

Embodying their own wheelchair modifies extrapersonal space perception in people with spinal cord injury

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Abstract

Despite the many links between body representation, acting and perceiving the environment, no research has to date explored whether specific tool embodiment in conditions of sensorimotor deprivation influences extrapersonal space perception. We tested 20 spinal cord injured (SCI) individuals to investigate whether specific wheelchair embodiment interacts with extrapersonal space representation. As a measure of wheelchair embodiment, we used a Body View Enhancement Task in which participants (either sitting in their own wheelchair or in one which they had never used before) were asked to respond promptly to flashing lights presented on their above- and below-lesion body parts. Similar or slower reaction times (RT) to stimuli on the body and wheelchair indicate, respectively, the presence or absence of tool embodiment. The RTs showed that the participants embodied their own wheelchair but not the other one. Moreover, they coded their deprived lower limbs as external objects and, when not in their own wheelchair, also showed disownership of their intact upper limbs. To measure extrapersonal space perception, we used a novel, ad-hoc designed paradigm in which the participants were asked to observe a 3D scenario by means of immersive virtual reality and estimate the distance of a flag positioned on a ramp. In healthy subjects, errors in estimation increased as the distance increased, suggesting that they mentally represent the physical distance. The same occurred with the SCI participants, but only when they were in their own wheelchair. The results demonstrate for the first time that tool-embodiment modifies extrapersonal space estimations.

Keywords:

1. *Body representation*
2. *Body ownership and disownership*
3. *Spinal cord injury*
4. *Space and Action representation*
5. *Tool incorporation*

Immersive Virtual Reality

Introduction

Embodied Cognition Theories (Shapiro et al, 2011) posit that higher-order cognitive functions are influenced by a variety of sensorimotor variables ranging from body representations to transient physiological conditions (e.g. fatigue, illness, carrying heavy objects).

The notion that information coming from the body can, at least in part, modulate cognition is nowadays readily accepted (Masson et al., 2015).

Changes in body representations may in principle affect the space that organisms inhabit (Aymerich-Franch 2018). There are a number of studies which have investigated the perception of extrapersonal space (i.e. distant space, where objects are not reachable without locomotion). It has been shown that wearing a heavy backpack leads to an overestimation of the inclination of a slope (Bhalla and Proffitt 1999) and of distances (Proffitt et al. 2003). This effect has been found in elderly participants, in people in poor physical health (Bhalla and Proffitt 1999) and in the presence of fatigue. The opposite effect has been observed after the assumption of energy beverages (Schnall et al. 2010). Moreover, the perceived distance of a target increases in tandem with the effort associated with mental representations relating to a specific action, indicating that corporeal states also impact on action planning. For example, if someone is asked to reach a target on foot, the perceived distance will be modulated by the effort specifically associated with the act of walking (and not by other actions, for example throwing an object, Witt et al. 2004).

These results may be explained within the Embodied Perception framework according to which perception is the result of the integration of body, action goals and facilitations or obstacles found in the environment (Proffitt, 2006). According to the Economy of Action principle, if perceivers have low physiological energy (e.g. fatigue) or are in physically demanding situations (e.g. wearing a heavy backpack), distances and slopes are perceived respectively longer or steeper and therefore more difficult (Proffitt, 2006). Thus, the more a mental action is demanding for the body, the greater the error in space perception.

The finding that perceptual errors increase in line with the effort required suggests that the process involved when a person mentally travels across a given distance is based on a spatial metric which is comparable to that implemented when actually performing the same action.

Despite this already established notion, to the best of our knowledge, no experimental research has thus far investigated whether permanent changes in body representations and action representations modify the perception of extrapersonal space.

People who have spinal cord injuries (SCI) suffer from below lesion motor and sensory deficits due to the disconnection of body-brain afferent and efferent tracts. A lesion below the seventh cervical spinal cord segment leads to sensorimotor deficits that affect the lower but not

upper limbs. Research on people with SCI has explored the effects of deafferentation and deafferentation on body-related cognitive functions, comparing responses with those of healthy and paralysed body parts (respectively upper and lower limbs) within individuals (Lenggenhager et al., 2012; Ionta et al. 2016; Scandola et al. 2014, 2016, 2017b, 2019a; Pozeg et al, 2017).

Given their sensorimotor deprivation, people with SCI represent a condition that makes it possible to test the assumptions of the Economy of Action principle. In order to move in the space around them, they use their wheelchairs constantly and it thus becomes a very special tool for them. Indeed the proficient use of a wheelchair enables them to independently navigate in the surrounding space. Importantly, each wheelchair is in principle tailored to its unique user. Studies suggest that wheelchair users report subjectively that their wheelchair becomes part of their own bodily self (Papadimitriou, 2008) and that people with SCI become experts in discriminating information associated with wheelchair use visually (Scandola et al., 2019a) or auditorily (Pazzaglia et al., 2018).

However, to the best of our knowledge, to date no study has experimentally explored whether there is in fact a special relationship between SCI people and their wheelchair. If there is, it might also be that the wheelchair user's space perception and action representation may be influenced by their own wheelchair (as compared to a different wheelchair).

This study aims to investigate the relationship between body and space representation, with particular reference to the effects of tool embodiment in terms of changes in the perception of distances in extrapersonal space. The main hypothesis of the present study is that the degree of wheelchair embodiment impacts the user's perception of extrapersonal space according to the Embodied Cognition and Economy of Action theories.

There were three consecutive steps relating to the rationale of the study. First, we investigated whether the body representation of chronic SCI individuals includes their own personal wheelchair but not another wheelchair. If this is the case, it indicates that a different wheelchair would cause a structural change in the user's body representation. Secondly, the effects of wheelchair embodiment on the user's representation of extrapersonal space were assessed by means of a novel Extrapersonal Space Perception task which was administered in a Virtual Reality environment. It was expected that varying the degree of tool embodiment would modulate the representation of the action and thus also have an effect on the estimates relating to extrapersonal space resulting in an increasing error trend typical of the Economy of Action theory. This would in theory occur only when the person's own wheelchair is embodied as embodiment ensures the user's representation relating to distances in the surrounding space. Lastly, the link between wheelchair

embodiment and extrapersonal space representation was directly investigated with the aim of discovering whether body representations and space representations are connected, in which case a systematic mutual variation in the two representations would be found.

Methods

In Experiment 1, a Body View Enhancement Task provided an objective measure of the embodiment of each participant's own wheelchair with respect to another wheelchair. Then, in order to estimate the impact of embodiment on extrapersonal space representation, the same individuals carried out a novel task involving an estimation of distances and inclinations (Experiment 2). The correlation between the results in the two tasks was then analysed.

Participants.

20 paraplegic adults (age ≥ 18 years, mean=44.20, SD=12.63; 2 females) with a traumatic complete lesion (ASIA Impairment Scale, AIS=A; Neurological level, NLI=T1 and below) participated in the study. Using G*Power software (version 3.1.9.2), an a-priori sample size computation indicated that 18 participants were sufficient to attain an a-priori power of 0.80 ($f^2=0.25$, $\alpha=0.05$). The participants were affected with complete deafferentation and deafferentation (i.e. the absence of sensations and voluntary motricity) in the below-lesion body parts (in this case the lower limbs), with normal sensory-motor functioning of the unaffected body parts (in this case the upper limbs; AIS: muscle strength=grade 3, sensory score=2). They were in a chronic phase after lesion onset (interval from lesion ≥ 1 year) and had been using their manual wheelchairs regularly to navigate in the space around them for at least 6 months. Patients with sensory-motor deficits in the upper limbs, a history of degenerative or tumour pathology, traumatic brain injury or psychiatric symptoms were excluded. The clinical and demographical data are reported in Table 1.

All of the participants signed the consent form. The study was approved by the Ethics committee of the Province of Verona (Prot. N. 355) and was conducted in accordance with the ethical standards of the Declaration of Helsinki (2008). The SCI participants were recruited on a voluntary basis thanks to the cooperation of the Spinal Units of the IRCSS Sacro Cuore Hospital (Negrar, Verona) and the Morelli Hospital of Sondalo, both of which are members of the International Group for Research into spinal cord injury (<http://profs.formazione.univr.it/npsy-labvr/spinal-cord-injury-research-center/>).

ID	Gender	Age	NLI	Benton
1	M	43	T4	28
2	F	47	T3	30
3	M	37	T6	25
4	M	53	T1	26
5	F	22	T6	27
6	M	37	T8	29
7	M	68	T2	26
8	M	45	T4	27
9	M	19	T5	27
10	M	44	T10	29
11	M	33	T5	26
12	M	64	T6	24
13	M	43	T5	20
14	M	51	T11	26
15	M	64	T4	29
16	M	37	T7	28
17	M	35	T4	29
18	M	44	T6	27
19	M	51	T5	27
20	M	47	T5	22

Table 1: The participants' demographic and clinical data. NLI=Neurological Level of Injury (i.e. the most rostral spinal cord segment where all the sensory-motor functions are spared). Benton=Judgment of Line Orientation- Form H, cut-off=17 (Benton 1991 It. Vers., 1990; Lezak et al. 2012, see Experiment 2)

Statistical analyses.

The statistical tests were computed within the framework of Bayesian statistics. In particular, the potential effects of independent variables (i.e. factors/covariates) on data were

analysed. The results are expressed in terms of Bayes Factors (BF_{10}). A $BF_{10} \geq 3$ indicates the presence of a difference between two or more groups of data (i.e. the alternative hypothesis), while $BF_{10} \leq 1/3$ indicates that data distributions are equal (i.e. confirmation of the null hypothesis). All of the BF_{10} factors within 3 and 1/3 were considered inconclusive, while $BF_{10} = 1$ meant an equivalence between the two hypotheses. For a complete description or the rationale behind the statistical analyses, see SM1.

Experiment 1. Body View Enhancement Task (BVET)

Materials and experimental setting.

12 Light Emitting Diodes (LEDs) were positioned (by means of velcro) on the participants' clothes and either on their own wheelchair (Own wheelchair) or on another wheelchair (Other wheelchair) which was not theirs but which they were using for the purposes of the task (i.e. the two conditions). The positions were as follows: for the upper part of the body (Upper Body), 2 LEDs were placed on the abdomen (5 cm on the right and left of the navel, respectively) and 2 on the chest (vertically aligned with the LEDs on the abdomen); for the lower part of the body (Lower Body), 2 LEDs were placed on the proximal and 2 on the distal parts of the thighs, in the centre; for the wheelchair (either Own or Other Wheelchair), 2 LEDs were placed on the armrests (aligned with the LEDs on the proximal part of the thighs) and two were on the upper part of the wheels (aligned with the LEDs on the distal part of the thighs) (See Figure 1a). All the LEDs were perfectly visible to the participants who were sitting in their own or in another wheelchair. The LEDs were controlled by means of an Arduino Uno TM microcontroller/home-made electronic toolbox which was connected to a computer. They were turned on one at a time in a randomised order and at randomised intervals (from 1500 to 3500 ms, mean 2500 ms) and they remained on until the participant pressed the response button. In the absence of a response, the LED was turned off after 1000 ms. Each LED was turned on 5 times, for a total of 60 randomised trials.

In two Control Conditions, the participants were sitting in the same position in a wheelchair (in some cases only in their own but in others in both their own and another wheelchair), but the LEDs were placed on a wooden board that was resting on the armrests of the wheelchair, hiding the wheelchair from sight. The spatial positions of the LEDs corresponded to the positions of those on the thighs and on the wheelchair in the experimental conditions, with the only difference being that these were aligned on a horizontal plane (i.e. all on the board, see Figure 1b). In these conditions, there were no LEDs on the upper body meaning that there were 8 LEDs in total, giving a total of 40 (5 times for each LED) randomised trials.

A preliminary experiment was carried out with a group of 15 healthy controls to confirm that the various different 3D distances from participants of the LEDs did not influence their responses (all $BF_{10} < 1/3$, more details in SM2.1).

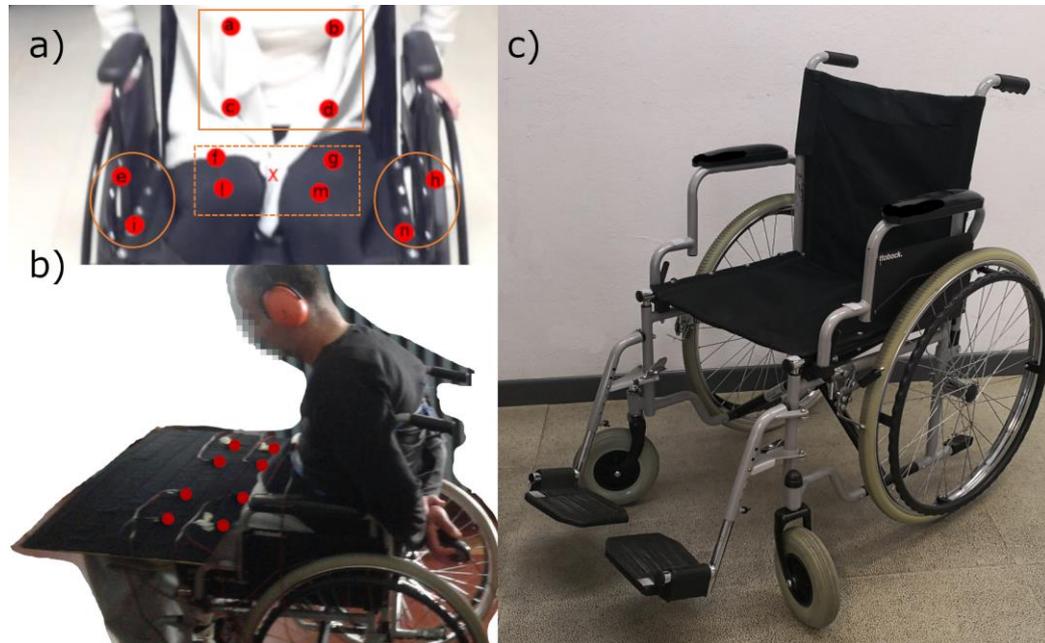


Figure 1: LED positions for the Body View Enhancement Task. A) the LED positions are represented by the red circles, separated into Upper Body (within the straight line rectangle), Lower Body (within the dotted line rectangle) and Wheelchair (within the ovals). B) the participant's position during the Control conditions. The LEDs are all positioned on the board, in correspondence with the Lower Body and Wheelchair LEDs. C) A photograph of the wheelchair used in the "Other wheelchair" condition

Procedure.

The participants were seated in their own or another wheelchair which they had never used before. This latter was a manual wheelchair of the type used in the hospital wards for hemiplegic patients. They wore anti-noise headphones to isolate themselves from the environment. Their arms were either at their sides (with the mouse in their right hand) or behind their back, in this latter case with the left hand holding the right hand. The Arduino Uno™ microcontroller and the computer were placed on the floor behind the wheelchair.

In a preliminary phase, the functioning of the LEDs was checked and the participants were familiarised with the task. This was a speeded-detection task in which the participants were asked to press a mouse button with their right hand as soon as they saw a target LED lighting up. The response times were automatically recorded.

The same procedure was followed for the Control condition in which case the LEDs were on a wooden board. As 9 of the participants only performed the task in this condition while they were sitting in their own wheelchair and the other 11 participants performed the task in both of the wheelchairs (i.e. their own and another one), a preliminary analysis was carried out to verify that there were no differences in the control condition responses due to the wheelchair used. A similar control test was also done for the hand positions (i.e. either arms at their sides or behind their back). No differences emerged in any of the comparisons allowing us to consider all of these data as a unique Control condition (SM2.2).

In this way, the three Conditions were counterbalanced across the participants (Latin square): i) with the participant's own wheelchair (Own condition); ii) with another wheelchair (Other condition) and iii) with the LEDs on a wooden board (Control condition). A 3x3 design was devised with Position (Upper Body, Lower Body and Wheelchair – or corresponding positions on the board) and Condition (Own, Other, Control) as factors. Reaction Times (RT) were analysed.

According to the Body View Enhancement effect (Kao and Goodale 2009), the RTs were expected to be shorter for the LEDs placed on the body as compared to the responses for the LEDs placed on the wheelchair. In addition, we expected that there would be differences between the responses corresponding to the LEDs on the body, with shorter RTs for the LEDs above the lesion as compared to below lesion body parts, representing an index of reduced embodiment of the deafferented and deafferented body parts. For the same reason it was crucial for the aim of the study that there was an indication of the embodiment of the participant's own wheelchair with respect to another wheelchair with shorter RTs for the LEDs positioned on their own wheelchair (Own condition) than for those on the other wheelchair (Other condition).

Results.

The main tendencies and variability of the distributions are reported in terms of mode and Highest Density Interval (with HDI 89% being the narrowest interval including 89% of the distribution). Behavioural results were analysed by means of Bayesian Multilevel Gamma models (see SM1.1).

In order to measure the degree of embodiment relating to the participants' own wheelchairs, we compared the RTs to LEDs in the various different Positions (i.e. Upper Body, Lower Body, Wheelchair) in the two Conditions (i.e. Own, Other) against the Control Condition. In this way, the presence or absence of differences with respect to the Control condition were considered as an index of embodiment or lack of embodiment, respectively.

It is worth noting that only in the Own Condition were differences found with respect to the Control Condition (Mode=450.22; HDI=[401.04, 510.16]), both in the Upper Body (410.12, [333.74, 461.98]) and the Own Wheelchair positions (414.54, [337.96, 466.16]) (both $BF_{10} > 150$). In all of the other conditions, there were no differences to the Control condition (all $BF_{10} < 0.01$, see SM2.3 for more details). This indicates that the person's own wheelchair had been processed as an embodied object, in a similar way to the upper, healthy body parts. Nevertheless, the Upper Body did not appear to be processed as embodied when the individuals were sitting in another wheelchair (446.85, [375.50, 520.68]). Crucially for the aim of the study, the other wheelchair (448.97, [378.11, 523.13]) did not appear to be embodied. Finally, the Lower Body did not appear to be embodied in either of the conditions (Own: 463.29, [386.08, 514.32], Other: 453.79, [381.83, 526.92]).

In addition, for the LEDs on the Wheelchair and the Upper Body, a comparison revealed differences between the Own and Other conditions (both $BF_{10} > 150$), while for the Lower Body the two conditions were equal ($BF_{10} < 0.01$) (see Figure 2).

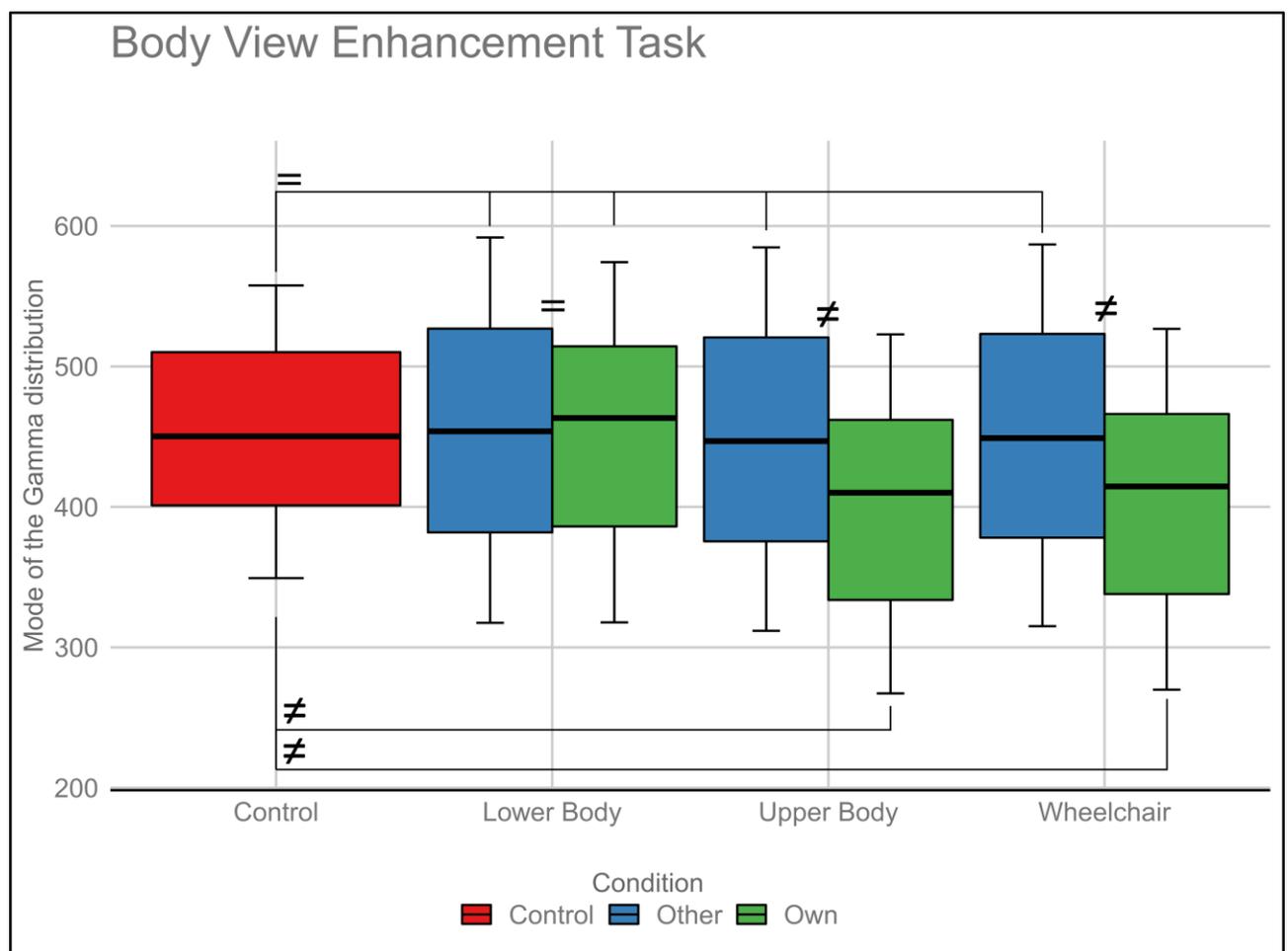


Figure 2: Body View Enhancement Task performance. The Aggregated posterior distributions resulting from the Bayesian Analysis are shown for the three experimental conditions and the various different positions of the LEDs. The boxes in the boxplots indicate the 89% Highest Density Interval, while the black lines in the middle are the Mode relating to the distributions, and

the whiskers are the range of the posterior distribution. =: comparisons with $BF_{10} < 1/3$; \neq : comparisons with $BF_{10} > 3$. Lower reaction times are an index of greater embodiment, while reactions times that are no different from the control condition are an index of a lack of embodiment.

Experiment 2. Extrapersonal space perception task

Once it was ascertained that the participants in the study perceived their own (but not the other) wheelchair as embodied, we investigated the hypothesis that tool embodiment impacts the subjects' perception of space in terms of their perception of angles and distances. To test this hypothesis, we devised a novel, virtual reality-based Extrapersonal Perception Task.

Participants and preliminary measures.

The group of 20 SCI patients who took part in Experiment 1 also participated in this part of the study (Table 1).

The presence of deficits in the visual discrimination of angles and inclinations was excluded by means of the Judgement of Line Orientation- Form H (Benton 1991, It. Vers. 1990). In this test, two target lines drawn in various different spatial orientations (with angles from 0 to 180 degrees) were shown to the participants who were then asked to identify which two lines were identical from those shown inside a geometrical semi-circular configuration formed of 11 lines. These lines were arranged in a sunburst configuration to cover 180 degrees. Each of the 11 lines was labelled with a number and the participants were asked to verbally report the number of those lines which were identical to the targets. The performance of all of the participants was normal in this task (Table 1).

Moreover, in order to normalise the data relating to depth perception in the experimental task, we assessed the participants' general ability in terms of the perception of distances by means of an *ad-hoc* virtual reality based task. The virtual reality scenario was designed in 3DS max 2015 (Autodesk, Inc.), implemented in XVR 2.0 and it was displayed by means of a Head Mounted Display (HMD) Oculus Rift DK1. The scenario consisted of an open space depicted in virtual reality with a flag placed on a ramp at various different distances from the participant's point of view (from 0.5 to 4.5 meters with graduations of 0.25 meters). The target distances (in this case 2, 3 and 4 meters) were showed three times, while other distances were showed only once with the mere purpose of reducing learning effects and habituation for the target distances. The participants were requested to identify the distance of the flag from themselves. The responses regarding the target distances were then used to normalise any errors in the estimate of the distance in the experimental task. This made it possible to check individual responses for various subjective sensitivities to virtual reality distance perception.

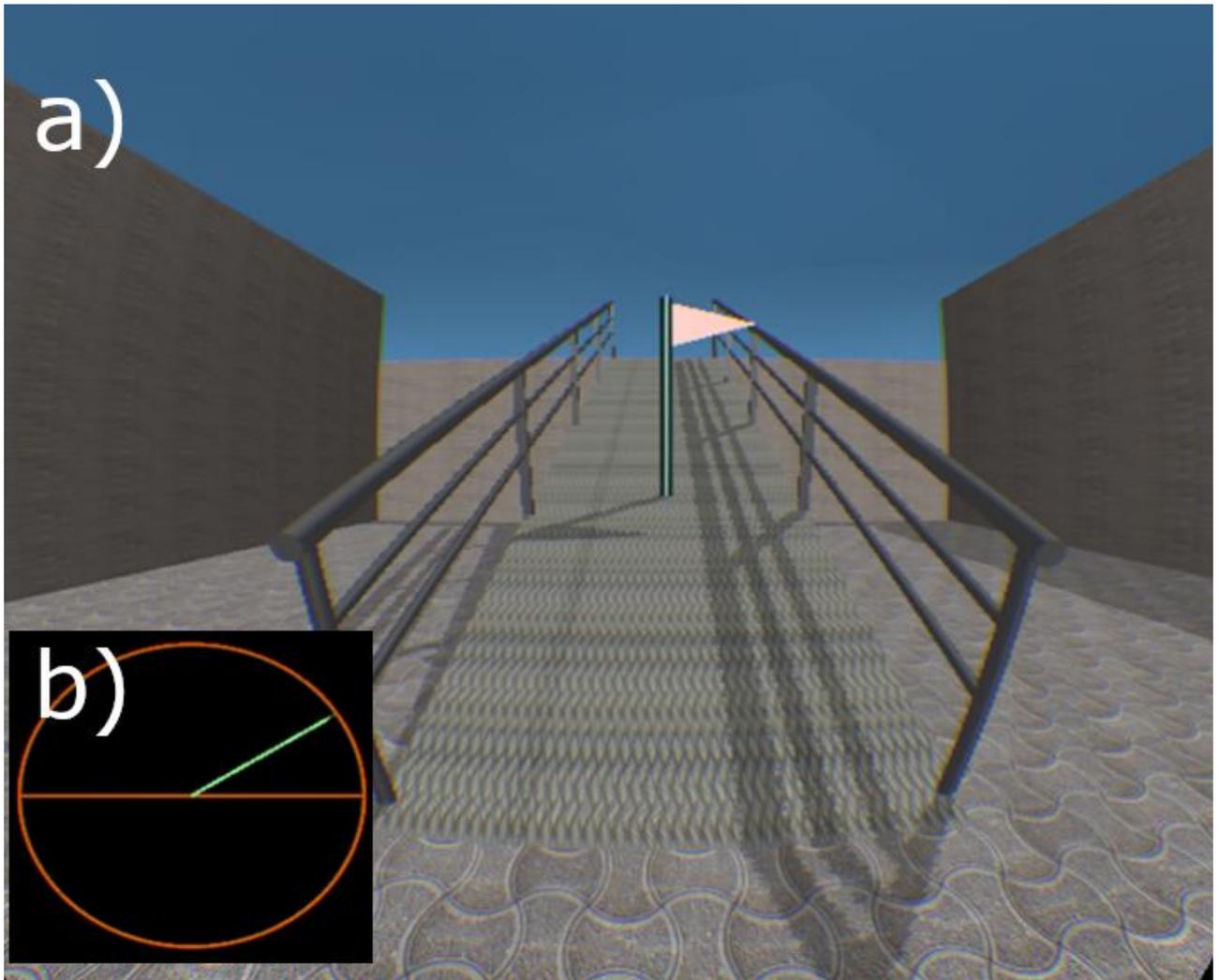


Figure 3: Virtual reality scenario and angle recorder. A) An example of the Virtual Reality scenario for the Extrapersonal Perception Task. B) The angle recorder used to estimate the inclination of the ramp.

Procedure

Participants sat in a wheelchair (either their own or another one which was not theirs). They wore the HMD and the anti-noise headphones to isolate themselves from the environment. In a preliminary habituation phase, they freely explored the virtual reality environment before starting the task.

The task consisted of a series of stimuli (46 per condition) involving a sloping ramp and a flag displayed in the HMD for 1 sec. When the stimulus disappeared, the participant had to give a verbal estimate of the distance of the flag (in cm) and of the inclination of the ramp by orienting a green line in a circle with a keyboard (Figure 3b). A new stimulus was then presented.

Results

Errors in the perception of the distance and the inclination of the ramp were analysed by means of Bayesian Multilevel Linear models (see SM1.2). The results are reported in terms of Bayes Factors, mode and HDI, as in Experiment 1.

Perception of the distance of the Flag

We investigated the hypothesis that the ability to discriminate distances (i.e. the position of the flag, with errors hereafter indicated as: distance errors) was influenced by the Condition (Own wheelchair, Other wheelchair), the actual Distance of the flag (2, 3, 4 meters), and the Inclination of the ramp (4%, 8%, 16%, 24%, 32%). The results reveal a linear effect of Distance ($BF_{10} > 150$; Mode=1.46, HDI=[1.42, 1.51]), and an interaction between Condition and Inclination ($BF_{10} > 150$; Mode=0.68, HDI=[0.60, 0.76]). In fact, only in the Own wheelchair condition did the expected linear effect relating to distance emerge, indicating that only in this case is extrapersonal space estimated by means of a representation of action. See Figure 4A for a graphical representation and SM3, SM3.2 and SM3.3 for further details.

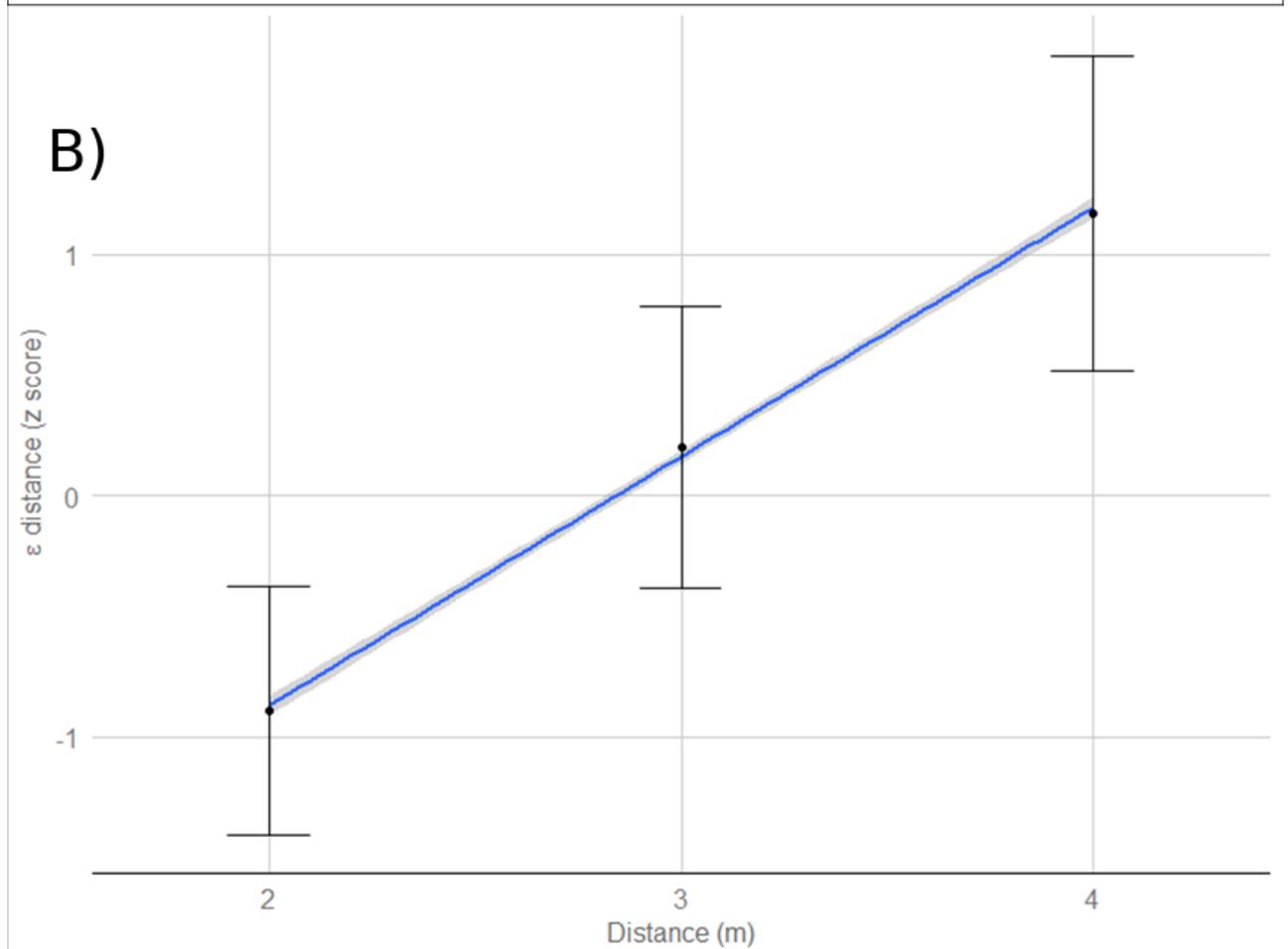
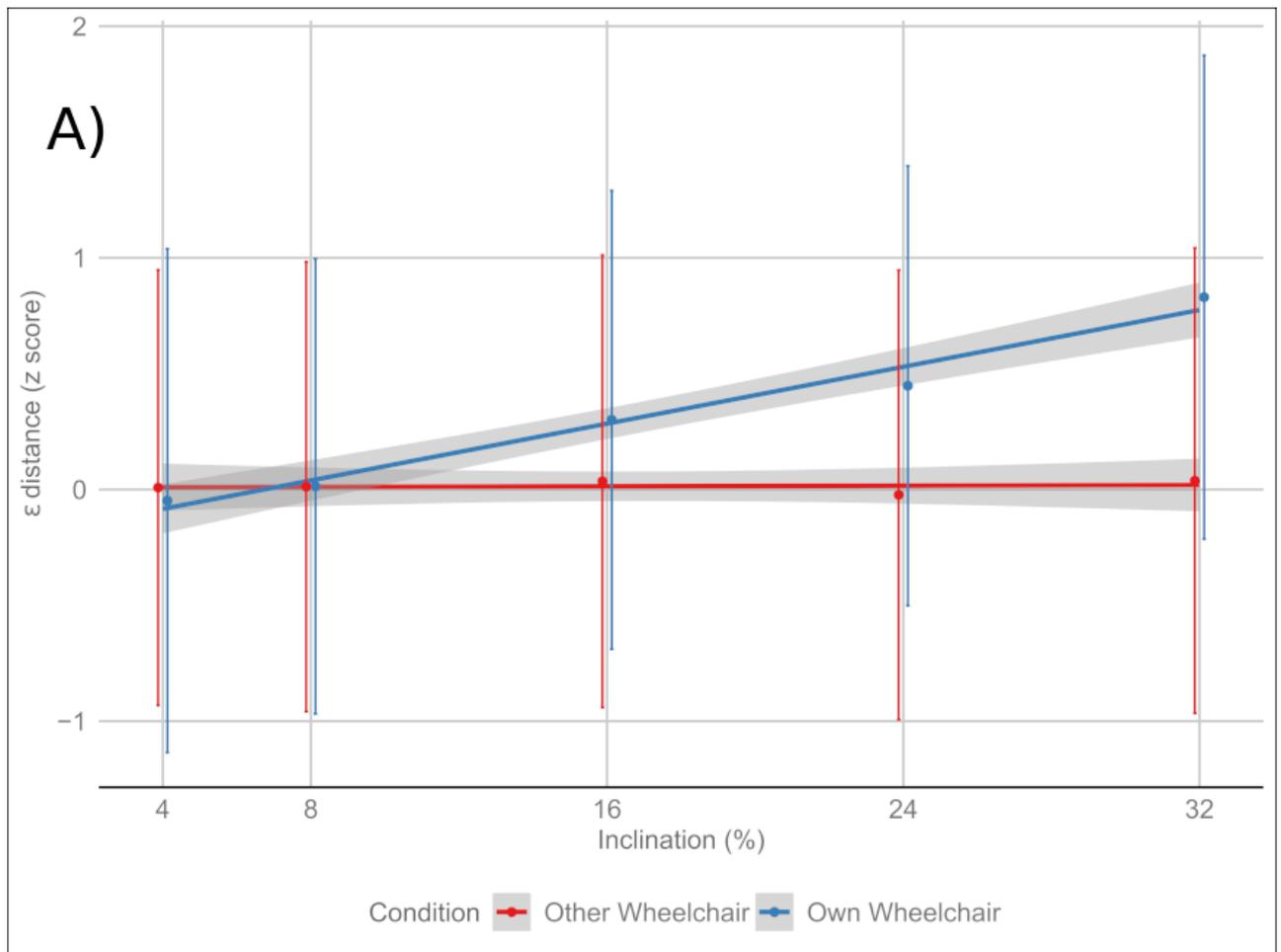


Figure 4: Perception of distance. A) Errors in estimates of the distance of the flag are shown for the various inclinations of the ramp and categorised by condition; B) Errors in estimates of the distance of the flag are shown for the various distances. The points represent the mean, error bars are the standard deviations.

Perception of the inclination of the ramp

The statistical analysis was the same as that done for flag distances, with the exception that the dependent variable was the errors in the estimate of the inclination of the ramp. Results showed a linear effect of the Inclination of the ramp relating to the errors ($BF_{10} > 150$; $Mode = 37.55$, $HDI = [25.46, 49.49]$). Thus, the steeper the slope, the greater the perceptual error. See Figure 4B and SM3, 3.3 and 3.4 for more details. However, with regard to the perception of the inclination of the ramp, the results did not show any effect due to the wheelchair ($BF_{10} = 0.30$; $Mode = 7.92$, $HDI = [-47.35, 46.57]$).

The correlation between the performance in the task and the neurological level of injury

The degree of embodiment of the wheelchair and the perception of the distance of the flag correlated negatively ($BF_{10} = 6.83$, $\rho = -0.41$ $[-0.61; -0.19]$), suggesting that the greater the embodiment, the nearer the flag was perceived to be. In contrast, no correlations were found between embodiment of the wheelchair and extrapersonal perception and the Neurological Level of Injury ($BF_{10} < 1/3$ in both cases). For further details, see SM4.

Discussion

The main aim of the study was to investigate the relation between body and space representations, with a focus on the impact of permanent changes in bodily sensory-motor functions and the continuous use of a wheelchair on extrapersonal space representation. The Economy of Action principle was used as a point of reference since according to this theory, estimates of extrapersonal space in terms of distance and inclination are grounded on the subject's mental representation of the target action executed in that space, which in turn correlates with the perceived current bodily state (Proffitt 2006).

Three results emerged from our experiments: i) in the case of people with SCI, their own wheelchair (but not another wheelchair) is incorporated in their body representations and perceptively treated as part of their own body; ii) the embodiment of the wheelchair modifies extrapersonal space perception (in fact, only when people are sitting in their own wheelchairs is their perception of space subject to the error trend which is typical of Embodied Cognition

Theories, indicating that in order to estimate a distance, they implicitly mentally represent moving across that space) and iii) there is a direct correlation between wheelchair embodiment and extrapersonal space estimations.

Altogether, these results shed new, significant light on the plasticity of body representations and on body-related cognitive modifications following Spinal Cord Injury.

Body representation changes: embodiment and disownership

For SCI individuals, their wheelchair is a special tool. Although they practise using various different, standard types of wheelchairs and become expert users, they report a very particular, unique feeling towards their own (Standal 2011; Papadimitriou 2008; Pazzaglia et al., 2013). Our results experimentally confirm this subjective sensation of wheelchair incorporation, showing that people with SCI respond to LEDs positioned on their own wheelchair (but not on another wheelchair) faster than LEDs on an external object (i.e. the wooden board in the control condition). In contrast, below lesion body parts are treated as external objects (i.e. reaction times are equal to the control condition), and this confirms previous data indicating that, although not verbally reported, a process of depersonalisation of deafferented and deafferented body parts occurs after SCI (Lenggenhager et al. 2012; Pernigo et al. 2012; Scandola et al. 2016, 2017a, b).

There was a novel result in the case of above lesion, healthy body parts. In fact, the responses to LEDs positioned on the trunk changed depending on the wheelchair in which the participants were sitting (i.e. they were faster or equal to control conditions when they were in their own or another wheelchair, respectively). Considered as a whole, these data demonstrate a great dynamicity in body representation and its close relation to and interaction with objects.

Previous research on the embodiment of tools has focused on their use/non-use, showing that embodiment is only possible after a short period of training involving active use of the tool (Maravita et al. 2002; Kao and Goodale 2009; Cardinali et al. 2016; Romano et al. 2018; Weser and Proffitt 2019). On the other hand, tools that do not extend the body modify body representation only after long-term use, while no modifications are found after short-term use (Cocchini et al. 2018; Coelho et al. 2018). In the present study, a modulation in body representation was found which involved both long and short-term use of the tool, but with two opposite effects. When the participants were sitting in their own wheelchair their body representation was extended to incorporate the wheelchair itself, but in the condition with the participant sitting in another, unknown wheelchair, disownership effects also seemed to be induced for the above lesion body parts. The results of the control phase of the experiment which was carried out with both the participant's own wheelchair and another wheelchair enabled us to exclude the possibility that

other factors (e.g. the awareness that the wheelchair was their own, or even just the fact that they were more used to seeing their own wheelchair around the lower part of their body) were playing a crucial role. Similar disownership effects were observed in the case of an experiment carried out with reference to the rubber hand illusion. In this paradigm, the participants were shown a rubber (or virtual) hand which was in a position that was consistent with the position of the body, while the person's real hand was not visible. While the subject was observing the fake hand, a visuo-tactile stimulation was applied to stimulate a sensation of ownership with regard to the fake hand (Botvinick and Cohen 1998). Even the mere sight of a fake or virtual hand can induce an illusory sense of ownership if it appears to be connected to the rest of the body (Tierl et al. 2015).

The embodiment of a fake hand may have parallel disownership effects on the real hand (but see de Vignemont 2011; Guterstam and Ehrsson 2012) as shown by the increased reaction times to tactile stimuli (Folegatti et al. 2009), differences in the temperature of the hand (Moseley et al. 2008; Tierl et al. 2017) and subjective reports of disownership sensations towards the real hand (Longo et al. 2008; Lane et al. 2017; Kannape et al. 2018). In all of these experiments, the disownership of a body part occurs when the participants in the experiment incorporate an equivalent representation of the same body part. Our data enrich these observations with two important concepts: i) disownership of body parts effects may be the consequence of the lack of embodiment of the tool the body is acting with and ii) it is not strictly necessary for the tool to be an extension of or similar to the body part in question.

Studies concerning the body schema of people with SCI indicate abnormal representations for the limbs which are paralysed (Conomy 1973; Ionta et al. 2016; Fusco et al. 2016; Scandola et al. 2017a) and body ownership abnormalities that are somato-topographically organised, hinting at the role of cortical remapping (Scandola et al. 2014; Pozeg et al. 2017). In addition, mental body rotations that involve the paralysed limbs (Ionta et al. 2016) are altered and illusory movements or the misplacement of paralysed limbs are reported during daily life activities (Bors 1951; Conomy 1973; Scandola et al. 2017a).

Conversely, in people with SCI the cognitive component of body representation (body image) is more stable and they are more resistant than healthy subjects to experimentally evoked illusions of movement (Lenggenhager et al. 2012; Scandola et al. 2014; Fusco et al. 2016). In fact, no changes in aspects concerning body image have been found (Stensman 1989; Fuentes et al. 2013), suggesting that this body representation is less prone to cortical neuroplasticity. Taken as a whole, these data confirm our hypothesis regarding a greater dynamicity of multiple body representations. This plasticity probably has an adaptive role which allows individuals to find new

post-lesion strategies to perform actions in the environment around them. Our data show that the body-object relationship plays an important role in this dynamicity.

Body representation and extrapersonal space estimations

External spaces may be perceived in two main ways: using purely visual strategies or by means of an implicit representation of the actions which are potentially executable or imaginable in that space. The Economy of Action Principle suggests that the latter is spontaneously used when an action is possible and that this is modulated by corporeal states (Proffitt 2006).

In effect, body form and actions affect the representation of peripersonal space. For example, in amputees, the presence of a prosthesis extends the person's peripersonal space representation around the whole prosthesis, while its absence produces a space restriction to the area around the stump (Canzoneri et al. 2013). In people with SCI, the extent of their peripersonal space representation around the paralysed lower limbs is reduced, but the application of 15' of passive mobilization leads to a temporary recovery (Scandola et al. 2016).

Fewer data are available regarding extrapersonal space in cases of SCI. Seminal studies have shown that corporeal states have an influence on extrapersonal space representation (Bhalla and Proffitt 1999; Proffitt et al. 2003; Witt et al. 2004). In particular, Schnall, and colleagues (2010) explored the effects of changes in corporeal states on discrimination relating to the inclination of a hill by means of glucose administration. Two groups of participants were asked to refrain from eating 3 hours prior to the experiment and were then randomly assigned to either drink an energy beverage (with the aim of increasing their corporeal energy) or to drink a sugar-free beverage (which would not change their level of corporeal energy). They subsequently participated in two unrelated tests to ensure that there was sufficient time for the glucose to be absorbed (10'). For the next part of the task, the participants wore a heavy backpack weighing approximately 20% of their body weight. They were then requested to estimate the inclination of a hill with an inclination of 29°. The physical fitness, mood, and levels of tiredness, nutrition, fatigue and stress of the participants were checked. The results indicated that the inclination of the hill was always overestimated, but those of the participants who had drunk the energy beverage overestimated less frequently than the sugar-free drink group.

In a similar way, our results provide evidence that changes in body representation (and not only in corporeal state) are associated with changes in extrapersonal space representation. Furthermore, the data indicate that when the tool which is being used to move in the surrounding space is embodied, people with SCI estimate extrapersonal space according to the Economy of Action principle (i.e. using action representation). In contrast, when the wheelchair they are sitting

in is not embodied, action representation becomes impossible and purely visual strategies are then used in order to estimate space. It is also worth noting that sitting in a different (i.e. non-embodied) wheelchair leads to the disownership of healthy, afferented/efferented body parts (as shown in Experiment 1). These results are in line with the observation that embodied knowledge containing the sensorimotor characteristics of a tool and the embodiment of tools shape space perception and action representation (Holt and Beilock 2006; Garbarini et al. 2015). This result sheds new light on the reciprocal modulation between body representation, action and space representation.

Previous studies have shown that in paraplegic individuals, the visual discrimination of bodily actions is specifically impaired for the lower part of the body but not for the upper part (Arrighi et al. 2011; Pernigo et al. 2012). Interestingly, paraplegic individuals who practise sport, due to their hyper-use of healthy body parts, are better at discriminating actions executed by upper limbs with respect to healthy individuals who practise sport, (Pernigo et al. 2012). This supports the role of motor expertise in the modulation of cognition following SCI.

There are also several studies which show that there are differences between people with SCI and healthy individuals in terms of motor imagery (Fiori et al. 2014; Chen et al. 2016; Scandola et al. 2017b; Ionta et al., 2016) and some document reduced activation in the motor imagery networks for the paralysed body parts in chronic SCI individuals (Hotz-Boendermaker et al. 2008; Chen et al. 2016). However, alongside these deficits, recent studies have reported that people with SCI carry out various tasks such as motor imagery by resorting to different strategies with respect to healthy controls (e.g. based on memory instead of on body representations, Fiori et al. 2014; Scandola et al., 2019b). They also develop new specific expertise (Scandola et al. 2019a). These cognitive strategies are influenced by corporeal body states (e.g. musculo-skeletal and neuropathic pain sensations, Scandola et al. 2017b).

Our results suggest that the close interaction between the body and a tool can modulate an individual's capacity to represent actions and, as a consequence, modulate the use of alternative strategies in order to execute cognitive tasks.

Conclusions

In spinal cord injured individuals only their own wheelchair is embodied, and this impacts on their representation of extrapersonal space. In fact, only when a wheelchair is embodied did the participants in the present study use a strategy based on action representations to estimate distances. Thus, changes induced by body representations do not regard only peripersonal but also extrapersonal space. Tellingly, a disembodied wheelchair leads to disownership effects relating to an

SCI individual's body, making it difficult for them even to represent the above lesion body parts which have been spared from sensorimotor problems. These results indicate that body representations are extremely dynamic and that their modulations are a result of a close relationship between the body, the capacity to execute an action or otherwise and the environment. In particular, our data shed new light on the embodiment/disembodiment, ownership/disownership phenomena, revealing for the first time the disownership effects caused by the disembodiment of a tool, although this is not directly connected for function or shape to the disowned body part.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Data availability:

Data and R code for Bayesian Analyses are retrievable at: osf.io/3gkvx

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