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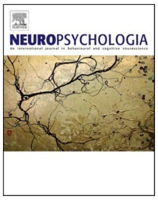

Limb apparent motion perception: Modification by tDCS, and clinically or experimentally altered bodily states

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ABSTRACT

Limb apparent motion perception (LAMP) refers to the illusory visual perception of a moving limb upon observing two rapidly alternating photographs depicting the same limb in two different postures. Fast stimulus onset asynchronies (SOAs) induce the more visually guided perception of physically impossible movements. Slow SOAs induce the perception of physically possible movements. According to the motor theory of LAMP, the latter perception depends upon the observer's sensorimotor representations. Here, we tested this theory in two independent studies by performing a central (study 1) and peripheral (study 2) manipulation of the body's sensorimotor states during two LAMP tasks. In the first sham-controlled transcranial direct current stimulation between-subject designed study, we observed that the dampening of left sensorimotor cortex activity through cathodal stimulation biased LAMP towards the more visually guided perception of physically impossible movements for stimulus pairs at slow SOAs. In the second, online within-subject designed study, we tested three participant groups twice: (1) individuals with an acquired lower limb amputation, either while wearing or not wearing their prosthesis (2) individuals with body integrity dysphoria (i.e., with a desire for amputation of a healthy leg) while sitting in a regular position or binding up the undesired leg (to simulate the desired amputation); (3) able-bodied individuals while sitting in a normal position or sitting on one of their legs. We found that the momentary sensorimotor state crucially impacted LAMP in individuals with an amputation and able-bodied participants, but not in BID individuals. Taken together, the results of these two studies substantiate the motor theory of LAMP.

1. Introduction

Embodied cognition theory advocates an essential contribution of the human body's structure, functionality, and sensorimotor state to perception, action, and cognition (Barsalou, 2010; Bechara and Damasio, 2005). In this framework, the repertoire of feasible movements and basic principles of physics, such as the implicit notion of mutual impenetrability of two solid entities (the law of impenetrability, Heinemann, 1945), may guide visual perception of body movements (Saetta et al., 2018). Since such movements are often partially occluded, accurate prediction about them is crucial (Kilner et al., 2007). Accordingly, there are dedicated mechanisms to extract the perception of coherent and dynamic bodily movement trajectories from partially occluded or even static visual cues (Downing et al., 2001; Giese and Poggio, 2003). For instance, human movement kinematics can be inferred from point-light displays applied to a human walker's joints in an otherwise darkened space (Blake and Shiffrar, 2007a). Moreover, the presentation of static photographs implying motion (e.g., an actor jumping off a cliff) biases spatial memory about the direction of the implied motion (Kourtzi and Shiffrar, 1999; Verfaillie and Daems, 2002).

A compelling illustration of such predictive mechanisms is the so-called limb apparent motion perception (LAMP, Shiffrar and Freyd, 1990). LAMP refers to the illusory perceptual completion of an actor's limb movements generated by alternating two motionless pictures

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depicting the same limb in two different positions. In LAMP tasks, the perception of the limb's movement trajectory is manipulated by the time interval between the two pictures' onset (i.e., stimulus-onset asynchrony, SOA). *Fast SOAs* typically induce the perception of a short movement trajectory that reflects physically impossible movements: in violation of the law of impenetrability, the limb is perceived as going through a solid object, or, in violation of the biomechanical constraints, the limb is perceived to move along a short angle of rotation incompatible with the joint's biomechanics. Therefore, this kind of perception has been supposed to be *visually guided*, i.e., relying on visual perception that is independent from the observer's motor capabilities (Saetta et al., 2018; Vannuscorps and Caramazza, 2016; Shiffrar and Freyd, 1990).

Slow SOAs, on the other hand, induce the perception of a large movement trajectory that reflects physically possible movements (i.e., the limb is perceived as moving around the solid object or as rotating around a joint consistent with its biomechanical constraints). This perception is thought to be *sensorimotorically guided* (Orgs et al., 2016; Stevens et al., 2000). Indeed, it relies on SOAs that are sufficiently slow to be consistent with the actual or simulated movement duration (Shiffrar and Freyd, 1990), and thus, sufficient timing might allow for bodily constraints and intuitive physics to influence LAMP. However, two main theories to account for the nature of the influences on LAMP are currently debated in the literature: the *motor* and the *visual theory of LAMP*.

According to the *motor theory of LAMP*, the perception of physically possible movements is grounded in the observer's sensorimotor representations acquired through motor experience (Funk et al., 2005; Orgs et al., 2016; Saetta et al., 2018; Stevens et al., 2000; Thornton, 1998). It is assumed that fronto-parietal networks tuned to motor control are also involved in the understanding of others' observed actions ("motor resonance", Fadiga et al., 1995), which can also be assumed for the LAMP phenomenon. In line with this assumption, the perception of physically possible movements induced by slow SOAs triggers the selective activation of motor areas representing the repertoire of the observer's possible movements, such as the premotor and primary motor cortices (Orgs et al., 2016; Stevens et al., 2000). Behavioral evidence supporting the motor theory comes, for instance, from studying phantom limb awareness. Experienced by most individuals with an amputation (Ramachandran and Hirstein, 1998), phantom limb awareness refers to the persistence of the motor and postural representations of a limb despite its physical absence (Brugger, 2006). The phantom limb might be intentionally moved to various degrees or completely immobilized (Saetta et al., 2020a). Training to execute impossible movements with a phantom limb has shown to enhance the visually guided perception of physically impossible movements, regardless of the SOAs (Moseley and Brugger, 2009). Furthermore, individuals with an amputation who typically experience a phantom limb to fade away or bend back once it crosses hindering solid objects ("obstacle shunning") are more likely to perceive a limb to move straight through an object in the LAMP task (Saetta et al., 2018). Taken together, these findings highlight a tight interrelation between the motor capabilities of a (phantom) limb and the LAMP phenomenon.

Conversely, the *visual theory of LAMP* states that the perception of physically possible movements merely relies on visual perception, and exclusively engages the observer's visual system (Vannuscorps and Caramazza, 2016). In this view, the extra-striate visual cortex processes static information on human bodies (fusiform body area) or specific body parts (extra-striate body area) (Downing et al., 2001; Peelen and Downing, 2007; Vangeneugden et al., 2014), while the posterior area of the superior temporal sulcus reconstructs the movement kinematics (Blake and Shiffrar, 2007b; Grosbras et al., 2012; Puce and Perrett, 2003). In support of this hypothesis, no movement trajectory differences in LAMP were found between able-bodied controls and individuals with congenital upper limb dysmelia who reported no phantom limb awareness (Vannuscorps and Caramazza, 2016). This suggests that almost complete deprivation of limb motor representations has no impact on LAMP. However, other evidence deriving from the LAMP task revealed that complete congenital amelia (without accompanying phantom percept) is associated with a bias towards a consistently more visually guided perception of physically impossible movements for all SOAs (Funk et al., 2005).

Here, we tested these two divergent theories in two independent studies. In the first study, we used transcranial direct current stimulation (tDCS) in healthy participants to causally interfere with cortical motor processing during the LAMP task. Increasing evidence shows that cathodal stimulation of the primary motor cortex (M1 c-tDCS) induces hyperpolarisation of the resting membrane potential of motor cortex neurons, reducing their spontaneous activity and excitability (Bindman et al., 1964; Nitsche and Paulus, 2000a; Nitsche et al., 2003). Furthermore, a sufficiently long stimulation (duration above 10 min) is accompanied by after-effects lasting up to 2 h (Jamil et al., 2017). Previous studies using M1 c-tDCS found reduced M1 activation during action observation and action execution (Qi et al., 2019). In support of the motor theory, we expected that dampening of primary motor cortex activity would reduce the motor simulation of perceived illusory movements and thus bias LAMP towards the visually guided perception of physically impossible movements. This was expected specifically for slow SOAs.

The second study was conducted in an online (web-based) setting and investigated LAMP in clinical samples presenting atypical alterations of sensorimotor limb representation. We investigated a) individuals with an involuntary lower limb amputation and b) individuals affected by body integrity dysphoria (BID) with a desire for, but not yet performed, lower limb amputation. BID is a rare condition characterized by dissatisfaction with a normal body morphology or functionality in non-psychotic individuals (Brugger et al., 2016; Saetta et al., 2020b). In its most common form, one limb can be experienced as non-belonging, despite normal anatomical development and integrity of sensory and motor functions. The feeling that a limb does not belong to oneself often leads to the desire for its amputation. Only very recently, with the release of the 11th Revision of the International Classification of Diseases (ICD-11 - Mortality and Morbidity Statistics), has BID been recognised as an official mental disorder. A distinctive behaviour displayed by the majority of BID individuals (to varying extent) is the so-called *pretending behaviour*, i.e., the mimicking of the desired body state resembling that of an amputee by using a wheelchair, using crutches, or binding up the disowned leg to obtain transient relief of symptoms. A sample of naïve, able-bodied individuals was also included.

Crucially, in all participants, we modulated the actual sensorimotor state by assessing LAMP twice in two different bodily states. Fig. 1 describes the three included groups and illustrates the manipulation of the bodily state as implemented in study 2. In support of the motor theory, we generally expected the sensorimotor states to influence LAMP exclusively for slow SOAs (see below for more specific hypotheses).

Individuals with an amputation performed the task twice, either with or without wearing their own prosthesis (counterbalanced order). Additionally, we measured the integration of the prosthesis into the sensorimotor system, i.e., the subjective sense of prosthesis ownership, defined as the feeling of a prosthetic limb constituting an integral part of the body (Niedernhuber et al., 2018). Accumulating evidence shows that prosthesis ownership positively correlates with prosthesis use (Bekrater-Bodmann et al., 2021). On the other hand, prosthesis use seems to counteract the effects of sensorimotor deprivation from limb amputation and may drive adaptive plasticity in the sensorimotor cortex (van den Heiligenberg et al., 2018). We expected that higher prosthesis ownership would predict greater bias towards the sensorimotor guided perception of physically possible movements on the LAMP task. This would be observed exclusively for slow SOAs, and only when participants performed the task while wearing the prosthesis.

BID individuals performed the LAMP task twice, while sitting in a normal position or while pretending. We expected that mimicking the

Fig. 1. Included groups and sensorimotor state manipulation. Individuals with an amputation (AMP) performed the task twice, either with or without wearing their own prosthesis; Individuals with Body Integrity Dysphoria (BID) sitting in a normal position or pretending (binding up the to-be removed leg; the transparent part of the leg indicates the area for which the amputation desire is reported); Able-bodied individuals (HC) while sitting in a normal position or sitting on one of their legs.

desired amputated state would bias LAMP towards the more visually guided perception of physically impossible movements, exclusively for slow SOAs.

Able-bodied participants in study 2 completed the experiment twice, either while sitting in a normal position or while sitting on one of their legs. On the basis of previous findings, which had demonstrated that both motor control and various cognitive processes can be affected by restrictions of body mobility (e.g. Ionta et al., 2007, 2012), we expected the peripheral and transient reduction of motor capabilities to bias LAMP towards the more visually guided perception of physically impossible movements, and exclusively for slow SOAs.

2. Study 1

2.1. Participants

Twenty-four right-handed participants (Males: 13, Females: 11, *M* age = 25.96 years, *SD* = 5.34) with no history of any psychiatric or neurological disorder took part in this study. Exclusion criteria were: presence of epilepsy or seizure, fainting spell or syncope, head trauma, metal implants in the brain/skull, cochlear and neurostimulator implants, cardiac pacemaker, use of recreational drugs, or consumption of more than 3 units of alcohol in the past 24 h. All participants had normal or corrected-to-normal vision. Participants received monetary compensation for their participation. All participants were informed about the scope of the study and provided written informed consent, complying with the Declaration of Helsinki (1984), and the approval of the local ethics committee of Utrecht University (protocol number: FETC 19–204).

2.2. Materials

Pairs of photographs, varying only in the position of one of the model's limbs, were presented. In one photograph, the limb was on the right, and in the other, on the left side of a solid object. In order for participants to select which of the two movement trajectories they perceived, the aforementioned two pictures were superimposed on one another to create a third picture, which showed two arrows depicting the two possible motion trajectories, i.e., the short and physically impossible (i.e., the limb moved through the object) or the long and

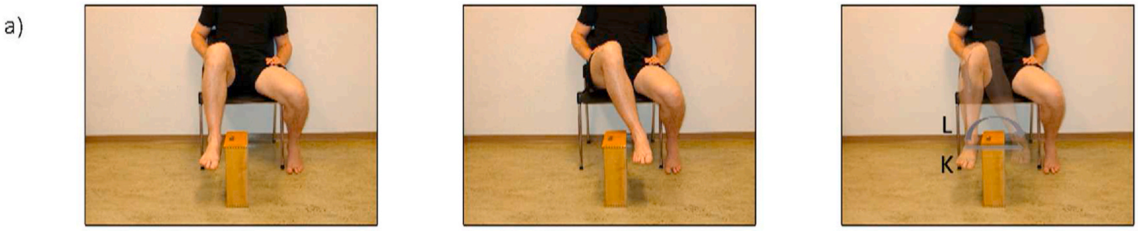

Fig. 2. Sample stimulus pair inducing the perception of leg moving through an object, or around the object depending on the SOA (illustrated here is a third person perspective). After the presentation of the stimulus pair, a picture showing two arrows depicting the two possible motion trajectories is presented. The arrow "L" indicates the more sensorimotor guided perception of physically possible movements, the arrow "K" the more visually guided perception of physically impossible movements.

physically possible (i.e., the limb moved above and around the object) trajectory. Fig. 2 represents a sample stimulus pair and the respective superimposed images for the response. The experiment consisted of 96 trials. The pairs of photographs featured left (n = 48) and right (n = 48) upper (n = 48) and lower (n = 48) limbs, and specifically four body parts: i) hand (n = 24), ii) forearm (n = 24), iii) foot (n = 24), and iv) shank (n = 24). The model's limbs were pictured in the first-person (1pp, n = 48) or the third-person (3pp, n = 48) perspective. All these conditions were considered for two reasons: i) to counteract participants' potential boredness, making the task more interesting to perform; ii) given a sufficient number of participants, we wanted to explore the effects of previously investigated factors, such as limb, laterality, and perspective (Saetta et al., 2018), as well as their interaction with the newly introduced factor tDCS stimulation.

2.3. Procedure

In a single-blind, sham-controlled between-subject design, participants were assigned to either the real stimulation condition, where cathodal tDCS was applied over the left motor cortex (experimental stimulation; n = 12, Males: 6, Females: 6, *M* age = 27.58 years, *SD* = 7.09) or the sham stimulation (n = 12, Males: 7, Females: 5, *M* age = 24.33 years, *SD* = 1.87), according to a Latin Square counterbalancing assignment to conditions. Given the role of the left hemisphere in initiating bimanual movements (Walsh et al., 2008), and that inhibition of the ipsilateral motor cortex has been shown to affect both ipsilateral and contralateral hand movements (review in Chen et al., 1997), we expected that stimulation of the left motor cortex would exert bilateral effects, rather than a specific effect for the contralateral limb. There was no statistically significant age difference between groups (two-tailed t (12.53) = 0.154, p = 0.15). The stimulation was delivered with a battery-driven, constant-current stimulator (neuroConn DC-stimulator) through 35 cm^2 sponge electrodes on which the Ten 20 conductive paste was spread. The voltage was set to 1 mA. In the experimental stimulation condition, the tDCS was applied for 20 min. The sham stimulation consisted of 20 min in total, with only the first 5 s applying tDCS stimulation, after which the stimulation was deramped within 10 s. The procedure lasted for 20 min irrespective of the stimulation condition (experimental or sham), and all participants perceived the current flow as an itching sensation, as they confirmed verbally.

The electrodes were placed over C3 and Fp2 according to the 10/20 EEG system, with the cathode being placed over the left motor cortex (Nitsche and Paulus, 2001) and the anode over the contralateral orbital/supraorbital region. The COMETS toolbox (Jung et al., 2013) implemented in MATLAB was used to simulate the electric field generated by the tDCS with the present electrodes' configuration and size. Results of the simulation are presented in Fig. 1 in the supplementary materials. This configuration has proven effective in down-regulating motor cortex excitability in replicated and multi-approach studies combining tDCS and single-pulse or repetitive transcranial magnetic stimulation (TMS) (Nitsche and Paulus, 2000b; Siebner et al., 2004). After the stimulation, participants were familiarized with the task via five practice trials before the actual experiment started.

Instructions were provided verbally by the experimenter. Additionally, before the start of the experiment, written instructions appeared on the center of the screen. A special emphasis was placed on explaining that there were no wrong or correct responses, as perception is highly subjective. Participants were asked to respond as quickly as possible and to not simulate the observed movement, but rather to remain relaxed in the sitting position. The distance from the screen was set to approximately 50 cm. The experiment was programmed in E-prime, version 3.

In each trial, after a central fixation cross was shown for 1 s, the pairs of photographs were presented alternately with different stimulus durations (StimD) and interstimulus intervals (ISI) at five SOAs. As in Shiffrar and Freyd (1990), the shortest SOA was 150 msec (SD = 100 msec, ISI = 50 msec). The other SOAs were 250 msec (SD = 200 msec, ISI = 150 msec), 450 msec (SD = 400 msec, ISI = 350 msec), 650 (SD = 600 msec, ISI = 550 msec), and 750 msec (SD = 700 msec, ISI = 650 msec). The experiment consisted of two blocks: one where the actor's movements were observed from 1pp and the other where they were observed from 3pp. The factor perspective was introduced based on previous studies (Ruby and Decety, 2001). In particular, we expected stimuli in 1pp, compared to 3pp, to more likely elicit a motor simulation of the observed movements, and therefore to bias LAMP towards the more sensorimotorically guided perception than stimuli in 3pp. These latter stimuli are associated with encoding processes in the observer's visual system and would therefore bias LAMP towards the more visually guided perception. The presentation of the blocks was counterbalanced across participants. The experiment lasted approximately 50 min in total.

2.4. Data analysis

Data were analysed with R Studio v. 1.3.1093, and packages R lme 4, sjPlot and ggplot 2. The R scripts and the dataset are deposited on the open science framework (OSF, https://osf.io/4z6yc/). The outcome variable was the perception of the limb's movement trajectory, represented by two binary values: 1 for the sensorimotorically guided perception of physically possible movements, and 0 for the visually guided perception of physically impossible movements. Logistic mixed models, estimated using maximum likelihood and Nelder-Mead optimizer, were fitted including the most relevant predictors according to our hypotheses. In particular, we fitted a logistic mixed model to predict the conditional probability that the outcome variable equals 1 as a function of the within-subject continuous predictor *SOA* (150, 250, 450, 650, 750), the between-subject categorical predictor *tDCS* (experimental/sham), and their interaction. The independent variables have been grand mean centered and scaled to assist with the interpretation of estimates (Sommet and Morselli, 2017).

Implementation of the logistic mixed models followed the well-established "three-steps" procedure described in Sommet and Morselli (2017):

1. The appropriateness and the need for a logistic mixed model was assessed by building a null model with no predictors to calculate the intra-class correlation (ICC). ICC expresses the degree of homeogenity of the outcome variables within the participants. Since the ICC was 0.217, indicating that 21.7% of the chance of reporting the sensorimotorically guided perception was explained by between-subjects (or 78.3% within-subjects) differences, a random intercept for each participant was included.
2. Two intermediate models, both including the predictors *SOA* and *tDCS* but no interaction, were built. The two models differed in that one included a random intercept for each participant, and the other additionally included a random slope for *tDCS*. A formal comparison of the two models was performed by examining the changes in the 2 log-likelihood (Bliese and Ployhart, 2002). The model's fit did not significantly improve as a result of setting a random slope for *tDCS* (X^2 (1) = 0, p = 0.999). That is, no significant variability in the effect of *tDCS* across participants was observed and therefore, the final model included only a random intercept for each participant.
3. The final model, additionally including the interaction *SOA* by *tDCS*, was built. Its equation is shown below:

$$\mathrm{Logit(odd)} = \mathrm{intercept} + \mathrm{p} + \beta 1(\mathrm{SOA}) + \beta 2(\mathrm{tDCS}) + \beta 3(\mathrm{SOA} * \mathrm{tDCS}) + \mathrm{e}$$

where *Logit(odd)* is the predicted probability of the sensorimotorically guided perception, "*p*" represents the random intercept for participants, "β_x" stands for the estimated parameters, "*e*" stands for the residuals.

The predictor effects were estimated as odds ratios (ORs) with their respective 95% confidence intervals (CIs). 95% CIs and p-values were computed using the Wald approximation. A significant effect was inferred when the CIs did not cross a value of 1 (Sommet and Morselli, 2017). For purposes of interpretation, the interaction term was decomposed using two dummy-coded models (Preacher et al., 2006). The first model estimated the effect of *tDCS* for the fast SOAs by *adding* 1 SD from the cluster-mean centered SOAs; the second model estimated the effect of *tDCS* for the slow SOA by *subtracting* 1 SD from the cluster-mean SOAs.

To avoid overparametrization (Bates et al., 2015), the predictor *Limb* was also modelled, but then excluded from the final model, as in line with our core hypothesis, including the interaction terms with the other predictors did not significantly improve the model's fit (X^2 (1) = 0.46, p = 0.50). Further analyses, including the predictors *Limb* and *Laterality*, are reported in the supplementary materials.

2.5. Results

With this procedure, a notable number of observations (n = 2304) was modelled while adjusting for the within-subject and within-group dependency, resulting in substantial explanatory power (conditional $R^2 = 0.44$) for the model. The final model results show a significant main effect of *SOA* (OR = 1.00, 95% CIs [1.00–1.01], p < 0.001), indicating that with slower SOAs, participants were more likely to perceive physically possible movements, and a significant main effect of *tDCS* (OR = 2.84, 95% CIs [1.20–6.72], p = 0.017), indicating that participants were more likely to perceive physically impossible movements in the experimental M1 c-tDCS, compared to the sham stimulation condition. Furthermore, a trend for an interaction of *SOA* by *tDCS* (OR = 1.00, 95% CIs [1.00–1.00], p = 0.054) was observed. The two dummy-coded models showed that there was no effect of *tDCS* for fast SOAs (OR = 2.30, 95% CIs [0.95–5.57], p = 0.066) but there was an effect for slow SOAs (OR = 3.52, 95% CIs [1.45–8.55], p = 0.005). That is, participants were more likely to perceive physically impossible movements after experimental M1 c-tDCS than after sham stimulation, but this stimulation-dependent effect was only observed when stimuli were presented at the slower SOAs. Results are visualized in Fig. 3. Fixed and random effects are reported in Table 1.

2.6. Discussion of Study I

In a sham-controlled M1 c-tDCS study, we confirmed the contribution of sensorimotor representations to LAMP by interfering with the cortical activity and excitability of the primary sensorimotor areas, thereby providing support for the motor theory. M1 c-tDCS has previously been shown to induce long-term depression effects in the sensorimotor cortex (Nitsche and Paulus, 2000a). In a recent study, a reduced amplitude of motor evoked potentials due to M1 c-tDCS was registered in connection with action observation and execution (Qi et al., 2019). Another study found that M1 c-tDCS lowers the accuracy of predictions of partially occluded human, but not non-human, reaching-grasping movements (Paracampo et al., 2018). These studies showed that the motor theory applies to action observation, execution, and prediction, as revealed by the inhibitory effects of M1 tDCS on all these processes. Our results extend these findings by showing an effect of M1 c-tDCS on the LAMP phenomenon. As in previous studies (Saetta et al., 2018; Shiffrar and Freyd, 1990; Stevens et al., 2000), we found that fast SOAs biased LAMP towards the visually guided perception of physically impossible

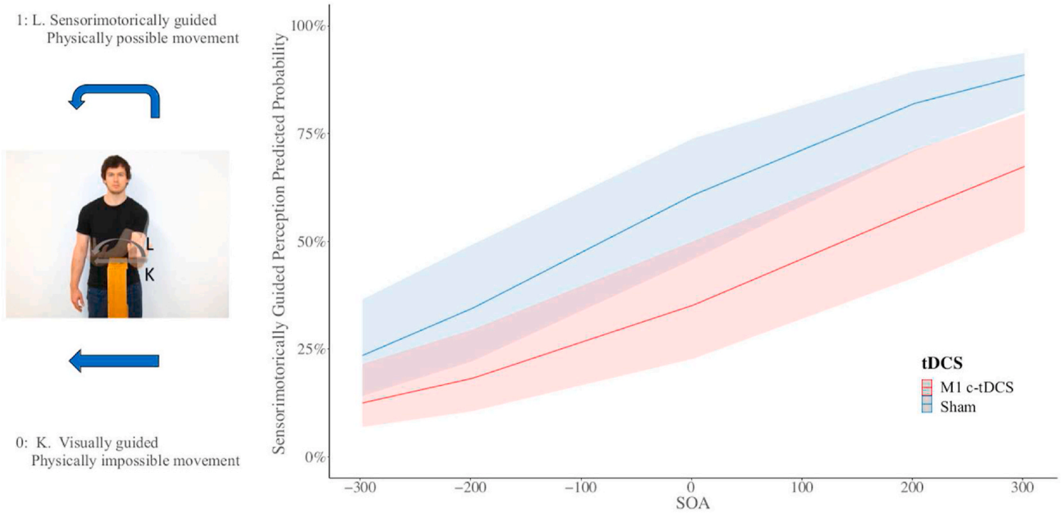

Fig. 3. Predicted probability and confidence intervals of the sensorimotorically guided perception in the LAMP task as a function of SOA and tDCS. Participants who underwent the experimental M1 c-tDCS compared to those who underwent the sham stimulation were biased toward the visually guided perception of physically impossible movements after the stimulation. This stimulation-dependent effect was only observed when stimuli were presented at the slower SOAs.

Table 1
Results of the logistic mixed model examining the predicted probability of the sensorimotorically guided perception in the LAMP task as a function of SOA and tDCS.

	Final Model			Interaction Model (fast SOAs)			Interaction Model (slow SOAs)		
Predictors	Odds Ratios	CI	p	Odds Ratios	CI	p	Odds Ratios	CI	p
(Intercept)	0.91	0.59–1.40	0.667	0.30	0.19–0.46	**<0.001**	2.79	1.79–4.34	**<0.001**
SOA	1.00	1.00–1.01	**<0.001**	1.00	1.00–1.01	**<0.001**	1.00	1.00–1.01	**<0.001**
tDCS	2.84	1.20–6.72	**0.017**	2.30	0.95–5.57	0.066	3.52	1.45–8.55	**0.005**
SOA* tDCS	1.00	1.00–1.00	**0.054**	1.00	1.00–1.00	**0.054**	1.00	1.00–1.00	**0.054**
Random Effects									
σ^2									3.29
τ_{00}									$1.08_{\text{subject ID}}$
ICC									0.25
N									$24_{\text{subject ID}}$
R^2 Marginal/Conditional									0.261/0.444

movements. Slow SOAs instead induced the perception of physically possible movements, which are, based on previous findings (Orgs et al., 2016; Stevens et al., 2000), sensorimotorically guided. More importantly, M1-tDCS biased LAMP towards more visually guided perception. This effect was specific for the slow SOAs. While previous studies applied correlational methods, such as positron emission tomography (Stevens et al., 2000, PET) and functional magnetic resonance imaging (Orgs et al., 2016, fMRI), we here implemented a causative method to corroborate the motor theory of LAMP for the first time (to the best of our knowledge).

3. Study 2

3.1. Participants

Twenty-nine individuals with unilateral lower limb amputation participated in the online study (Males: 24, Females: 5, Right-sided amputation: 12, Left-sided amputation: 17, Mean age = 52.66 years, SD = 5.09). These individuals were recruited using the PHANTOMMIND database (first description by Bekrater-Bodmann et al., 2015). Inclusion criteria for the present study were a) acquired major (involuntary) lower limb amputation, b) age between 18 and 80 years, and c) using a prosthesis. Frequency of prosthesis use, prosthesis ownership, and sense of control over the prosthesis, as well as presence, frequency, and strength of phantom limb awareness over the last four weeks were assessed using a questionnaire. Table 2 reports used questions, the scale types, and the scale values.

Individuals with an amputation used their prosthesis with a high frequency (Median frequency of prosthesis use = 4 per week (scale ranging from 0 to 4, MAD = 0, see Table 2), indicating daily use. Overall, prosthesis ownership (Mean = 7.45, SD = 2.63) and sense of control over the prosthesis (Mean = 8.38, SD = 1.40) were rated as high. Nineteen individuals with an amputation reported current phantom limb awareness, 5 had experienced a phantom limb in the past, and 5 had never experienced a phantom limb.

Ten individuals with BID were recruited through online forums or personal contacts established in previous studies (Saetta et al., 2020b) (Males: 8, Females: 2, Right-sided amputation desire: 7, Left-sided amputation desire: 3, Mean age = 41.00 years, SD = 12.36). The desire for amputation was assessed using the Zurich Xenomelia Scale (Aoyama et al., 2012). This 12-item scale consists of 3 subscales assessing different aspects: “amputation desire” (identity restoration as the main motivation for the amputation), “erotic attraction” (sexual arousal to amputated bodies), and “pretending” (inclination to mimic an individual with amputation). The subscores for each scale are the sum of 4 item scores. The subscore can range from 1 = not intense to 24 = most intense. The average subscores were: amputation desire: Mean = 22.70, SD = 1.70, erotic attraction: Mean = 16.70, SD = 6.07, pretending: Mean = 17.00, SD = 2.49.

Twenty-nine naïve able-bodied men (Males: 25, Females: 4, Mean age = 40.66, SD = 4.88), not included in study 1, were recruited through the platform “Prolific” (https://www.prolific.co/).

All participants gave their informed consent. The informed consent was displayed prior to starting the online survey, and participants had to actively give their consent by ticking a box. The study was approved by the Local Ethics Committee of the Faculty of Arts and Social Sciences at the University of Zurich (Approval number: 17.12.8).

3.2. Materials

Participants were confronted with pairs of photographs varying only in the position of one of the model’s limbs. In one condition, as in study 1, the limb was once on the right and once on the left side of an object (object solidity condition). Additionally, in another condition, in one

Table 2
Questions asked to individuals with lower limb amputation with the type of scales and the scale values.

Item	Question	Scale type	Scale Values
Prosthesis frequency of use	How often do you wear your prosthesis in a week?	ordinal	0 = not at all, 1 = less than twice, 2 = every second day, 3 = almost daily, 4 = daily
Prosthesis ownership	How much do you perceive your prosthesis as part of your body when you wear it?	continuous	0 = prosthesis feels like a foreign body – 10 = prosthesis is like a part of the body
Prosthesis sense of control	How much control do you have over the movements of your prosthesis when you wear it?	continuous	0 = I have no control – 10 = I have full control)
Phantom limb sensation presence (last 3 months)	Have you recently (over the past three months) experienced the presence of a phantom limb?	categorical	0 = No, I have never experienced the presence of a phantom limb, 1 = No, but I used to experience the presence of a phantom limb, 2 = Yes, I currently am experiencing the presence of a phantom limb
Phantom limb sensation strength (last 4 weeks)	How strong were these experiences on average over the past four weeks?	continuous	0 = not present – 10 = very strong
Phantom limb sensation frequency	How often does the phantom limb emerge?	ordinal	(0 = never, 1 = less than once a month, 2 = once a month, 3 = every other week, 4 = 1–2 a week, 5 = at least 3 days a week, 6 = at least 5 days a week, 7 = once a day, 8 = several times a day, 9 = all the time)

photograph the limb was on the right and in the other on the left side of the contralateral limb (limb solidity condition; see Fig. 2b). As in study 1, for response selection, the two pictures of a pair were superimposed onto one another to create a third picture that showed two arrows depicting the two possible motion trajectories (i.e., limb moving through or around the object). This was done so participants could select their perceived movement trajectory.

The experiment consisted of the presentation of 256 stimulus pairs. They featured left (n = 128) and right (n = 128), upper (n = 128) and lower (n = 128) limbs, and specifically four body parts: i) hand (n = 64); ii) forearm (n = 64), iii) foot (n = 64), iv) shank (n = 64). The model's limbs were pictured in the first-person (1pp, n = 128) or third-person (3pp, n = 128) perspective, and belonged to the object solidity constraint (n = 128) or limb solidity constraint (n = 128) condition. These two conditions were included on the basis of two strains of evidence: i) whether individuals with amputations show obstacle shunning or not depends on whether the phenomenal space occupied by the phantom limb overlaps with that of biological (i.e., the contralateral limb) or non-biological (a wall) matter (Saetta et al., 2020a), and ii) obstacle shunning experience is related to LAMP (Saetta et al., 2018).

3.3. Procedure

The jsPsych software (https://www.jspsych.org) (de Leeuw, 2015) was used to program the online experiment. A trial consisted of a central fixation cross shown for 1 s, followed by 256 stimulus pairs that were presented alternately with different stimulus duration (StimD) and interstimulus interval (ISI) at four SOAs. The shortest SOA was 150 msec (SD = 100 msec, ISI = 50 msec). The other SOAs were 250 msec (SD = 200 msec, ISI = 150 msec), 650 (SD = 600 msec, ISI = 550 msec), and 750 msec (SD = 700 msec, ISI = 650 msec). The experiment consisted of a single block, in which all the trial types were randomised. The duration of the experiment was approximately 15 min.

Before the start of the experiment, as in study 1, all the instructions were presented at the center of the screen. Participants' sensorimotor states were manipulated by performing the experiment twice (in individuals with an amputation: either while wearing a prosthesis or while not wearing a prosthesis; in BID individuals: either while binding up their unwanted leg (pretending) or while sitting in a normal position; in able-bodied participants: either while sitting on one of their legs or while sitting in a normal position, see Fig. 1). Eleven participants sat on the right leg, 18 on the left leg. For each group, the order of conditions was counterbalanced. The two assessments were performed on two separate days, with a mean delay of 7 days.

3.4. Data analysis and results

Logistic mixed models were fitted following the statistical methods described for study 1. R Studio v. 1.3.1093 was used. The R scripts and the dataset are deposited on the open science framework (OSF, https://osf.io/4z6yc/). Separate analyses were conducted on the three samples.

3.4.1. Individuals with an amputation

A logistic mixed model examined the impact of the categorical predictors *SOA*, *Sensorimotor State* and the continuous predictor *Prosthesis Ownership* (a continuous variable) on the illusion experience. Predictors were grand mean centered and scaled. This model also included the two-way and the three-way interactions between these parameters. A random intercept for each participant was set given the random structure of the data (ICC = .34). A random slope for sensorimotor slope was initially modelled, but then omitted from the final model as it did not improve the model's fit (X^2 (1) = 0, p = 0.999). To avoid overparametrization (Bates et al., 2015), the predictor *Limb* was also modelled, but then excluded from the final model, as in line with our core hypothesis, including the interaction terms with the other predictors did not improve the model's fit (X^2 (7) = 9.75, p = 0.2034). Further analyses, including the predictors *Limb*, *Correspondence of the side of the amputation with the laterality of the stimuli*, *Solidity* and *Perspective* are reported in the supplementary materials. The number of the modelled observation was 7424 and the model's total explanatory power was substantial (conditional R^2 = 0.38).

The results show a main effect of *SOA* (OR = 1.00, 95% CIs [1.00–1.01], p < 0.001). We also found a significant two-way interaction *SOA* by *Sensorimotor State* (OR = 1.00, 95% CIs [1.00–1.01], p <0.001) and three-way interaction effect of *SOA* by *Sensorimotor State* by *Prosthesis Ownership* (OR = 1.00, 95% CIs [1.00–1.01], p < 0.001). As shown in Fig. 4, the more the prosthesis was felt as part of the body, the more individuals with an amputation were likely to perceive a physically possible movement, but only while *wearing the prosthesis*. This effect was observed exclusively for the slowest SOAs, as shown by the green and the violet lines representing the grand mean centered SOA650 and SOA750, respectively, that have slopes that are opposite to each other for the two different sensorimotor states. Fixed and random effects are reported in Table 3.

3.4.2. BID individuals

A logistic mixed model examined the predictors *SOA* and *Sensorimotor State* and their interaction in the LAMP task. Predictors were grand mean centered and scaled. A random intercept for each participant was set, given the random structure of the data (ICC = .20). A random slope for *Sensorimotor State* was included and improved the model's fit significantly (X^2 (1) = 20.96, p < 0.0001). To avoid overparametrization (Bates et al., 2015), the predictor *Limb* was also modelled, but then excluded from the final model, as in line with our core hypothesis, including the interaction terms with the other predictors did not significantly improve the model's fit (X^2 (3) = 5.78, p = 0.1226). Further analyses including the predictors *Limb*, *Correspondence of the side of the amputation with the laterality of the stimuli*, *Solidity* and *Perspective* are reported in the supplementary materials.

The number of the modelled observation was 2560 and the model's total explanatory power was moderate (conditional R^2 = 0.24). The results show a significant main effect of *SOA* (OR = 1.00, 95% CIs [1.00–1.01], p < 0.001). We found no significant effect of *Sensorimotor State* (OR = 0.83, 95% CIs [0.56–1.23], p = 0.353) and no significant interaction *SOA* by *Sensorimotor State* (OR = 1.00, 95% CIs [1.00–1.00], p = 0.463). Fixed and random effects are reported in Table 3.

3.4.3. Able-bodied individuals

A logistic mixed model examined the impact on the illusion experience of the predictors *SOA*, *Sensorimotor State*, *Limb*, and their interaction. Predictors were grand mean centered and scaled. A random intercept for each participant was set given the random structure of the data (ICC = 0.1). A random slope for *Sensorimotor State* was included and improved the model's fit significantly (X^2 (1) = 71.69, p < 0.0001). The number of the modelled observation was 7168 and the model's total explanatory power was moderate (conditional R^2 = 0.13). We found a significant main effect of *SOA* (OR = 1.00, 95% CIs [1.00–1.01], p < 0.001). No main effect of *Sensorimotor State* (OR = 1.00, 95% CIs [0.75–1.33], p = 0.996) was found. However, the interaction of *Sensorimotor State* by *SOA* was significant (OR = 1.00, 95% CIs [1.00–1.00], p = 0.005). Able-bodied individuals were thus more likely to perceive physically impossible movements when sitting on their leg than when sitting in a normal position, but only for the slowest SOAs. We also found a main effect of *Limb* (OR = 1.41, 95% CIs [1.28–1.56], p <0.001), i.e., leg stimuli as compared to arm stimuli were more likely to elicit the perception of phsysically impossible movements, and an interaction effect *Sensorimotor State* by *Limb* (OR = 0.75, 95% CIs [0.62–0.91], p = 0.004). While sitting on their legs, able-bodied individuals were more likely to perceive physically impossible movements for leg stimuli and physically possible movements for arm stimuli. No three-way interaction SOA by Sensorimotor State by Limb was observed (OR = 1.0, 95%

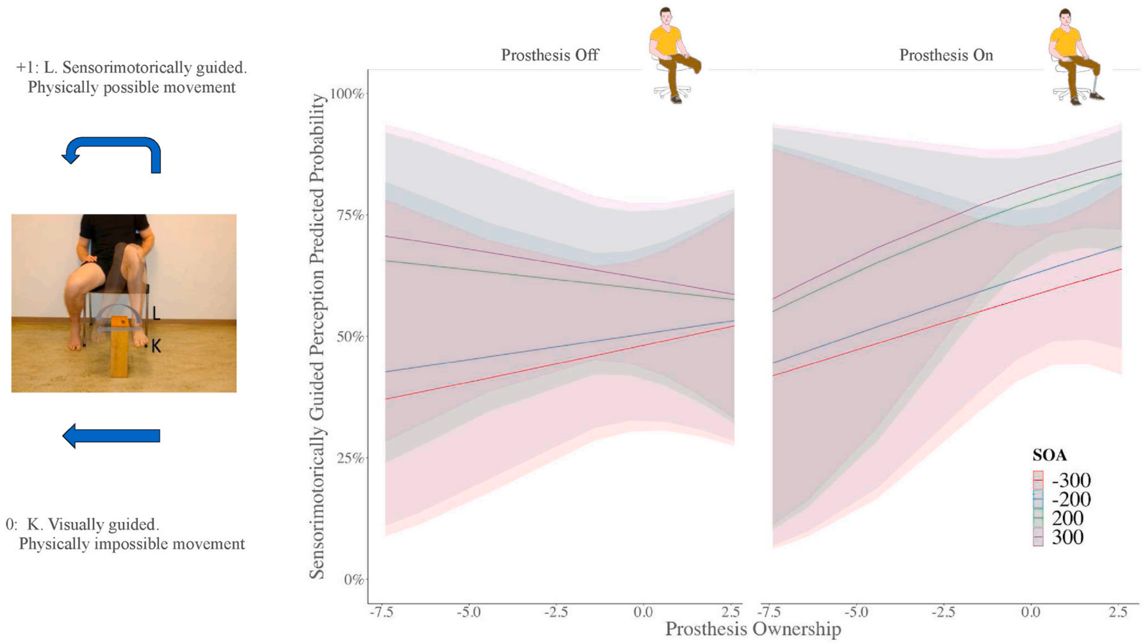

Fig. 4. Predicted probability and confidence intervals of the sensorimotorically guided perception in individuals with a lower limb amputation as a function of SOA, Sensorimotor State, and Prosthesis Ownership. The more the prosthesis was felt as part of the body, the more participants were biased towards the more sensorimotorically guided perception of physically possible movement, but exclusively while they wore the prosthesis compared to when they did not. As predicted, this was only observed when stimuli were presented at the slower SOAs.

Table 3
Results of the logistic mixed model examining the predicted probability of the sensorimotorically guided perception in individuals with a lower limb amputation and with body integrity dysphoria as a function of SOA and Sensorimotor State, and in able-bodied individuals, as a function of SOA, Sensorimotor State, and Limb.

	Individuals with Lower Limb Amputation			Individuals with Body Integrity Dysphoria			Able-bodied Individuals		
Predictors	Odds Ratios	CI	p	Odds Ratios	CI	p	Odds Ratios	CI	p
Intercept	1.73	1.06–2.81	**0.028**	1.41	0.78–2.57	0.258	1.08	0.85–1.36	0.534
SOA	1.00	1.00–1.00	**<0.001**	1.00	1.00–1.00	**<0.001**	1.00	1.00–1.00	**<0.001**
Sensorimotor State	1.97	0.74–5.21	0.172	0.83	0.56–1.23	0.353	1.00	0.75–1.33	0.987
Prosthesis Ownership	1.06	0.88–1.29	0.516						
SOA * Sensorimotor State	1.00	1.00–1.00	**<0.001**	1.00	1.00–1.00	0.463	1.00	1.00–1.00	**0.006**
SOA * Prosthesis Ownership	1.00	1.00–1.00	0.262						
Sensorimotor State * Prosthesis Ownership	1.12	0.77–1.64	0.546						
SOA * Sensorimotor State * Prosthesis Ownership	1.00	1.00–1.00	**<0.001**						
Limb							1.41	1.28–1.56	**<0.001**
SOA * Limb							1.00	1.00–1.00	0.389
Sensorimotor State * Limb							0.75	0.62–0.91	**0.004**
SOA * Sensorimotor State * Limb							1.00	1.00–1.00	0.288
Random Effects									
σ^2	3.29			3.29			3.29		
τ_{00}	1.63 Subject ID			0.91 Subject ID			0.39 Subject ID		
τ_{11}				0.31 Subject ID, Sensorimotor State			0.50 Subject ID, Sensorimotor State		
ICC	0.33			0.22			0.11		
N	29 Subject ID			10 Subject ID			29 Subject ID		
Marginal R^2/Conditional R^2	0.065/0.375			0.026/0.238			0.029/0.131		

CIs [1.00–1.00], p = 0.288). Results are displayed in Fig. 5. Fixed and random effects are reported in Table 3.

Further exploratory analyses of the effects of *Correspondence of the side of the leg on which participants sat with the laterality of the stimuli*, *Solidity*, and *Perspective* are reported in the supplementary materials.

3.5. *Discussion of the Study II*

This web-based study revealed an influence of the current (peripherally modulated) sensorimotor states on LAMP in three different participant samples. Specifically, we showed that i) the higher the prosthesis ownership, the more likely individuals with an amputation

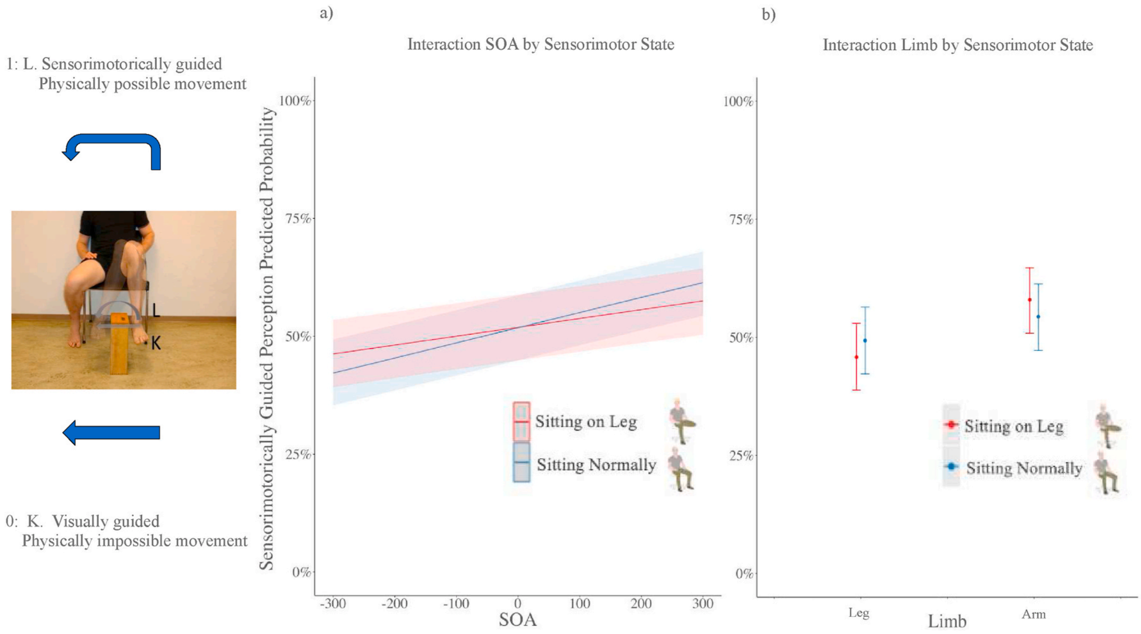

Fig. 5. Predicted probability and confidence intervals of the sensorimotorically guided perception in able-bodied individuals as a function of SOA and Sensorimotor state (panel a), and Limb and Sensorimotor State (panel b). Participants were biased towards the visually guided perception of physically impossible movements while sitting on their leg compared to while sitting in a normal position, for stimuli at the slower SOAs (panel a), and for leg stimuli (panel b).

were to report a sensorimotorically guided perception, when they *wore the prosthesis*, and when the SOAs were slow; b) transitory pretending during the task (i.e., when mimicking their desired, amputated state by binding up their legs) did not influence LAMP in BID individuals; and c) healthy controls were more likely to show a visually guided LAMP when sitting on their legs, but only for the slow SOAs. While the results for each sample will be discussed in more detail below, our findings are in line with the motor theory of LAMP. Additionally, we replicated the well-known effect of the SOA in the LAMP task for the first time in a web-based setting.

Our first finding indicates a modulation of wearing a prosthesis in the perception of the LAMP task that was dependent on the degree of prosthesis ownership. Most individuals with a lower limb amputation wore their prosthesis daily, and experienced high ownership over them. Accumulating theoretical and empirical evidence suggest that the integration of a prosthesis into an amputee's body representation enhances prosthesis use (Bekrater-Bodmann, 2021). Prosthesis use has been identified as a key factor in the development of alternative motor representations adapting to limb loss (van den Heiligenberg et al., 2018). In particular, it has been shown that prosthesis use may recruit the same large scale visual and motor neural networks that would have normally been recruited by the limb prior to amputation. This "replacement" of the neural representation by the prosthesis in sensorimotor areas that had hosted the representation of the limb prior to amputation is not dependent on the visual exposure to, or familiarity with, the prosthesis, but specific to its use (van den Heiligenberg et al., 2018). In line with the motor theory, we found that wearing the prosthesis, compared to not wearing it, induced more sensorimotorically guided perceptions in the LAMP task. Notably, this bias was dependent on the degree of prosthesis ownership and was specific for slow SOAs. Our results suggest that for the LAMP task, a prosthesis that is felt as part of the body and is frequently used poses the same physical constraints as the intact limb does (see also below, but see Bekrater-Bodmann et al., 2021, who caution simply equating "embodiment" with "frequency of use" of a prosthesis). Future studies combining fMRI with the LAMP task should look at the relationship between LAMP and the neural activation related to prosthesis perceptions to verify this link on a neural level. We also found no significant interaction of *Limb* by *Sensorimotor State*. The lack of the specificity effects of the experimental manipulation for lower limb stimuli is compatible with the results by Simoes et al. (2012), observing a functional expansion of the leg sensorimotor representation in lower limb amputees that spreads to neighbouring regions that represent the trunk and upper limbs. Remarkably, the strength of their approach rested in their exclusion of amputees with painful phantom limb sensations. This allowed for dissection of cortical activity due to preserved neural representation of the body from that strictly related to pain perception (Bramati et al., 2019; Makin et al., 2013). Here, we speculate that perception of either upper or lower limb movements may trigger the activation of all the limb sensorimotor representations.

The second finding demonstrated no effect of the bodily posture in the LAMP task in BID individuals. A unique phenomenological signature of BID, typically originating in early childhood, is the self-reported feeling of "over-completeness" with four limbs and the feeling of one limb as a "nuisance or annoying appendage to the body" (Hilti and Brugger, 2010, p. 321). Thus, 'pretending', i.e., sitting on one leg to simulate the desired amputation state, may allow for the temporary alignment of the actual and phenomenal body, and provide an instant and transient relief from BID symptoms (First, 2005). In keeping with this, virtual reality or multisensory illusions to experimentally induce visual disappearance of the affected limb have proven effective to transiently alleviate the BID symptoms (Stone et al., 2018; Turbyne et al., 2021). Recent neural accounts of BID highlight that such a phenomenal experience might be mirrored by the lack of functional and structural connectivity between the primary sensorimotor areas of the affected limb and the areas involved in a coherent and unitary representation of the body as a whole, such as the right superior parietal lobule (Saetta et al., 2020b, 2021). Notably, the gray matter density of the latter area has been found to correlate negatively with the strength of the subjectively reported desire for amputation and pretending behavior (Saetta et al., 2020b). In accordance with these phenomenological and neural perspectives, the results of the present study show, on a behavioral level, that momentarily pretending during the task does not influence perception in the LAMP task. This may provide additional support to the view that the to-be removed limb's peripheral sensorimotor representations might be, at least to some extent, not integrated into central higher-order body representations. Alternatively, the absence of effects of the experimental manipulation might be attributable to the repetition over time in the everyday life of pretending behaviors. Such repetitive and prolonged immobilization may have induced a shrinking of the corresponding sensorimotor cortical representations, in line with observed alterations in the right superior parietal lobule, i.e., a key node for both motor execution and motor imagery networks (Solodkin et al., 2004). Indeed, Liepert et al. (1995) showed, in able-bodied participants, a linear relationship between the duration of lower limb immobilization and shrinking of the spatial extent of the leg sensorimotor representation, as revealed by TMS. Relatedly, middle-term immobilization has been shown to induce significant structural brain changes, such as a reduction of cortical thickness in the primary sensorimotor cortex of the corresponding limb (Langer et al., 2012). Furthermore, limb disuse has been shown to be accompanied by reduced neural activity in the corresponding primary motor cortex (Gandola et al., 2017, 2019). Opposite viewpoints regarding the nature-nurture debate on the determinants of BID may favor one or the other, or both interpretations (Brugger et al., 2018; Carmon et al., 2021).

Contrary to the findings in BID individuals, and in line with our hypothesis, we found that able-bodied individuals were more biased towards the more visually guided perception during transient immobilization of the leg (i.e., while sitting on it) for slow SOAs and for leg stimuli. This pattern was presumably observed due to a reduction of peripheral sensorimotor signalling (cp. e.g., Ionta et al., 2007, 2012). The results are consistent with the motor theory, and consistent with previous findings demonstrating an influence of body posture and peripheral body movement restraint on other motor-related cognitive processes, such as the mental rotation of body parts (Ionta et al., 2007) and action perception (Zimmermann et al., 2013).

4. General discussion

Across two studies using a similar LAMP task, and in line with the motor theory, we showed that both central (study 1) and peripheral (study 2) manipulations of sensorimotor states affected LAMP. In study 1, the dampening of the activity of the motor cortex induced a bias towards the more visually guided perception of impossible movements. In study 2, assuming different (clinically relevant) bodily states critically modulated LAMP in a way that was consistent with the observers' sensorimotor representations accumulated through motor experience. In particular, in individuals with an amputation, the integration of the prosthesis into the sensorimotor system induced the more sensorimotorically guided perception of physically possible movements. In parallel, able-bodied individuals were also biased toward the more sensorimotorically guided perception while performing the task in a fully functional sensorimotor state. However, when this full body sensorimotor state was affected by not wearing the prosthesis, or, in able-bodied individuals, by the transient peripheral immobilization of the leg by sitting on it, visually guided perception was more likely to occur. This was not case for BID individuals, who often engage in pretending to be an amputee in everyday life. "Pretending" in the form of sitting on the unwanted leg during the LAMP task did not impact perception, further confirming the pivotal role of the observer's sensorimotor experiences in this task.

Both studies come with important limitations. First, while our sample size in study 1 was comparable to or larger than that of previous studies (Saetta et al., 2018; Shiffrar and Freyd, 1990; Stevens et al., 2000), and the statistical power was adequate, the sample sizes remain modest. Therefore, replication studies in bigger sample sizes would be desirable. Second, M1 tDCS has shown to exert minor or no effects on corticospinal activity in almost 50% of the cases (Wiethoff et al., 2014). As the present study lacks an objective measure of cortical excitability, we cannot accurately infer whether this might have been the case in our sample. However, such a lack of neural modulation should be reflected in a *smaller* effect of the stimulation, and there is no reason to assume confounding effects in our included groups. Third, despite the use of a well-established M1 ctDCS setup supposedly targeting the upper limbs, we found the stimulation to affect both upper and lower limbs. Therefore, it might be the case that the effects spread from the sensorimotor regions representing the upper limbs to neighboring regions, including those representing the lower limbs (for a discussion see Stagg et al., 2018). For the same reason, it might be impossible to accurately disentangle the effects of sensory and motor processes on LAMP. The weaknesses inherent to the M1 c-tDCS would require the integration of a single-pulse TMS protocol as a more robust technique to target specific regions of M1 and systematically quantify the effects of this stimulation on cortical excitability. The use of this technique in future studies may provide useful insights to further substantiate the motor theory. Furthermore, another potential weakness of the study is the lack of a baseline condition, which would have ensured that the observed across-group effects could be ascribed to the c-tDCS stimulation, and not to a general bias of one or the other group towards the visually or sensorimotorically guided perception. However, our analytic approach allowed us to establish that there was no significant variability in the effect of c-tDCS across participants. Moreover, in future studies, the c-tDCS should be applied to a control site to exclude that the effects are due to the inhibition of the sensorimotor areas rather than due to a general effect of the M1 c-tDCS. In study 2, due to its web-based nature, there were no means to control whether the manipulation of the sensorimotor states was in fact realized, other than a manipulation check question asking the participants to answer truthfully whether they had followed the required procedure. Future replications in a laboratory setting would thus be advantageous. However, the non-compliance to the manipulation should have reduced the evinced effects of sensorimotor state rather than enhance them. Futhemore, the replication of the main effect of SOA in all three samples alludes to the validity of the results, and justifies an online application of the task. By administering the task online, we were able to recruit a sample of 29 individuals with an amputation to perform the task twice, resulting in a larger sample size than in classical LAMP studies. Although the number of BID individuals is admittedly small, the presumed rarity and secrecy of the disorder (First, 2005) often sets hurdles in recruiting an adequately powered sample size. Furthermore, while we were able to follow up with amputees with a reminder in the case of non-participation in the second session a after one week, the anonymous nature of the BID recruitment and participation made the identification (and therefore targeted reminder) of individual participants (who had not yet participated in the second round) impossible, despite emailing general follow-up participation reminders. Given these circumstances, we consider our sample size acceptable, especially in view of the fact that participants had to perform the task twice. Finally, the specific hypotheses were based on the findings of the more adequately powered study 1, and were supported by these preliminary analyses. Nevertheless, the number of participants and the statistical power were rather low, and a replication study in a larger sample size would prove informative.

The focus of the present studies was on the interaction between the manipulation of sensorimotor states and LAMP. However, other factors such as (upper or lower) *Limb*, *Laterality*, *Correspondence of the laterality of the stimuli with the side of the (desired) amputation*, *Solidity*, and *Perspective*, were not fully considered, given the small number of participants. For the interested reader, we thus provide a table with the results of the explorative analyses including all these factors in the supplementary materials and, for further analyses, the datasets are deposited on the open science framework (OSF, https://osf.io/4z6yc/).

Building upon the results of the two studies that visual input of bodily movements triggers a cross-modal activation of sensorimotor and visual limb representations, the LAMP task may bring forth the fascinating potential to clinically evaluate the state of peripheral and central aspects of body representation. From a more practical stance, the LAMP task might, for example, be used to assess the outcomes of rehabilitative programs for clinical conditions marked by reduced reliance of the central limb representations on sensorimotor processing in favor of visual processing. Such a disintegration of the interplay between visual and sensorimotor processing may occur after disconnection between peripheral and central limb sensorimotor signalling (as in spinal cord injury, see Scandola et al., 2019), or as a consequence of a profound disturbance in the body schema (as in asomatognosia, i.e., the somaesthetic experience that a limb has ceased to exist, see Saetta et al., 2020c). To prove the effectiveness of the physiotherapy treatment in re-establishing this interplay, Scandola et al. Scandola et al. (2019) administered a mental rotation task (i.e., a limb laterality task) to patients with spinal cord injury, where the visual presentation of static limb stimuli activates the visual or the sensorimotor processing depending on the depicted limb's orientation and the observer's biomechanical constraints. While patients generally tended to adopt visual processing, after physiotherapy, their performances were biased again by the biomechanical constraints. Analogously, in the LAMP task, the switching between the visually and the sensorimotorically guided perception depending on SOAs may confirm the effectiveness of therapeutic interventions on the level of an individual, and thus foster the definition of more customized forms of therapy. Future studies might look more carefully into the individual timing courses of such visual and sensorimotor interactions, as it has previously been done using a limb laterality task (Perruchoud et al., 2018).

Furthermore, the performances in the LAMP task might be taken as signs to evaluate the impact of different neurological and psychiatric disorders on visual as compared to sensorimotor processing. Indeed, in a previous study (Saetta et al., 2018), we showed that the perception of a phantom limb of individuals with an amputation, and its interaction with the environment in everyday situations, was intrinsically related to LAMP. The results of the present study emphasize that limb amputation may bias individuals towards visual processing, but that the integration of the prosthesis as a part of the body within the sensorimotor system may promote a healthy interplay between visual and sensorimotor processing (see also Fritsch et al., 2021,). In a separate clinical population of BID individuals, we here showed that transient limb immobilization to simulate the desired bodily state does not exert any influence on the adoption of visual or sensorimotor processing, thus suggesting the presence of profound alterations in sensorimotor processing (i.e., lack of integration of peripheral aspect of body representation into a central body representation). Therefore, in BID individuals, we predict that a restoration of limb ownership through non-invasive techniques such as brain-computer interfaces may be accompanied by successful experimental manipulations of the bodily posture in the LAMP task (for a recent opinion paper on BID treatment see Chakraborty et al., 2021); for methodological considerations see Pisotta et al. (2015).

To conclude, our findings extend the accumulating evidence for the functional role of sensorimotor processing in perception by showing a systematic influence of the sensorimotor state on LAMP. They are thus in line with the embodied cognition framework, suggesting a strong anchoring of perception and cognition in sensorimotor bodily states.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.neuropsychologia.2021.108032.

Credit author statement

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References

Aoyama, A., Krummenacher, P., Palla, A., Hilti, L.M., Brugger, P., 2012. Impaired spatial-temporal integration of touch in Xenomelia (body integrity identity disorder). Spatial Cognit. Comput. 12 (2–3), 96–110. https://doi.org/10.1080/13875868.2011.603773.

Barsalou, L.W., 2010. Grounded cognition: past, present, and future. Topics Cognitive Sci. 2 (4), 716–724. https://doi.org/10.1111/j.1756-8765.2010.01115.x.

Bates, D., Kliegl, R., Vasishth, S., Baayen, H., 2015. Parsimonious Mixed Models. ArXiv:1506.04967 [Stat].

Bechara, A., Damasio, A.R., 2005. The somatic marker hypothesis: a neural theory of economic decision. Game. Econ. Behav. 52 (2), 336–372. https://doi.org/10.1016/j.geb.2004.06.010.

Bekrater-Bodmann, R., 2021. Factors associated with prosthesis embodiment and its importance for prosthetic satisfaction in lower limb amputees. Front. Neurorob. 14 https://doi.org/10.3389/fnbot.2020.604376.

Bekrater-Bodmann, R., Schredl, M., Diers, M., Reinhard, I., Foell, J., Trojan, J., Fuchs, X., Flor, H., 2015. Post-amputation pain is associated with the recall of an impaired body representation in dreams—results from a nation-wide survey on limb amputees. PLoS One 10 (3), e0119552. https://doi.org/10.1371/journal.pone.0119552.

Bekrater-Bodmann, R., Reinhard, I., Diers, M., Fuchs, X., Flor, H., 2021. Relationship of prosthesis ownership and phantom limb pain: results of a survey in 2383 limb amputees. Pain 162 (2), 630–640. https://doi.org/10.1097/j.pain.0000000000002063.

Bindman, L.J., Lippold, O.C.J., Redfearn, J.W.T., 1964. The action of brief polarizing currents on the cerebral cortex of the rat (1) during current flow and (2) in the production of long-lasting after-effects. J. Physiol. 172 (3), 369–382.

Blake, R., Shiffrar, M., 2007a. Perception of human motion. Annu. Rev. Psychol. 58, 47–73. https://doi.org/10.1146/annurev.psych.57.102904.190152.

Blake, R., Shiffrar, M., 2007b. Perception of human motion. Annu. Rev. Psychol. 58, 47–73. https://doi.org/10.1146/annurev.psych.57.102904.190152.

Bliese, P.D., Ployhart, R.E., 2002. Growth modeling using random coefficient models: model building, testing, and illustrations. Organ. Res. Methods 5, 362–387. https://doi.org/10.1177/109442802237116.

Bramati, I.E., Rodrigues, E.C., Simões, E.L., Melo, B., Höfle, S., Moll, J., Lent, R., Tovar-Moll, F., 2019. Lower limb amputees undergo long-distance plasticity in sensorimotor functional connectivity. Sci. Rep. 9 (1), 2518. https://doi.org/10.1038/s41598-019-39696-z.

Brugger, P., 2006. From phantom limb to phantom body: varieties of extracorporeal awareness. In: Knoblich, G., Thornton, I.M., Grosjean, M., Shiffrar, M. (Eds.), Human Body Perception from the inside Out. Oxford University Press, pp. 171–209.

Brugger, P., Christen, M., Jellestad, L., Hänggi, J., 2016. Limb amputation and other disability desires as a medical condition. *The Lancet*. Psychiatry 3 (12), 1176–1186. https://doi.org/10.1016/S2215-0366(16)30265-6.

Brugger, P., Kurthen, I., Rashidi-Ranjbar, N., Lenggenhager, B., 2018. Grey matter or social matters? Causal attributions in the era of biological psychiatry. Eur. Psychiatr. 52, 45–46.

Carmon, J., Bammel, M., Brugger, P., Lenggenhager, B., 2021. Uncertainty promotes neuroreductionism: a behavioral online study on folk psychological causal inference from neuroimaging data. Psychopathology. https://doi.org/10.1159/000518476.

Chakraborty, S., Saetta, G., Simon, C., Lenggenhager, B., Ruddy, K., 2021. Could brain–computer interface Be a new therapeutic approach for body integrity dysphoria? Front. Hum. Neurosci. 15, 433. https://doi.org/10.3389/fnhum.2021.699830.

Chen, R., Cohen, L.G., Hallett, M., 1997. Role of the ipsilateral motor cortex in voluntary movement. Can. J. Neurol. Sci. 24, 284–291.

de Leeuw, J.R., 2015. jsPsych: a JavaScript library for creating behavioral experiments in a Web browser. Behav. Res. Methods 47 (1), 1–12. https://doi.org/10.3758/s13428-014-0458-y.

Downing, P.E., Jiang, Y., Shuman, M., Kanwisher, N., 2001. A cortical area selective for visual processing of the human body. Science (New York, N.Y.) 293 (5539), 2470–2473. https://doi.org/10.1126/science.1063414.

Fadiga, L., Fogassi, L., Pavesi, G., Rizzolatti, G., 1995. Motor facilitation during action observation: a magnetic stimulation study. J. Neurophysiol. 73 (6), 2608–2611. https://doi.org/10.1152/jn.1995.73.6.2608.

First, M.B., 2005. Desire for amputation of a limb: paraphilia, psychosis, or a new type of identity disorder. Psychol. Med. 35 (6), 919–928. https://doi.org/10.1017/s0033291704003320.

Fritsch, A., Lenggenhager, B., Bekrater-Bodmann, R., 2021. Prosthesis embodiment and attenuation of prosthetic touch in upper limb amputees–A proof-of-concept study. Conscious. Cognit. 88, 103073.

Funk, M., Shiffrar, M., Brugger, P., 2005. Hand movement observation by individuals born without hands: phantom limb experience constrains visual limb perception. Exp. Brain Res. 164 (3), 341–346. https://doi.org/10.1007/s00221-005-2255-4.

Gandola, M., Bruno, M., Zapparoli, L., Saetta, G., Rolandi, E., De Santis, A., Banfi, G., Zerbi, A., Sansone, V., Paulesu, E., 2017. Functional brain effects of hand disuse in patients with trapeziometacarpal joint osteoarthritis: executed and imagined movements. Exp. Brain Res. 235, 3227–3241. https://doi.org/10.1007/s00221-017-5049-6.

Gandola, M., Zapparoli, L., Saetta, G., De Santis, A., Zerbi, A., Banfi, G., Sansone, V., Bruno, M., Paulesu, E., 2019. Thumbs up: imagined hand movements counteract the adverse effects of post-surgical hand immobilization. Clinical, behavioral, and fMRI longitudinal observations. NeuroImage: Clinical 23, 101838. https://doi.org/10.1016/j.nicl.2019.101838.

Giese, M.A., Poggio, T., 2003. Neural mechanisms for the recognition of biological movements. Nat. Rev. Neurosci. 4 (3), 179–192. https://doi.org/10.1038/nrn1057.

Grosbras, M.-H., Beaton, S., Eickhoff, S.B., 2012. Brain regions involved in human movement perception: a quantitative voxel-based meta-analysis. Hum. Brain Mapp. 33 (2), 431–454. https://doi.org/10.1002/hbm.21222.

Heinemann, F.H., 1945. Toland and leibniz. Phil. Rev. 54 (5), 437–457. https://doi.org/10.2307/2181293.

Hilti, L.M., Brugger, P., 2010. Incarnation and animation: physical versus representational deficits of body integrity. Exp. Brain Res. 204 (3), 315–326. https://doi.org/10.1007/s00221-009-2043-7.

ICD-11—Mortality and Morbidity Statistics. (n.d.). Retrieved October 20, 2018, from https://icd.who.int/browse11/l-m/en#/http://id.who.int/icd/entity/256572629.

Ionta, S., Fourkas, A.D., Fiorio, M., Aglioti, S.M., 2007. The influence of hands posture on mental rotation of hands and feet. Exp. Brain Res. 183 (1), 1–7. https://doi.org/10.1007/s00221-007-1020-2.

Ionta, S., Perruchoud, D., Draganski, B., Blanke, O., 2012. Body context and posture affect mental imagery of hands. PLoS One 7 (3), e34382. https://doi.org/10.1371/journal.pone.0034382.

Jamil, A., Batsikadze, G., Kuo, H.-I., Labruna, L., Hasan, A., Paulus, W., Nitsche, M.A., 2017. Systematic evaluation of the impact of stimulation intensity on neuroplastic after-effects induced by transcranial direct current stimulation. J. Physiol. 595 (4), 1273–1288. https://doi.org/10.1113/JP272738.

Jung, Y.-J., Kim, J.-H., Im, C.-H., 2013. COMETS: a MATLAB toolbox for simulating local electric fields generated by transcranial direct current stimulation (tDCS). Biomed. Eng. Lett. 3 (1), 39–46. https://doi.org/10.1007/s13534-013-0087-x.

Kilner, J.M., Friston, K.J., Frith, C.D., 2007. Predictive coding: an account of the mirror neuron system. Cognit. Process. 8 (3), 159–166. https://doi.org/10.1007/s10339-007-0170-2.

Kourtzi, Z., Shiffrar, M., 1999. Dynamic representations of human body movement. Perception 28 (1), 49–62. https://doi.org/10.1068/p2870.

Langer, N., Hänggi, J., Müller, N.A., Simmen, H.P., Jäncke, L., 2012. Effects of limb immobilization on brain plasticity. Neurology 78, 182–188. https://doi.org/10.1212/WNL.0b013e31823fcd9c.

Liepert, J., Tegenthoff, M., Malin, J.-P., 1995. Changes of cortical motor area size during immobilization. Electroencephalogr. Clin. Neurophysiol. Electromyogr. Mot. Control 97, 382–386. https://doi.org/10.1016/0924-980X(95)00194-P.

Makin, T.R., Scholz, J., Filippini, N., Henderson Slater, D., Tracey, I., Johansen-Berg, H., 2013. Phantom pain is associated with preserved structure and function in the former hand area. Nat. Commun. 4 (1), 1570. https://doi.org/10.1038/ncomms2571.

Moseley, G.L., Brugger, P., 2009. Interdependence of movement and anatomy persists when amputees learn a physiologically impossible movement of their phantom limb. Proc. Natl. Acad. Sci. U.S.A. 106 (44), 18798–18802. https://doi.org/10.1073/pnas.0907151106.

Niedernhuber, M., Barone, D.G., Lenggenhager, B., 2018. Prostheses as extensions of the body: progress and challenges. Neurosci. Biobehav. Rev. 92, 1–6. https://doi.org/10.1016/j.neubiorev.2018.04.020.

Nitsche, M.A., Paulus, W., 2000a. Excitability changes induced in the human motor cortex by weak transcranial direct current stimulation. J. Physiol. 527 (Pt 3), 633–639. https://doi.org/10.1111/j.1469-7793.2000.t01-1-00633.x.

Nitsche, M.A., Paulus, W., 2000b. Excitability changes induced in the human motor cortex by weak transcranial direct current stimulation. Pt 3 J. Physiol. 527 (Pt 3), 633–639. https://doi.org/10.1111/j.1469-7793.2000.t01-1-00633.x. PubMed.

Nitsche, M.A., Paulus, W., 2001. Sustained excitability elevations induced by transcranial DC motor cortex stimulation in humans. Neurology 57 (10), 1899. https://doi.org/10.1212/WNL.57.10.1899.

Nitsche, M.A., Nitsche, M.S., Klein, C.C., Tergau, F., Rothwell, J.C., Paulus, W., 2003. Level of action of cathodal DC polarisation induced inhibition of the human motor cortex. Clin. Neurophysiol.: Off. Int. Federation Clin. Neurophysiol. 114 (4), 600–604. https://doi.org/10.1016/s1388-2457(02)00412-1.

Orgs, G., Dovern, A., Hagura, N., Haggard, P., Fink, G.R., Weiss, P.H., 2016. Constructing visual perception of body movement with the motor cortex. Cerebr. Cortex 26 (1), 440–449. https://doi.org/10.1093/cercor/bhv262.

Paracampo, R., Montemurro, M., de Vega, M., Avenanti, A., 2018. Primary motor cortex crucial for action prediction: a tDCS study. Cortes J. Devot. Study Nervous Syst. Behav. 109, 287–302. https://doi.org/10.1016/j.cortex.2018.09.019.

Peelen, M.V., Downing, P.E., 2007. The neural basis of visual body perception. Nat. Rev. Neurosci. 8 (8), 636–648. https://doi.org/10.1038/nrn2195.

Perruchoud, D., Fiorio, M., Cesari, P., Ionta, S., 2018. Beyond variability: subjective timing and the neurophysiology of motor cognition. Brain Stimul. 11 (1), 175–180.

Pisotta, I., Perruchoud, D., Ionta, S., 2015. Hand-in-hand advances in biomedical engineering and sensorimotor restoration. J. Neurosci. Methods 246, 22–29.

Preacher, K.J., Curran, P.J., Bauer, D.J., 2006. Computational tools for probing interactions in multiple linear regression, multilevel modeling, and latent curve analysis. J. Educ. Behav. Stat. 31 (4), 437–448.

Puce, A., Perrett, D., 2003. Electrophysiology and brain imaging of biological motion. Phil. Trans. Biol. Sci. 358 (1431), 435–445. https://doi.org/10.1098/rstb.2002.1221.

Qi, F., Nitsche, M.A., Zschorlich, V.R., 2019. Modulating observation-execution-related motor cortex activity by cathodal transcranial direct current stimulation. Brain Sci. 9 (5), 121. https://doi.org/10.3390/brainsci9050121.

Ramachandran, V.S., Hirstein, W., 1998. The perception of phantom limbs. The D. O. Hebb lecture. Brain: J. Neurol. 121 (Pt 9), 1603–1630.

Ruby, P., Decety, J., 2001. Effect of subjective perspective taking during simulation of action: a PET investigation of agency. Nat. Neurosci. 4 (5), 546–550. https://doi.org/10.1038/87510.

Saetta, G., Grond, I., Brugger, P., Lenggenhager, B., Tsay, A.J., Giummarra, M.J., 2018. Apparent motion perception in lower limb amputees with phantom sensations: "obstacle shunning" and "obstacle tolerance". Cortex 104, 220–231.

Saetta, G., Cognolato, M., Atzori, M., Faccio, D., Giacomino, K., Mittaz Hager, A.-G., Tiengo, C., Bassetto, F., Müller, H., Brugger, P., 2020a. Gaze, behavioral, and clinical data for phantom limbs after hand amputation from 15 amputees and 29 controls. Scientific Data 7 (1), 60. https://doi.org/10.1038/s41597-020-0402-1.

Saetta, G., Hänggi, J., Gandola, M., Zapparoli, L., Salvato, G., Berlingeri, M., Sberna, M., Paulesu, E., Bottini, G., Brugger, P., 2020b. Neural correlates of body integrity dysphoria. Curr. Biol. https://doi.org/10.1016/j.cub.2020.04.001. S0960982220304814.

Saetta, G., Zindel-Geisseler, O., Stauffacher, F., Serra, C., Vannuscorps, G., Brugger, P., 2020c. Asomatognosia: structured interview and assessment of visuomotor imagery. Front. Psychol. 11 https://doi.org/10.3389/fpsyg.2020.544544.

Saetta, G., Ruddy, K., Zapparoli, L., Gandola, M., Salvato, G., Sberna, M., Bottini, G., Brugger, P., Lenggenhager, B., 2021. White Matter Abnormalities in Body Integrity Dysphoria. https://doi.org/10.1101/2021.08.18.21262224, 2021.08.18.21262224.

Scandola, M., Dodoni, L., Lazzeri, G., Arcangeli, C.A., Avesani, R., Moro, V., Ionta, S., 2019. Neurocognitive benefits of physiotherapy for spinal cord injury. J. Neurotrauma 36 (12), 2028–2035. https://doi.org/10.1089/neu.2018.6123.

Shiffrar, M., Freyd, J.J., 1990. Apparent motion of the human body. Psychol. Sci. 1 (4), 257–264. https://doi.org/10.1111/j.1467-9280.1990.tb00210.x.

Siebner, H.R., Lang, N., Rizzo, V., Nitsche, M.A., Paulus, W., Lemon, R.N., Rothwell, J.C., 2004. Preconditioning of low-frequency repetitive transcranial magnetic stimulation with transcranial direct current stimulation: evidence for homeostatic plasticity in the human motor cortex. J. Neurosci.: Off. J. Soc. Neurosci. 24 (13), 3379–3385. https://doi.org/10.1523/JNEUROSCI.5316-03.2004.

Simoes, E.L., Bramati, I., Rodrigues, E., Franzoi, A., Moll, J., Lent, R., Tovar-Moll, F., 2012. Functional expansion of sensorimotor representation and structural reorganization of callosal connections in lower limb amputees. J. Neurosci. 32 (9), 3211–3220.

Solodkin, A., Hlustik, P., Chen, E.E., Small, S.L., 2004. Fine modulation in network activation during motor execution and motor imagery. Cerebr. Cortex 14 (11), 1246–1255.

Sommet, N., Morselli, D., 2017. Keep calm and learn multilevel logistic modeling: a simplified three-step procedure using Stata, R, Mplus, and SPSS. Int. Rev. Soc. Psychol. 30 (1) https://doi.org/10.5334/irsp.90.

Stagg, C.J., Antal, A., Nitsche, M.A., 2018. Physiology of transcranial direct current stimulation. J ECT 34, 144–152. https://doi.org/10.1097/YCT.0000000000000510.

Stevens, J.A., Fonlupt, P., Shiffrar, M., Decety, J., 2000. New aspects of motion perception: selective neural encoding of apparent human movements. Neuroreport 11 (1), 109–115.

Stone, K.D., Bullock, F., Keizer, A., Dijkerman, H.C., 2018. The disappearing limb trick and the role of sensory suggestibility in illusion experience. Neuropsychologia 117, 418–427.

Thornton, I.M., 1998. The visual perception of human locomotion. Cogn. Neuropsychol. 15 (6–8), 535–552. https://doi.org/10.1080/026432998381014.

Turbyne, C., de Koning, P., Zantvoord, J., Denys, D., 2021. Body integrity identity disorder using augmented reality: a symptom reduction study. BMJ Case Rep. 14 (1), e238554 https://doi.org/10.1136/bcr-2020-238554.

van den Heiligenberg, F.M.Z., Orlov, T., Macdonald, S.N., Duff, E.P., Henderson Slater, D., Beckmann, C.F., Johansen-Berg, H., Culham, J.C., Makin, T.R., 2018. Artificial limb representation in amputees. Brain 141 (5), 1422–1433. https://doi.org/10.1093/brain/awy054.

Vangeneugden, J., Peelen, M.V., Tadin, D., Battelli, L., 2014. Distinct neural mechanisms for body form and body motion discriminations. J. Neurosci. 34 (2), 574–585. https://doi.org/10.1523/JNEUROSCI.4032-13.2014.

Vannuscorps, G., Caramazza, A., 2016. The origin of the biomechanical bias in apparent body movement perception. Neuropsychologia 89, 281–286. https://doi.org/10.1016/j.neuropsychologia.2016.05.029.

Verfaillie, K., Daems, A., 2002. Representing and anticipating human actions in vision. Vis. Cognit. 9 (1–2), 217–232. https://doi.org/10.1080/13506280143000403.

Walsh, R.R., Small, S.L., Chen, E.E., Solodkin, A., 2008. Network activation during bimanual movements in humans. Neuroimage 43 (3), 540–553. https://doi.org/10.1016/j.neuroimage.2008.07.019.

Wiethoff, S., Hamada, M., Rothwell, J.C., 2014. Variability in response to transcranial direct current stimulation of the motor cortex. Brain Stimul. 7 (3), 468–475. https://doi.org/10.1016/j.brs.2014.02.003.

Zimmermann, M., Toni, I., de Lange, F.P., 2013. Body posture modulates action perception. J. Neurosci.: Off. J. Soc. Neurosci. 33 (14), 5930–5938. https://doi.org/10.1523/JNEUROSCI.5570-12.2013.