



OPEN Virtual body continuity during action observation affects motor cortical excitability

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Body ownership, the sense that the body belongs to oneself, can be altered by inducing body manipulations in Virtual Reality, such as by increasing the visual discontinuity between the avatar's hand and body. Body representation manipulations can also influence motor cortex excitability. We hypothesized that the degree of body continuity between one's body and the observed virtual body would affect ownership feelings and impact motor cortex excitability during action observation. Participants observed virtual hand movements from a first-person perspective with the virtual hand presented with different level of connection with their real hand; the virtual hand could be part of a full virtual body co-located with the real body (Full-Body condition), it could appear as connected to an upper limb visually discontinuous from the real body (Upper Limb condition), or the virtual hand appeared in isolation, fully discontinuous (Detached Hand condition). Results showed increased corticospinal excitability when body continuity is higher (Full-Body and Upper Limb). This effect was mediated by ownership and disownership feelings, supporting the relationship between body perception and motor system.

Keywords Virtual embodiment, Action observation, Non-invasive brain stimulation, Motor excitability

The sense of embodiment (SoE) has been defined as the sense of having a body, and the body can be considered both the subject and object of medical science and practice¹. The capability of our brain to have a representation of our body results in a mental construction composed of perceptions and ideas about the dynamic organization of our own body, involving vision, touch, proprioception, interoception, motor control, and vestibular sensations². Indeed, the SoE refers to the sense of having a body, achieved through processing the different sensory inputs arriving at our body, which are integrated and interpreted by our brain to create a coherent representation of ourselves. Accordingly, De Vignemont, defines the SoE as “(an object) *E* is embodied if and only if some properties of *E* are processed in the same way as the properties of one's own body”³. The SoE is induced when the following components are present: (i) the *Sense of Body Ownership*, which is the feeling that a specific body part belongs to one's body⁴; (ii) the *Sense of Agency*, which is the sense of intending executing actions and the feeling of controlling one's body movements⁵; and (iii) the *Sense of Co-location*, which is the one's spatial experience of being inside a body⁶.

Immersive virtual reality (IVR) systems have been widely used to induce the SoE, showing how and to what extent we can experience a virtual body as our own⁷. Remarkably, even simply observing a virtual body, positioned spatially aligned with one's physical body, can induce ownership towards it⁶. IVR systems provide unique advantages, such as the ability to easily manipulate specific factors associated with the embodied virtual body in a controlled way that would hardly be possible in physical reality⁸. In detail, it is possible to manipulate body representation in terms of body continuity (i.e. continuity of the connection between the body and its parts) potentially promoting a dissociation between one's physical body and the virtual body observed from an egocentric visual perspective^{9,10}. Body continuity refers to the visual and structural coherence between different

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parts of the body. Here, we use the term ‘body continuity’ to refer to the visual and structural coherence between different parts of the body. In IVR, it is possible to manipulate body continuity by presenting virtual body parts as either detached from the virtual body or misaligned with the real body. For instance, it has been shown that visual discontinuity between the virtual hand and arm significantly decreased participants’ sense of ownership over the virtual hand^{9,10}. Thus, when a virtual limb is attached to the rest of the virtual body, it promotes a stronger sense of ownership over the virtual body. Conversely, when the virtual hand is completely detached from the virtual body, the sense of ownership is reduced.

Moreover, manipulations of body representation have an impact on motor performance¹¹ and on the activation of the primary motor cortex. In this regard, changing the morphological characteristics of the affected virtual limb using IVR can improve motor functions in patients with stroke^{12,13}. A recent fMRI study revealed that observing virtual body movements while being embodied in a virtual body lead to stronger activation of the motor and premotor cortex¹⁴. Similarly, motor improvements after observing virtual body movements had been shown in patients with distal radius fracture¹⁵ and in patients with stroke¹⁶. Indeed, observing virtual body movements while being embodied in a virtual body has shown positive effects in the activation of the motor and premotor cortex¹⁴, as well as on motor recovery in patients with distal radius fracture¹⁵ and in patients with stroke¹⁶.

Some evidence showed a relationship between the activation of the motor cortex and the SoE when observing involuntary hand movements evoked by transcranial magnetic stimulation (TMS) over the primary motor cortex (M1)¹⁷. In fact, it is well known that corticospinal excitability is enhanced during the (passive) observation of biological movements (the so-called ‘motor resonance’ phenomenon¹⁸, and the magnitude of this facilitation is modulated according to the features of the depicted actions^{19,20}). Hence, one may postulate that observing hand movements from a first-person perspective while fully embodied in a virtual body increases motor cortical facilitation during action observation. Even though some evidence demonstrates that virtual body discontinuity decreases the sense of ownership towards the virtual body^{9,10}, to date, none investigated the role of virtual body representation in terms of body continuity on M1 cortical excitability during action observation. Based on prior evidence^{21–23}, we hypothesized that greater virtual body continuity would enhance the sense of ownership and increase motor cortical excitability during action observation.

The present study aimed to investigate the impact of observing virtual hand movements from a first-person perspective on motor cortex excitability while fully immersed in a virtual environment. Specifically, the study counted with different conditions in terms of visual continuity of the moving virtual hand with the body of the observer: (i) Full Body, where the virtual hand is integrated into a full body first-person perspective, (ii) Upper Limb, where the hand is integrated into a virtual upper limb that is visually discontinuous from the participant’s body, (iii) Hand detached, in which the virtual hand is in isolation and fully discontinuous with the participant’s body (see Fig. 1). In all conditions, the bodily stimuli were observed from a first-person perspective in an immersive virtual environment. During the action observation task, participants observed a static (static condition, with the virtual hand at rest) or (movement condition showing the index finger abduction) moving left virtual hand. To measure M1 cortical excitability, motor evoked potentials (MEPs) induced by single-pulse TMS over the right M1 were recorded from the participant’s left hand during the action observation task.

Here, considering previous findings using the same visual stimuli of movements^{22,24,25}, we expected that MEPs recorded during movement observation would be higher than the ones recorded during the observation of static stimuli, suggesting the presence of motor resonance during action observation. Furthermore, corticospinal excitability facilitation during action observation is specific for the muscles involved in the observed action, at least for simple movements like the one we adopted^{18,20}. For instance, an study by Guidali and colleagues²², showed that during the observation of index finger abduction movements (that is, the same action depicted in the IVR tasks of the present work) MEPs enhancement was detectable only from the *first dorsal interosseus* (FDI) muscle but not from other muscles not involved in the viewed hand movement (i.e., *abductor digiti minimi* – ADM –²²). Hence, we recorded MEPs from both FDI and ADM muscles. Embodiment feelings were assessed through a questionnaire^{9,26}. Consistent with previous studies demonstrating an enhancement in corticospinal excitability by the observation of similar hand movements using non-immersive paradigms (i.e., motor resonance effect)^{21–23}, we expected to find this effect only for the muscle involved in executing the observed movement. Furthermore, we expected that both motor resonance and embodiment feelings would increase as the visual continuity between the real and virtual body increased.

Results

The experiment followed a 3(Condition) × 2(Type of Movement) × 2(Muscle) factorial within-subject design (see Fig. 1). We considered MEPs amplitude as an index of motor cortex excitability and questionnaire scores as a measure of embodiment sensations (see Table 1 for questionnaire details). We employed a mixed-effects design to analyze our dependent variables (MEPs), with a multilevel linear regression test (*mixed function* in Stata), considering as fixed effects: body continuity condition (Full Body, Upper Limb, Detached Hand), type of virtual hand movement (static or moving), and muscle (FDI or ADM). Significant effects were further explored with Post-hoc Scheffe test. We used a multilevel linear regression test (*mixed function* in Stata) to identify differences in the embodiment questionnaire scores across conditions.

To further explore the mechanism through which body continuity influences corticospinal excitability, we conducted a mediation analysis using a seemingly unrelated regression (*sureg function* in Stata). This analysis examined whether the sensation of embodiment, experienced during virtual body exposure, mediates the effect of body continuity on corticospinal excitability. In all analyses, we included participants as a random effect variable to properly account for inter-subject variability.

Ownership	Q1	During the virtual reality experience, I felt as if the virtual environment was real
	Q4	During the experimental session, I felt as I had more than one body
Agency	Q2	During the experimental session, I felt like I had control over the arm represented on the screen.
	Q6	During the experimental session, I felt that even if I moved my real arm, the arm represented on the screen would not move.
Disownership	Q3	During the experimental session, it seemed like I was unable to move my real hand.
	Q5	During the experimental session, it felt like my real hand was disappeared.
	Q7	During the experimental session, I couldn't tell where my real hand was located.

Table 1. Embodiment questionnaire statements.

	Coef.	z	p	Lower, 95% CI	Upper, 95% CI
Condition _{Upper Limb}	-0.004	-0.10	0.917	-0.076	0.068
Condition _{Detached Hand}	-0.047	-1.28	0.200	-0.119	0.025
Type of movement _{Movement}	0.018	0.50	0.617	-0.054	0.091
Muscle _{FDI}	0.680	18.42	<0.001	0.607	0.752
Condition _{Upper Limb} × Type of movement _{Movement}	0.075	1.44	0.151	-0.027	0.176
Condition _{Detached Hand} × Type of movement _{Movement}	-0.007	-0.14	0.889	-0.109	0.095
Condition _{Upper Limb} × Muscle _{FDI}	-0.007	-0.14	0.885	-0.110	0.095
Condition _{Detached Hand} × Muscle _{FDI}	-0.157	-3.00	0.003	-0.259	-0.054
Type of movement1 × Muscle _{FDI}	0.183	3.52	<0.001	0.081	0.286
Condition _{Upper Limb} × Type of movement1 × Muscle _{FDI}	-0.094	-1.27	0.204	-0.238	0.051
Condition _{Detached Hand} × Type of movement _{Movement} × Muscle _{FDI}	-0.197	-2.67	0.007	-0.341	-0.052

Table 2. The table shows the results of the 3(condition) × 2(type of movement) × 2(muscle) on meps amplitude. Significant values are in bold.

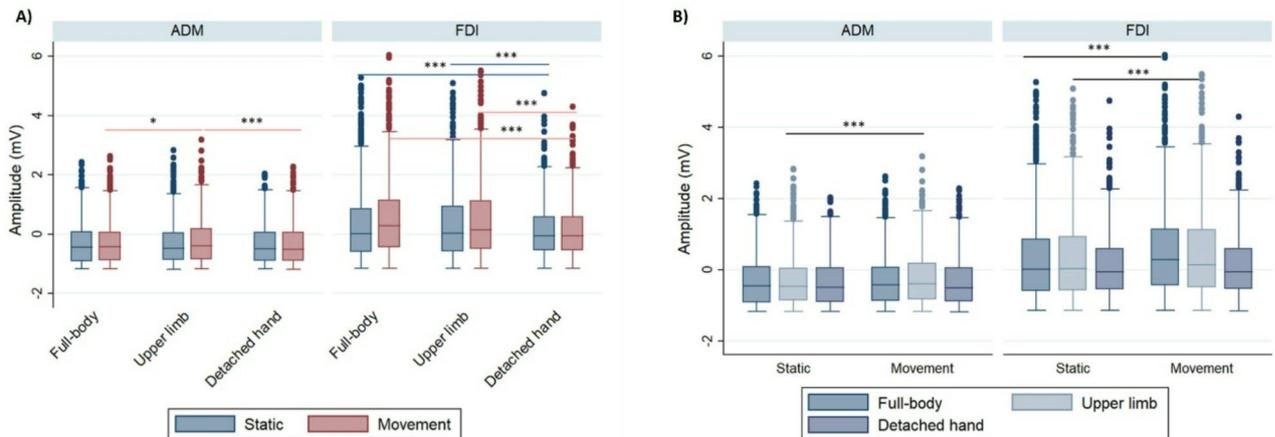


Fig. 2. (A) Different degrees of body continuity between the real and the virtual body modulate MEPs amplitude. The Full Body and Upper Limb conditions presented higher MEPs in the FDI than the Detached Hand condition in the Static condition. During movement conditions, the Full Body and Upper Limb conditions presented higher MEPs in FDI muscle compared to the Detached Hand condition. The Upper Limb condition presented higher MEPs in the ADM, during movement condition, compared to the Full Body and Detached Hand condition. (B) Moving virtual hand induced higher MEPs compared to static virtual hand. The Full Body and Upper Limb conditions presented higher MEPs in the FDI in the moving virtual hand condition compared to the static virtual hand condition. The Upper Limb conditions presented higher MEPs in the moving virtual hand condition compared to the static virtual hand in the ADM. In the boxplots, the medians are shown as horizontal lines, and the boxes are the interquartile ranges (IQR). The whiskers are between max (min score, lower quartile - 1.5 IQR) to min (max score, upper quartile + 1.5 IQR). If there are values outside the whiskers, these are conventionally called “outliers” and are shown by (o). **p* < 0.05, ***p* < 0.01, ****p* < 0.0001.

	Movement		Static	
	ADM	FDI	ADM	FDI
Full body vs. detached hand	n.s	$z = -9.01, p < 0.001$	n.s	$z = -5.59, p < 0.001$
Upper limb vs. detached hand	$z = -5.31, p < 0.0001$	$z = -9.01, p < 0.001$	n.s	$z = -4.89, p < 0.001$
Upper limb vs. full body	$z = -2.93, p < 0.01$	n.s	n.s	n.s

Table 3. Multiple comparisons Sheffe test.

action observation emerged in conditions with higher visual body continuity between the real and the virtual body (i.e., Full Body and Upper Limb). Moreover, FDI MEP amplitudes were significantly higher during action observation in the Full Body ($z = -10.37, p < 0.001$) and Upper Limb ($z = -9.65, p < 0.001$) conditions compared to the Detached Hand condition. Additionally, there was a significant difference in MEPs amplitude in the FDI muscle during the observation of static hand stimuli when comparing the Full Body ($z = -5.51, p < 0.001$) and Upper Limb ($z = -5.15, p < 0.001$) conditions with the Detached Hand condition (Fig. 2; Table 3 form multiple comparisons (Sheffe test)). These results suggest that a higher degree of visual continuity between the real and virtual body can enhance M1 activation during the observation of a hand in both static and dynamic conditions.

At the same time, MEPs amplitude recorded from the control muscle (i.e., ADM) did not significantly differ between the static and moving conditions in the Full Body (n.s) and Detached Hand (n.s). Unexpectedly, MEPs facilitation by action observation emerged in the ADM muscle in the Upper Limb condition ($z = 4.67; p < 0.001$). Additionally, no significant differences were observed in the MEPs amplitude for the ADM muscle across conditions during the observation of static hand stimuli (n.s). However, significant differences were found during action observation when comparing the Full Body ($z = -2.93, p < 0.01$) and Detached Hand ($z = -5.31, p < 0.001$) conditions (see Fig. 2; Table 3 for multiple comparisons (Sheffe test)).

The results indicated a gradient in the motor facilitation effect relative to the degree of body continuity. Specifically, in the Full Body condition, a muscle-specific response was observed, with a difference between movement and static conditions emerging exclusively in the FDI muscle. In contrast, the Upper Limb condition produced a muscle-unspecific response, with the facilitation effect appearing in both the ADM and FDI muscles. No motor facilitation effect was observed in the Hand Detached condition. See Table 3 for detailed table results.

Higher body continuity between the real and the virtual body induces a stronger sense of embodiment toward the virtual body

The reported levels of ownership showed a statistically significant difference between the Upper Limb ($z = -81.48, p < 0.001$) and Detached Hand ($z = -117.26, p < 0.001$) condition compared with the Full Body condition, being higher in the Full Body condition. Further, there was a significant difference between the Detached Hand and the Upper Limb conditions ($z = 35.86, p < 0.001$), showing higher levels of ownership in the upper limb condition. In addition, there was a significant difference between conditions in terms of agency, where participants reported higher scores in the Full Body condition compared to the Upper Limb ($z = -55.19, p < 0.001$), and Detached Hand condition ($z = -59.75, p < 0.001$). Again, a significant difference between Upper Limb and Detached Hand condition was found, showing higher score in the Upper limb condition ($z = 4.60, p < 0.001$). Overall, participants rated significantly higher scores related to disownership (Q3, Q5, and Q7) in the Full Body condition compared to the Upper Limb ($z = -38.07, p < 0.001; z = -63.15, p < 0.001; z = -48.44, p < 0.001$) and Detached Hand ($z = -42.93, p < 0.001; z = -73.05, p < 0.001; z = -55.04, p < 0.001$) conditions. Moreover, the results also showed higher scores related to disownership in the Upper Limb condition compared to the Detached Hand condition ($z = 4.89, p < 0.001; z = 9.96, p < 0.001; z = 6.65, p < 0.001$) (Fig. 3).

Mediation analyses, by using the seemingly unrelated regressions (sur) method which allows to analyze multiple regression equations when their errors (disturbances) are correlated²⁷, predict the possible relationship between the scoring reported in the virtual embodiment questionnaire and the MEPs responses obtained after being exposed to the three different conditions in terms of virtual body continuity (Full Body, Upper Limb, and Detached Hand), also revealed that the sense of ownership (Q1), and the disownership index (Q3, Q5, and Q7) mediates differences in MEPs amplitude among the different virtual body continuity conditions. Results showed a significant relationship between the independent factor virtual body continuity and the mediation variable sense of ownership, and disownership (see Table 4).

Presence of a feeling of immersion during the VR experience

The assessment of the sense of presence (i.e., the belief of being in another world than where the body is located) during the VR experience was conducted using the Virtual Reality Experience scale^{28,29} (see Supplementary Table 1). Overall, participants seem to perceive themselves as being immersed in a real environment, as if they were visiting it ($M = 0.43; SE = 0.20$). Specifically considering the three dimensions, we observed a positive score for each dimension (sense of being there: $M = 0.58; SE = 0.23$; feeling real or present in the virtual environment: $M = 0.17, SE = 0.30$; Locality: $M = 0.47; SE = 0.27$). The collected scores during the experimental sessions indicate that the participants felt immersed in the VR environment and experienced a sense of presence within the virtual environment (see Supplementary Materials for additional details).

Absence of side effects within the immersive virtual reality environment

The possible side effects of cybersickness were assessed after the VR experience using the Simulator Sickness Questionnaire³⁰; Supplementary Table 2). This questionnaire comprises 16 items designed to evaluate various

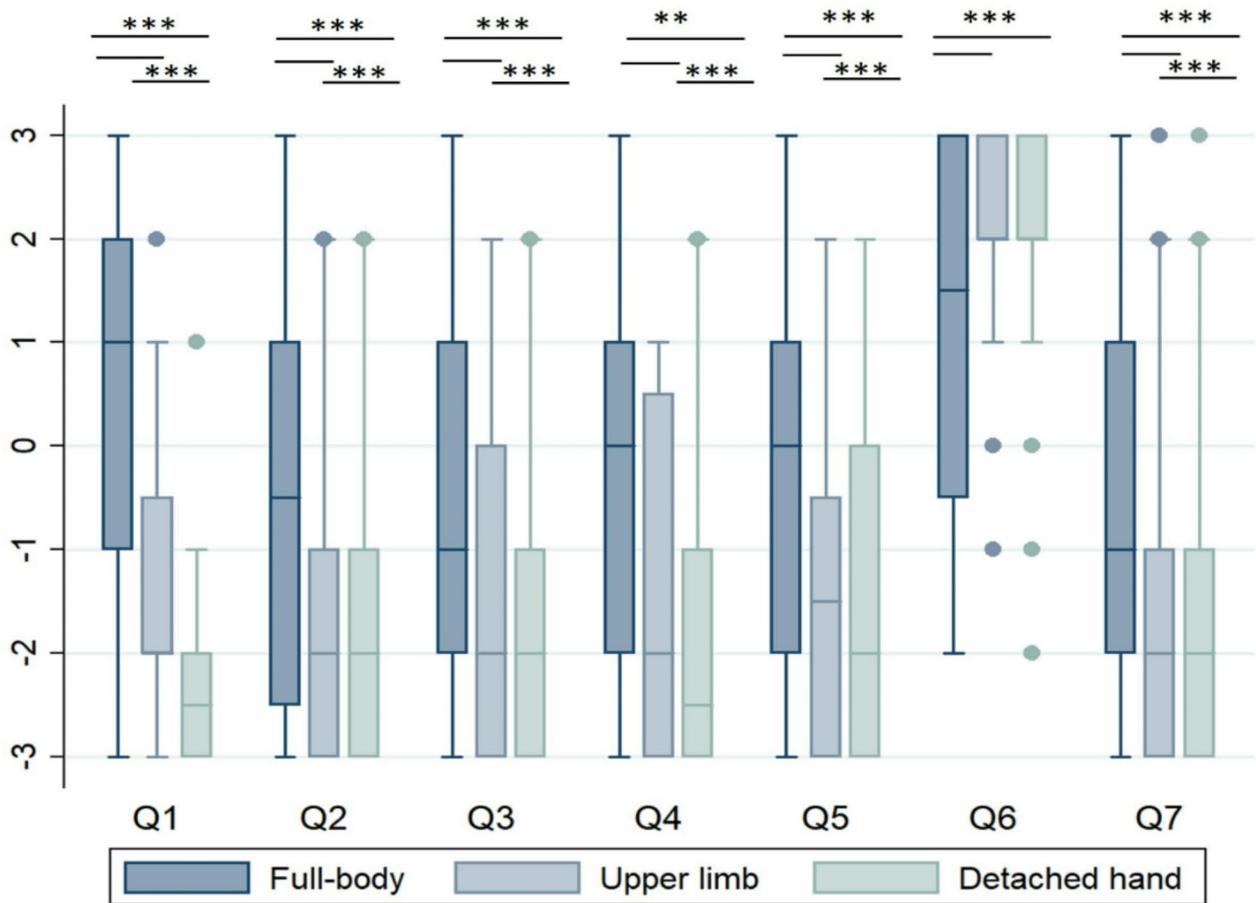


Fig. 3. Different degrees of continuity between the real and the virtual body affect sense of embodiment toward the virtual body. There were significant differences between conditions for all the questions of the virtual embodiment questionnaire, showing higher scores of ownership and agency in the Full Body condition compared to the Upper Limb, and Detached Hand conditions. Further, the Upper Limb condition presented significant higher scores related to ownership and agency compared to the Detached Hand condition. In the boxplots, the medians are shown as horizontal lines, and the boxes are the interquartile ranges (IQR). The whiskers are between max (min score, lower quartile - 1.5 IQR) to min (max score, upper quartile + 1.5 IQR). If there are values outside the whiskers these are conventionally called “outliers” and are shown by (o). * $p < 0.05$, ** $p < 0.01$, *** $p < 0.0001$.

Embodiment component	Coefficient	Confidence interval	z	p-value
Ownership (Q1)	0.16	0.12–0.19	9.63	<0.0001
Agency (Q2)	-0.004	-0.32–0.02	-0.33	0.74
Disownership index (Q3, Q5, Q7)	0.57	0.32–0.81	4.50	<0.0001

Table 4. Results of mediation analysis.

symptoms, utilizing a four-point scale (0 = None, 3 = Severe). By applying a subjective threshold that considered participants reporting only slight symptoms (score = 1) for each item, it was observed that all participants recorded a raw score below 16 ($M = 4.47$; $SE = 0.599$). Our results indicate that side effects were rated, on average, below the “slight” level for all items. Importantly, no participants found it necessary to interrupt the immersive experience due to the sensation of sickness. More specifically, we also considered the scores related to the two main factors of the questionnaire (i.e., Nausea and Oculomotor factors). A higher score was observed for the Oculomotor factor ($M = 3.56$, $SE = 0.477$) in comparison to the Nausea Factor ($M = 0.906$, $SE = 0.231$). This finding implies that the side effects attributed to our VR environment were more related to oculomotor symptoms, such as eye strain, difficulty on concentrating and focusing, blurred vision, and the sensation of “Fullness of the Head,” fatigue, and headache. More details are reported in the Supplementary materials.

Discussion

The present study investigated motor cortex excitability modulations while observing hand movements under varying conditions of visual body continuity between the virtual hand and the observer's body. Participants were immersed in a virtual environment through an HMD and observed a virtual body from a first-person in three different conditions of visual continuity with the real body: (i) Full Body, (ii) Upper Limb, (iii) Detached Hand. Body continuity refers to the visual and structural coherence between different parts of the body. In IVR, it is possible to manipulate body continuity by presenting virtual body parts as either detached from the virtual body or misaligned with the real body. In detail, the results of the present study showed that participants reported higher feelings of embodiment in the Full Body and Upper Limb conditions (conditions showing higher visual continuity between the real and the virtual body), compared to the Detached hand conditions (lower body continuity). To measure M1 corticospinal excitability, left-hand MEPs were recorded following single-pulse TMS applied to the right M1 while participants observed a static or moving left virtual hand. Embodiment feelings were assessed through a questionnaire. Results showed that feelings of embodiment were enhanced as the visual continuity between the virtual and real body increased (i.e., Full Body, and Upper Limb). Moreover, the Full-Body and Upper Limb conditions induced higher MEPs amplitude in the FDI muscle either when the virtual hand was static or moving compared to the Hand Detached conditions, suggesting higher M1 motor excitability, regardless of action observation. Crucially, these two conditions induced higher MEPs on moving than static hand observation trials, suggesting, besides a more general facilitation effect on M1 excitability in these conditions, also an increase of motor resonance effects during action observation^{21,22}. Finally, the results indicate that the effect on M1 excitability is mediated by the subjective sense of ownership and disownership, as assessed through the questionnaire. Specifically, mediation analyses revealed that differences in MEPs amplitude across virtual body continuity conditions were significantly influenced by the sense of ownership toward the virtual body and disownership toward one's body. Our findings underscore the central role of these sensations in shaping motor excitability, as mediators of the relationship between virtual body continuity and MEP amplitude.

The sense of ownership towards a virtual body may be favored by body continuity. When we look down at our own bodies, we know that the limbs we see belong to us because they maintain a continuous connection with our shoulders or hips. This anatomical connection between contiguous body parts creates a sense of coherence and belonging, reinforcing our perception of the body as an integrated whole. Indeed, continuity between body parts is crucially stored in the so-called body structural description, which is critical for body representation and may be logically linked to "continuity"³¹. According to this, previous studies demonstrated that in VR, the physical continuity of the virtual hand with the shoulder is a crucial factor in inducing the subjective illusion of ownership over a virtual arm⁹. Tieri and colleagues demonstrate that small visual incongruences in a body's visual integrity can fundamentally affect the sense of body ownership in VR¹⁰. Furthermore, the authors found that passive observation of a virtual hand detached from the body similarly modulates the sense of ownership and agency in both static and dynamic contexts of the virtual hand observed from a first-person perspective. However, a full sense of body continuity between the real and the virtual body can be fully achieved when using immersive virtual reality. It is well-known that through non-immersive VR, it is not possible to induce full body-illusion². Indeed, some studies have demonstrated that the co-location of the real body with the virtual body when using immersive virtual reality systems is crucial to induce the sense of ownership toward the virtual body³². This is in line with previous studies using the well-known rubber hand illusion (RHI), in which the concept of bodily continuity was linked to the constraint of anatomical plausibility³³. Specifically, in the RHI, the fake hand is placed in an anatomically coherent position and partially occluded by a cloth resembling an arm, thereby maintaining the sense of bodily continuity. Such structural constraints are crucial for inducing the illusion. In this regard, other studies have shown that body ownership illusions decrease as postural incongruence between the real body and the fake one increases^{34,35}.

Such an impact of body discontinuity on embodiment in terms of a sense of ownership and agency was previously revealed by Newport and Preston where the authors showed that detaching the tip of the finger destroyed the underlying ownership for the remaining stump as well as for the tip itself, even when the tip was under participants' control³⁶. Moreover, it has been shown that the mere manipulation of the visual appearance of a virtual limb could influence the subjective feeling of ownership and the physiological responses (skin conductance response, SCR) associated with a threatening stimulus approaching the virtual hand³⁷. In this study, the authors exposed the participant to four different virtual arm conditions in terms of body continuity from a first-person perspective: (i) a virtual body with the right hand and forearm connected by a physiological wrist (Full-Limb), (ii) connected by a thin rigid wire, (iii) disconnected due to a missing wrist, and (iv) disconnected with a missing wrist plus a plexiglass panel positioned between the hand and forearm. The results revealed that visual discontinuity between the virtual hand and forearm affected the physiological reactivity associated with a virtual threat in terms of SCR. SCR was stronger when the virtual hand was connected to the rest of the body (Full-Limb and Wire conditions) compared to other conditions where the virtual hand was disconnected from the virtual body³⁷. In the present work, we further demonstrated that the visual continuity between one's body and the virtual body can affect embodiment sensations. Specifically, embodiment feelings were incrementally stronger as the visual continuity between the virtual and real body increased. The present study results supported the relation between body representation and the motor system, highlighting the importance of a coherent visual continuity between the virtual and one's own body in modulating motor excitability.

The patterns found on corticospinal excitability highlight that the muscle-specific MEP facilitation during action observation (i.e., higher MEPs for the muscle actually involved in the observed movement²⁵ –FDI) is found only during the Full Body condition. In the Upper Limb condition, M1 excitability during action observation was enhanced for both FDI and ADM muscles compared to static stimuli, revealing a generalized corticospinal facilitation at the sight of the moving index finger. As was commented above (see introduction section), muscle specificity is one of the main properties characterizing the motor resonance phenomenon

for simple movements^{18,38}. Overall, it is highly possible that the features of the depicted hand may have contributed to the patterns found in the present work on corticospinal excitability^{19,20}. For instance, the absence of motor resonance in the Detached Hand condition could be interpreted as evidence that, in an immersive environment, action observation per se is not mandatory to facilitate corticospinal excitability. Rather, the sense of embodiment and visual continuity toward the upper limb may be the key factors allowing the emergence of this phenomenon. Hence, in the Upper Limb condition, FDI and ADM increased excitability cannot be interpreted as ‘motor resonance’ given that the muscle-specificity of the effect is not detectable. Conversely, it suggests a general increase of M1 excitability during action observation, regardless of the type of viewed action (movements of the index finger, but not of the little finger), given that the depicted hand cannot be fully felt as the participant’s own hand due to body discontinuity. Still, this visual stimulus is more salient for visuomotor mirroring processes and activates the motor system to a greater extent than the previous condition. However, this activation is not fully superimposable to the typical, muscle-specific, motor resonance phenomenon – which instead is found in the Full Body condition – likely due to a less specialized motor system recruitment to compensate for visual discontinuity. Hence, the complex pattern found on corticospinal excitability in the different experimental conditions may underlie intertwined and complementary effects reflecting mirroring, attentional, and embodiment processes. Likely, M1 mirror recruitment in VR environment follows more complex patterns at variance with standard settings where the movement is simply observed on a screen in front of the participants^{18,38}. However, from the present data, our suggestion remains a speculation. Further studies are needed to clarify better the neurophysiological substrates underlying action observation in immersive environments like the ones adopted here.

Regardless of the specific modulation responsible for the MEP patterns, our results further suggest that stronger visual continuity between the virtual and real body (i.e., Full Body condition) is a vital condition for inducing muscle-specific motor resonance, at least when the subject is embodied into a virtual body. This evidence could be highly informative for future studies and clinical treatments exploiting action observation VR settings³⁹. It must be noted that, in the present study, regardless of the observation of a static or moving virtual hand, participants presented higher motor cortex excitability in the FDI muscle during the Full Body and Upper Limb conditions compared to the Detached Hand one. This evidence further advises that, in an immersive environment and when the continuity between the real and virtual body is increased, even simple observation of a static hand would induce increased cortical activation in M1, as if the stimulus would be interpreted in terms of the potential movement of one’s body part^{40,41}.

Overall, our patterns suggest that the sense of embodiment toward the virtual body and the continuity of the virtual body with the real one can have an impact on M1 excitability. Indeed, the results from this study show that the sense of ownership and disownership toward the real body mediated the corticospinal excitability effects. Accordingly, previous investigations demonstrated a relationship between the sense of embodiment and motor cortex activation when embodied in a virtual body^{15,42–44}. In the study conducted by Gonzalez-Franco and colleagues⁴³, participants were fully embodied in a virtual body observed from a first-person perspective. The virtual right hand was visually aligned with their real hand. Event-related brain potentials (ERPs) were recorded in two conditions: a condition where the participant’s virtual hand was attacked with a knife and a control condition where the knife only struck the virtual table. In this study, the authors observed mu-rhythm Event-Related Desynchronization (ERD) and Readiness Potential negativity in the motor cortex when the virtual hand was threatened, as would be expected if the real hand was threatened and the participant tried to avoid harm⁴³. Mu-rhythm desynchronization has been highly related to motor cortex activation⁴⁵. Moreover, another study has revealed that changing the physical characteristics of an embodied virtual body can increase motor cortex excitability⁴⁴. In this study, the authors induced the “stone arm illusion” while participants were embodied in a virtual body and provided single-pulse TMS to evaluate changes in motor cortical excitability associated with the stone arm illusion. To investigate if the “stone illusion” affected motor control, participants performed a reaching task with the human and “stone” virtual body. The results indicated that the strength of the illusion was associated with enhanced motor cortical excitability measured by MEPs, suggesting a sort of motor compensation having embodied the illusory stiffness of the body. Moreover, it has been shown that feeling fully embodied in a virtual body can enhance motor rehabilitation processes in patients with upper limb motor disorders, along with a positive relationship between the functional recovery of the upper limb and the reported levels of ownership and agency over the virtual arm¹⁵. Kilteni and co-authors also demonstrated that inducing the illusion of losing a virtual arm when observing the virtual body from a first-person perspective decreases MEPs of the extensor digitorum communis muscle for the contralateral sensorimotor cortex⁴⁶. This finding suggested that inducing short-term illusory perception of missing a body-part can trigger inhibitory effects on corticospinal pathways. Consistent with this study, our results have also shown that feeling disownership toward the real body mediates MEPs responses. Additionally, previous work has provided physiological evidence for a reduction of M1 motor excitability in the hand region when the feeling of disembodiment toward the real hand is induced by bodily illusions²⁶.

The present study sheds new light on understanding the role of virtual embodiment on motor cortex excitability. Results show how observing virtual hand movements connected to the rest of the virtual body or virtual arms from a first-person perspective increases motor excitability in the contralateral M1. Such an effect is mainly mediated by the sense of ownership and disownership toward the virtual body. These results may help in designing new applications that combine non-invasive technologies (IVR and TMS) to increase M1 excitability in clinical populations presenting motor disorders.

Limitations of the study

This study has some limitations that should be acknowledged. First, overall, the participants reported low scores regarding the sense of embodiment in the questionnaire. Even though the scores related to the sense of body

ownership are higher in the Full Body condition compared to the Upper Limb and Detached Hand conditions, still the scores are above 1 in a Likert scale going range from -3 to 3 . One possible reason for this result is that the sense of embodiment has been induced by using a 360° camera (body capture from a first-person perspective), as in the study from¹³. Even though the induction of sense of embodiment through 360° images has been demonstrated, it is more complicated to perfectly co-locate the position of the real body with the virtual one. Regarding this, some studies have shown that co-location is a crucial aspect to induce the sense of embodiment toward the virtual body⁴⁷. Given the demonstrated role of multisensory correlations (visuo-tactile or visuo-motor correlations) in enhancing the sense of embodiment in virtual reality compared to mere visual exposure⁴⁸, future studies using 360° video to induce the sense of embodiment will benefit from incorporating multisensory correlations before the action observation task to enhance the sense of embodiment.

Moreover, the sample size in this study was relatively small regarding the mediation analyses, larger sample sizes are necessary for future research to confirm and extend these results, ensuring more robust and widely applicable conclusions. Lastly, for rehabilitation purposes, it would be beneficial to test the effects using more ecological movements to increase the applicability of these findings in a clinical setting.

Methods

Participants

Thirty-two healthy participants were recruited for the experiment (female=21, male=11, mean age \pm SD = 23.2 ± 3.08 , age range = 19–29). All participants were right-handed as assessed by the Edinburgh Handedness Inventory³⁶. All participants filled in a questionnaire directed to evaluate any possible contraindications to participate in TMS study (TMS Safety Questionnaire⁴⁹). The study received ethical approval from the University of Milano-Bicocca's Ethical Committee and conducted in accordance with the standards of the Declaration of Helsinki. All participants provided written informed consent for their participation in the experiment.

Experimental procedure

Participants were seated in a chair, with their left arm resting on the table positioned in front of them and their right arm resting on the legs, under the table, and out of their view. This placement replicated the position of the virtual body in the Full Body condition. Subsequently, the three phases of the experiment began (Fig. 1A): (i) *Neuronavigation procedures and resting Motor Threshold (rMT) determination*. The experimental session began with the localization of the left-hand FDI hotspot and with the determination of the individual rMT. (ii) *Single-pulse TMS over the right M1 during an Action Observation Task in an IVR scenario*. Corticospinal excitability was assessed by recording MEPs, elicited by single-pulse TMS over the right M1, in both the left-hand FDI and the ADM muscles while participants viewed static or moving left-virtual hand images in a randomized order (i.e., Action Observation Task). During the Action Observation Task, three different conditions in terms of the visual continuity of the hand-stimulus image to the observer's body were presented in an IVR scenario from a first-person perspective: Full Body, Upper Limb, Hand Detached (Fig. 1B). During the Full Body condition, participants observed the virtual hand integrated in a full-body perspective, without discontinuity between the virtual and the participant's body. During the Upper Limb condition, participants observed the virtual hand integrated in an Upper Limb visually discontinuous from the participant's body. In the Detached Hand condition, participants observed the virtual hand in isolation, fully discontinuous with the participant's body. The experimental conditions were counterbalanced among the participants.

The virtual reality scenarios were presented through the HMD (Oculus Quest 2) connected to a computer (Notebook Dell Alienware; M15CPU: intel i7-8750 H, 8GB RAM, GPU NVIDIA RTX 2070 Max-q, Fig. 1C). Trials randomization and timing of the stimuli presentation were all implemented using Unity 2021 software. (iii) *Questionnaires*. At the end of each condition, participants filled out an adapted questionnaire measuring the sense of Embodiment. Specifically, the questionnaire assessed the sense of ownership and agency toward the virtual avatar, and disownership of the real body^{9,26}. To account for the potential effects of virtual reality, we also administered two additional questionnaires to measure the level of discomfort or sickness experienced (Simulator Sickness Questionnaire³⁰), and the extent to which participants felt immersed within the virtual environment^{28,29} (see Supplemental Materials, Tables 1 and 2). The entire experiment took approximately 1 h to complete.

VR action observation task

Participants performed a standard Action Observation Task, which involved the presentation of two pictures depicting a left hand in either static or moving conditions (Fig. 1A). Thus, two distinct types of visual stimuli were presented: static, where the hand remained stationary, and moving, in which the index finger performed an abduction-adduction movement (adapted from^{22,25}). Participants observed and focused on these visual stimuli presented in three distinct conditions (Fig. 1B), all involving complete immersion in a VR environment using an HMD. (i) In the Full Body condition, participants were immersed in the experimental room, which could be explored from a 360° -degree perspective. In this setting, the virtual body's position precisely matched that of the participant's real body, and the virtual environment replicated the experimental laboratory. This setup was designed to guarantee that participants experienced the same viewpoint as if they were looking at their own bodies. To achieve this, we captured 360° -degree photos (stereoscopic images) with a 360° camera (Insta360 ONE X2) mounted on the forehead of a seated female or male experimenter with their arm resting on the table. This setting ensured that participants experienced the same perspective of their own posture and surroundings and that stimuli matched the gender of each participant. (ii) In the Upper Limb condition, a 180° picture of the arm placed on the table against a 360° black background was presented, i.e., similar to a cinema mode. Importantly, participants in this condition did not see the virtual body: there was a separation between the

observed arm and the participant's own body, without a visual continuity between the two. (iii) In the Hand Detached condition, participants observed an isolated hand against a 360° black background, completely detached from any associated body. Before starting each block of a given condition, participants observed the static stimulus for one minute to familiarize themselves with the virtual scenario. Then, trials depicting the static and the moving hand were presented in a randomized order, for a total of 60 trials (30 depicting the static left hand, 30 depicting the moving left-hand index finger) in each block. Regardless of the VR condition, each trial started with the presentation of the static hand for a jittered variable duration lasting from 2250 to 3250 msec. Subsequently, a second frame, lasting 750 msec, was displayed. In the “moving hand” trials, the second frame depicted the abduction movement of the index finger, inducing the perception of the finger movement. In the “static hand” trial, the second frame was again the static hand, with the finger maintaining the same position throughout the trial (i.e., no movement). To evaluate motor system excitability by action observation, a TMS pulse was delivered over the right M1 after 250 msec from the onset of this second frame^{22,25} and MEPs were simultaneously recorded from FDI and ADM muscles (see TMS and EMG recording sections). Given previous evidence using such kind of biological movements, we expected that MEP facilitation would be recorded only, implicated in the observed index-finger movement^{22,24,25}.

During the task, participants were instructed to count the occurrences of finger movement to ensure that they paid attention to the visual stimuli (similar to Matamala-Gomez and colleagues¹⁵). This approach was chosen to keep participants engaged without overloading their cognitive resources. We did not prioritize accuracy in the counting task, focusing instead on maintaining attention to the visual stimuli, which helped minimize distractions. No participants reported the task as overly demanding. In addition, MEPs were also recorded during a control condition, in which only a fixation cross was presented, both at the beginning and at the end of the session (20 trials each). Refer to Supplementary materials for detailed analysis and results for the control condition.

TMS

A figure-of-eight coil (diameter = 70 mm) connected to a biphasic Magstim Super Rapid2 stimulator (Magstim, Whitland, UK), was employed to administer TMS pulses. Each session began with the localization of the left-hand FDI motor hotspot and the determination of individual rMT. The individual rMT was calculated by employing the parameter estimation by sequential testing (PEST) procedure, which is a maximum-likelihood threshold-hunting procedure optimized for rMT detection using the software MTAT 2.0^{38,39}. On average, participants presented an rMT of $63.3\% \pm 11.4\%$ of the maximum stimulator's output. During the Action Observation Task, TMS intensity was set at 120% rMT^{22,50}. On average, in our sample, this intensity induced MEPs' peak-to-peak amplitude of about 1.5 mV in the contralateral FDI muscle. When stimulating the right M1, the coil was positioned tangentially to the scalp, with the handle oriented backward and laterally at a 45° angle to the sagittal plane, to induce an anterior-to-posterior (first phase)/posterior-to-anterior (second phase) current flow in the precentral gyrus. The placement and positioning of the TMS coil during the experiment were rigorously monitored using a neuronavigation system composed of IR Polaris optical tracking system (SofTactic 3.0, E.M.S., Bologna, Italy, www.softaxic.com).

EMG recording

Pre-gelled surface electrodes (15 × 20 mm Ag-AgCl, Friendship Medical, Xi'an, China) were applied on the left hand to record the EMG signal (Fig. 1A, C). The active electrodes were positioned over the muscle bellies of left-hand FDI and ADM muscles. The reference electrodes were placed over the metacarpophalangeal joint of the index finger (for FDI) and of the corresponding joint of the little finger (for ADM). The ground electrode was positioned over the wrist. Before data acquisition, the signal from FDI and ADM channels was visually inspected to ensure that the background noise remained below 20 µV. Signal software (version 3.13) connected to a Digitimer D360 amplifier and a CED micro1401 A/D converter (Cambridge Electronic Devices, Cambridge, UK, www.ced.co.uk) were employed to record MEPs with a sampling rate of 5000 Hz. During the action observation task, they were collected from 100 ms before to 200 ms after the TMS pulse and stored for subsequent offline analysis.

Behavioral assessment (questionnaires)

The perceived sense of ownership and agency over the virtual body (adapted from⁹), along with the disownership over the real body²⁶, were measured using a 7-point questionnaire (ranked from -3 to +3), administered after being exposed to each experimental condition (See Table 1). After completing the experimental session, two supplementary questionnaires assessing the potential impact of IVR were administered. The first questionnaire assessed the degree of discomfort or sickness felt, utilizing the Simulator Sickness Questionnaire by Kennedy and colleagues³⁰. The second questionnaire focused on participants' perceived immersion within the virtual environment, as measured by the Virtual Reality Experience scale^{28,29}. The 7-point questionnaire investigated the VR experience through 7 items, ranked from -3 to +3, assessing three different dimensions: (i) the sense of “being there”, measuring the psychological state within the VR environment (Item 1, 3, and 5), (ii) the degree to which the experience in the virtual environment feels more “real or present” compared to daily reality (Item 2, and 4), and (iii) the *locality*, the feeling of visiting somewhere rather than just seeing something (Item 6 and 7) (see Supplemental Materials for detailed analysis and results concerning these two additional questionnaires).

Statistical analysis

For MEP analysis, the Signal software was employed, and the standard preprocessing pipeline adopted in our laboratory was applied^{25,50}. In detail, EMG signal was amplified and band-pass filtered within the 10 to 1000 Hz range with a 50-Hz notch filter applied. Trials containing artefacts, such as muscular or background noise, that

deviated from 200 μV within the 100ms window preceding the TMS pulse were automatically excluded. Finally, MEPs peak-to-peak amplitude was calculated for each muscle in each trial in a time window between 5ms and 60ms from the TMS pulse. Trials in which MEP amplitude was lower than 50 μV were excluded from analysis. MEP amplitudes that fell beyond ± 2 SD from the mean of each condition and in each participant were considered as outliers and subsequently removed from the analysis. This procedure resulted in the removal of 2.08% of recorded MEPs. Finally, to take under control variability in cortical excitability across subjects, we normalized MEP amplitudes within each participant. Specifically, for each participant, we subtracted the individual's mean MEP amplitude from each raw MEP value and then divided the result by the standard deviation of their MEP amplitudes. This procedure reduces inter-individual differences, controls fluctuations in motor cortex excitability over time, and enhances comparability across participants and conditions.

We employed a mixed-effects design to analyze our dependent variables (*mixed function* in Stata), considering as fixed effects: virtual body continuity condition (Full Body, Upper Limb, Detached Hand), type of virtual hand movement (static or moving), and muscle (FDI or ADM) and random effects over the individual subjects. In detail, we analyzed differences in MEPs amplitude and embodiment questions scoring across conditions with a multilevel mixed-effects linear regression test (the *mixed function* in Stata). The significance level was set at $p < 0.05$. Furthermore, a pairwise comparison with the Scheffe test for multiple comparisons was used to identify differences between virtual body continuity conditions. For differences in embodiment scores across conditions, we used a multilevel linear regression test (*mixed function* in Stata). Lastly, to further explore the mechanism through which body continuity influences corticospinal excitability, we conducted a mediation analysis using a seemingly unrelated regression (*sureg function* in Stata). This analysis examined whether the sensation of embodiment, experienced during virtual body exposure, mediates the effect of body continuity on corticospinal excitability. In all analyses, we included participants as a random effect variable to properly account for inter-subject variability. Analyses were performed using Stata13 (StataCorp LP, College Station, TX, USA; <https://www.stata.com/>).

Data availability

Data have been deposited at the Open Science Framework (OSF) and are publicly available at https://osf.io/473wg/?view_only=c89faf2295bd4178a0446fab4027c1a5.

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Declarations

Competing interests

The authors declare no competing interests.

Additional information

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