



Agency and responsibility over virtual movements controlled through different paradigms of brain–computer interface

Running title

Inducing agency and responsibility through BCI

Keywords

BCI, agency, visual evoked potentials, mu rhythm, brain-machine interfaces, motor imagery, embodiment, body ownership, virtual reality, motor action, motor activity, sense of agency,

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Key points summary

- We induced embodiment of a virtual body and its movements were controlled by two different BCI paradigms – one based on signals from sensorimotor versus one from visual cortical areas.
- BCI-control of movements engenders agency, but not equally for all paradigms.
- Cortical sensorimotor activation correlates with agency and responsibility.
- This has significant implications for neurological rehabilitation and neuroethics.

Footnote

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Abstract

Agency is the attribution of an action to the self and is a prerequisite for experiencing responsibility over its consequences. Here we investigated agency and responsibility by studying the control of movements of an embodied avatar, via brain computer interface (BCI) technology, in immersive virtual reality. After induction of virtual body ownership by visuomotor correlations, healthy participants performed a motor task with their virtual body. We compared the passive observation of the subject's 'own' virtual arm performing the task with (1) the control of the movement through activation of sensorimotor areas (motor imagery) and (2) the control of the movement through activation of visual areas (steady-state visually evoked potentials). The latter two conditions were carried out using a brain-computer interface (BCI) and both shared the intention and the resulting action. We found that BCI-control of movements engenders the sense of agency, which is strongest for sensorimotor areas activation. Furthermore, increased activity of sensorimotor areas, as measured using EEG, correlates with levels of agency and responsibility. We discuss the implications of these results for the neural basis of agency.

Introduction

The feeling of generating actions that can influence the course of events in the outside world is a central feature of human experience and is important for our perception of the self (Haggard, 2017). The attribution of actions to ourselves is referred to as “agency” (Gallagher, 2000), which gives us a feeling of control and results in a sense of responsibility over an action’s outcome.

Through brain-computer interfaces (BCI) it is feasible to control the actions of surrogate bodies, prostheses, robots, or other effectors. Such BCI systems are based on a closed feedback loop, in which neural activity related to an intention is transformed in real-time into a command to a device that then gives feedback to the participant (Pfurtscheller & Neuper, 2001; Birbaumer, 2006; Hochberg *et al.*, 2012). Different types of BCI are available, some of which rely on changes in the sensorimotor mu-rhythm induced through motor imagery. For such motor-imagery-related BCI it has been shown that discrepancies between the neural activity and the resulting visual feedback can result in a decreased sense of agency (Evans *et al.*, 2015; Marchesotti *et al.*, 2017). However, whether and how agency can be modulated by the usage of other BCI systems has not been investigated.

Agency is closely linked to body ownership—the feeling that “this body is my body”—and although agency and body ownership can be dissociated (Tsakiris *et al.*, 2010; Kalckert & Ehrsson, 2012; Imaizumi & Asai, 2015), agency has been shown to significantly correlate with body ownership (Kalckert & Ehrsson, 2012).

Both body ownership and agency are aspects of self-consciousness, which might not be a unique elemental percept or qualia but rather a cluster of subjective experiences, feelings, and attitudes (Synofzik *et al.*, 2008; Tsakiris *et al.*, 2010). The neural underpinnings of agency have been extensively investigated (for an overview see David (2012) and Haggard (2017)) and might lie in the connectivity between several brain areas, rather than in any single brain structure. A possible candidate is the connectivity between areas involved in action initiation and areas involved in monitoring of perceptual events, which have been proposed as neural correlates (Haggard, 2017). For events caused by an external agent (external agency), neuroimaging studies report activation of a complex brain network including the dorsomedial prefrontal cortex, precuneus, temporoparietal junction and pre-supplementary motor area (pre-SMA). However, for agency-related activity the insula seems to be the most consistently reported area (Sperduti *et al.*, 2011; Haggard, 2017). On the other hand, interference with activity in the pre-SMA by means of transcranial stimulation has been shown to alter agency (Moore *et al.*, 2010; Cavazzana *et al.*, 2015), pointing to an involvement of motor areas in the development of the sense of agency. The role of motor areas in the sense of agency

is theoretically supported by a computational model of agency, the comparator model (Frith *et al.*, 2000), which is based on a model for sensorimotor integration (Wolpert *et al.*, 1995) and describes agency as the result of a matching between predicted and actual sensory feedback of a planned motor action (Blakemore *et al.*, 2000; Frith *et al.*, 2000). Further, brain regions related to BCI control not related to the comparator model have been identified in the basal ganglia, the anterior cingulate cortex and the left superior frontal gyrus (Marchesotti *et al.*, 2017).

Under certain conditions, we can perceive agency over an agent's action without performing that action with our own body, which is referred to as "illusory agency". For example, one can perceive agency over another person's hand movements when seeing that hand at the position where one would expect one's own hand to be and when there is a prior command to carry out the later seen actions (Wegner *et al.*, 2004). Experiments on agency have also been conducted in immersive virtual environments, where a virtual body can be felt as one's own after inducing adequate sensorimotor correlations (Slater *et al.*, 2008, 2009; Sanchez-Vives *et al.*, 2010). Impressively, during this "virtual embodiment" experience, people may attribute actions of the virtual body to themselves even though they are not performing those actions with their real body (Banakou & Slater, 2014; Kokkinara *et al.*, 2016).

Drawing upon these premises, our objective was to investigate whether and how the sense of agency over a virtual limb movement controlled through a BCI was generated. In order to generate a movement through BCI there is first an intention. Next, the brain signal is used by the BCI to initiate the movement, however different signals (or paradigms) can be used. Here we questioned: do agency levels differ between different BCI methods? How relevant is the cortical area that the BCI uses for the initiation of the movement? And, if agency over a BCI-controlled action is induced, is there also a feeling of responsibility with respect to the results of that action?

To answer these questions we designed and carried out an experiment to measure cortical activation patterns, sense of agency, and the sense of responsibility with respect to movements of an "embodied" virtual body in an immersive virtual environment (Slater *et al.*, 2008, 2010) and compared three different paradigms to initiate the movements of a virtual arm: motor imagery, activating sensorimotor areas, (Pfurtscheller & Neuper, 1997; Pfurtscheller *et al.*, 2006); visually evoked potentials, activating visual cortical areas (Middendorf *et al.*, 2000; Vialatte *et al.*, 2010); and passive, non-triggered movements.

Methods

Participants

Sixty-two healthy, right-handed females with normal or corrected-to-normal vision, no neurological or psychological disorders, and no medication intake that could influence their perception were screened for the experiment. After the screening procedure, a sample of 40 participants completed the experiment. All participants were novices to BCI. To maintain a similar level of accuracy for BCI conditions, we used the inverse of the binomial cumulative distribution for finding the threshold for non-random (at $P=0.001$) classification of epochs. This threshold was in our case $30/40=0.75$ (i.e. 75%), leaving a remaining sample of 29 participants (mean age=21.5 years, $SD=2.6$; laterality quotient (Oldfield, 1971): mean=71.0, $SD=23.4$). All participants were naïve to the research question, gave written informed consent before starting the experiment, and received €5–20 for their participation. The experiment was approved by the local ethics committee (Comité Ético de Investigación Clínica de la Corporación Sanitaria, Hospital Clínic de Barcelona; approval number HCB/2014/0474) and is in accordance with the Declaration of Helsinki, except for registration in a database.

Virtual environment and tracking system

The virtual environment was programmed and controlled using the Unity game engine (Unity Technologies, www.unity3d.com) and displayed through a HMD (Oculus Rift Development Kit 2, www.oculus.com) with a nominal field-of-view of 100° , a resolution of 960×1080 pixels per eye, and a 75 Hz frame rate. The virtual bodies were taken from the Rocketbox library (Rocketbox Studios GmbH, www.rocketbox.de). Further details about the laboratory setups to create and measure virtual embodiment illusions can be found in Spanlang et al. (2014). The virtual room was a custom-made replica of a virtual reality laboratory. During the embodiment phase, movements of the right hand were tracked with the right arm setup of Perception Neuron (Noitom, Beijing, China), a full-body tracking system. See Fig.1 for experimental setup.

Electroencephalographic recordings

Electrographic data were captured with 64 active Ag/AgCl ring electrodes (g.LADYbird, g.tec, Schiedlberg, Austria), amplified with g.HIamp (g.tec) and recorded with Matlab R2013a Simulink software (The MathWorks, Inc., Natick, USA) on a separate computer. During the data acquisition, signals were band-pass filtered between 0.5 and 250 Hz, notch filtered at 50 Hz, and digitized at a rate of 512 Hz. Fifty-nine EEG electrodes were mounted on a g.Gamma cap (g.tec) and had standard positions in accordance with the 10-percent electrode system (Chatrian *et al.*, 1985). The ground electrode was located at AFz. The two electrooculographic (EOG) electrodes were placed next to the outer canthus and below the right eye. EOG and EEG electrodes were referenced to the right ear. The

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two electromyographic (EMG) electrodes had a bipolar montage and were located over the distal section and belly of the anterior deltoid muscle. Data were analyzed offline using Matlab and the Berlin Brain-Computer Interface toolbox (https://github.com/bbci/bbci_public) (Blankertz *et al.*, 2016) and online using Matlab Simulink. To compensate for network latencies between the two computers, we synchronized them by using the network time protocol and time-stamped triggers with the times of the Unity and the Matlab computer. Triggers were then adapted in the analysis so that the time stamps would match.

SMR-based BCI

The sensorimotor rhythm (SMR)-based BCI used the Common Spatial Pattern (CSP) approach (Fukunaga, 1990; Koles *et al.*, 1995; Müller-Gerking *et al.*, 1999; Graimann & Pfurtscheller, 2006; Blankertz *et al.*, 2008) to extract event-related desynchronization (ERD) over sensorimotor areas from 27 channels (see Fig. S1, biorxiv 735548) and was provided by g.tec (“Common Spatial Patterns 2-class BCI”, V2.14.01). This is an established approach for distinguishing two classes of motor imagery, which were in our case imagination of a right arm pressing a button (similar to the movement they saw in the virtual environment) and a left foot movement (extension and flexion of the ankle joint). The foot movement served to create the classifier.

Motor imagery training

Before the actual experiment, participants undertook motor imagery training consisting of two parts, both outside virtual reality. In the initial part we taught participants how to imagine the movement in order to produce the greatest changes in the SMR (this took up to 25 min), and in the second part participants did up to four training sessions with the BCI, which followed the training procedure recommended by g.tec (Guger, Edlinger, Harkam, Niedermayer, & Pfurtscheller, 2003). In the majority of the participants one of the four training session was done directly before the motor imagery condition. The initial part of the training was inspired by Ethan *et al.* (2008) and participants were asked (1) to repeatedly press a button in front of them with their right arm, (2) to imagine the action of the right arm, (3) to repeatedly lift the heel and the tip of their left foot, (4) to imagine the action of their left foot, (5) to alternately imagine the hand and foot action. The SMR-BCI training sessions were performed in front of a computer screen. Participants were sitting on a chair with their arms on a table in front of them, they were instructed not to move and to keep their body relaxed. The training started with a fixation cross displayed in the middle of the screen. After 3 s an arrow was shown for 1.25 s which pointed either to the right or down. The participants were instructed to imagine the previously learned arm movement when the arrow pointed to the right or the foot movement when the arrow pointed down for the next 5 seconds until the arrow disappeared. In the following training sessions feedback on the classification result of the BCI was given to the

participant between seconds 4.25 and 8. Specifics of the procedure can be found in Guger et al. (2003).

SSVEP-based BCI

The visual-evoked potential this BCI system was based on were steady-state visual-evoked potentials (SSVEP), which can be evoked by a visual stimulus flickering at a specific frequency. The SSVEP-based BCI extracted the signal from eight occipital channels (see Fig. S1, [biorxiv 735548](#)), was provided by g.tec (“SSVEP BCI”, V2.14.01), and modified for its use in a virtual environment. SSVEP stimuli were two buttons in the virtual environment; one blinked at a frequency of 7.5 Hz and the other at 9.4 Hz. An extra, dummy frequency (20 Hz) was also used during the SSVEP training phase to be able to form a better classifier.

SSVEP training

The SSVEP-training was performed while participants wore the HMD and was adapted from Guger et al. (2012). Each frequency required five training trials and took about 4 min. Only the frequency of interest was displayed during the training phase; during the experiment, both frequencies (7.5 and 9.5 Hz) were displayed at the same time. Participants were sitting in a chair with their hands on the table in front of them and wore the head-mounted display. First, a 20 Hz flickering visual frequency was utilized as dummy frequency in order to obtain a precise classifier. This frequency was not displayed during the training phase nor during the experiment. Participants were instructed to look in the middle of the two (not blinking) buttons (a fixation cross was displayed at beginning of each trial at that point). The SSVEP training had 15 trials, 5 for each frequency used during the experiment (7.5 and 9.4 Hz). In order to get a better classifier, only the frequency of interest was displayed during the training phase. Later, during the experiment, both frequencies were displayed simultaneously.

Experimental procedure

All instructions were pre-recorded and given to participants through headphones. Preparation of EEG electrodes took about 40 min. Before starting the experiment, participants did the training for the SMR- and SSVEP-based BCIs. The classifiers of both training programs were calculated using gBSanalyze (Version 5.16.00, g.tec).

Executed Movement

Executed Movement was recorded in 18 out of the 29 participants in order to capture the brain activity for each participant while moving their real right arm. Through headphones participants heard a beep every 8 s with a jitter of ± 1 s. They were instructed to move their right hand and press a button in front of them (within 2 s) whenever they heard a beep, performing a movement that resembled the virtual movement.

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Experimental conditions

Participants were asked to sit comfortably on a chair with their arms lying on a table in front of them keeping a distance of 55 cm between their middle fingers (Fig. S2, biorxiv 735548). Each experimental condition started with an embodiment phase followed by the action phase. In both phases participants saw a virtual body from a first person perspective in the same position and collocated with their real body.

Embodiment phase. When visualizing the virtual environment, participants were instructed to look around and describe what they saw, thereby inducing a feeling of presence in the virtual environment. They were further instructed to look down at the virtual body. Next, they were instructed to move their right hand and fingers for 1 min. These movements were tracked and mapped onto the movements of the virtual body, so that participants saw the right virtual arm moving in the same way. This procedure was carried out to induce a sense of body ownership and agency over the virtual body regardless of the condition. Directly after this, the questionnaire items IControlledArm and MyBody were presented on the virtual screen in randomized order (see Table 1).

Action phase. Directly after the embodiment phase, participants were instructed to keep still for the rest of the experimental condition and to only move the left hand when giving responses to the questionnaire items. The virtual environment was the same as during the embodiment phase, except that now they saw two buttons on the table in front of them (Fig. S3, biorxiv 735548), each blinking at one of the SSVEP frequencies.

All participants went through the following three conditions: the MotorImagery condition, the SSVEP condition, and the Observe condition, each consisting of 40 trials. The order of conditions was balanced over participants (the order of conditions after exclusion of participants from the analysis can be found in the supplementary information). Each trial started with a fixation cross displayed between the two buttons, followed 2 s later by an arrow indicating the target button for that particular trial. In the following 6 s participants had to either imagine the arm movement (MotorImagery condition), focus on the indicated button (SSVEP condition), or simply observe what was happening (Observe condition). During MotorImagery and SSVEP conditions the previously trained classifiers detected whether participants imagined the arm movement (MotorImagery) or to which button they looked (SSVEP); that is, if the frequency of the indicated button or if sensorimotor activity in arm areas were detected, the virtual arm would move toward the target button; if not, participants would hear an error sound to indicate a missed trial and the arm would not move. Missed trials were repeated one additional time. In the Observe condition, the arm moved in each trial to the target button. Fig. S3 (biorxiv 735548) displays the timeline of one trial. Every 10 trials participants responded to the IControlledArm item (Table 1). During each experimental condition the virtual arm accidentally threw an object off the table resulting in a breaking sound (Fig. S4, biorxiv 735548). This happened

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four times throughout each condition at a random trial once during each block of 10 trials (but not directly before or after they were answering the IControlledArm item). The objects were a pencil stand, a vase, a coffee cup, and a glass, and they appeared in random order. Directly after the virtual arm broke an object, participants answered the IBrokeObject item (Table 1). One of the four trials was a catch trial, which was included to test our items' internal validity.

Questionnaires

Table 1 displays all questionnaire items. Some items were displayed inside the virtual reality environment (MyBody, IControlledArm, IBrokeObject) and others outside on a computer screen (MyBody, MySound, ITouchedObject, MyMovement, ArmMovedItself). In the horizontal visual analogue scale for item 3, 0 corresponded to “the movement of another person” and 10 to “my movement” (see Table 1). Note that we used reverse wording when designing question 4, therefore its scale was reversed for the analysis.

Questionnaire items inside the virtual environment were displayed on a virtual screen. Participants gave their responses by turning a button (Power Mate, Griffin Technologies, Nashville, USA) located next to their left hand. VAS ratings, indicated by a little red bar, increased when the button was turned right and decreased when it was turned left. Participants confirmed their rating by pressing the button. In order to avoid interfering with the sense of body ownership, while rating the questionnaire items and therefore moving the left hand, the view of the virtual forearms was blocked by a virtual board.

Directly after each condition participants answered five questionnaire items outside the virtual environment, which were displayed on a laptop screen. In this case, participants answered the items using the keyboard. Questionnaire items were displayed in random order (see Table 1). Using a principal component factor analysis which resulted in one variable, the items IBrokeObject and ITouchedObject were merged to the variable ResponsibilityPCF, and the items IControlledArm, MyMovement, and ArmMovedItself were merged to the variable AgencyPCF. Initially we included also MySound, but excluded it later, because the resulting variable AgencyPCF explained more variance without this item (81% of variance *versus* 75% when including MySound). The continuous ratings of the MyBody item were down-scaled into ordinal ratings ranging from 1 to 10.

Processing of EEG data

Artifact identification

Very noisy EEG channels were visually identified and removed from further analysis (this affected on average one to two channels in five participants). During data collection, one electrode (F5) broke and we continued without it (this affected 12 participants). For artifact detection the signal was filtered between 0.5 Hz and 40 Hz. Eye blink artifacts were identified and projected from EEG data with

Independent Component Analysis (ICA) performed on concatenated epoched data (FastICA (Hyvärinen & Oja, 2000)). Epochs were generated around the onset of the arrow and consisted of 1000 ms of pre-stimulus and 6000 ms of post-stimulus interval. The epochs were visually inspected for the presence of muscular and mechanical artifacts, indicated by the variance of the maximal activity and by the Mahalanobis distance (Nikulin *et al.*, 2008). Within different subjects we identified between 0% and 8% of epochs.

Executed Movement

Artifacts in the Executed Movement data were visually identified in epochs ranging from –1000 to 3000 ms around the tone indicating the start of the movement and those epochs containing them were removed at a later step in the analysis (0–25% of epochs).

Amplitude modulation of spontaneous alpha oscillations

We were interested in alpha oscillations because they have the largest signal-to-noise ratio of all spontaneous oscillations and therefore allow a reliable estimation of ERD (Pfurtscheller & Lopes da Silva, 1999; Nikouline *et al.*, 2000; Nierula *et al.*, 2013), which is important for obtaining clear spatial patterns. Moreover, alpha oscillations have been previously shown to be a reliable indicator of engagement of cortical areas in different experimental conditions including sensory and motor tasks (Berger, 1929; Gastaut & Bert, 1954; Pfurtscheller & Aranibar, 1977; Pfurtscheller & Lopes da Silva, 1999).

Identifying individual sensorimotor alpha range

The individual sensorimotor alpha peak frequencies were identified in the pre-stimulus spectrum of Laplace transformed channel C3 (Hjorth, 1975; Graimann & Pfurtscheller, 2006). The signal of all conditions and the executed movement was then filtered in a range of ± 2 Hz around the individual peak frequency.

Identifying individual ERD peak latencies in executed movement data

The filtered and Laplace transformed signal was Hilbert transformed in order to obtain its amplitude envelope (Clochon *et al.*, 1996; Rosenblum & Kurths, 1998; Graimann & Pfurtscheller, 2006). The signal was next cut into epochs from –1000 to 3000 ms around the tone and epochs containing artifacts were removed from further analysis. ERD% was calculated using the following equation: $ERD\% (t) = (AMP (t) - PRE) / PRE \cdot 100$, where AMP (amplitude) refers to the activity at each time point t of the averaged epochs and PRE is the mean amplitude in the pre-stimulus interval (from –500 to 0 ms). Time points with lowest ERD% were identified between 0 and 1500 ms in Laplace transformed channel C3 ($n=18$, latency: mean=808 ms, $SD=228$ ms).

Extracting CSP in Executed Movement data

The filtered, Hilbert-transformed, epoched, and cleaned executed movement signal was used for CSP analysis. No ICA was applied because prior application of another spatial filtering could lead to possible deterioration in the performance of CSP (Blankertz *et al.*, 2008; Nierula *et al.*, 2013). For CSP, pre-stimulus epochs, filtered in the individual alpha range, were merged from executed movement and all three experimental conditions, and the mean was subtracted from single epochs in the post-stimulus interval. The CSP algorithm is commonly used to separate two classes of data by determining the spatial filters W that maximize the variance of one class while simultaneously minimizing the variance of another class. In our data, one class contained the data of the pre-stimulus interval (from -500 to 0 ms) and the other class contained the data of the post-stimulus interval (± 250 ms around the ERD peak previously identified in Laplace transformed C3 channel). In the case of bandpass-filtered EEG-signals, variance is equivalent to power in a given frequency range (Dornhege *et al.*, 2003; Blankertz *et al.*, 2005; Nikulin *et al.*, 2008; Nierula *et al.*, 2013), which means that CSP can be also used to optimize ERD (Lemm *et al.*, 2009). CSP has been successfully used to classify single EEG epochs during motor imagery (Koles *et al.*, 1995; Dornhege *et al.*, 2003; Blankertz *et al.*, 2005; Nikulin *et al.*, 2008). The inverse of the filter matrix W is the CSP and it contains components/patterns that were sorted by the size of their eigenvalue from high to low. Within the first four patterns we selected the pattern with the strongest eigenvalue that represented activity in sensorimotor areas. Patterns were validated by splitting all epochs into two sets. Only patterns that appeared in both sets were considered for further analysis.

Source reconstruction of CSP patterns

Source reconstruction of CSP patterns was performed using Brainstorm (Tadel *et al.*, 2011). The forward model was generated with OpenMEEG using the symmetric Boundary Element Method (Kybic *et al.*, 2005; Gramfort *et al.*, 2010) on the cortical surface of a Montreal Neurological Institute (MNI) brain template (non-linear MNI-ICBM152 atlas (Fonov *et al.*, 2011)) with a resolution of 1 mm. Cortical sources were then estimated using the Tikhonov-regularized minimum-norm (Baillet *et al.*, 2001) with a Tikhonov parameter of $\lambda=10\%$ of maximum singular value of the lead field, and mapped to a distributed source model consisting of 15 000 current dipoles. Sources of CSP patterns were visually inspected for their origin in sensorimotor areas. Fig. 3A displays the inverse solutions averaged over all 18 participants, which was strongest at coordinates $X=-52.5$, $Y=-7.5$ and $Z=52.9$ in the MNI space. Mean sources were located in the precentral gyrus (Fig. 3A).

ERD

The extracted spatial filter W from the CSP pattern used for source analysis was also used to project the data X from the three conditions (MotorImagery, SSVEP, and Observe) using the following formula: $Z=WX$. To obtain ERD%, we extracted the amplitude envelope of the analytic signal with the

Hilbert transform and then calculated ERD% (Nierula *et al.*, 2013) using the formula above. The minimum value of ERD% during the preparation phase was later used for statistical comparisons.

EMG and EOG

The EMG recordings were high-pass filtered at 10 Hz and EOG recordings were low-pass filtered at 50 Hz. Both filtered EMG and EOG recordings were then segmented into epochs from –2000 to 8000 ms with respect to the arrow indicating one of the two buttons. The root-mean square values were calculated during the motor preparation phase (from 0 to 6000 ms) to obtain measures of motor activation (MA) in the right anterior part of the deltoid muscle and eye movement (EM).

MA and EM served as covariates in order to control for experiences of agency triggered by attributing eye or muscle movements to the virtual movement. Therefore, before fitting a statistical model we checked whether MA or EM could explain some of the variance.

Statistics

All statistical tests were performed using Stata 13 (StataCorp LP, College Station, TX). Residuals were tested for normality when necessary using the Shapiro–Wilk test. Violations of the sphericity assumption were tested with Mauchly’s sphericity test. IBrokeObject and ITouchedObject were merged to the variable ResponsibilityPCF, and the items IControlledArm, MyMovement, and ArmMovedItself were merged to the variable AgencyPCF using a principal component factor analysis. The resulting interval scaled variables were analyzed with a multilevel mixed-effects regression (the “mixed” function in Stata) with “condition” as fixed-effects and “individual subject” as random effects. For post hoc analyses we used the Scheffé post hoc criterion for significance. ERD% was analyzed using repeated measures ANOVA with factor “condition” and post hoc comparisons were performed using the Scheffé criterion. Because of its ordinal nature, MyBody reports were analyzed with a multilevel mixed-effects ordered logistic regression (the “meologit” function in Stata) with “condition” as fixed effects and “individual subject” as random effects. Likelihood ratio tests were used to identify if the variables MA or EM should be added as covariates to each model. Relationships between variables were assessed with mixed-effects regression (the “mixed” function in Stata).

Results

Task performance across BCI-paradigms

Task performance plays an important role for agency and responsibility. We therefore compared the levels of accuracy in the two BCI-conditions with a paired *t*-test. Even with a slight absolute difference in accuracy between SSVEP condition (Mean = 90.9%) and the MotorImagery condition (Mean=87.4%), this difference was statistically significant ($t(28)=2.03$, $P=0.052$).

Agency ratings

Agency has been measured in the literature as the sense of control over an action (Synofzik *et al.*, 2008), as the sense of having caused/produced an outcome (Bednark & Franz, 2014; Kumar & Srinivasan, 2014), and as the sense that an action is one's own and not another person's (Weiss *et al.*, 2014). In order to have a single measure for agency, we performed a principal component factor analysis on the questionnaire items indicating agency (IControlledArm, MyMovement, and ArmMovedItself; see Table 1), which resulted in a single variable accounting for 81% of variance. We refer to this variable as AgencyPCF. Median and IQR of all questionnaire items can be found in the Supplementary Table S2.

A mixed-effects regression revealed an effect of condition on AgencyPCF ($z=6.64$, $P<0.001$), indicating that participants experienced higher levels of AgencyPCF over the virtual movement during the Motor Imagery than during the Observe condition (*Scheffé* $z=6.64$, $P<0.001$) and during the SSVEP conditions (*Scheffé* $z=2.53$, $P=0.041$), and participants experienced higher levels of AgencyPCF during the SSVEP than during the Observe condition (*Scheffé* $z=4.12$, $P<0.001$). Our data show that activating motor areas to induce the movement of the virtual arm elicited a higher sense of agency over the action than activating visual areas, while merely observing the virtual arm move elicited the lowest sense of agency (see Fig. 2A).

Responsibility ratings

Agency is closely related to the feeling of responsibility because it tells us when we are responsible for the results of action and when we are not (Haggard & Tsakiris, 2009). To measure the levels of experienced responsibility, we introduced for each condition four random trials in which the virtual arm “accidentally” threw an object off the table and broke it (Supplementary Information, video). We asked participants directly after this incident how strongly they felt responsible for breaking the object (item IBrokeObject). One of these four trials was a catch trial, which we used to test if our measure was working. In this trial the object fell off the table although the virtual hand did not touch it. This trial was not part of the IBrokeObject measure (see Methods for more details). The results on how well our measure worked are reported in the Supplementary Material. Moreover, once the condition (Motor Imagery, SSVEP or Observe) was over, participants were also asked whether they considered

they had touched the object out of sloppiness (item ITouchedObject). We merged these two responsibility-related questionnaire items to the variable ResponsibilityPCF using a principal component factor analysis (Median and IQR of all questionnaire items can be found in the Supplementary Table S2). A mixed-effects regression revealed an effect of condition on ResponsibilityPCF ($z=4.66$, $P<0.001$), wherein participants gave higher ratings during MotorImagery than during Observe (*Scheffé* $z=4.66$, $P<0.001$) or during SSVEP (*Scheffé* $z=3.34$, $P=0.004$), whereas there was no difference between the SSVEP and the Observe conditions (*Scheffé* $z=1.18$, $P=0.499$). Our results show therefore that activating motor areas to induce the virtual arm movement led to a significantly higher sense of responsibility than using visual areas or merely observing the movement (Fig. 2B).

Note that because responsibility can only be experienced when there is agency, the two variables agencyPCF and responsibilityPCF are correlated (mixed-effects regression with condition as covariate, $\beta=0.68$, $z=8.58$, $P<0.001$).

Body ownership ratings

Body ownership and agency are closely related. For example, only when feeling high levels of body ownership over a surrogate body can people experience illusions of agency over the actions of that body (Banakou & Slater, 2014; Kokkinara *et al.*, 2016) or even perceive action errors as their own (Padrao *et al.*, 2016). To capture the participant's experienced level of body ownership we asked them to rate it at the end of each condition (see Table 1 questionnaire item MyBody). A mixed-effects ordered logistic regression revealed an effect of condition on MyBody ($z=3.40$, $P=0.001$; Fig. 2), showing that ratings were highest during Motor Imagery compared to Observe (*Scheffé* $z=3.40$, $P=0.001$) and SSVEP (*Scheffé* $z=2.22$, $P=0.026$); during the Observe and SSVEP conditions ratings did not differ (*Scheffé* $z=1.37$, $P=0.170$). Our data show that participants had highest levels of body ownership during Motor Imagery, while during SSVEP and Observe conditions they reported body ownership at similarly intermediate levels (Fig. 2C).

Activity in sensorimotor areas

Agency has been proposed to result from the match between predicted and actual sensory feedback of a planned motor action, a process that involves sensorimotor areas (Frith *et al.*, 2000; Giummarra *et al.*, 2008). To test the different levels of sensorimotor activity induced by the experimental conditions we first recorded EEG activity in 18 of the 29 included participants while they pressed a button with their right arm (a movement that replicates the virtual one). Applying common spatial pattern (CSP) analysis to the executed movement data, we obtained spatial filters of sensorimotor activity, which we used to project the EEG signal of the three conditions and then calculate the event-related desynchronization (ERD) of the somatosensory alpha rhythm in 18 participants (Fig. 3B displays

ERD% of the projected signal). We compared minimum ERD% in the different conditions during the preparation phase, which corresponds to a time window of 6 s before participants saw the virtual movement and in which they either imagined the movement, focused at the blinking light, or simply observed. A repeated measures analysis of variance (ANOVA) with fixed-effect condition revealed that there was an effect of condition on ERD% ($F(2,34)=12.70, P<0.001$), wherein ERD% was highest during MotorImagery compared to SSVEP (*Scheffé* $t=-3.29, P=0.009$) and Observe (*Scheffé* $t=-4.95, P<0.001$). The SSVEP and Observe conditions did not differ (*Scheffé* $t=-1.66, P=0.267$) (Table 1). Our data show that our experimental paradigm triggered processing in the sensorimotor cortex during the preparation phase and that corresponding levels of neural activity were highest during MotorImagery, and low during SSVEP and Observe conditions.

In order to relate sensorimotor activity to the sense of agency, as has been proposed by computational models of agency (Blakemore *et al.*, 2000; Frith *et al.*, 2000) as well as models that take a cognitive component of agency into account (Synofzik *et al.*, 2008), we investigated the relationship between ERD% and agency-related questionnaire reports. It has been demonstrated that anticipating an action leads to activity in sensorimotor areas (Mauritz & Wise, 1986; Denis *et al.*, 2017), and the situation of body ownership could contribute to this (e.g. Banakou & Slater, 2017). We therefore looked at the correlation between ERD% and agency-related questionnaire reports (as well as responsibility and body ownership related questionnaire reports) over all three conditions and specifically in the MotorImagery condition. We found that greater sensorimotor activity, which is reflected in negative ERD%, was associated with a higher sense of agency and responsibility. Specifically, a mixed-effects regression revealed a negative relationship between ERD% and both AgencyPCF (Fig. 3C; $z=-3.02, P=0.003$) and ResponsibilityPCF (Fig. 3D; $z=-4.56, P<0.001$). There was no significant relationship between ERD% and MyBody ($z=-2.22, P=0.026$). We then examined whether these relationships were also present within conditions. A mixed-effects regression revealed a negative relationship between ERD% and ResponsibilityPCF ($z=-2.84, P=0.004$) in the MotorImagery condition, but not in the two other conditions (Observe: $z=-1.27, P=0.202$; SSVEP: $z=1.33, P=0.183$), indicating that when participants intentionally activated sensorimotor areas, the strength of sensorimotor activity was related to their feeling of responsibility; that is, the stronger the activity the higher the feeling of responsibility. There was no relationship between ERD% and AgencyPCF in any of the three conditions (Observe: $z=-0.10, P=0.922$; SSVEP: $z=-0.25, P=0.805$; Motor Imagery: $z=-0.50, P=0.617$) and no relationship between ERD% and MyBody (Observe: $z=-0.70, P=0.486$; SSVEP: $z=1.97, P=0.048$; MotorImagery: $z=-1.13, P=0.258$).

There was no relationship between activity in occipito-parietal areas and AgencyPCF or ResponsibilityPCF during the SSVEP condition (see Supplementary Material).

Debriefing

Finally, in order to get an overall idea of how much control participants felt over the virtual movement during the different conditions, we asked them to give an overall rating at the end of the experiment. For this rating, participants were asked to order the conditions from strongest to weakest according to their experienced sense of control over the virtual arm movement (IControlledArm). Out of 29 participants, 22 reported strongest feelings of control during Motor Imagery, followed by SSVEP, and during the Observe condition the lowest feeling of control over the virtual arm movement was reported (Fig. S5, biorxiv 735548).

Discussion

With the present work we have demonstrated that BCI-controlled movements engender agency, being higher during this conditions than during the observation of a passive movement of the ‘own’ body. Furthermore, the highest agency is induced by BCI based on the activation of sensorimotor areas (motor imagery paradigms). Interestingly, BCI based on activation of visual areas (SSVEP paradigms), engendered elevated levels of agency compared to movement observation, but not a higher sense of responsibility. Our analysis also revealed that the higher the activation of sensorimotor areas, the higher the reported levels of agency and responsibility. The implications of these findings should be considered at different levels: (1) on the neural basis of agency and responsibility for actions, (2) on executive aspects of which BCI paradigms should be used for different purposes, and (3) on the ethical implications of controlling actions by thinking and the subjective responsibility over the consequences that this may imply.

Higher agency but not responsibility levels for intended movements

Voluntary actions can be described by an intention–action–outcome chain (Roskies, 2010). In this chain, intentions are linked to actions by an action selection process, which is the basis for the motor plan. In addition to the selected action, the motor plan also computes its expected sensory feedback (Frith *et al.*, 2000), and a comparison between intended and expected sensory feedback has been proposed to produce a sense of initiation (de Vignemont & Fournieret, 2004). The action selection process occurs after the formation of the intention but before its execution through an action. In an experimental setup priming can be used to bias the action selection process by making some actions easier to access than others. Participants report reduced feelings of agency when such breaks between the intention–action link are present (Wenke *et al.*, 2010; Chambon *et al.*, 2013, 2014). Actions are also linked to their outcome through a comparator mechanism (Frith *et al.*, 2000), which has been proposed to create a sense of one’s own movement and contribute, together with the sense of initiation (de Vignemont & Fournieret, 2004) and other cognitive processes (Synofzik *et al.*, 2008), to the sense

of agency. One difference between inducing the movement of a virtual limb through BCI and merely observing the movement is that in the latter condition no intention is generated, while to operate a BCI it is necessary to generate intention. Therefore, BCI-control should lead to a greater sense of agency than mere observation. Our data confirmed this prediction for perceived levels of agency but not for responsibility. Participants perceived higher levels of agency when an intention was generated before seeing the virtual movement, such as in the two BCI conditions, compared to when there was no intention; that is, when participants observed the movement (see Fig. 2). On the other hand, participants' feelings of responsibility over the consequences of a given action, such as the virtual arm accidentally breaking an object in the virtual scenario, were higher only when they induced the virtual movement by the activation of sensorimotor areas. Contrarily, when the movement was induced by visual-evoked potentials the feeling of responsibility was similar to when participants simply observed the movement without being able to control it. One possible interpretation is that the intention to perform a task, *per se*, is not a determining factor for the feeling of responsibility to arise.

An important factor for the sense of agency and responsibility is task performance. However, this is only the case when the percentage of successful BCI trials is below 75%; BCI accuracies above this rate add only little to the perceived feeling of control (Fard & Grosse-Wentrup, 2014). In our data, which included only participants with accuracies of 75% or higher, BCI accuracies were actually higher during the SSVEP condition. Therefore, if task performance had an influence our data, it would be in exactly the opposite direction to our findings.

Importance of body ownership

Illusory agency is a phenomenon that can also give clues about the neural basis of agency. When experiencing illusory agency, one attributes to the self the visual or auditory feedback of an action that was not performed by oneself (Wegner *et al.*, 2004; Banakou & Slater, 2014; Kokkinara *et al.*, 2016). Such illusory experiences of agency have been reported for example when participants feel high levels of body ownership over a surrogate body (Banakou & Slater, 2014; Kokkinara *et al.*, 2016). Body ownership over virtual bodies can be induced by visuotactile (Slater *et al.*, 2008) and visuomotor (Sanchez-Vives *et al.*, 2010) correlations. Furthermore, ownership over a virtual arm can be induced through an SMR-based BCI, such that imagining a movement and seeing a virtual arm move from a first-person perspective is sufficient to induce certain levels of body ownership (Perez-Marcos *et al.*, 2009). Our findings are in line with the existing literature and expand the current knowledge on this topic: participants reported the highest feelings of body ownership when they induced the virtual movement through motor imagery; when inducing it through visually evoked potentials or when simply observing, the levels of body ownership were lower (see Fig. 2). Since in the present study self-attribution of the virtual body's movement was mainly based on visual feedback, the role of body ownership is crucial for attributing an action to the self (Wegner *et al.*,

2004; Banakou & Slater, 2014; Kokkinara *et al.*, 2016; Kilteni & Ehrsson, 2017). Motor imagery and motor execution of the same movement are believed to activate similar neural networks (Gerardin *et al.*, 2000; Ehrsson *et al.*, 2002; Pfurtscheller *et al.*, 2008). This could mean that the brain predicts not only the sensory feedback of a planned (and executed) action, but also the feedback of an imagined one. If this holds true, it could explain why all agency-related questionnaire items have the highest ratings when participants imagined the movement.

The sense of responsibility for BCI actions

In order to feel responsible for the outcome of an action, the action should be performed by oneself. The sense of agency can give us this information and thereby creates the basis for a feeling of responsibility over that action (Haggard & Tsakiris, 2009). Experiencing high levels of agency over one's own movements should therefore lead to high levels of responsibility. Based on this we measured in this study the sense of agency and the sense of responsibility, and expected both to show similar response patterns. Indeed, we found a similar pattern in agency and responsibility: for both, imagining the movement induces the highest levels, while observing the movement induces the lowest levels. Interestingly, however, we found a dissociation of agency and responsibility when the movement was induced by visually evoked potentials. While visually evoked potentials induced higher levels of agency compared with observation, and lower levels compared to imagining the movement, BCI through SSVEP did not induce higher responsibility levels than mere movement observation. Importantly, we also found that when imagining the movement, the level of activity in sensorimotor areas was positively correlated with the level of reported responsibility, meaning more sensorimotor activity was associated with higher responsibility ratings. On the other hand neither agency nor responsibility rating were associated with activity in visual areas. It has been previously shown that when people see another person's hand making movements at a position where they would expect their real hand to be, and when they are primed with auditory instructions given via headphones to make the hand movements, people feel illusory agency over the other person's movements (Wegner *et al.*, 2004). This priming can also be seen as an expectation of movement and when the participant creates an intention instead of the expectation, as is the case in the two BCI conditions, its effect should be at least similar, and possibly even stronger. Therefore, for responsibility, the combination of intention and seeing the virtual arm movement at an expected position is not sufficient. It has also been suggested that for BCI actions the visual feedback dominates the sense of agency (Evans *et al.*, 2015), meaning that poorly controlled BCI actions can result in a high sense of agency when the visual feedback matches the participant's intended direction. In this experiment we manipulated the level of sensorimotor involvement and whether there is an intention or not. In line with Evans *et al.*, (2015) our data shows that the sense of agency is higher when participants had formed an intention. However, our data further shows that when sensorimotor

areas are involved in a BCI action participants report higher levels of agency and only then report responsibility. Therefore, in order to induce high feelings of responsibility it seems reasonable to suggest that the brain should create a motor plan.

Clinical perspective

Immersive virtual reality allows the combination of virtual embodiment with motor imagery controlling motor action of the own avatar body. This is a promising approach for neurological rehabilitation (see Buccino (2014) and Buccino et al. (2006) for reviews). Other possible applications are in the field of chronic pain where body image might be distorted (Moseley, 2004; Llobera *et al.*, 2013), or for improving the integration of prosthesis into the body representation.

References

- Baillet S, Moshier JC & Leahy RM (2001). Electromagnetic brain mapping. *IEEE Signal Process Mag* **18**, 14–30.
- Banakou D & Slater M (2014). Body ownership causes illusory self-attribution of speaking and influences subsequent real speaking. *Proc Natl Acad Sci U S A* **111**, 17678–17683.
- Banakou D & Slater M (2017). Embodiment in a virtual body that speaks produces agency over the speaking but does not necessarily influence subsequent real speaking. *Sci Rep* **7**, 14227.
- Bednark JG & Franz EA (2014). Agency attribution: event-related potentials and outcome monitoring. *Exp Brain Res* **232**, 1117–1126.
- Berger H (1929). Über das Elektrenkephalogramm des Menschen. *Arch Psychiatr Nervenkr* **87**, 527–570.
- Birbaumer N (2006). Breaking the silence: Brain–computer interfaces (BCI) for communication and motor control. *Psychophysiology* **43**, 517–532.
- Blakemore S-J, Wolpert D & Frith C (2000). Why can’t you tickle yourself? *Neuroreport* **11**, R11-6.
- Blankertz B, Acqualagna L, Dähne S, Haufe S, Schultze-Kraft M, Sturm I, Ušćumlic M, Wenzel MA, Curio G & Müller K-R (2016). The Berlin Brain-Computer Interface: Progress beyond communication and control. *Front Neurosci* **10**, 530.
- Blankertz B, Dornhege G, Krauledat M, Müller K-R & Curio G (2005). The Berlin brain-computer interface: Report from the feedback sessions. *FIRST Reports*.
- Blankertz B, Tomioka R, Lemm S, Kawanabe M & Muller K r. (2008). Optimizing spatial filters for robust EEG single-trial analysis. *IEEE Signal Process Mag* **25**, 41–56.
- Buccino G (2014). Action observation treatment: a novel tool in neurorehabilitation. *Philos Trans R Soc Lond B Biol Sci* **369**, 20130185.
- Buccino G, Solodkin A & Small SL (2006). Functions of the mirror neuron system: implications for neurorehabilitation. *Cogn Behav Neurol Off J Soc Behav Cogn Neurol* **19**, 55–63.
- Cavazzana A, Penolazzi B, Begliomini C & Bisiacchi PS (2015). Neural underpinnings of the “agent brain”: New evidence from transcranial direct current stimulation. *Eur J Neurosci* **42**, 1889–1894.
- Chambon V, Sidarus N & Haggard P (2014). From action intentions to action effects: How does the sense of agency come about? *Front Hum Neurosci* **8**, 320.
- Chambon V, Wenke D, Fleming SM, Prinz W & Haggard P (2013). An Online Neural Substrate for Sense of Agency. *Cereb Cortex* **23**, 1031–1037.
- Chatrian GE, Lettich E & Nelson PL (1985). Ten percent electrode system for topographic studies of

- spontaneous and evoked EEG activities. *Am J EEG Technol* **25**, 83–92.
- Clochon P, Fontbonne J, Lebrun N & Etevenon P (1996). A new method for quantifying EEG event-related desynchronization: amplitude envelope analysis. *Electroencephalogr Clin Neurophysiol* **98**, 126–129.
- David N (2012). New frontiers in the neuroscience of the sense of agency. *Front Hum Neurosci*; DOI: 10.3389/fnhum.2012.00161.
- Denis D, Rowe R, Williams AM & Milne E (2017). The role of cortical sensorimotor oscillations in action anticipation. *Neuroimage* **146**, 1102–1114.
- Dornhege G, Blankertz B & Curio G (2003). Speeding up classification of multi-channel brain-computer interfaces: Common spatial patterns for slow cortical potentials. *First Int IEEE EMBS Conf Neural Eng 2003 Conf Proc*.
- Ehrsson HH, Kuhtz-Buschbeck JP & Forssberg H (2002). Brain regions controlling nonsynergistic versus synergistic movement of the digits: A functional Magnetic Resonance Imaging study. *J Neurosci* **22**, 5074–5080.
- Ethan B, Cornelia W, G. CL, Christoph B, A. DM, Tyler A, Jurgen M, Andrea C, Surjo S, Alissa F & Niels B (2008). Think to Move: a Neuromagnetic Brain-Computer Interface (BCI) System for Chronic Stroke. *Stroke* **39**, 910–917.
- Evans N, Gale S, Schurger A & Blanke O (2015). Visual feedback dominates the sense of agency for brain-machine actions. *PLoS One*; DOI: 10.1371/journal.pone.0130019.
- Fard PR & Grosse-Wentrup M (2014). The influence of decoding accuracy on perceived control: A simulated BCI study.
- Fonov V, Evans AC, Botteron K, Almli CR, McKinstry RC & Collins DL (2011). Unbiased average age-appropriate atlases for pediatric studies. *Neuroimage* **54**, 313–327.
- Frith CD, Blakemore & Wolpert DM (2000). Abnormalities in the awareness and control of action. *Philos Trans R Soc London Ser B Biol Sci* **355**, 1771–1788.
- Fukunaga K (1990). *Introduction to statistical pattern recognition*, 2. ed. Academic Press, San Diego, CA.
- Gallagher S (2000). Philosophical conceptions of the self: Implications for cognitive science. *Trends Cogn Sci* **4**, 14–21.
- Gastaut HJ & Bert J (1954). EEG changes during cinematographic presentation (Moving picture activation of the EEG). *Electroencephalogr Clin Neurophysiol* **6**, 433–444.
- Gerardin E, Sirigu A, Lehericy S, Poline J-B, Gaymard B, Marsault C, Agid Y & Le Bihan D (2000). Partially Overlapping Neural Networks for Real and Imagined Hand Movements. *Cereb Cortex* **10**, 1093–1104.
- Giummarra MJ, Gibson SJ, Georgiou-Karistianis N & Bradshaw JL (2008). Mechanisms underlying embodiment, disembodiment and loss of embodiment. *Neurosci Biobehav Rev* **32**, 143–160.

- Graimann B & Pfurtscheller G (2006). Quantification and visualization of event-related changes in oscillatory brain activity in the time–frequency domain. In *Progress in brain research: Event-related dynamics of brain oscillations*, ed. Neuper C & Klimesch W, pp. 79–97. Elsevier, Amsterdam.
- Gramfort A, Papadopoulo T, Olivi E & Clerc M (2010). OpenMEEG: opensource software for quasistatic bioelectromagnetics. *Biomed Eng Online* **9**, 45.
- Guger C, Allison BZ, Großwindhager B, Prückl R, Hintermüller C, Kapeller C, Bruckner M, Krausz G & Edlinger G (2012). How many people could use an SSVEP BCI? *Front Neurosci* **6**, 169.
- Guger C, Edlinger G, Harkam W, Niedermayer I & Pfurtscheller G (2003). How many people are able to operate an EEG-based Brain-Computer Interface (BCI)? *IEEE Trans Neural Syst Rehabil Eng* **11**, 145–147.
- Haggard P (2017). Sense of agency in the human brain. *Nat Rev Neurosci* **18**, 196–207.
- Haggard P & Tsakiris M (2009). The Experience of Agency: Feelings, Judgments, and Responsibility. *Curr Dir Psychol Sci* **18**, 242–246.
- Hjorth B (1975). An on-line transformation of EEG scalp potentials into orthogonal source derivations. *Electroencephalogr Clin Neurophysiol* **39**, 526–530.
- Hochberg LR, Bacher D, Jarosiewicz B, Masse NY, Simeral JD, Vogel J, Haddadin S, Liu J, Cash SS, van der Smagt P & Donoghue JP (2012). Reach and grasp by people with tetraplegia using a neurally controlled robotic arm. *Nature* **485**, 372–375.
- Hyvärinen A & Oja E (2000). Independent component analysis: algorithms and applications. *Neural Networks* **13**, 411–430.
- Imaizumi S & Asai T (2015). Dissociation of agency and body ownership following visuomotor temporal recalibration. *Front Integr Neurosci* **9**, 35.
- Kalckert A & Ehrsson H (2012). Moving a rubber hand that feels like your own: A dissociation of ownership and agency. *Front Hum Neurosci* **6**, 40.
- Kilteni K & Ehrsson HH (2017). Body ownership determines the attenuation of self-generated tactile sensations. *Proc Natl Acad Sci* **114**, 8426–8431.
- Kokkinara E, Kilteni K, Blom KJ & Slater M (2016). First person perspective of seated participants over a walking virtual body leads to illusory agency over the walking. *Sci Rep* **6**, 28879.
- Koles ZJ, Lind JC & Soong ACK (1995). Spatio-temporal decomposition of the EEG: A general approach to the isolation and localization of sources. *Electroencephalogr Clin Neurophysiol* **95**, 219–230.
- Kumar D & Srinivasan N (2014). Naturalizing Sense of Agency with a Hierarchical Event-Control Approach. *PLoS One* **9**, e92431.
- Kybic J, Clerc M, Abboud T, Faugeras O, Keriven R & Papadopoulo T (2005). A common formalism for the Integral formulations of the forward EEG problem. *IEEE Trans Med Imaging* **24**, 12–28.

- Lemm S, Müller K-R & Curio G (2009). A generalized framework for quantifying the dynamics of EEG Event-Related Desynchronization. *PLOS Comput Biol* **5**, e1000453.
- Llobera J, González-Franco M, Perez-Marcos D, Valls-Solé J, Slater M & Sanchez-Vives M V (2013). Virtual reality for assessment of patients suffering chronic pain: a case study. *Exp Brain Res* **225**, 105–117.
- Marchesotti S, Martuzzi R, Schurger A, Blefari ML, del Millán JR, Bleuler H & Blanke O (2017). Cortical and subcortical mechanisms of brain-machine interfaces. *Hum Brain Mapp* **38**, 2971–2989.
- Mauritz K-H & Wise SP (1986). Premotor cortex of the rhesus monkey: neuronal activity in anticipation of predictable environmental events. *Exp Brain Res* **61**, 229–244.
- Middendorf M, McMillan G, Calhoun G & Jones KS (2000). Brain-computer interfaces based on the steady-state visual-evoked response. *IEEE Trans Rehabil Eng* **8**, 211–214.
- Moore JW, Ruge D, Wenke D, Rothwell J & Haggard P (2010). Disrupting the experience of control in the human brain: pre-supplementary motor area contributes to the sense of agency. *Proc R Soc B Biol Sci* **277**, 2503–2509.
- Moseley GL (2004). Graded motor imagery is effective for long-standing complex regional pain syndrome: A randomised controlled trial. *Pain* **108**, 192–198.
- Müller-Gerking J, Pfurtscheller G & Flyvbjerg H (1999). Designing optimal spatial filters for single-trial EEG classification in a movement task. *Clin Neurophysiol* **110**, 787–798.
- Nierula B, Hohlefeld FU, Curio G & Nikulin V V (2013). No somatotopy of sensorimotor alpha-oscillation responses to differential finger stimulation. *Neuroimage* **76**, 294–303.
- Nikouline V V, Linkenkaer-Hansen K, Wikström H, Kesäniemi M, Antonova E V, Ilmoniemi RJ & Huttunen J (2000). Dynamics of mu-rhythm suppression caused by median nerve stimulation: A magnetoencephalographic study in human subjects. *Neurosci Lett* **294**, 163–166.
- Nikulin V V, Hohlefeld FU, Jacobs AM & Curio G (2008). Quasi-movements: A novel motor--cognitive phenomenon. *Neuropsychologia* **46**, 727–742.
- Oldfield RC (1971). The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia* **9**, 97–113.
- Padrao G, Gonzalez-Franco M, Sanchez-Vives M V, Slater M & Rodriguez-Fornells A (2016). Violating body movement semantics: Neural signatures of self-generated and external-generated errors. *Neuroimage* **124**, 147–156.
- Perez-Marcos D, Slater M & Sanchez-Vives M V. (2009). Inducing a virtual hand ownership illusion through a brain-computer interface. *Neuroreport* **20**, 589–594.
- Pfurtscheller G & Aranibar A (1977). Event-related cortical desynchronization detected by power measurements of scalp EEG. *Electroencephalogr Clin Neurophysiol* **42**, 817–826.
- Pfurtscheller G, Brunner C, Schlögl A & Lopes da Silva FH (2006). Mu rhythm (de)synchronization and EEG single-trial classification of different motor imagery tasks. *Neuroimage* **31**, 153–159.

- Pfurtscheller G & Lopes da Silva FH (1999). Event-related EEG/MEG synchronization and desynchronization: basic principles. *Clin Neurophysiol* **110**, 1842–1857.
- Pfurtscheller G & Neuper C (1997). Motor imagery activates primary sensorimotor area in humans. *Neurosci Lett* **239**, 65–68.
- Pfurtscheller G & Neuper C (2001). Motor imagery and direct brain-computer communication. *Proc IEEE* **89**, 1123–1134.
- Pfurtscheller G, Scherer R, Muller-Putz GR & Lopes da Silva FH (2008). Short-lived brain state after cued motor imagery in naive subjects. *Eur J Neurosci* **28**, 1419–1426.
- Rosenblum M & Kurths J (1998). Analysing synchronization phenomena from bivariate data by means of the Hilbert transform. In *Nonlinear analysis of physiological data*, ed. Kantz H, Kurths J & Mayer-Kress G, pp. 91–99. Springer Berlin Heidelberg, Berlin, Heidelberg.
- Roskies AL (2010). How Does Neuroscience Affect Our Conception of Volition? *Annu Rev Neurosci* **33**, 109–130.
- Sanchez-Vives M V, Spanlang B, Frisoli A, Bergamasco M & Slater M (2010). Virtual hand illusion induced by visuomotor correlations. ed. Greenlee MW. *PLoS One* **5**, e10381.
- Slater M, Perez-Marcos D, Ehrsson HH & Sanchez-Vives M V (2008). Towards a digital body: The virtual arm illusion. *Front Hum Neurosci* **2**, 6.
- Slater M, Perez-Marcos D, Ehrsson HH & Sanchez-Vives M V (2009). Inducing illusory ownership of a virtual body. *Front Neurosci* **3**, 214–220.
- Slater M, Spanlang B, Sanchez-Vives M V & Blanke O (2010). First person experience of body transfer in virtual reality. *PLoS One* **5**, e10564.
- Spanlang B, Normand J-M, Borland D, Kilteni K, Giannopoulos E, Pomes A, Gonzalez-Franco M, Pérez-Marcos D, Arroyo-Palacios J, Navarro Muncunill X & Slater M (2014). How to Build an Embodiment Lab: Achieving Body Representation Illusions in Virtual Reality. *Front Robot AI*; DOI: 10.3389/frobt.2014.00009.
- Sperduti M, Delaveau P, Fossati P & Nadel J (2011). Different brain structures related to self- and external-agency attribution: A brief review and meta-analysis. *Brain Struct Funct* **216**, 151–157.
- Synofzik M, Vosgerau G & Newen A (2008). I move, therefore I am: A new theoretical framework to investigate agency and ownership. *Soc Cogn Emot Self-Consciousness* **17**, 411–424.
- Tadel F, Baillet S, Mosher JC, Pantazis D & Leahy RM (2011). Brainstorm: A user-friendly application for MEG/EEG analysis. *Comput Intell Neurosci* **2011**, 13.
- Tsakiris M, Longo MR & Haggard P (2010). Having a body versus moving your body: Neural signatures of agency and body-ownership. *Neuropsychologia* **48**, 2740–2749.
- Vialatte F-B, Maurice M, Dauwels J & Cichocki A (2010). Steady-state visually evoked potentials: Focus on essential paradigms and future perspectives. *Prog Neurobiol* **90**, 418–438.
- de Vignemont F & Fournieret P (2004). The sense of agency: A philosophical and empirical review of

the “Who” system. *Conscious Cogn* **13**, 1–19.

Wegner DM, Sparrow B & Winerman L (2004). Vicarious agency: experiencing control over the movements of others. *J Pers Soc Psychol* **86**, 838–848.

Weiss C, Tsakiris M, Haggard P & Schütz-Bosbach S (2014). Agency in the sensorimotor system and its relation to explicit action awareness. *Neuropsychologia* **52**, 82–92.

Wenke D, Fleming SM & Haggard P (2010). Subliminal priming of actions influences sense of control over effects of action. *Cognition* **115**, 26–38.

Wolpert DM, Ghahramani Z & Jordan MI (1995). An internal model for sensorimotor integration. *Science (80-)* **269**, 1880.

Data statement

Data is available from the corresponding author on reasonable request.

Competing interests

The authors declare no competing financial interests.

MVSV is founder of Virtual Bodyworks Inc (virtualbodyworks.com). The publication of this article is unrelated to the commercial activities of VBWs and has not received any funding from the company.

BS is founder and currently an employee at Virtual Bodyworks Inc. His work in the article was performed as senior postdoc at the University of Barcelona.

Author contributions

MVSV, MM, and BN designed the experiment. MVSV supervised the different aspects of the study. BN and BS worked on the implementation and integration of the virtual reality and BCI. BN, MM and MB ran the experiments. BN, VVN and MVSV analyzed the data. BN and MVSV wrote the paper and all authors contributed to the final version.

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Tables

Table 1. Questionnaire items answered by participants before, during, or after each experimental condition (in Spanish in the original). Responses were given on a visual analogue scale (VAS) ranging from 0 (“strongly disagree”) to 10 (“strongly agree”), except for item 3. Note that reversed wording was used for item 4 and therefore the inverse of the original scale was used for further analysis.

Variable	Questionnaire item	Item tag
MyBody	(1) It felt as if the right virtual arm were my arm.	<i>MyBody</i>
	(2) It felt as if it were me who controlled the movement of the virtual arm.	<i>IControlledArm</i>
AgencyPCF	(3) It felt as if the movement of the virtual arm were... the movement of another person (= 0 on VAS) / my movement (= 10 on VAS).	<i>MyMovement</i>
	(4) It felt as if the virtual arm moved by itself.	<i>ArmMovedItself</i>
	(5) It felt as if it were me who produced the sound (when the hand touched the button).	<i>MySound</i>
ResponsibilityPCF	(6) It felt as if it were me who broke the vase/pencil holder/glass/cup.	<i>IBrokeObject</i>
	(7) It felt that out of sloppiness I touched the objects with my hand when they fell off the table.	<i>ITouchedObject</i>

Figures and legends

Fig. 1. Experimental setup. (A) Participants sat with both hands resting on a table and saw through a head mounted display (HMD) a virtual body co-located with their real body, over which body ownership was induced in an initial embodiment phase. (B) During the action phase, in which participants were instructed not to move their arms, each trial started with a fixation cross, (C) followed by an arrow indicating one of two buttons to indicate the task, which was to bring the hand towards to pointed to-button. (D) In two conditions participants controlled the movement of the virtual arm through a BCI and in a third control condition they simply observed the virtual arm move.

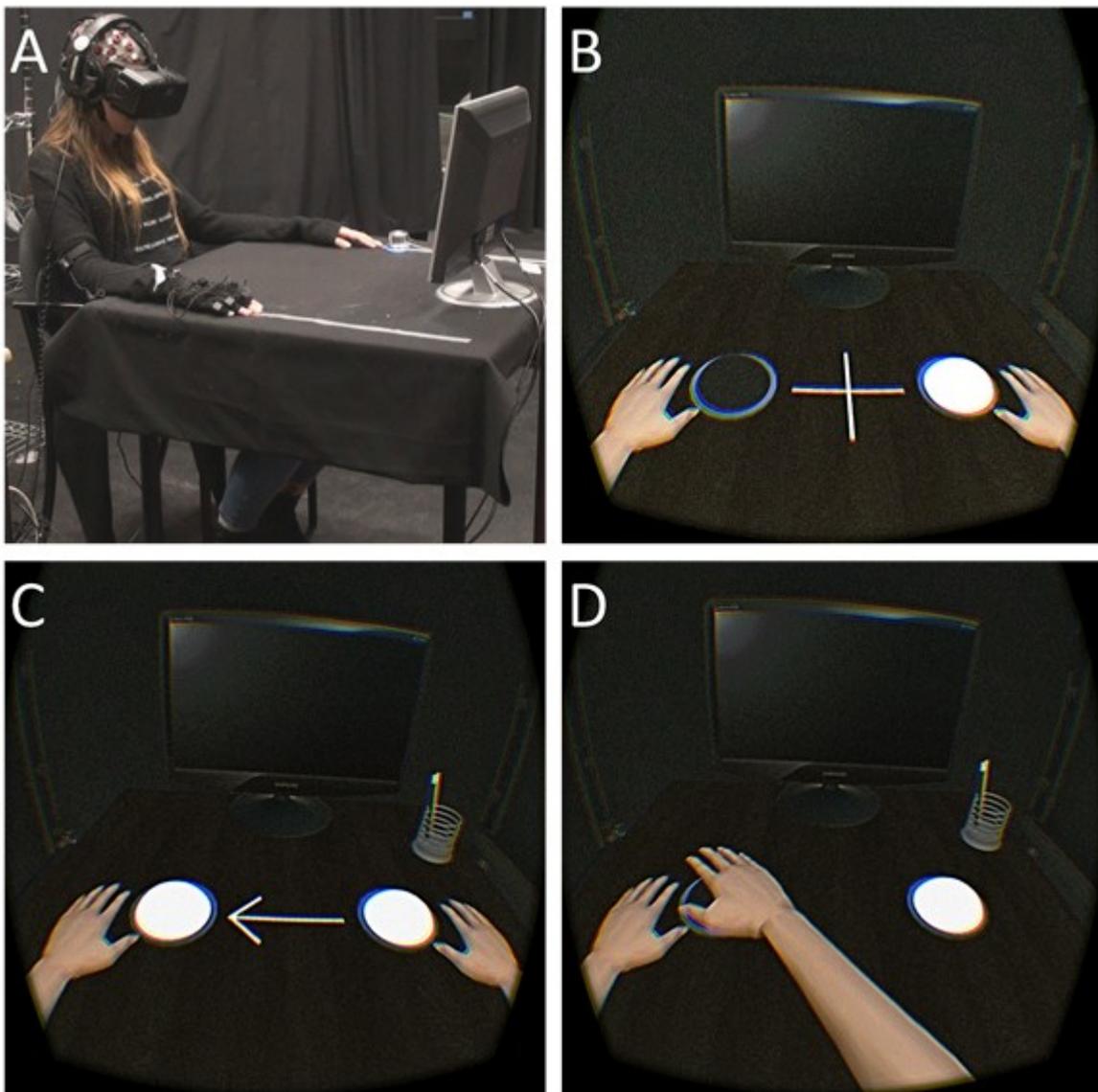


Fig. 2. Agency, responsibility and body ownership ratings in the three experimental conditions (passive observation, SSVEP-BCI and motor imagery-BCI). AgencyPCF (A), ResponsibilityPCF (B), and MyBody (C) ratings. The Boxplots include all participants (n=29) who completed all conditions. The definition of these variables can be found in Results and Methods. See Table 1 for the questionnaire items associated with the variables. *: $P \leq 0.05$, **: $P \leq 0.01$, *: $P \leq 0.001$.**

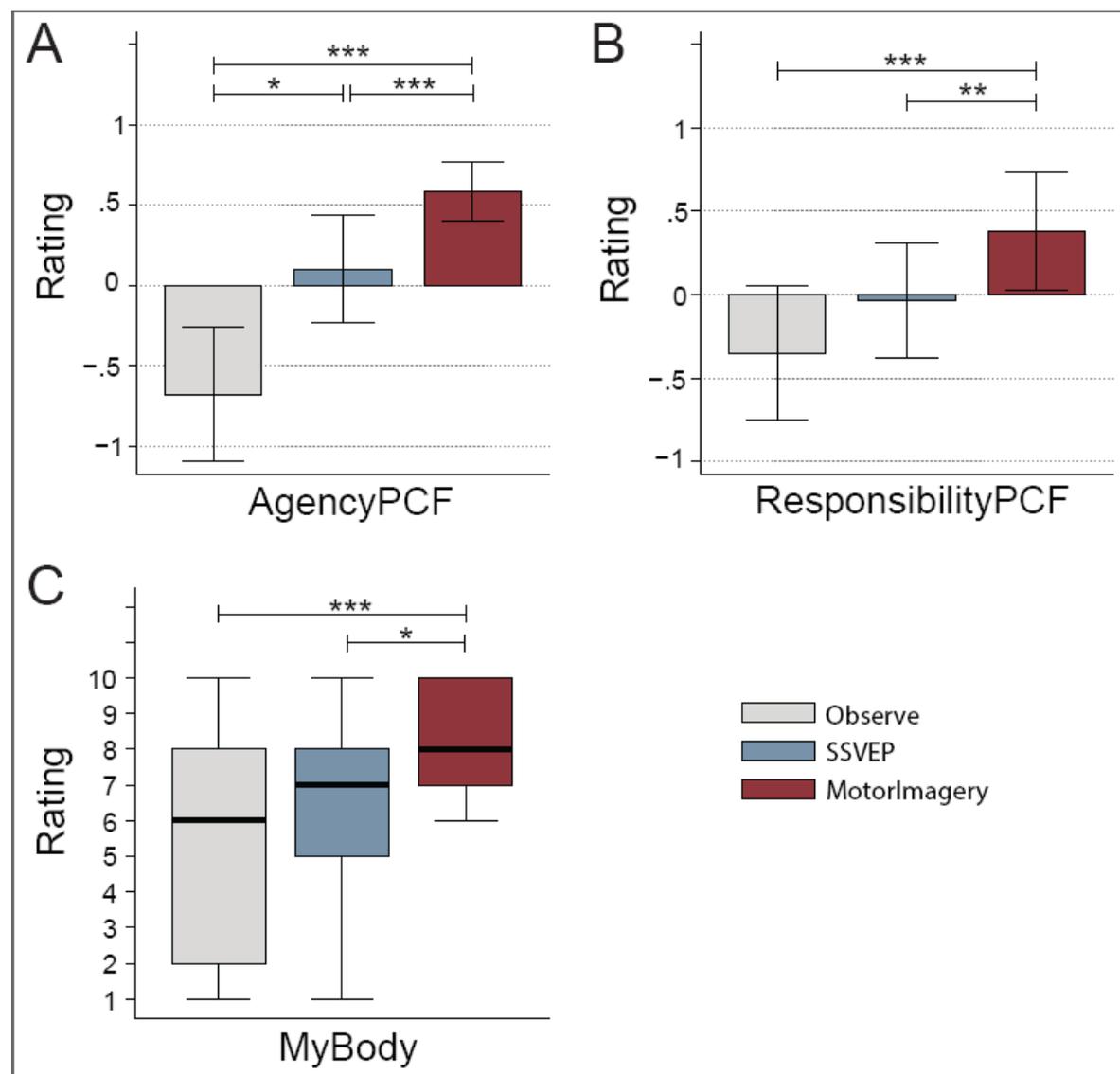
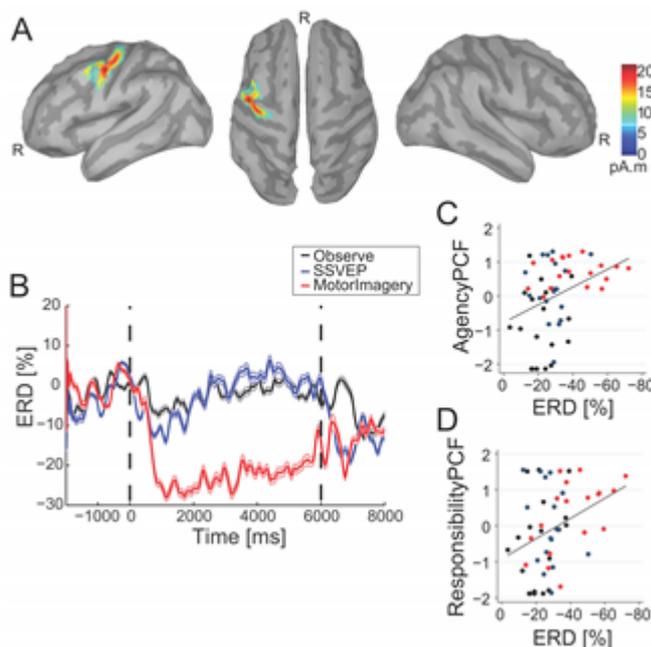


Fig. 3. Brain activation during BCI-controlled and passive movements of the virtual arm and its relation to agency and responsibility. (A) Average sources of Executed Movement from 18 participants. The active area during this task coincides with the precentral gyrus (Brodmann's area 6). The images display left hemisphere, top view with both hemispheres, and right hemisphere from left to right. R=rostral. (B) Event-related desynchronization (ERD) of the alpha rhythm as a marker of sensorimotor activation in the three conditions MotorImagery, SSVEP, and Observe. The signals, recorded during the three conditions, were projected through spatial filters, obtained by applying CSP on executed movement data, and transformed to ERD%. Zero (0) indicates the display of the arrow, after which participants started to observe, look at the blinking light or imagining the movement (depending on the condition). After 6000 ms the virtual arm started moving—in the Observe condition in every trial and in the BCI conditions when the action was classified accordingly. The plotted signal is averaged over $n=18$ participants. Only correctly classified trials were taken into account. (C) Minimum ERD% activity in the time window between 0–6000 ms during Observe (in black), SSVEP (in blue), and MotorImagery (in red) plotted against AgencyPCF, (D) and ResponsibilityPCF. Note that the x -axis is inverted. More negative ERD% values indicate higher sensorimotor cortex activity. Lines indicate the linear fit of the questionnaire item on ERD%.





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