayesian repeated measures ANOVA showed no evidence for an effect (H1) of the type of avatar on the duration of the illusion (BF_{incl}= 1.5) with a mean $\pm$ SD duration of 3.2 $\pm$ 1.8 with realistic avatars and 2.5 $\pm$ 1.8 with point light avatars when the three modalities were pooled. Finally, the Bayesian ANOVA revealed no evidence for an interaction between sensory modalities and type of avatars (BF_{incl}= 0.8) (Figure 4).

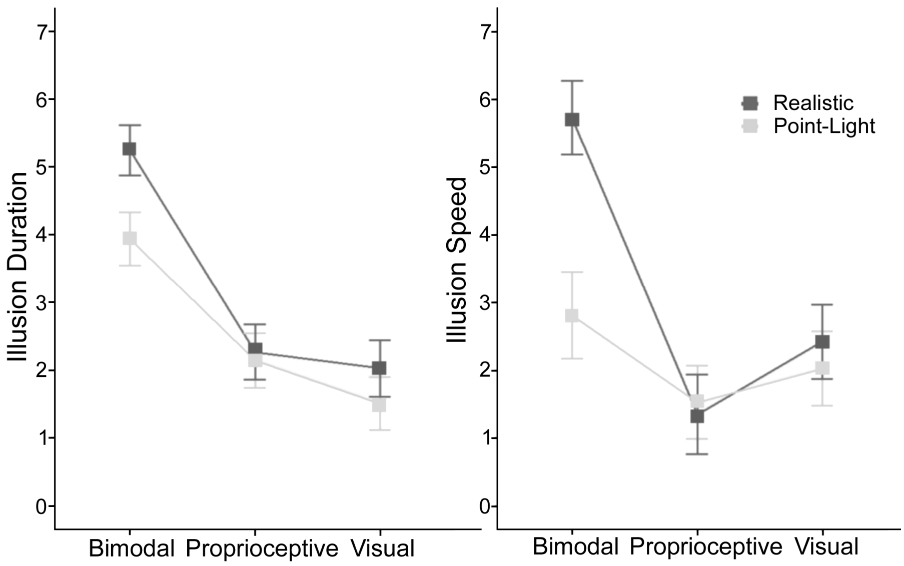

Figure 4: The mean duration (left panel) and speed (right panel) of the kinaesthetic illusion, as a function of the sensory modality (bimodal, visual, or proprioceptive) and the type of avatar (realistic or point-light) in the dark environment. The error bars correspond to confidence intervals after Cousineau-Morey correction for within-subject designs.

The velocity of the kinaesthetic illusion

The Bayesian repeated measures ANOVA showed very strong to extreme evidence for an effect (H1) of the sensory modality (BF_{incl}= 6.33e^{+6}), the type of avatar (BF_{incl}= 75.8) and for an interaction between these two factors (BF_{incl}= 69.4). As can be seen in Figure 4, a difference between the two types of avatars occurred mainly in the bimodal condition, what is confirmed by a Bayesian repeated sample t-test (BF_{10}= 2132). In contrast, moderate evidence for an absence of effect (H0) of the type of avatar was observed for the proprioception (BF_{10}=0.21) and vision (BF_{10}= 0.34) unimodal conditions.

With realistic avatars, the mean $\pm$ SD speed of the illusion was higher in the bimodal condition (5.7 $\pm$ 2.4) than in the two unimodal conditions (proprioception: 1.3 $\pm$ 2.9; vision: 2.4 $\pm$ 2.6). Bayesian repeated sample t-tests provides extreme evidence of a higher velocity of the illusion in the bimodal condition as compared to the two unimodal conditions (bimodal vs proprioception: BF_{10}= 70124; bimodal vs vision: BF_{10}= 1597). In contrast, there is anecdotal evidence for an absence of difference (H0) between the two unimodal conditions (BF_{10}= 0.59). With point light avatars, there was no evidence of a difference (H1) between any of the three sensory modalities (bimodal vs proprioception: BF_{10}= 0.81; bimodal vs vision: BF_{10}= 0.32; proprioception vs vision: BF_{10}= 0.27).

Experiment in an illuminated environment

The embodiment score

In the illuminated environment, all but one of the 30 participants embodied the realistic avatar and 27 embodied the point-light avatar. The difference between the embodiment score for the realistic avatar (*me*=1.58) and the score for the point-light avatar (me=1.51) was not significant (z=0.76, p=.45). This was also true for each subcomponent of the embodiment score (Body Ownership: z = 0.68, p=.50; Agency: z = 1.84, p=.07 and Location: z = -0.05, p=.96)

Occurrence of the kinaesthetic illusion

In the illuminated environment, the kinaesthetic illusion with the realistic avatar occurred in 82% of the bimodal trials, 51% of the visual unimodal trials and 27% of the proprioceptive unimodal trials. With the point-light avatar, the kinaesthetic illusion occurred in 62.8% of the bimodal trials, 36% of the visual unimodal trials, and 30% of the proprioceptive unimodal trials. As in the dark environment, the great majority of the illusions were in the same direction as the avatars' displacements. However, the illusion occurred in the opposite direction in a few trials (<4%).

The duration of the kinaesthetic illusion (in seconds)

Mean duration of the kinaesthetic illusion in the different experimental conditions is represented in figure 5 (left panel). The Bayesian repeated measures ANOVA showed extreme evidence for an effect of both the sensory modality (BF_{incl}= 4.4e^{+10}) and the type of avatar (BF_{incl}= 139) on the duration of the illusion. There was no evidence of an interaction between these two factors (BF_{incl}= 1.2). The mean $\pm$ SD duration was longer in the bimodal condition than in the two unimodal conditions. This was confirmed by Bayesian t-tests that revealed extreme evidence for a longer duration of the illusion, when the two avatars conditions were pooled, in the bimodal condition (4.3 $\pm$ 2.2) as compared to the two unimodal conditions (bimodal vs proprioception (1.5 $\pm$ 1.7): BF_{10}= 2.1e^{+6}; bimodal vs vision (2.3 $\pm$ 2.1): BF_{10}= 1182). In contrast, there was no evidence for a difference between the two unimodal conditions (BF_{10}= 0.9). As indicated by the main effect of the type of avatar, the duration of the illusion was longer with realistic avatars as compared to point-light avatars, with mean $\pm$ SD duration when the three sensory modalities are combined, of 3.2 $\pm$ 1.8 and 2.2$\pm$ 1.6 respectively.

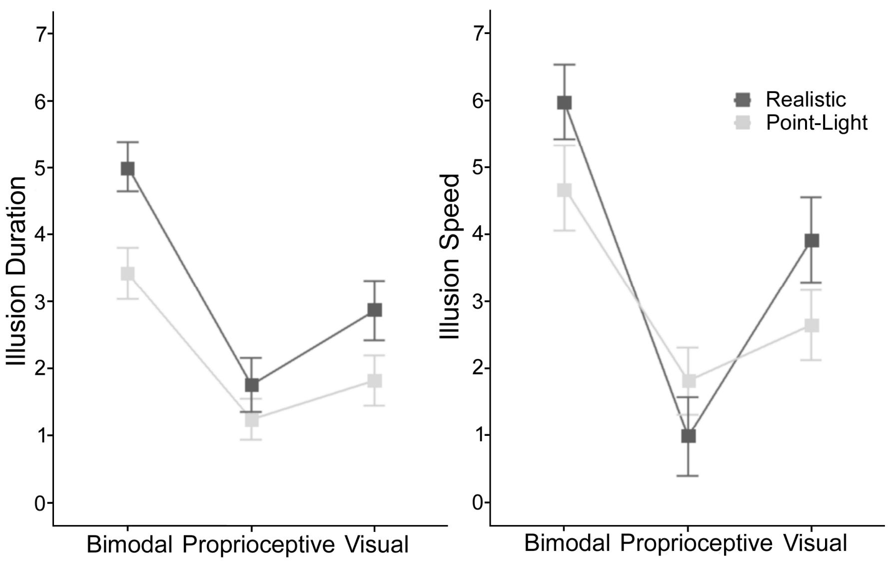

Figure 5. The mean duration (left panel) and speed (right panel) of the kinaesthetic illusion, as a function of the sensory modality (bimodal, visual, and proprioceptive) and the type of avatar (realistic vs. point-light) in the illuminated environment. The error bars correspond to the confidence intervals after Cousineau-Morey correction for within-subject designs.

The velocity of the kinaesthetic illusion

The Bayesian repeated measures ANOVA showed extreme evidence for a main effect of the sensory modality (BF_{incl}= 5.5e^{+10}). When the two avatar conditions were combined, the mean $\pm$ SD speed was indeed higher in the bimodal condition (5.3 $\pm$ 3.2) as compared to the vison condition (3.3 $\pm$ 2.6), the latter being higher than in the proprioception condition (1.4 $\pm$ 2.6). Bayesian repeated sample t-test confirmed with very strong to extreme evidence that the three sensory modalities differ from each other (bimodal vs proprioception: BF_{10}= 1.1e^{+6} ; bimodal vs vision: BF_{10}= 94.5; vision vs proprioception BF_{10}= 42.4).

In contrast, we found no evidence of a main effect of the type of avatar (BF_{incl}= 0.8) and only an anecdotal evidence for an interaction between sensory modalities and type of avatar (BF_{incl}= 2.2). Bayesian repeated sample t-tests revealed either anecdotal or no evidence for a difference between realistic and point-light avatars in the different sensory modalities (bimodal: BF_{10}= 2.8; vision: BF_{10}= 0.75; proprioception: BF_{10}=0.64).

DISCUSSION

Our present results confirmed that the combination of passive movement of the participant's left forearm with movement of realistic avatar's forearms (viewed from a first-person perspective) induced a kinaesthetic sensation of the same direction of movement in the static (right) arm in most participants and most trials (both in a dark and in an illuminated environment). Our results also showed that such kinaesthetic illusions occurred when the realistic avatars were replaced by point-light ones, albeit less frequently, with a shorter duration and a little slower. Moreover, the appearance of kinaesthetic illusion with point-light avatars appears to be conditioned by the richness of the virtual environment, whether it facilitates visual detection of motion of the point-light display. It must also be borne in mind that visuo-motor appropriation of the avatar's arms (as measured with the embodiment questionnaire derived from Gonzalez-Franco and Peck (2018)) was just as effective with a point-light avatar as with a realistic avatar.

Embodiment of the point light display

Embodiment (incorporation) of an object is constrained by top-down processes and a certain degree of similarity between the object or avatar and the representation of what the human body is like, is usually considered as necessary for incorporation (embodiment) to occur. Indeed, synchronous visuo-motor or visuo-tactile stimulation is not always enough for an object to become self-attributed; anatomic, morphological and body part identity can act as top-down processes that modulate self-attribution (Tsakiris and Haggard 2005, Lugrin et al., 2015a,b; Tsakiris et al., 2010; Haans et al., 2008, de Vignemont and Farné 2010, Waltemate et al., 2018). Accordingly, the incorporation of realistic humanoid avatars via virtual reality is rather straightforward (Petkova and Ehrsson 2008; Jung et al., 2017). This knowledge prompted our initial decision to use a realistic humanoid avatar (seen from a first-person perspective) to test whether visual--motion information from the avatar could be integrated for inference of one's own movements. The kinaesthetic illusions observed here with realistic forearm's showed that visual-motion information originating from embodied avatar's segments are indeed integrated for the purpose of kinaesthesia (see also Giroux et al., 2018). The point-light avatar's forearms used here in both the dark and illuminated environment were very unlike anyone's representation of human forearms. Despite this disparity, visuo-motor coupling with such point-light avatars proved to be enough for embodiment (as evaluated with a questionnaire) to occur in both environments. These results may appear surprising since the realism of the avatar has been shown to have an impact on the degree of embodiment and presence (Argelaguet, Hoyet, Trico, & Lecuyer, 2016; Jung, Sandor, Wisniewski, & Hughes, 2017; Lin & Jörg, 2016). However, the violation of avatar's realism does not systematically prevent ownership (Lin & Jörg, 2016; Schwind, Lin, Di Luca, Jörg, & Hillis, 2018; Tran, Shin, Stuerzlinger, & Han, 2017), especially with visuo-motor combination. Indeed, body ownership is more strongly and positively influenced by a congruent visuo-motor combination than by visuo-tactile or visuo-proprioceptive combinations (Kokkinara and Slater 2014) and can lead to ownership of non-humanoid objects such as a virtual hand represented by a wooden block (Lin & Jörg, 2016), a cat's paw (Zhang & Hommel, 2016), a 2D square (Ma & Hommel, 2015) or by dots placed at the fingertips locations (Schwind et al., 2018). In our experiments, the level of embodiment as measured with the embodiment questionnaires (Gonzalez-Franco & Peck, 2018) was similar with the realistic and point-light forearms. This similarity likely stem from the use of such visuo-motor combination during the embodiment periods.

The avatar's visual appearance and the sense of movement

As mentioned above, both the physical (Chancel et al., 2016, 2017) and virtual mirror illusions (Giroux et al., 2018) arise from the integration of visual and contralateral proprioceptive afferents. The results observed here with realistic avatars in both the dark and the illuminated environment confirmed the presence of visuo-proprioceptive integration, since the kinaesthetic illusion was more intense, in terms of duration and speed, in the bimodal condition (i.e. when congruent visual and contralateral proprioceptive signals were provided) than in the unimodal stimulation conditions. It must be noticed that in the illuminated environment and with realistic avatars, the speed of the kinaesthetic illusions was higher in the unimodal visual condition as compared to unimodal proprioceptive stimulation. No difference between the two unimodal conditions (visual or proprioceptive) did otherwise occur, thus confirming the importance of multisensory integration in kinaesthesia.

When the point-light avatars were viewed in the dark, this integration process was not evidenced. Indeed, the illusion produced under the bimodal condition only differed from that produced under unimodal conditions when its duration was considered but not when its speed was considered. In that respect, the illusion was much weaker (same duration but with a much lower speed) with the point-light display than with realistic avatars when seen in otherwise total darkness. The absence of a clear integrative pattern with the point-light avatars in the dark environment may well be related to the central nervous system's difficulties in capturing visual motion cues from point-lights moving at a slow speed (3.8°/s) in otherwise total darkness. Indeed, the threshold for perceiving the displacement of a single object in complete darkness is higher than that for perceiving relative motion between objects (Abadi et al., 1999; Snowden 1992). In contrast, visuo-motor coupling with such point-light avatars, with voluntary flexion-extension movements at a natural speed (which is much higher than 3.8°/s), proved to be enough for embodiment to occur both in the dark and illuminated environments.

The visual illuminated environment in our second experiment was designed to enhance the detection of visual motion cues from the point-light avatars. Our results showed that a combination of passive movement of the participant's left forearm with visual movement of the point-light avatar's forearms (seen from a first-person perspective) was sufficient to evoke a kinaesthetic illusion in the participant's right (static) arm. Those kinaesthetic illusions in the bimodal condition were more intense, in terms of duration and speed than in the unimodal stimulation conditions. These results with point-light avatars in the illuminated environment confirmed the presence of visuo-proprioceptive integration as previously observed with realistic avatars. These results echo those reported by Chancel et al. (2016) for the physical mirror paradigm; the kinaesthetic mirror illusion could even be induced when the arm's reflection in the mirror was strongly degraded. In the present study, the forearms were represented by three point-lights only - one of which corresponded to the pivot of the elbow and thus remained static. Therefore, individuals can (i) make out their body segments described by three aligned but unconnected point-lights, and (ii) integrate visual motion cues from the point-light display to build a unified perception of arm movement.

It must be noted that even in the illuminated environment, the kinaesthetic illusions evoked in the bimodal condition, were both shorter and slightly slower compared to those observed with realistic avatars. Several hypotheses could be put forward to explain such a difference. First, the weight allocated to a given sensory signal in multisensory perception is usually proportional to its reliability (see Ernst and Bülthoff, 2004 for a review). A lack of reliability of the point-light display might stem from the movement speed used to evoke illusions here (3.8°/s; see Guerraz et al., 2012 for a rational), which is well below that of most "natural" biological movements. Alternatively, although facilitated by the illuminated environment, the central nervous system's might still have more difficulties in capturing visual motion cues from two point-lights moving at 3.8°/s than from a full realistic arm moving at the same speed. As mentioned above, visuo-motor coupling through movements performed at a natural speed was sufficient to give rise to embodiment, either in the dark or illuminated environment. The slow speed used here to evoke kinaesthetic illusion might therefore not be optimal to fully appreciate the role of biological motion in the context of kinaesthesia.

Point-light displays are known to bring meaningful perception when they are in movement but not when they are static (Johansson, 1973; Kozlowski & Cutting, 1977). This is the reason why, in the context of understanding perception of one's own forearms movements, we chose not to use a full Point-Light avatar's body but only point-light forearms, those forearms being the only moving body parts (with the exception of the head) in our experiments. In that respect, the point-light avatar's forearms displayed here, although deviating slightly from conventional point-light displays, fulfilled their role as they were selectively conveying only biological motion.

The clinical relevance of feature-poor avatars

The mirror box arrangement is often used to treat amputees suffering from phantom limb pain (Deconinck et al., 2015, see also Mercier & Sirigu 2009 for related techniques). Although mirror-like virtual displays may be effective in the treatment of phantom limb pain (e.g. Ambron et al., 2018, Perry et al., 2018), virtual reality remains a highly technical and might not provide more clinical benefit than a conventional (physical) mirror box (Brunner et al., 2014, Laver et al., 2017). However, some amputees cannot bear to see a reflection mimicking a lost limb that they are still mourning. Virtual reality might therefore be a relevant way of providing virtual limbs that cannot be confused with real limbs. In this respect, the point-light limb avatar is positioned at one end of a continuum ranging from the real limb (such as that reflected in the physical mirror paradigm) to an empty space. Given that i. embodiment of the point-light avatar's forearms is just as effective as that of realistic ones, ii. visual motion cues from both realistic and point-light avatars can be used for the purpose of kinaesthesia (just as it does with a real reflected limb in the physical mirror paradigm), point-light avatars could be a relevant clinical alternative to patients that cannot bear to see a reflection mimicking their lost limb.

Taken as a whole, our present results show that beneficial visual motion cues for kinaesthesia do not require a very elaborate, fine-grained, human-like representation of a body segment. In fact, individuals can (i) make out their body segments represented by as few as three aligned point-lights, and (ii) integrate the corresponding visual motion cues to yield a unified perception of arm movement.

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AUTHORS CONTRIBUTION

MGx, JB, and MGz participated in the conception and design of the study. MGx, JB and MGz conducted the study. PAB designed the motorized manipulandum. All the authors participated to the interpretation of the data and critically revised the manuscript before approving the final version.

COMPETING INTERESTS

None of the authors have any conflicts of interests.

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Legends

Figure 1. The virtual reality setup. The panels show the participant's view (i.e. a first-person perspective) when the avatar's forearms were either (A) visible and realistic, (B) visible and represented as points of light, or (C) masked by virtual white boxes.

Figure 2. Experimental session. Each participant carried out two sessions of three randomised blocks (Bimodal, Visual, Proprioceptive), one session with realistic avatars and the other one with point-light avatars. A block comprised six trials (alternating flexions F and extensions E). Kinaesthesia was rated (arrows) after each trial. Each block was preceded by an embodiment phase. The first embodiment phase lasted 60s and was followed by an embodiment rating (B). These two sessions were performed in either a dark (first experiment) or an illuminated background (second experiment).

Figure 3. Representation of the illuminated virtual environment in the second experiment.

Figure 4. The mean duration (left panel) and speed (right panel) of the kinaesthetic illusion, as a function of the sensory modality (bimodal, visual, or proprioceptive) and the type of avatar (realistic or point-light) in the dark environment. The error bars correspond to confidence intervals after Cousineau-Morey correction for within-subject designs.

Figure 5. The mean duration (left panel) and speed (right panel) of the kinaesthetic illusion, as a function of the sensory modality (bimodal, visual, and proprioceptive) and the type of avatar (realistic vs. point-light) in the illuminated environment. The error bars correspond to the confidence intervals after Cousineau-Morey correction for within-subject designs.

Appendix: Embodiment questionnaire based on Gonzalez-Franco & Peck (2018)

Participants had to give their degree of agreement concerning the following assertions, basing on the following 7-point Likert-scale ranging from:

-3	-2	-1	0	+1	+2	+3
Strongly disagree	**Disagree**	**Somewhat disagree**	**Neither agree nor disagree**	**Somewhat agree**	**Agree**	**Strongly agree**

"During the preceding experimental phase, there were moments in which…"

Q1 – "I felt as if the virtual arms were my own arms"

Q2 – "It felt as if the virtual arms I saw were someone else's arms"

Q3 – "It seemed as if I might have more than two arms"

Q6 - "It felt like I could control the virtual arms as if they were my own arms"

Q7. "The movements of the virtual arms were caused by my own movements"

Q8. "I felt as if the movements of the virtual arms were influencing my own movements"

Q9. "I felt as if the virtual arms were moving by themselves"

Q14. "I felt as if my arms were located where I saw the virtual arms"

Q15. "I felt out of my body"