# Agency in the sensorimotor system and its relation to explicit action awareness

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## ABSTRACT

People generally have a strong and immediate intuition whether they are the author of an action or not. Nevertheless, recent psychological studies focused on situations of ambiguous agency. These studies concluded that agency is an inference rather than a direct perception, and is, at least sometimes, illusory. Moreover, shared representations of executed and merely observed actions within the sensorimotor system pose a challenge to the idea that a sense of agency can be grounded within that system. Here, we sought to investigate whether the human motor system is indeed sensitive to whether observed actions are linked to agency or not. In addition, we investigated whether the mere observation of an action has comparable effects on low-level, sensorimotor measures of agency, and on high-level, explicit representations of agency. To this end, we instructed participants to make simple manual movements, and manipulated the temporal correspondence between the movement that they made and the movement that they observed. Motor-evoked potentials to single-pulse TMS were taken as a low-level, sensorimotor measure of agency. To assess explicit representations of agency, participants verbally judged whether or not the observed movement temporally corresponded to the movement they executed. The results showed that corticospinal excitability varied with the degree of temporal correspondence of the executed and observed movements. Moreover, explicit agency judgments could be predicted from corticospinal excitability. This suggests that explicit judgments of agency could be directly based on information within the sensorimotor system.

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## 1. Introduction

The capability to produce actions so as to achieve goals is a fundamental component of human behavior and social life (Baumeister, 1998). Beyond this outward-directed role, the experience of our own actions also makes a key contribution to the sense of self (Gallagher, 2000; Gallese & Sinigaglia, 2010; Jeannerod, 2003; Marcel, 2003). In particular, voluntary actions are usually accompanied by an experience of agency. That is, oneself is experienced as the cause of the initiation and the way an action and its perceptual consequences are achieved. It has been suggested that specific processes of motor prediction (Blakemore, Wolpert, & Frith, 2002; Frith, Blakemore, & Wolpert, 2000) and the cognitive inference of agency (Wegner, 2002) form the basis of the distinction between self-generated actions and perceptual events generated by other sources. This distinction in turn allows formation of a self as a specific entity distinct from other objects and from other agents (Gallagher, 2000; Jeannerod, 2003). However, the basis of the self–other distinction remains unclear. In particular, the respective contributions to the self–other distinction of lower-level resonance to observed action within the motor system, and higher-order, cognitive representations of action generation has not previously been investigated.

Although the sense of agency appears as a straightforward experience during our own actions, its computational basis in the brain is surprisingly complex. At least two different levels (Synofzik, Vosgerau, & Newen, 2008; cf. Bayne & Pacherie, 2007; Gallagher, 2012) of this experience are identified in recent theories. *Judgments of agency* (Synofzik et al., 2008) are reflective propositions or interpretations that one is the agent of an action. These judgments depend on belief-like processes and rationalization modules. Many previous studies focused on these judgments by measuring agency in terms of verbal reports. For instance, participants are asked to judge explicitly whether they were the author of an action or whether a presented sensory feedback of an action corresponds to the action they made (e.g., Aarts, Custers, &

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Wegner, 2005; Daprati et al., 1997; Franck et al., 2001; Metcalfe & Greene, 2007; Repp & Knoblich, 2007; Sato & Yasuda, 2005; Tsakiris, Haggard, Franck, Mainy, & Sirigu, 2005; van den Bos & Jeannerod, 2002). However, our everyday actions are usually carried out without such explicit judgments or verbal reports, yet they are still accompanied by a sense of agency, and an automatic recognition of when events are self-generated. Therefore, a basic, non-conceptual *feeling of agency* (Synofzik et al., 2008) was proposed. A feeling of agency could be provided by efference copies within forward models of motor control (Wolpert & Flanagan, 2001; Wolpert, Ghahramani, & Jordan, 1995). Specifically, it is assumed that during self-generated actions, a forward model uses the efference copy (von Holst & Mittelstaedt, 1950) of the motor command to predict the sensory consequences resulting from this action. These predictions are then compared against the actual sensory consequences (see Frith et al., 2000). Stronger correspondence is associated with stronger experience of agency (Pacherie, 2001; Synofzik et al., 2008). Conversely, the higher the discrepancy, the more an action is experienced as caused not by oneself, but by another cause, such as another agent. Feelings of agency are thought to have the format of basic sensorimotor experiences, in contrast to the propositional content of agency judgments (Bayne & Pacherie, 2007; Berberian & Cleeremans, 2010; David, Newen, & Vogeley, 2008; Synofzik et al., 2008). The link between these two levels is poorly understood. One simple model would suggest that high-level, cognitive judgments of agency rely on low-level indicators of agency generated within the sensorimotor system. However, this model has never, to our knowledge, been formally tested. Testing it would first require a suitable measure of the low-level sense of agency. The model then predicts that this measure would differ systematically between situations where people do and do not judge that they are the agent over an observed action.

However, the idea of a low-level, sensorimotor basis of agency is challenged by the discovery of a "mirror matching mechanism" which appears to map an observed action onto a motor representation of the same action in the observer (Rizzolatti, Fogassi, & Gallese, 2001; for a recent review see Rizzolatti & Sinigaglia, 2010). For example, excitability of the primary motor pathway occurs not only during preparation and execution of an action, but also during the mere observation of another agent's action. More precisely, observation of a specific manual action has been shown to cause an increase in motor-evoked potentials (MEPs) elicited by motor cortical transcranial magnetic stimulation (TMS) in the specific muscles involved in executing those actions (e.g., Avenanti, Bolognini, Maravita, & Aglioti, 2007; Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995; Romani, Cesari, Urgesi, Facchini, & Aglioti, 2005; Strafella & Paus, 2000; see also Caetano, Jousmaki, & Hari, 2007; Hari et al., 1998 for similar findings from magentoencephalographic measures of oscillatory activity). Moreover, the timing of these changes in corticospinal excitability tracks the temporal detail of the action itself (e.g., Borroni, Montagna, Cerri, & Baldissera, 2005; Gangitano, Mottaghy, & Pascual-Leone, 2001; Montagna, Cerri, Borroni, & Baldissera, 2005). It has been suggested therefore that the motor system simulates an observed action by implementing some of the processes involved in action execution (Fadiga, Craighero, & Olivier, 2005; Jeannerod, 2006). This process implies "shared", or agent-neutral representations (de Vignemont & Haggard, 2008; Decety & Sommerville, 2003; Georgieff & Jeannerod, 1998; Jeannerod & Pacherie, 2004), since the observed action is typically not one's own but that of another agent, while the executed action is necessarily one's own. This equivalence seems to directly contradict the everyday experience that we directly register whether we are the agent or not (Schütz-Bosbach, Avenanti, Aglioti, & Haggard, 2009).

On the other hand, even though the sensorimotor system might be activated for both self- and other-produced actions, this does not necessarily imply that these activations are neutral with regard to agency. Alternatively, the responsive characteristics of these activations could provide an indication of agency. Evidence for such differential, sensorimotor activations with respect to agency was provided by two recent studies (Schütz-Bosbach et al., 2009; Schütz-Bosbach, Mancini, Aglioti, & Haggard, 2006). These studies used a social version of the rubber hand illusion (RHI: Botvinick & Cohen, 1998) to compare observation of actions that are physically equivalent, but either are or are not linked to the self. Observing actions that were (illusorily) linked to the self were associated with decreased corticospinal excitability and increased cortical inhibition, whereas observation of actions linked to another person produced the opposite, facilitatory effects. This suggests that a sense of agency might be associated with changes in low-level, sensorimotor representations. Therefore, although several previous studies emphasized changes in corticospinal excitability during both executed and observed actions (for a review see Fadiga et al., 2005), our previous work suggests that corticospinal excitability can also provide a reliable low-level, sensorimotor marker of agency. Whether this low-level, sensorimotor marker is actually responsible for explicit judgments of agency, however, is not clear. In previous studies, participants were not required to give any explicit judgment of agency, but just passively observed actions linked to self or other. Thus, while these studies showed that corticospinal excitability was sensitive to the facts of agency, they did not show that lower-order, sensorimotor level information was available and used at the cognitive level for forming explicit judgments of agency. Here we tried to investigate the latter possibility.

Specifically, in the present study, we studied the link between agency and sensorimotor excitability by parametrically varying the relation between executed and observed action, while recording both corticospinal excitability and verbal self-reports of agency. We used an established paradigm (e.g., David, Stenzel, Schneider, & Engel, 2011; Farrer et al., 2008; Franck et al., 2001; Leube et al., 2003; MacDonald & Paus, 2003; Spengler, von Cramon, & Brass, 2009) that systematically varies the correspondence between self-produced actions and their sensory feedback. Participants performed simple finger movements without direct view. They received indirect visual feedback that varied between being completely temporally corresponding to the executed movement and being substantially delayed. Varying the temporal delay parameter could provide evidence for or against one's own agency over the visually displayed action. That is, increasing temporal discrepancies between action and feedback should produce a shift from feeling one observed a self-generated movement to feeling one was watching another person's movement (cf. Farrer et al. 2003). Farrer et al. (2008) confirmed the strong relation between the awareness of a temporal correspondence or non-correspondence between execution and observation, and the attribution of the observed action either to the self or another agent. Specifically, they found that the same network of brain areas, notably the angular gyrus, was involved both in the detection of a temporal correspondence or non-correspondence of the visual feedback relative to the actually executed movement and in self–other attribution. Furthermore, other studies showed that, similar to the detection of temporal correspondence or non-correspondence between execution and sensory feedback (e.g., Franck et al., 2001; Leube et al., 2003), the tendency to attribute a perceived action (effect) to another agent increases the more it temporally deviates from the actual execution (e.g., David et al., 2011; Sato & Yasuda, 2005; Spengler et al., 2009). Self–other attribution judgments, however, typically exhibit a self-bias: people overattribute observed actions to themselves (see e.g.,

Daprati et al., 1997; Sirigu, Daprati, Pradat-Diehl, Franck, & Jeannerod, 1999; Tsakiris et al., 2005; van den Bos & Jeannerod, 2002). For this reason, we have preferred to use judgments of correspondence (i.e., temporal corresponding or non-corresponding) as an explicit judgment related to agency rather than a classical self–other judgment. Judgments of correspondence are based on the same information as self–other judgments, but lack the self-bias (see also Materials and methods).

Crucially, we obtained proxy measures of both low-level, sensorimotor-based coding of agency and high-level, explicit judgments of agency, for the same events and in the same participants. This approach allowed a direct comparison of these two measures and thus, their possible relation or dissociation. Specifically, modulations of excitability to single-pulse TMS over the primary motor cortex (M1) were measured as a function of temporal correspondence between movement execution and visual feedback as a proxy for the sensorimotor representation of agency (i.e., feeling level). Based on previous results, we predicted an increase in the excitability of the motor system with higher temporal non-correspondence (Schütz-Bosbach et al., 2006, 2009). We also asked participants to verbally report whether the observed movement did or did not correspond their own executed movement as a proxy for the explicit representation of agency (i.e., judgment level). If there is a functional link between a low-level, sensorimotor and a high-level, explicit representation of agency, enhanced corticospinal excitability should be associated with a judgment that the observed movement does not correspond to the executed one.

## 2. Materials and methods

### 2.1. Participants

Thirty-one healthy participants (mean age 25.4 years, $SD$=3.8 years, 18 female, all right-handed), free from any contraindication to TMS (Wassermann, 1998) took part in this study. Two participants had to be excluded due to technical problems, leaving a sample of 29 participants (mean age 25.5 years, $SD$=3.8 years, 17 female, all right-handed). All of them had normal or corrected-to-normal vision. Informed written consent was obtained from each participant prior to the experiment and they received a small reimbursement for their participation. The study was conducted in accordance with the Declaration of Helsinki and was approved by the local ethics committee of the University of Leipzig. No discomfort or adverse effects associated with TMS were reported or noticed.

### 2.2. Electromyographic (EMG) recording and TMS

Motor-evoked potentials (MEPs) to single-pulse TMS over the left primary motor cortex (M1) were recorded simultaneously from two muscles of the right hand: (1) the first dorsal interosseus (FDI), the target muscle specifically involved in the executed/observed abduction movement of the index finger (see below) and (2) the abductor digit minimi (ADM; involved in abduction movements of the little finger), a control muscle that was irrelevant to the executed/observed movement. EMG recordings were obtained with disposable Ag/AgCl surface electrodes placed over the muscle belly (active electrode) and over the associated tendon (reference electrode). A ground electrode was placed over the dorsal surface of the right forearm. EMG signals were amplified (1000 ×) and band-pass filtered between 10 and 2000 Hz with a mains hum notch filter at 50 Hz by a D360 amplifier (Digitimer Ltd., Welwyn Garden City, UK). The signals were digitized at 5 kHz using a CED Power 1401 data acquisition interface (Cambridge Electronic Design, Cambridge, UK) and stored on a personal computer for display and later off-line data analysis.

TMS was performed with a 70 mm figure-of-eight coil connected to a Magstim $200^2$ (The Magstim Company Ltd., Whitland, UK) and positioned over the optimum scalp location of the left motor cortex, tangentially to the scalp with the handle pointing backward at 45° from the midline. The coil orientation was chosen based on the findings that the lowest motor threshold is achieved when the induced current in the neural tissue is flowing approximately perpendicular to the central sulcus (Brasil-Neto et al., 1992; Mills, Boniface, & Schubert, 1992). The optimum scalp location was defined as the position at which maximum amplitude MEPs were produced in both muscles at rest. It was detected by moving the coil in steps of 1 cm around the motor-hand area of the left motor cortex and by delivering TMS pulses with a constant, slightly suprathreshold intensity. The optimum scalp location was then marked on the scalp and the position of the coil with respect
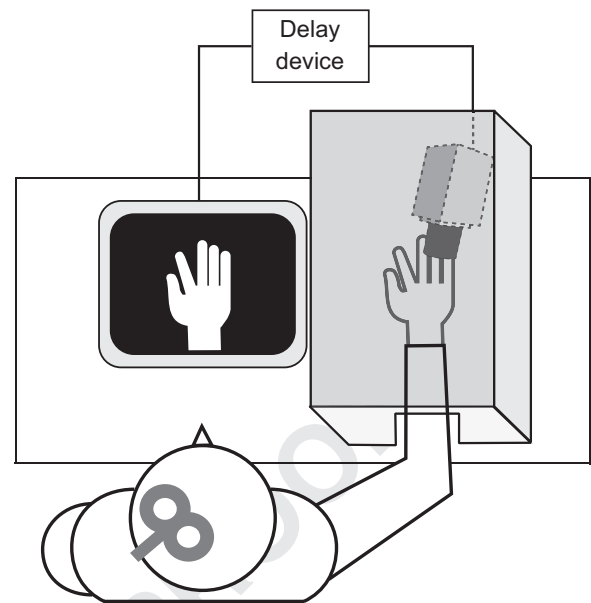


**Fig. 1.** Experimental setup. Participants sat comfortably in front of a horizontally aligned monitor. Their right hand was hidden from direct view, placed inside a box standing on the right side of the monitor. Participants had to perform abduction movements of their right index finger that were filmed vertically from above. The movements were projected on the monitor in front of participants either in approximate real-time (with an intrinsic delay inferior to 17 ms) or delayed by 100, 200 or 300 ms. On 75% of trials, a single TMS pulse was delivered over participants' right motor cortex shortly after observing/performing the movement. At the end of each trial, participants had to judge whether the observed movement on the monitor temporally corresponded to their executed movement.

to the mark was continuously checked throughout the experiment. The resting motor threshold (rMT) was defined as the lowest level of stimulation at the optimal scalp location that produced MEPs of at least 50 μV in both muscles at rest in at least five out of 10 consecutive trials (Rossini et al. 1994). During the experiment, stimulation intensity was set at 110% of the rMT and ranged from 30% to 47% ($M$=37.3%, $SD$=4.5%) of the maximum stimulator output.

### 2.3. Apparatus

Participants were seated in front of a table whose surface was formed by a 19-inch monitor. Their right hand was placed palm down in a box standing on the right side of the monitor, hiding the hand from direct view. Their right forearm rested in a relaxed position on the table. A video camera (1/3″ Color CCD Camera, ELV Elektronik AG, Leer, Germany) was mounted inside the box and filmed the right hand of participants vertically from above. The filmed hand image was presented on the monitor in front of participants (resolution 800 × 600 pixels, refresh frequency 60 Hz). A delay device (DelayLine, Ovations Systems Limited, Oxford, UK) was connected between the video camera and the monitor that allowed for a delayed presentation of the hand image (see Fig. 1).

### 2.4. Procedure

At the beginning of the experimental session, baseline MEP amplitudes of the FDI and ADM were measured (fixation baseline). To this end, participants fixated on a small cross presented in the midline with their right hand resting in the experimental position inside the box. Fifteen TMS pulses were delivered.

Then, participants were familiarized with the experimental setup and instructed to perform simple index finger abduction movements while watching the visual feedback of these movements on the monitor in front of them. The participants' right hand was covered with a white glove throughout the whole experimental session in order to hide any morphological cues to authorship. Before the main part of the experiment started, participants underwent 20 movement practice trials during which they were trained to perform the required abduction movements with a comparable onset and duration of each movement. To prepare participants for the onset of the movement, an auditory countdown was presented that consisted of two short beeps (200 ms duration each) separated by 800 ms. Then, 800 ms after the second beep of the countdown, a 1000 ms duration auditory signal (movement tone) was presented during which participants had to perform an abduction movement of the right index finger. More specifically, this "movement tone" consisted of a 500 ms duration ascending pitch during which participants should move the index finger to the side (initial position: fingers

closed) and a 500 ms duration descending pitch during which they should move the finger back to the initial position. If participants failed to synchronize their movement performance with the "movement tone", the experimenter informed them about it and corrected them accordingly. Tone stimuli were presented via headphones. Participants were instructed to fully relax their muscles before and after the movement. This was continuously monitored by the experimenter via visual feedback of the EMG signal. Further, participants were instructed to avoid making any other movements except for the instructed abduction of the index finger. During this practice phase, visual feedback of the movements was always presented in real-time and no TMS pulses were delivered.

Afterwards, the main experiment started. Participants were instructed to perform the abduction movements trained previously. However, they were told that the visual feedback on the monitor could now either temporally correspond to the movement they generated or could be temporally manipulated. Participants were informed that the amount of deviation could vary from trial to trial, and that after each trial, they had to answer the question: "Did the movement you saw on the screen correspond to the movement you made?" with a yes-or-no response. The trial sequence of the main part of the experiment was as follows: Each trial started with a two-beep auditory go-signal (see above) delivered via headphones. During this period the monitor was blank. Directly after the occurrence of the second beep, the filmed hand image of the participants' right hand was displayed on the monitor. Participants performed a simple ~1000 ms duration abduction movement with their right index finger approximately 800 ms after the second beep (following previous training). The video recording of this movement was displayed with a delay of either 0, 100, 200 or 300 ms (these figures do not include an intrinsic delay within the video hardware, which did not exceed 17 ms). In the main experiment, the "movement tone" from the training phase was omitted. This avoided any possible interference with the movement execution and any potential additional cues for detecting temporal non-correspondence by monitoring the relation between tone and visual movement feedback. The screen turned blank after a random time interval after the end of the movement. The duration of this interval was pseudo-randomized with the following restrictions: (1) the minimum duration was defined as the time necessary to observe the whole movement (depending on the delay level; i.e., if the delay was 200 ms, then 200 ms were added after the end of the executed movement) and (2) the maximum duration was limited to 50 ms before the subsequent TMS pulse (see below). This procedure ensured that there was no fixed temporal relationship between the delay level and the duration of the appearance of the hand image, or between the disappearance of the hand image and the subsequent TMS pulse. In 75% of trials, a single TMS pulse was randomly delivered after the executed/observed movement. Timing of the TMS pulse is described in greater detail below. The remaining 25% of trials were catch trials where no TMS pulse was delivered. Following a 500 ms blank after the TMS pulse in TMS trials and 500 ms after the screen turned blank in catch trials, participants were cued (auditory signal via headphones) to give a yes-or-no response whether the observed movement corresponded to their executed movement or not (see above).[1] Unspeeded verbal responses were recorded by an experimenter on a keyboard. The experimenter's key press elicited an intertrial interval randomized between 2.5 and 3 s after which the next trial started.

Each level of delay (0, 100, 200, and 300 ms) of the visual movement feedback was presented 56 times (42 TMS trials and 14 catch trials) in randomized order, resulting in 224 trials overall. The whole experimental session lasted about 90 min.

As a manipulation check, participants completed a short questionnaire about their experience at the end of the experimental session. This included two ratings on 10-point visual analogue scales about their experience of agency over the observed movement on the monitor in front of them: (1) "If the movement on the monitor temporally corresponded to my executed movement (according to my subjective impression), I had the feeling that the movement on the monitor was: My own movement (0) – The movement of another person (10)"; (2) "If the movement on the monitor was temporally delayed with respect to my executed movement (according to my subjective impression), I had the feeling that the movement on the monitor was: My own movement (0) – The movement of another person (10)". A paired *t*-test revealed – as a validation of expected results – that when participants perceived the observed movement on the monitor as temporally corresponding to their actual executed movement, they indeed more strongly felt that they observed their own movement (rating 1: $.68 \pm SEM.19$) compared to when they perceived the observed movement on the monitor to be temporally

delayed with respect to their actual executed movement (rating 2: $4.2 \pm SEM.49$) ($t(28)=8.88, p < .001$).

#### 2.4.1. Timing of TMS pulse delivery

In the present experimental design, participants were both executing and observing a movement. Both these events are known to increase corticospinal excitability. With regard to execution, TMS studies have shown that corticospinal excitability peaks at movement onset and gradually decreases thereafter (Chen, Yaseen, Cohen, & Hallett, 1998; Zaaroor, Pratt, & Starr, 2003), with facilitatory after-effects on corticospinal excitability up to approximately 600 ms following the movement (Zaaroor et al., 2003). Although we are not aware of any TMS studies that systematically investigated the time-course of corticospinal excitability following movement observation, the temporal pattern of the corticospinal excitability *during* observation has been shown to correspond to the actual execution (Borroni et al., 2005; Gangitano et al., 2001; Montagna et al., 2005). Furthermore, a recent MEG study suggests a similar temporal stabilization of the primary motor cortex activation after execution and observation (Caetano et al., 2007). Therefore, it is plausible that movement observation induces comparable (although weaker) facilitatory after-effects on corticospinal excitability just as they occur after movement execution.

Our experimental design faced an important methodological issue, because participants always both executed and observed a movement. Specifically, if the TMS pulse were simply time-locked to the end of the *observed* movement, facilitatory after-effects due to movement execution would inevitably be stronger with smaller execution-observation delays (i.e., the end of the *executed* movement would be temporally closer to the TMS pulse in trials with smaller delays). This would counteract our prediction of an increased corticospinal excitability with larger temporal incongruence, that is, with larger delays. In contrast, if the TMS pulse were time-locked to the end of the *executed* movement, facilitatory after-effects due to movement observation would be stronger with larger delays (i.e., the end of the *observed* movement would be temporally closer to the TMS pulse in trials with larger delays). This would bias the results in the predicted direction, but for a trivial reason unconnected with sense of agency.

To solve this problem, the TMS pulse was time-locked to occur with a random jitter 350, 400 or 450 ms after (1) the end of the executed movement in 50% of trials and after (2) the end of the observed movement in the remaining 50% of trials (for two illustrative examples see Fig. 2). These timings were randomized within participants. Each method of timing the TMS pulse occurred equally often at each delay level. Both method of timing and delay level were presented in fully randomized order. This procedure ensured first that the time point of the TMS pulse was highly variable and therefore unpredictable. Second, for each delay level, shorter time distances to the end of the observed movement (as in (1)) were compensated with equivalent longer time distances to the end of the executed movement (as in (2)). In all cases, visual feedback of the movement was fully provided before the TMS pulse was applied. That is, when the TMS-pulse was time-locked to occur with the earliest jitter of 350 ms after the end of the executed movement in the 300 ms delay condition, it still occurred 50 ms after the end of the observed movement (see Fig. 2A). Overall, this protocol was still conservative with respect to our expected results because the influence of movement execution on corticospinal excitability (counting against our hypothesis) is assumed to be stronger than the influence due to movement observation counting in favor of our hypothesis (see e.g., Clark, Tremblay, & Ste-Marie, 2004; Léonard & Tremblay, 2007).

### 2.5. Data analysis

#### 2.5.1. Calculation of behavioral indices (correspondence judgments)

For each delay condition, the probability of "correspondence" judgments was calculated (ranging between 0=no trial judged as corresponding and 1=all trials judged as corresponding) as the number of trials in which participants judged the observed movement as corresponding to their own executed movement divided by the total number of trials of each delay level, separately for TMS trials and catch trials.

#### 2.5.2. EMG data pre-processing and calculation of MEP/EMG indices

EMG data were analyzed off-line. All trials were visually inspected and trials with detectable background EMG activity in the 50 ms prior to the TMS, technical artifacts or no clearly detectable MEP were discarded (1.4% of the total; maximum 3 trials per delay condition per participant). For the remaining trials, MEP amplitudes and background EMG level were obtained.

Individual peak-to-peak MEP amplitudes were calculated as the absolute distance between minimum and maximum values within a time window 10–80 ms after the TMS pulse. Mean MEP amplitudes were obtained for each delay condition and muscle. For a control analysis about potential influences of the time point of the TMS pulse delivery (i.e., global influences due to movement execution/observation per se), MEPs in the 100, 200 and 300 ms delay condition were further subdivided according to whether they were time-locked to the end of the executed or observed movement and averaged accordingly. The 0 ms delay condition was excluded because in this condition, the time of the TMS pulse locked to the end of

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[1] This approach allowed us to divide trials into those where participants felt they were the agent (i.e., recognized the correspondence between executed and observed movement) and those where they did not. Clearly, we could not control the exact proportions of "Correspondence" and "Non-correspondence" judgments. Many previous studies noted that direct questions about self–other attribution (Was that your hand movement or another person's hand movement?) generally produce a strong self-bias (see Introduction). This would make any comparison between the two different judgments impossible or at least highly unbalanced. In pilot testing, we found that questions about correspondence/non-correspondence produced a much more equal distribution of judgments. For this reason, we have used a question about correspondence as an explicit judgment of agency rather than a self–other attribution question.
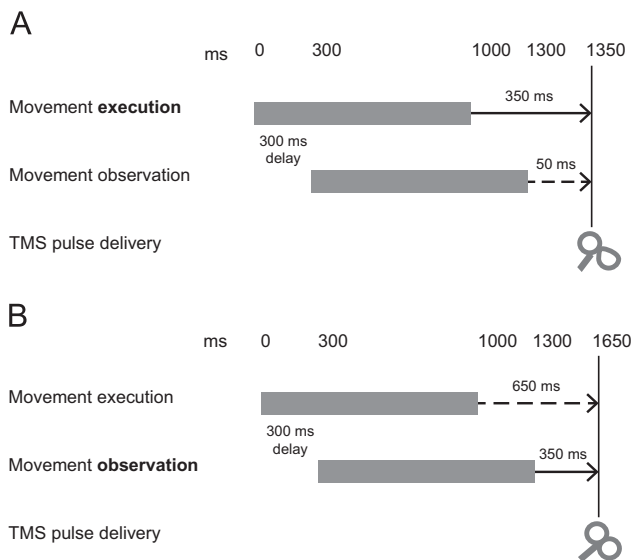
Fig. 2. Two illustrative examples of the timing of the TMS pulse delivery in the 300 ms delay condition. In the example above (A), the TMS pulse was time-locked to occur 350 ms after the end of the executed movement (solid line). Accordingly, the time distance of the TMS pulse with respect to the end of the observed movement was 50 ms (dashed line). In the example below (B), the TMS pulse was time-locked to occur 350 ms after the end of the observed movement (solid line). Accordingly, the time distance of the TMS pulse with respect to the end of the observed movement was 650 ms (dashed line).

the executed movement equals the time of the TMS pulse locked to the end of the observed movement. To further analyze the relation between corticospinal excitability and correspondence judgments, MEPs were divided into trials in which participants explicitly judged the observed movement as corresponding to their own executed movement and those in which they judged it as non-corresponding. This classification was restricted to the high ambiguity trials with 100 ms and 200 ms delays in which participants sometimes recognized and sometimes failed to recognize non-correspondence (cf. Farrer et al., 2008). Because most participants showed an unequal distribution between trials in which they judged the observed movement as corresponding versus non-corresponding, for each condition and muscle the median instead of the mean MEP was calculated to minimize the effect of outlier MEPs on the central tendency.

Finally, participants' mean and median MEP values for each experimental condition were expressed as a facilitation ratio compared to the pre-recorded fixation baseline to account for the large interindividual variability in MEP size (Rossini & Rossi, 1998): For each muscle, facilitation ratios were calculated by dividing each participant's mean MEP value or median MEP value into each condition by that participant's average MEP value of the fixation baseline.

The background EMG level was calculated for additional control analyses addressing whether potential MEP differences between conditions were confounded by modulations in background EMG activity that are known to influence MEP amplitudes (e.g., Devanne, Lavoie, & Capaday, 1997; Flament, Goldsmith, Buckley, & Lemon, 1993). The level of background EMG activity was calculated as the average rectified EMG signal during the 50 ms prior to the TMS pulse and the mean and the median of the respective values were obtained for each condition und muscle.

## 3. Results

### 3.1. Correspondence judgments (explicit agency) as a function of delay

The probabilities of "correspondence" judgments were entered into a repeated measures analysis of variance (ANOVA) with trial type (TMS trial vs. catch trial) and delay (0 vs. 100 vs. 200 vs. 300 ms) as within-subject variables. Degrees of freedom were corrected for deviance from sphericity using the Greenhouse and Geisser (1959) coefficient. The probability to judge the observed movement as corresponding to one's own executed movement decreased with increasing delay (see Fig. 3) as validated by a significant main effect of delay ($F(3,84)=152.36$, $p<.001$).
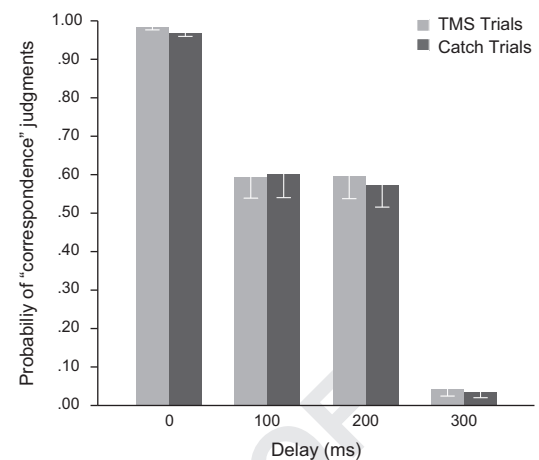


Fig. 3. Means and standard errors of the probability of "correspondence" judgments as a function of the delay of the visual movement feedback and trial type.

The mean values of the probabilities of "correspondence" judgments were $.98\pm SEM.01$ ms for the 0 ms delay, $.59\pm SEM.05$ ms for the 100 ms delay, $.58\pm SEM.06$ ms for the 200 ms delay, and $.04\pm SEM.02$ ms for the 300 ms delay. Neither the main effect of trial type nor the interaction between trial type and delay were significant ($F(1,28)=.92$, $p=.346$ and $F(3,84)=.69$, $p=.522$), indicating that correspondence judgments were comparable across TMS trials and catch trials for all levels of delay.

To further specify the pattern of the significant influence of the delay of the visual movement feedback on the probability to judge the observed movement as corresponding or non-corresponding, planned contrasts (t-tests) of adjacent levels of delay were conducted (i.e., 0 vs. 100 ms, 100 vs. 200 ms, 200 vs. 300 ms), collapsed across TMS trials and catch trials. There was a significant decrease in the probability of "correspondence" judgments from the 0 ms delay to the 100 ms delay ($t(28)=7.56$, $p<.001$), no further difference between the 100 ms delay and the 200 ms delay ($t(28)=.30$, $p=.765$), but again a significant decrease from the 200 ms delay to the 300 ms delay ($t(28)=10.49$, $p<.001$).

These results indicated that the correspondence judgments followed a step-wise function from a level at which the observed movement was clearly recognized as corresponding to one's own execution (0 ms delay) to a level of high ambiguity (100 and 200 ms delay) to a level at which the observed movement was clearly recognized as non-corresponding to one's own execution (300 ms delay).

### 3.2. MEPs (sensorimotor agency) as a function of delay

Averaged MEP facilitation ratios for FDI and ADM were entered into separate repeated measures ANOVAs with delay (0 vs. 100 vs. 200 vs. 300 ms) as a within-subject variable. Degrees of freedom for the analysis on the MEP facilitation ratios for FDI were corrected for deviance from sphericity using the Greenhouse and Geisser (1959) coefficient. Corticospinal excitability in the FDI muscle increased with increasing delay (see Fig. 4A) as validated by a significant main effect of delay ($F(3,84)=8.28$, $p<.001$). The mean values of the MEP facilitation ratios for FDI were $1.89\pm SEM.21$ mV for the 0 ms delay, $1.99\pm SEM.24$ mV for the 100 ms delay, $1.98\pm SEM.22$ mV for the 200 ms delay, and $2.07\pm SEM.24$ mV for the 300 ms delay. For the ADM, the main effect of delay was not significant ($F(3,84)=.49$, $p=.689$), indicating that the delay of the visual movement feedback had no meaningful influence on corticospinal excitability in a control muscle that was unrelated to the executed/observed movement (see Fig. 4B).
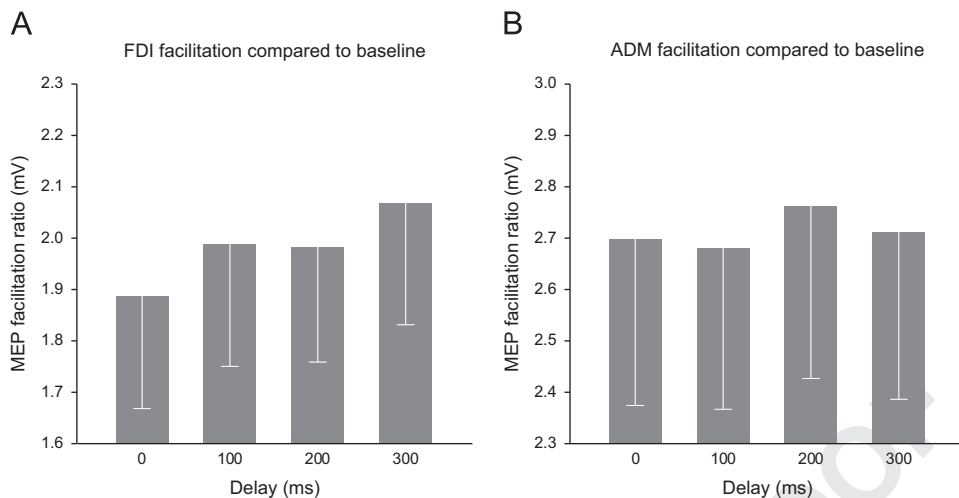
**Fig. 4.** Means and standard errors of the averaged MEP facilitation ratios of FDI (A) and ADM (B) as a function of the delay of the visual movement feedback.

As in the analysis on the correspondence judgments, planned contrasts (t-tests) of adjacent levels of delay were conducted in order to further specify the pattern of the significant influence of delay of the visual movement feedback on the MEP facilitation ratios for FDI. There was a significant increase from the 0 ms delay to the 100 ms delay ($t(28)=2.53$, $p=.017$), no further increase between the 100 ms delay and the 200 ms delay ($t(28)=.18$, $p=.855$), but again a significant increase from the 200 ms delay to the 300 ms delay ($t(28)=2.13$, $p=.042$). This pattern resembles an inverted mirroring of the step-wise pattern found for the correspondence judgments and confirms an increase in corticospinal excitability from the 0 ms delay level to an intermediate level at 100 and 200 ms delay and a further increase to the 300 ms delay level.

### 3.2.1. Control analyses

The pattern of results found in the FDI muscle was corroborated by further control analyses. First, we analyzed whether the observed differences between delay conditions were confounded by potential facilitatory after-effects of movement execution/observation per se. Although the protocol of the TMS pulse delivery was carefully and conservatively designed to compensate for these potential influences, we nevertheless investigated whether the time-locked procedure of the TMS pulse influenced corticospinal excitability in general and/or to a different degree under different levels of delay. Therefore, a repeated measures ANOVA was performed on the averaged MEP facilitation ratios for FDI in the 100, 200 and 300 ms delay with delay (100 vs. 200 vs. 300 ms) and timing of TMS pulse delivery (TMS pulse time-locked to end of executed movement vs. end of observed movement) as within-subject variables. As expected from the previous analysis, the main effect of delay was significant ($F(2,56)=3.64$, $p=.033$), indicating increased corticospinal excitability with increasing delay. Importantly, neither the main effect of timing of TMS pulse delivery nor the interaction between delay and timing of TMS pulse delivery were significant ($F(1,28)=.90$, $p=.350$ and $F(2,56)=1.43$, $p=.248$). This suggests that there was no significant modulation of corticospinal excitability – neither in general nor to a different degree under different levels of delay – according to whether the TMS pulse was time-locked to the end of the executed or observed movement. Therefore, the observed differences between delay conditions were unlikely to be due to potential facilitatory after-effects of movement execution/

observation per se. Rather, the protocol of the TMS pulse delivery obviously successfully compensated for these global influences.

Second, we investigated whether any variations in the background EMG activity might have contributed to the observed differences between delay conditions in the FDI muscle. Therefore, the averaged background EMG values for FDI were entered into a repeated measures ANOVA with delay (0 vs. 100 vs. 200 vs. 300 ms) as within-subject variable. No significant main effect of delay was found ($F(3,84)=.33$, $p=.801$), indicating only little variations in background EMG in the FDI muscle across conditions. Therefore, the differences between delay conditions observed for the FDI were unlikely to be due to differences in background EMG activity.

### 3.3. Relation of correspondence judgments (explicit agency) and MEPs (sensorimotor agency)

#### 3.3.1. Correlations between correspondence judgments, MEPs (FDI) and delay

To further examine the relation between correspondence judgments and corticospinal excitability, the correlation between the probability of "correspondence" judgments (TMS trials only) and averaged MEP facilitation ratio for FDI was calculated for each participant, across the levels of delay. Correlation coefficients were then converted into Fisher's Z transforms. A significant correlation between correspondence judgments and corticospinal excitability in the FDI muscle was found ($M$ Fisher's $Z=-.68$; $t(28)=4.16$, $p<.001$).

In addition, we analyzed whether the manipulation of the delay of the visual movement feedback induced similar, parallel variations of the correspondence judgments and corticospinal excitability, or, on the other hand, affected both measures in different ways. If a large part of the variance in correspondence judgments as a function of the delay is shared with the variance in corticospinal excitability, one might conclude that explicit judgments of agency are strongly grounded in low-level, sensorimotor representations of agency. Conversely, a significant influence of the delay on one measure (e.g., corticospinal excitability) after controlling for its shared variance with the other measure (e.g., correspondence judgments) would suggest that the two dependent variables are independently related to the manipulation of the delay of the visual movement feedback. Since the previous analysis revealed – as expected – no significant influence of the delay manipulation on ADM, the present analysis focused on the FDI only (averaged MEP facilitation ratios).
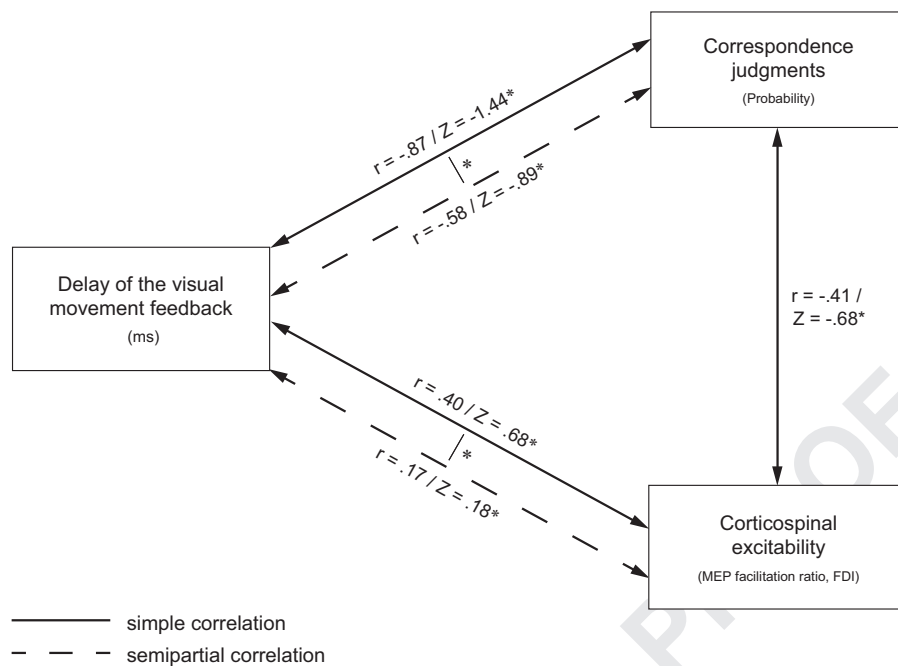
**Fig. 5.** Correlation structure for the relation between the delay of the visual movement feedback (in ms), corticospinal excitability (i.e., averaged MEP facilitation ratios for FDI), and correspondence judgment (i.e., probabilities to judge the observed movement as corresponding to one's own executed movement). Correlations were performed separately for each participant, converted into Fisher's *Z* transforms, and tested using *t*-tests. Note the significant reduction in the (semipartial) correlations between the delay and each dependent variable when the influence of the respective other dependent variable was partialled out.

For each participant (TMS trials only), we therefore calculated (1) the simple correlation between delay and probability of "correspondence" judgments, and (2) the simple correlation between delay and MEP facilitation ratio for FDI. Then, we used a semipartial correlation technique to assess (3) the relation between delay and probability of "correspondence" judgments, while controlling for the relation between probability of "correspondence" judgments and MEP facilitation ratio for FDI. This effectively assessed whether the delay influenced correspondence judgments, after the variation in correspondence judgments explained by the variation in corticospinal excitability had been removed. Similarly, we computed (4) the semipartial correlation between delay and MEP facilitation ratio for FDI, controlling for the relation between MEP facilitation ration for FDI and probability of "correspondence" judgments. All correlation coefficients were converted into Fisher's *Z* transforms. The structure of these correlations is shown in Fig. 5.

The simple correlations between delay and probability of "correspondence" judgment, and between delay and MEP facilitation ratio for FDI were both were significantly different from zero (*M* Fisher's *Z* = −1.44; *t*(28) = 21.65; *p* < .001 and *M* Fisher's *Z* = .68; *t*(28) = 3.89; *p* = .001). Both these relations remained significant after the contribution of the other dependent variable was removed using semipartial correlations (*M* Fisher's *Z* = −.89; *t*(28) = 7.01, *p* < .001 and *M* Fisher's *Z* = .18; *t*(28) = 2.75, *p* = .010). However, a direct comparison between the simple and semipartial correlation coefficients was significant for both cases. Specifically, the relation between delay and probability of "correspondence" judgments was significantly reduced, when the relation between probability of "correspondence" judgments and MEP facilitation ratio for FDI was controlled for (*t*(28) = 4.69, *p* < .001). Similarly, the relation between delay and MEP facilitation ratio for FDI was significantly reduced, when the relation between MEP facilitation ratio for FDI and probability of "correspondence" judgments was controlled for (*t*(28) = 3.13, *p* = .004). In summary, these analyses suggested that the influence of the delay of the visual movement feedback on high-level, explicit judgments and on low-level,

sensorimotor measures was partly independent, and partly overlapping.

### 3.3.2. MEPs as a function of delay and correspondence judgments

An additional analysis was performed to further investigate the covariation between correspondence judgments and corticospinal excitability and most importantly, to determine whether this covariation occurred due to a direct relation between the two measures rather than merely reflecting a similar influence of the delay manipulation on both measures. To this end, median MEP facilitation ratios were analyzed as a function of the delay of the visual movement feedback and correspondence judgments. The analysis was restricted to the high ambiguity trials in which participants sometimes recognized and sometimes failed to recognize the non-correspondence between executed and observed movement (i.e., 100 and 200 ms delay; cf. Farrer et al., 2008). Because a sufficient number of trials in each condition (minimum of 10 MEPs) were required, only a sub-sample of 12 participants could be included in this analysis.

Median MEP facilitation ratios for FDI and ADM were entered into separate repeated measures ANOVAs with delay (100 vs. 200 ms) and correspondence judgment (judged as corresponding vs. non-corresponding) as within-subject variables. The analysis on the MEP facilitation ratios for FDI revealed a significant main effect of correspondence judgment (*F*(1,11) = 5.85, *p* = .034), indicating a decrease in corticospinal excitability for trials in which the observed movement was judged as corresponding to one's own executed movement (1.99 ± *SEM*.31 mV) compared to trials in which it was judged as non-corresponding (2.19 ± *SEM*.32 mV) (see Fig. 6A). The main effect of delay and the interaction between delay and correspondence judgment were not significant (*F*(1,11) = .27, *p* = .617 and *F*(1,11) = .63, *p* = .444). Accordingly, the covariation between modulations of the corticospinal excitability in the FDI muscle and correspondence judgments (i.e., main effect of correspondence judgment) could not be attributed to any differences in the delay manipulation because first, the latter
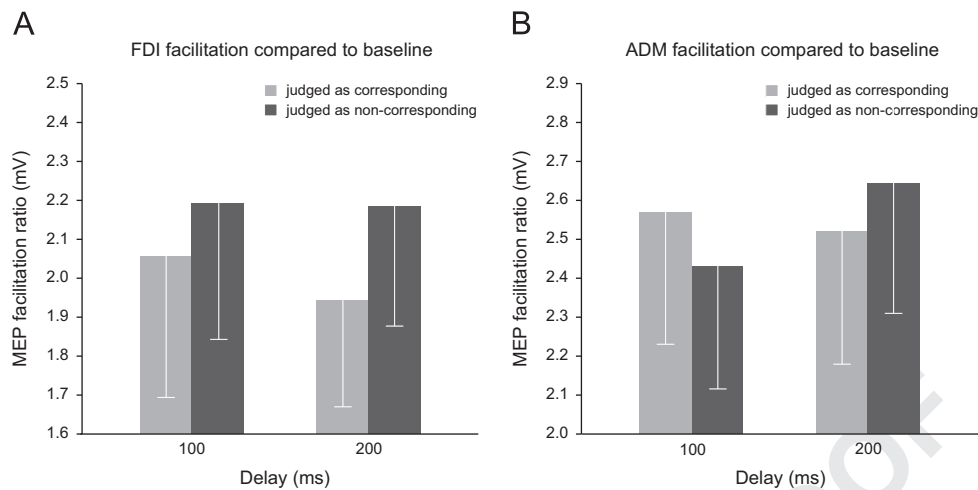
**Fig. 6.** Means and standard errors of the median MEP facilitation ratios for FDI (A) and ADM (B) as a function of the delay of the visual movement feedback and correspondence judgments.

seemed to not influence MEP facilitation ratios for FDI per se as indicated by a non-significant main effect of delay and second, this covariation appeared to be constant across the two levels of delay as suggested by the non-significant interaction between delay and correspondence judgment. The analysis on the MEP facilitation ratios for ADM revealed neither significant main effects of delay ($F$(1,11)=.23, $p$=.640) or correspondence judgment ($F$(1,11)=2.72, $p$=.127) nor a significant interaction between delay and correspondence judgment ($F$(1,11)=2.66, $p$=.131) (see Fig. 6B). The absence of a significant main effect of correspondence judgment indicated that no meaningful covariation between corticospinal excitability and correspondence judgments was present in a control muscle that was unrelated to the executed/observed movement.

### 3.3.3. Control analysis

The pattern of results found in the FDI muscle was corroborated by a further control analysis that tested whether any variations in the background EMG activity might have contributed to the observed covariation between modulations of the corticospinal excitability in the FDI muscle and correspondence judgments. Therefore, the median background EMG values for FDI were entered into a repeated measures ANOVA with delay (100 vs. 200 ms) and correspondence judgment (judged as corresponding vs. non-corresponding) as within-subject variables. Neither significant main effects of delay ($F$(1,11)=1.41, $p$=.260) or correspondence judgment ($F$(1,11)=.22, $p$=.647) nor a significant interaction between delay and correspondence judgment were found ($F$(1,11)=.06, $P$=.804), indicating only little variations in background EMG in the FDI muscle across conditions. Most importantly, the absence of a significant main effect of correspondence judgment indicated that the observed covariation between modulations of the corticospinal excitability in the FDI muscle and correspondence judgments were unlikely to be due to differences in background EMG activity.

### 4. Discussion

The present study sought to investigate the relation between low-level, sensorimotor-based feelings of agency and high-level, explicit judgments of agency. To this end, a paradigm was applied that allowed a parametric manipulation of the temporal correspondence between an executed finger movement and the visual feedback of the movement (see e.g., Farrer et al., 2008; Franck

et al., 2001). The experience of agency over the observed movement was expected to gradually decrease with increasing temporal non-correspondence. This expectation was corroborated by participants' reports. The effects of this parametric modulation were assessed by measuring corticospinal facilitation to TMS during movement observation as well as by assessing explicit verbal judgments about the presence/absence of temporal correspondence on a given trial. The resulting pattern of corticospinal facilitation was considered as a low-level, sensorimotor proxy for feelings of agency (Schütz-Bosbach et al., 2006, 2009) and the pattern of correspondence judgments was considered as a high-level, explicit proxy for judgments of agency.

### 4.1. Corticospinal excitability as a sensorimotor marker of agency

Corticospinal excitability increased as the temporal correspondence between the visual movement feedback and actual movement execution decreased. This modulation of corticospinal excitability could not be attributed to any global influences of the time elapsed between the executed/observed movement and the TMS pulse per se. Moreover, the degree of correspondence between executed and observed movement only influenced the excitability of circuits controlling the FDI muscle that was involved in the executed/observed abduction movement of the index finger, but was not present for a control muscle (ADM) that was irrelevant to the executed/observed movement (cf. e.g., Fadiga et al., 1995; Maeda, Kleiner-Fisman, & Pascual-Leone, 2002; Romani et al., 2005; Strafella & Paus, 2000). The muscle specificity of the observed effect is in line with the notion of a motor mapping between observed actions and execution of the same actions (Fadiga et al., 2005). The modulation of corticospinal excitability thus appeared to be a specific response linked to the correspondence between the execution and observation of the movement.

We assume that the differential excitability of the motor system can be regarded as a pre-reflective, sensorimotor-based marker of agency (i.e., *feeling* of agency; Synofzik et al., 2008) for the following reasons. First, the modulation of corticospinal excitability reflected the parametric degree of correspondence between execution and visual feedback of the movement and, in this way, the degree to which participants would instantaneously feel that the observed movement was self-generated. Previous studies emphasized the agent-neutral, shared representation between execution of one's own actions and observation of the actions of others within the sensorimotor system (see e.g., Fadiga et al., 1995; for overviews see Fadiga et al., 2005; Jeannerod, 2003;

Rizzolatti & Sinigaglia, 2010; Sommerville & Decety, 2006). Here, we show that, *within* the class of observed actions, corticospinal excitability to observed actions is strongly related to whether one is or is not a plausible agent of the observed action. Second, previous studies (Schütz-Bosbach et al., 2006; cf. Schütz-Bosbach et al., 2009) have shown this relation between corticospinal excitability and agency in an experimental situation where participants were not required to form any explicit judgments about agency, but merely observed actions (illusorily) linked to oneself or someone else. Accordingly, the differential response of the motor system with respect to agency of an observed action might occur rather automatic without the need for any explicit processes or judgments. This immediateness as well as the nature of the signal (i.e., responsivity of primary motor cortex) suggests that corticospinal excitability seems to not be a correlate of an explicit judgment itself, but rather of its more basic registration (i.e., feeling of agency).

Thus, the present study further supports the idea that corticospinal excitability following an observed action varies with the immediate feeling of agency over this action. The directionality of this relation, that is, a gradual increase in corticospinal excitability with a decreasing feeling agency over an observed movement replicates the previous findings of Schütz-Bosbach et al. (2006; cf. Schütz-Bosbach et al., 2009) who operationalized agency as two distinct categories (i.e., agency of oneself vs. agency of another person). In a similar vein, Fourkas, Avenanti, Urgesi, and Aglioti (2006) showed an enhanced corticospinal excitability when participants imagined an action performed by another person compared to when they imagined themselves performing the action. Furthermore, Désy and Théoret (2007) reported an increase in corticospinal excitability during observed actions of hands that were rather dissimilar to oneself in terms of skin color compared to when the hands matched the observer's skin color. Finally, a recent study suggests that the belief that one performs a joint task (i.e., playing a piano piece together) with another person was associated with an increase of corticospinal excitability to co-represented actions of the other person, compared to a condition where action representations were exclusively related to self-performance (Novembre, Ticini, Schütz-Bosbach, & Keller, 2012). The present study extends these previous findings by using a parametric manipulation of agency, based on temporal correspondence rather than a simple self/other dichotomy (e.g., Daprati et al., 1997; Sirigu et al., 1999). Moreover, ours is the first study, to our knowledge, that included a comparison of a low-level, sensorimotor and high-level, explicit proxy of agency for the same actions.

## 4.2. Relationship between sensorimotor and explicit agency representation

A specific goal of the present study was to investigate whether the low-level, sensorimotor representation (our proxy for feeling of agency) relates to the high-level, explicit representation of agency (judgment of agency). Our results revealed that the degree of temporal correspondence of the observed compared to the executed movement modulated both representational levels in a similar way. The step-wise increase in corticospinal excitability of the FDI muscle with decreasing agency due to larger temporal non-correspondence was mirrored in the explicit, verbal judgments as to whether the observed index finger movement did or did not correspond to participants' own executed movement. More specifically, in the veridical condition (i.e., no delay), when corticospinal facilitation to the observed movement was comparatively low, participants clearly judged the observed movement as corresponding to their own executed one. In parallel with an increase in corticospinal facilitation with intermediate levels of

temporal non-correspondence (100 ms and 200 ms delay), participants started to recognize that the observed movement deviated from their executed movement on approximately half the trials. Finally, in the condition with the highest non-correspondence (300 ms delay), participants almost always recognized that the observed movement did not correspond to their executed one. This was again paralleled by a further increase in corticospinal facilitation.

Further analyses revealed that the delay of the visual movement feedback induced partially covarying as well as partially independent variations of corticospinal excitability and correspondence judgments. With regard to the latter, independent variations of both measures might be considered to support the distinction of a sensorimotor-based feeling and an explicit judgment level of agency (Synofzik et al., 2008; cf. Bayne & Pacherie, 2007; Gallagher, 2012). That is, these sensorimotor and explicit representations may not be reducible to one another, but rather reflect two different and (partly) independent facets of the sense of agency. Nevertheless, this finding needs to be treated with caution because it might also reflect a simple measurement problem. Both measures represent indirect proxies for the sensorimotor and explicit representations of agency and are thus hardly a perfectly valid capture of these underlying representations. Therefore, independent variations could also reflect independent measurement noise inherent in one or both of these measures.

Moreover and more importantly, though, it was found that a substantial part of the variance was shared between corticospinal excitability and correspondence judgments. Additional analyses confirmed that the parallel modulations of these two measures appeared to be directly related instead of merely occurring as two separate consequences of the manipulation of the temporal correspondence between executed and observed movement. Corticospinal excitability showed a clear covariation with explicit judgments, even for intermediate levels of temporal non-correspondence (i.e., 100 ms and 200 ms delay) to which neither of the two measures were strongly sensitive per se. This indicates that the parallel modulation of corticospinal excitability and explicit judgments resulted (at least partially) from a direct link between them rather than reflecting a pseudo-relation, or in other words, an indirect effect due to similar influences of the temporal correspondence on either measure. More specifically, judgments of agency could be predicted based on the extent of corticospinal excitability to the observed index finger movement. This covariation indicates a strong interconnection between the two levels of agency described above. More specifically, it suggests that agency-related judgments are not purely inferentially mediated reconstructions (cf. Wegner, 2002), but could be directly based on a "readout" of information within the sensorimotor system.

Few previous studies have tried to bridge sensorimotor-based feelings of agency and explicit judgments of agency. Fourneret and Jeannerod (1998) showed that participants were able to perform a sensorimotor transformation to adjust their movements to compensate for spatially distorted visual feedback presented on-screen, without being consciously aware of their motor adaptation (cf. Knoblich & Kircher, 2004). This finding suggests a clear dissociation between sensorimotor aspects of motor behavior and movement awareness. In a similar vein, Berberian and Cleeremans (2010) reported a (putatively) sensorimotor-based sensitivity to externally but not self-generated changes in a visual stimulus, in the absence of any explicit awareness of the change or the causation of the change. Finally, a recent study showed that participants could explicitly deny agency over the effect of an action, even though the kinematics of an actual motor response indicated that it was treated as a self-generated effect, and vice versa (Preston & Newport, 2010). Even though different agency levels can obviously be experimentally dissociated in such studies,

the present study shows that they are nevertheless functionally related. Accordingly, the explicit judgment of agency does not appear to be decoupled from the sensorimotor evidence, but rather may often exploit low-level markers within the sensorimotor system. An interesting avenue for future research could be to further specify how the transition from the lower-order, sensorimotor to the higher-order, explicit representation of agency is implemented at the neural level. In particular, it is currently unknown where the information processed in the primary motor cortex might propagate to or where exactly this information is integrated to form explicit judgments of agency. Neuroimaging studies based on connectivity analyses might be able to shed further light on these underlying neural pathways.

## Acknowledgments

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