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ORIGINAL ARTICLE

Do movements contribute to sense of body ownership? Rubber hand illusion in expert pianists

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Abstract
Currently, it is still debated whether, how and to what extent movements contribute to the sense of body ownership (i.e., the feeling that one's body belongs to oneself). To answer this question, here we examined if a prolonged increase of the amount of movements affects body ownership. Specifically, we administered the rubber hand illusion paradigm within a natural condition of long-term motor practice, namely in expert pianists. We compared the illusory effects of both static (visuotactile stimulation) and dynamic (active/passive movements) versions of that paradigm in a group of expert pianists and a group of non-musicians. The illusion was measured behaviorally (proprioceptive drift) and subjectively (questionnaire). Our results showed that pianists were significantly less susceptible to any type of the illusion, compared to the non-musicians. Moreover, they did not experience the illusion in general (presenting neither the proprioceptive drift, nor the subjective feeling of ownership). These findings suggest that the increased amount of motor-related afferent and efferent signals does affect the construction and the coherence of body ownership, thus showing the role of movements in this process.

Introduction

Body ownership is defined as the conscious experience that one's body belongs to oneself (Gallagher, 2000). Such omnipresent perceptual status stands at the root of human nature, since each human being senses what it is like to have the body and what are its boundaries with respect to the environment (James, 1890).

There is a large consensus on the fact that body ownership is strongly rooted in both bottom-up and top-down signals. With respect to the former source, it emerges whenever incoming afferent sensory information (e.g., visual, tactile, proprioceptive, interoceptive, etc.) that continuously reaches our own body is integrated in both spatial and temporal terms (Kilteni, Maselli, Kording, & Slater, 2015; Pyasik, Burin, & Pia, 2018; Tsakiris, 2010). This interpretation comes from neurologically based alteration of body ownership (e.g., Bottini, Sedda, Ferre, Invernizzi, Gandola, & Paulesu, 2009; Jenkinson, Haggard, Ferreira, & Fotopoulou, 2013; Pia et al., 2014; Pia, Garbarini, Fossataro, Burin, & Berti, 2016; Piedimonte, Garbarini, Pia, Mezzanato, & Berti, 2016; Vallar & Ronchi, 2009), and mainly from the most employed experimental manipulation of normal body ownership, the rubber hand illusion (RHI) (Botvinick & Cohen, 1998; Burin, Pyasik, Ronga, Cavallo, Salatino, & Pia, 2018; Burin, Pyasik, Salatino, & Pia, 2017; Costantini & Haggard, 2007; Ehrsson, Spence, & Passingham, 2004; Farnè, Pavani, Meneghello, & Ladavas, 2000; Kalckert & Ehrsson, 2014; Kammers, de Vignemont, Verhagen, & Dijkerman, 2009; Longo, Schüür, Kammers, Tsakiris, & Haggard, 2008; Makin, Holmes, & Ehrsson, 2008). During the RHI, a realistic human-like fake hand is placed congruently with the participant's body (aligned with the shoulder and parallel to the matching real hand), while the real hand is hidden from the view. When the two hands are synchronously stroked, a compelling feeling of ownership over the fake hand arises; on the contrary, if the strokes are asynchronous, the illusion does not occur [although several studies reported some degree of embodiment also after the asynchronous stimulation (Costantini, Robinson, Migliorati, Donno, Ferri, & Northoff, 2016; Ismail & Shimada, 2016;

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Shimada, Fukuda, & Hiraki, 2009)]. The illusory effects, which are measured by the perceived mislocalization of the own hand towards the fake hand (i.e., proprioceptive drift) and/or by the subjective experience of owning the fake hand (an ad hoc questionnaire), are explained by the fact that vision, with respect to touch and proprioception, is given a higher weighting in the construction of the final percept (Costantini & Haggard, 2007; Makin et al., 2008; Tsakiris, 2010). Therefore, the initial conflict between vision of the rubber hand and tactile and proprioceptive sensation of the own hand is resolved by shifting the perceived location of the own hand towards the rubber hand. It is worth emphasizing, however, that the human body receives afferent signals not only in static conditions, but also during movements. Indeed, under these circumstances, vision, proprioception and touch are complemented with some additional signals, such as those coming from skin/joint receptors and muscle spindles. Hence, one might wonder whether the integration of sensory signals processed during passive and active movements also contributes to the sense of body ownership. As regards the role of top-down information in body ownership, it is known that some efferent signals impose constraints on what can, or cannot, be embodied during the RHI. Indeed, the illusion does not occur when the fake hand is placed in an incongruent position (e.g., rotated 180° or located far from the participant's body midline and real hand) (Botvinick & Cohen, 1998; Burin, Pyasik, et al., 2017; Costantini & Haggard, 2007; Lloyd, 2007; Preston, 2013). Given the fact that voluntary movements are based on efferent signals [e.g., centrally generated motor commands, forward models and sensory predictions (Blakemore, Frith, & Wolpert, 1999; Blakemore, Wolpert, & Frith, 1998; Frith, 2005)], one might ask whether motor-related efferent signals also contribute to the emergence of body ownership.

So far, most of the literature that attempted to answer the question of whether movements contribute to body ownership modified the original RHI paradigm in order to compare the conditions of passive and/or active movements with static conditions (Dummer, Picot-Annand, Neal, & Moore, 2009; Kalckert & Ehrsson, 2012, 2014; Kammers et al., 2009; Longo & Haggard, 2009; Riemer, Kleinbohl, Holzl, & Trojan, 2013; Tsakiris, Prabhu, & Haggard, 2006; Walsh, Moseley, Taylor, & Gandevia, 2011). The rationale of such approach was investigating whether movements further modulate body ownership. Overall, these studies reported contrasting findings. Indeed, some of them showed that the illusion was equally strong when it was evoked by tactile stimulation, active or passive movements (Kalckert & Ehrsson, 2014); others showed that movements increased the feeling of ownership (Dummer et al., 2009; Ma & Hommel, 2015; Tsakiris et al., 2006); and others more demonstrated that the sense of ownership decreased in the presence of movements (Walsh et al., 2011). Other studies employed a different approach that consisted in investigating whether the prolonged absence of movements affects body ownership. Accordingly, the RHI has been investigated in paraplegia/tetraplegia caused by spinal cord injury (Scandola, Tidoni, Avesani, Brunelli, Aglioti, & Moro, 2014), stroke-induced limb paralysis (Burin et al., 2015), and in healthy participants after a period of mechanical limb immobilization (Burin, Garbarini, et al., 2017). In all of those cases, the susceptibility to the illusion was affected by the absence of movements. Specifically, tetraplegic patients did not present proprioceptive drift, but experienced embodiment of the fake hand on the subjective level even after asynchronous stimulation (Scandola et al., 2014); hemiplegic patients experienced stronger illusion for their plegic hand (Burin et al., 2015); and healthy participants had more illusory effects for the hand that had been immobilized for 1 week (Burin, Garbarini, et al., 2017).

Findings obtained in the conditions of long-lasting periods of movement absence seem to suggest that motor-related signals are necessary for the construction of the coherent sense of body ownership. However, those studies did not clarify the specific role of afferent (e.g., vision, proprioception, kinesthetic information) and efferent (e.g., motor intention and sensory predictions) signals. Additionally, they provided only indirect evidence, since the role of movements was inferred from their absence. In order to fill this gap, in the present study we employed the opposite, direct logic, that is investigating the illusion in a condition where movements are naturally boosted, and therefore, there is an objective increase in the amount of motor-related signals. We capitalized on the condition of long-term motor practice of professional pianists. We therefore compared the RHI with three different types of stimulation (visuotactile, active movements and passive movements) in a group of expert pianists and in a group of non-musicians. Indeed, comparing different types of movement conditions would allow to clarify the role of efferent signals, such as motor intention, and afferent motor-related signals. Specifically, in the active moving RHI, the illusion is evoked by participant's voluntary movements (hence, it implies both efferent and afferent signals); in the passive moving RHI, there are no motor intentions or predictions but there are afferent motor-related signals, while neither type of motor-related signals is present in the visuotactile RHI (Kalckert & Ehrsson, 2014). Firstly, we predicted that pianists would experience less (or none) illusory effects in all types of the RHI because of the long-lasting increase of motor-related signals. We reasoned that, if in the condition of movements reduction (e.g., hemiplegia or movement prevention with a cast), the RHI effects were stronger because the multisensory conflict was more likely to be resolved in favor of vision due to the lack of motor-related signals to the hand

(Burin et al., 2015; Burin, Garbarini, et al., 2017), then an increased amount of those signals should result in the opposite pattern, i.e., lower susceptibility to the illusion. Secondly, we predicted a further decrease of the illusory effects in the active movement condition, because efferent motor-related signals, such as motor intention and planning, might additionally contribute to the construction of ownership of one's own hand.

Methods

Participants

Twenty expert pianists (9 females, 11 males; right-handed (Oldfield, 1971), mean age 24.6 ± 6.3 years, mean number of years of playing the piano 13.5 ± 5.0, mean time currently spent playing the piano 11.2 ± 11.9 h/week) and 20 age- and gender-matched control participants without any experience in playing a musical instrument (9 females, 11 males; right-handed (Oldfield, 1971), mean age 23.6 ± 1.8) participated in the study. Informed consent was obtained from all individual participants included in the study.

Experimental design

We used the moving RHI procedure (Kalckert & Ehrsson, 2012, 2014), which included three types of the RHI—visuotactile, active moving and passive moving, and two types of stimulation—synchronous and asynchronous, in a within-subject design. Therefore, there were total of six experimental conditions (3 × 2) administered in two groups of participants. We tested only the right (dominant) hand, since it has been shown that the RHI susceptibility is not affected by the hand laterality (Adamo, Scotland, & Martin, 2012; Ocklenburg, Rüther, Peterburs, Pinnow, & Güntürkün, 2011; Smit, Kooistra, van der Ham, & Dijkerman, 2017). The experiment was performed in a single session that lasted approximately 1 h.

Setup

The setup is presented in Fig. 1. Participants sat in front of a wooden box (40 cm × 30 cm × 20 cm) that was set on a table. A life-sized model right hand (a plastic glove filled with flour) was placed on an upper shelf of the box, while the participant's right hand (wearing an identical plastic glove) was placed on a lower shelf, 15 cm below the fake hand and vertically aligned with it. The two hands were

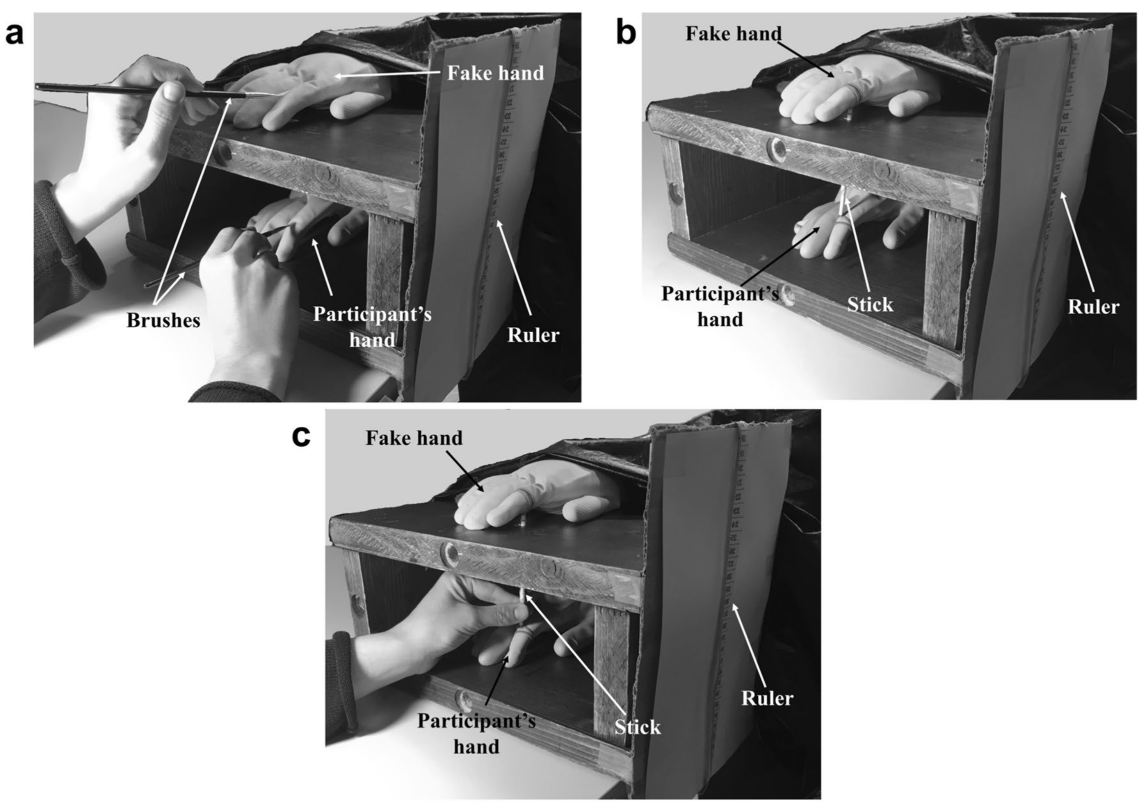

Fig. 1 Experimental setup: **a** visuotactile RHI; **b** active moving RHI; **c** passive moving RHI

placed congruently with the participant's body, and a barber cape covered the space between participant's neck and the wrist of the fake hand; thus, the participant's hand and arm were hidden from the view, which created the impression that the fake hand was the participant's own outstretched hand. During the active and passive moving RHI procedures, a plastic ring was placed on the participant's and the fake-hand's index fingers. Then, a plastic stick was attached to both rings in order to connect the participant's index finger with the index finger of the fake hand.

Procedure

The three types of RHI had the same procedure, except for the type of stimulation. In each type of RHI, the illusory effects were measured behaviorally (i.e., proprioceptive drift) and subjectively (i.e., questionnaire on the sense of body ownership).

In each type of RHI, firstly, participants were blindfolded and asked to indicate the perceived position of their right index finger by pointing their left index finger towards a rectangular piece of cardboard that was placed vertically on the left side of the box (six trials). Between the trials, the participants were asked to return their left hand to the initial position (placing it on the lap and keeping it relaxed) to avoid stereotypic responses. In each trial, the indicated position was recorded on a ruler that was attached to the piece of cardboard, and the recorded values were averaged between the six trials and referred to as pre-stimulation proprioceptive judgment. This measurement was followed by the stimulation phase that lasted for 2 min.

In the *visuotactile RHI* (Fig. 1a), the participants were asked to maintain their gaze on the index finger of the fake hand and to remain still; then, the touches were applied to the participant's and fake-hand's index fingers with two paintbrushes. In the condition of *synchronous* stimulation, the touches were applied simultaneously at 1 Hz frequency with randomly applied faster touches and occasional double touches at the tip of finger, while in the condition of *asynchronous* stimulation, the stimulation was temporally incongruent, i.e., the visual stimuli preceded the tactile ones by approximately 500–1000 ms (the experimenter was trained in advance with the backdrop of metronome beats occurring accordingly to the above-mentioned intervals).

In the *active RHI* (Fig. 1b), the participant's index finger was connected to the fake-hand's index finger with a plastic stick. The participants were asked to perform a tapping movement with their right index finger in a semi-regular rhythm of approximately 1 Hz with occasional double taps [since it has been shown that regular rhythm produced weaker illusion (Kalckert & Ehrsson, 2012)]. Before the beginning of this RHI procedure (i.e., during the instructions before pre-stimulation proprioceptive judgments), the participants were briefly trained to perform the tapping in the requested rhythm by following a metronome (which was no longer present during the experimental phase). During the experimental phase, in the condition of *synchronous* stimulation the participants performed the tapping movements and were instructed to keep their gaze on the index finger of the fake hand, which moved synchronously with the participant's movements. In the condition of *asynchronous* stimulation, the plastic stick between participant's and fake-hand's index fingers was disconnected in the middle. The participants followed the same instructions as in the *synchronous* condition, but the index finger of the fake hand was moved by the experimenter (who sat opposite from the participant and moved the finger using the plastic stick inside the box) in asynchrony with the participant's finger movements, i.e., the experimenter moved the fake finger as soon as the participant completed the movement of her finger.

In the *passive RHI* (Fig. 1c), participants were instructed to maintain their gaze on the index finger of the fake hand and keep their hand still and relaxed. In the *synchronous* condition, the participant's and fake-hand's index fingers were connected with the plastic stick, and the experimenter (seating opposite from the participant) moved the plastic stick, thus synchronously moving both fingers up and down. In the *asynchronous* condition, the stick was disconnected in the middle, and the experimenter first performed the complete movement of the participant's finger and then the complete movement of the fake finger.

Then, in each type of RHI and in each stimulation condition, immediately after the stimulation phase, the participants were blindfolded again and asked to indicate the perceived position of their right index finger by pointing towards the piece of cardboard on the left side of the box with their left index finger (six trials). The indicated position was averaged between the six trials and referred to as post-stimulation proprioceptive judgment. After that, the participants were presented with a questionnaire on the subjective experience of ownership over the fake hand. The questionnaire consisted of six statements—three illusion statements, which reflected the experience of different aspects of the illusion, and three control statements (see Table 1). The statements were read to the participants by the experimenter, and the participants were asked to verbally report their agreement with each statement by using a 7-point Likert scale from −3 ("completely disagree") to +3 ("completely agree"). The statements were selected from a previous study (Kalckert & Ehrsson, 2014), and their order was randomized for each participant in each experimental condition.

Between the experimental conditions (i.e., between each type of RHI and stimulation), participants were instructed to take their hand out of the box and move it in order to avoid possible lasting effects of the illusion from the previous

Table 1 Questionnaire on the sense of body ownership

Real	Q1. I felt as if I was looking at my own hand Q2. I felt as if the fake hand was part of my body Q3. I felt as if the fake hand was my hand
Control	Q4. It seemed as if I had more than one right hand Q5. It felt as if I had no longer a right hand, as if my right hand had disappeared Q6. I felt as if my real hand was turning rubbery

condition. The order of experimental conditions was counterbalanced between participants.

Statistical analysis

Firstly, we compared pre-stimulation proprioceptive judgments in each type of RHI between the groups of participants to evaluate whether the groups were comparable in terms of initial proprioceptive accuracy.

Then, in each experimental condition, pre-stimulation proprioceptive judgments were subtracted from post-stimulation judgments, and this value was referred to as proprioceptive drift (Tsakiris et al., 2006). Within the ownership questionnaire in each condition, the ratings were averaged for the illusion statements (Q1–Q3) and the control statements (Q4–Q6).

Proprioceptive drift and subjective ownership ratings (represented by the ratings in the illusion statements of the questionnaire) were compared between the groups of participants for each type of the RHI in the synchronous condition [i.e., the condition that is supposed to induce the illusion (Botvinick & Cohen, 1998)]. Then, within each group, for each type of the RHI the proprioceptive drift was compared between synchronous and asynchronous condition, and the ratings in illusion and control statements of the questionnaire were compared within synchronous and asynchronous condition, to evaluate whether each group of participants experienced each type of the illusion. Within each group, we also compared the illusion susceptibility (proprioceptive drift and the ratings in illusion statements of the questionnaire in synchronous condition) between the three types of RHI.

Since at least one variable for each required analysis failed to meet the criteria for normality of distribution on a Shapiro–Wilk test ($p > .05$), we performed nonparametric tests. The effect size was estimated with r. Bonferroni correction for multiple comparisons was used to adjust the alpha level for statistical significance according to the number of comparisons performed in each analysis.

Data availability

All data generated and analyzed during this study are included in this article (see Supplementary Material).

Results

Proprioceptive drift

According to Mann–Whitney U test, pre-stimulation proprioceptive judgments did not differ between the groups of participants in any type of RHI in any condition: *visuotactile synchronous* ($Z = 0.70$, $p = .48$; pianists median = 3.08, IQR = 2.83, control group median = 2.58; IQR = 3.00), *visuotactile asynchronous* ($Z = -1.26$, $p = .21$; pianists median = 2.33, IQR = 3.50, control group median = 4.08; IQR = 4.42), *active synchronous* ($Z = 0.89$, $p = .37$; pianists median = 2.75, IQR = 2.92, control group median = 2.17; IQR = 3.67), *active asynchronous* ($Z = 0.27$, $p = .80$; pianists median = 2.08, IQR = 2.52, control group median = 3.08; IQR = 4.08), *passive synchronous* ($Z = -0.32$, $p = .75$; pianists median = 2.00, IQR = 2.42, control group median = 2.25; IQR = 2.42), *passive asynchronous* ($Z = -1.18$, $p = .24$; pianists median = 2.08, IQR = 3.75, control group median = 4.33; IQR = 4.33). These results show that there was no a priori between-group difference in the ability to localize one's own hand.

The results of proprioceptive drift are presented in Fig. 2. As regards the between-group differences, Mann–Whitney U test showed that pianists presented significantly lower drift in *visuotactile* ($Z = -2.60$, $p = .001$, $r = -0.41$; pianists median = −0.17, IQR = 2.83, control group median = 1.83, IQR = 3.83) and *active* ($Z = -3.72$, $p < .001$, $r = -0.59$; pianists median = 0.17, IQR = 1.83, control group median = 2.00, IQR = 2.17) RHI in the condition of synchronous stimulation, compared to the control group. As for the *passive* RHI, the groups of participants did not differ significantly ($Z = -1.28$, $p = .20$; pianists median = −0.33, IQR = 1.33, control group median = 0.75, IQR = 3.67).

As for the within-group analysis, in the group of pianists, Wilcoxon signed rank test showed no significant differences between proprioceptive drift in the condition of *synchronous* and *asynchronous* stimulation in any type of the RHI: *visuotactile* RHI—$Z = 0.34$, $p = .74$; *synchronous* median = −0.17, IQR = 2.83, *asynchronous* median = −0.42, IQR = 1.50; *active* RHI—$Z = 1.43$, $p = .15$; *synchronous* median = 0.17, IQR = 1.83, *asynchronous* median = −0.08, IQR = 1.50; *passive* RHI—$Z = 1.75$, $p = .08$; *synchronous* median = −0.33, IQR = 1.33, *asynchronous* median = −0.50, IQR = 1.08. The proprioceptive

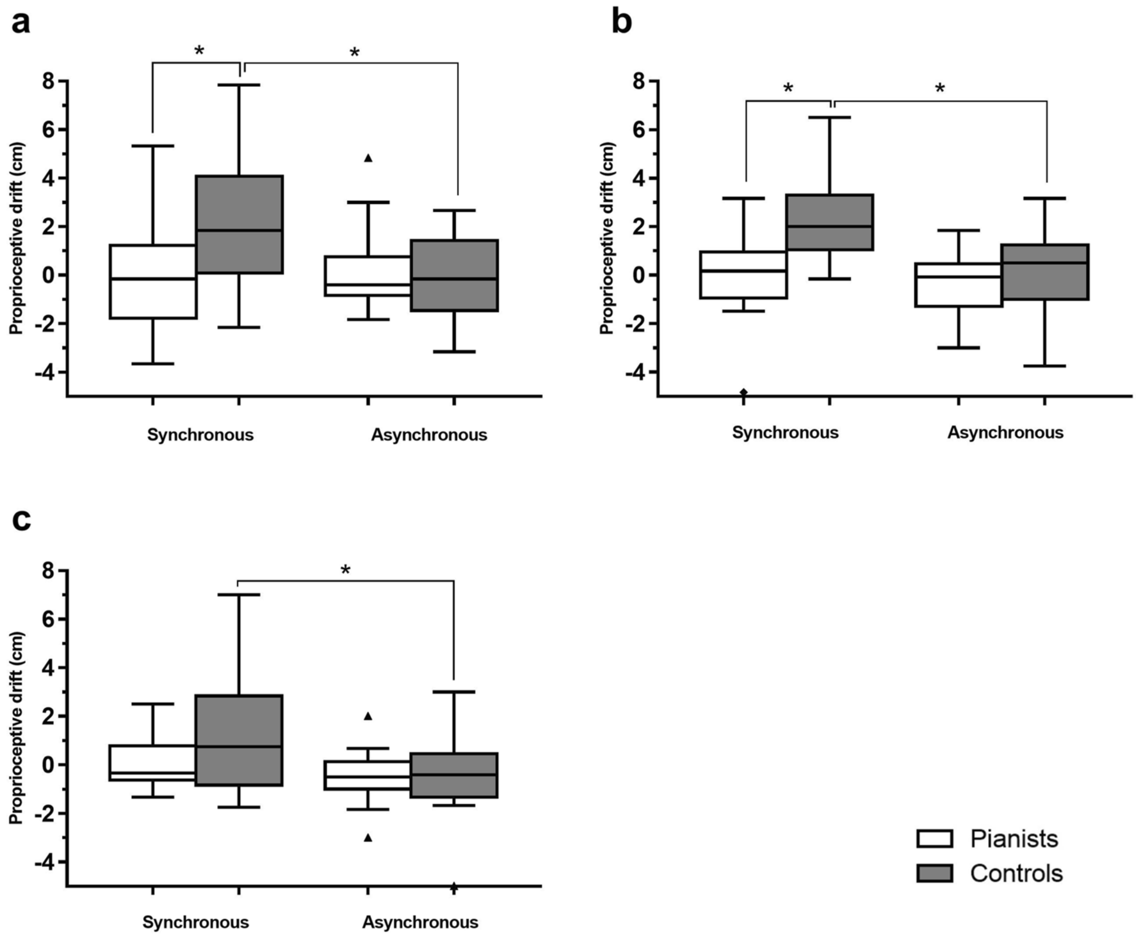

Fig. 2 Proprioceptive drift (cm) in the condition of synchronous and asynchronous stimulation in the group of pianists and the control group: **a** visuotactile RHI; **b** active moving RHI; **c** passive moving RHI. The box represents the first and the third quartile with the line in the middle of the box representing the median, and the bottom and top whiskers represent the first quartile minus 1.5*IQR and the third quartile plus 1.5*IQR; *represents significant differences

drift in *synchronous* condition did not differ significantly between the three types of RHI (*visuotactile* vs *active* RHI: $Z = 0.06$, $p = .95$; *visuotactile* vs *passive* RHI: $Z = 0.11$, $p = .91$; *active* vs *passive* RHI: $Z = 0.54$, $p = .59$).

In the control group in all types of RHI, proprioceptive drift was significantly higher in the condition of *synchronous* stimulation compared to *asynchronous: visuotactile* RHI—$Z = 3.17$, $p = .002$, $r = 0.50$; *synchronous* median = 1.83, IQR = 3.83, *asynchronous* median = − 0.17, IQR = 2.75; *active* RHI—$Z = 3.47$, $p < .001$, $r = 0.55$; *synchronous* median = 2.17, IQR = 2.17, *asynchronous* median = 0.50, IQR = 2.17; *passive* RHI—$Z = 2.15$, $p = .03$, $r = 0.34$; *synchronous* median = 0.75, IQR = 3.67, *asynchronous* median = − 0.42, IQR = 1.75. Similarly to the group of pianists, there were no significant differences in proprioceptive drift in *synchronous* condition between the three types of RHI (*visuotactile* vs *active* RHI: $Z = 0.09$, $p = .93$; *visuotactile* vs *passive* RHI: $Z = 1.62$, $p = .10$; *active* vs *passive* RHI: $Z = 1.47$, $p = .14$).

In summary, these results show that after the synchronous stimulation in *visuotactile* and *active* RHI, the group of pianists had significantly less proprioceptive drift with respect to the control group. Moreover, pianists did not experience the proprioceptive drift in any type of the RHI, while the control group, on the contrary, presented typical drift in all types of the illusion; neither of the groups had significant differences between the three types of RHI.

Ownership questionnaire

The results are presented in Fig. 3. As regards the between-group differences, on a Mann–Whitney *U* test, the ratings in illusion statements of the ownership questionnaire were significantly lower in the group of pianists in *active* ($Z = -3.12$, $p = .002$, $r = -0.50$) and *passive* RHI ($Z = -2.06$, $p = .04$, $r = -0.33$) RHI with synchronous stimulation. In *visuotactile* RHI, the ratings did not differ significantly between the groups of participants ($Z = -1.77$, $p = .08$).

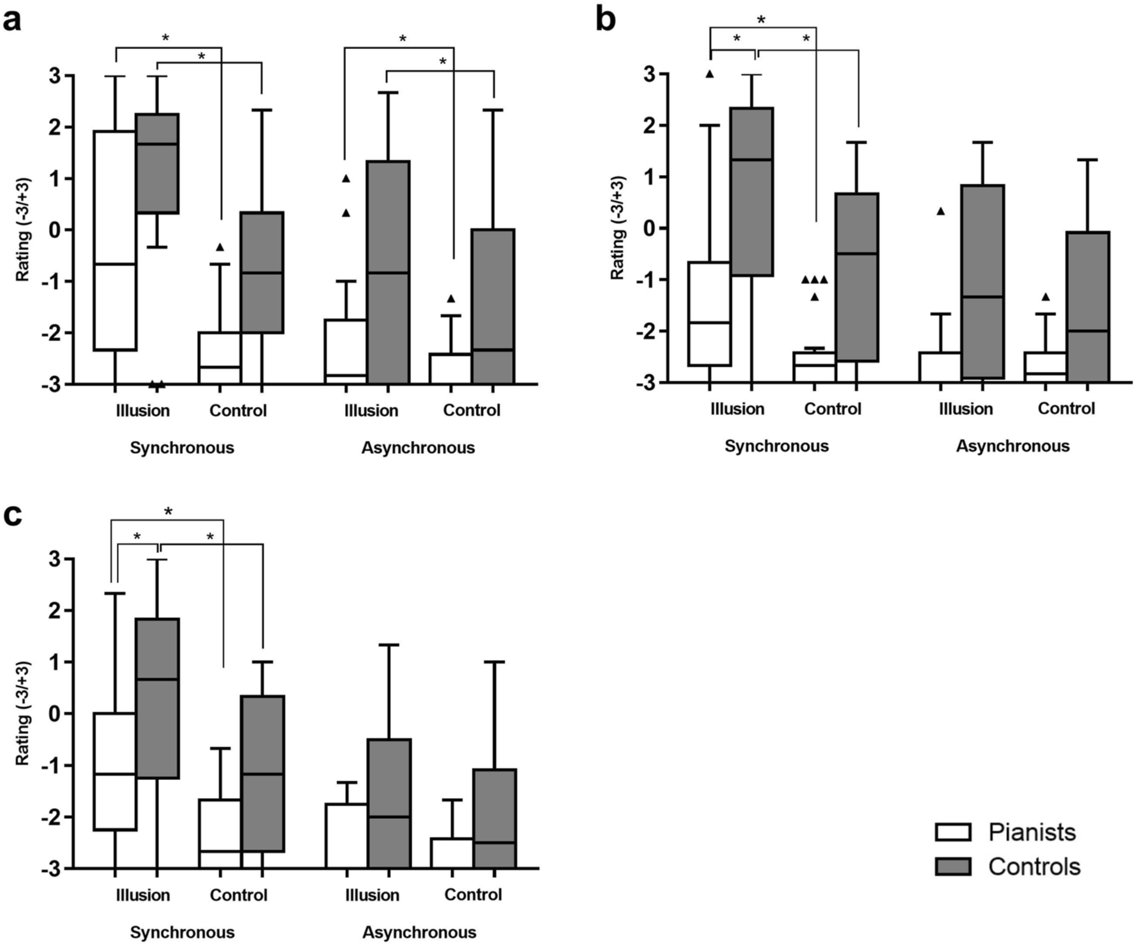

Fig. 3 Ownership questionnaire (ratings in illusion and control statements; − 3/+ 3 Likert scale) in the condition of synchronous and asynchronous stimulation in the group of pianists and the control group: **a** visuotactile RHI; **b** active moving RHI; **c** passive moving RHI. The box represents the first and the third quartile with the line in the middle of the box representing the median, and the bottom and top whiskers represent the first quartile minus 1.5*IQR and the third quartile plus 1.5*IQR; *represents significant differences

In the within-group analysis we compared the ratings in illusion and control statements in each experimental condition using the Wilcoxon signed rank test. In the group of pianists, the ratings in illusion statements were significantly higher than in control statements in *synchronous* condition in all types of RHI (*visuotactile:* $Z=3.11$, $p=.002$, $r=0.52$; illusion median $=-.67$, IQR $=4.17$; control median $=-2.67$, IQR $=1.00$; *active:* $Z=2.97$, $p=.003$, $r=0.48$; illusion median $=-1.83$, IQR $=2.00$; control median $=-2.67$, IQR $=0.50$; *passive:* $Z=3.39$, $p=.001$, $r=0.53$; illusion median $=-1.17$, IQR $=2.17$; control median $=-2.67$, IQR $=1.33$). In *asynchronous* condition, the ratings in illusion statements were significantly higher only in *visuotactile* RHI ($Z=2.01$, $p=.04$, $r=0.32$; illusion median $=-2.83$, IQR $=1.17$; control median $=-3.00$, IQR $=0.50$), but not in *active* ($Z=0.21$, $p=.83$; illusion median $=-3.00$, IQR $=0.50$; control median $=-2.83$, IQR $=0.50$) or *passive* ($Z=1.77$, $p=.08$; illusion median $=-3.00$, IQR $=1.17$; control median $=-3.00$, IQR $=0.50$). The ratings in illusion statements in *synchronous* condition did not differ significantly between the three types of RHI: *visuotactile* vs *active* RHI: $Z=2.33$, $p=.02$ (N.S. after Bonferroni correction; alpha level: $p=.017$); *visuotactile* vs *passive* RHI ($Z=1.44$, $p=.15$); *active* vs *passive* RHI ($Z=0.57$, $p=.57$).

In the control group, the pattern of significant differences was the same as in pianists: in *synchronous* condition, the ratings in illusion statements were significantly higher than in control statements in all types of RHI (*visuotactile:* $Z=3.59$, $p<.001$, $r=0.58$; illusion median $=1.67$, IQR $=1.83$; control median $=-0.83$, IQR $=2.33$; *active:* $Z=3.18$, $p=.001$, $r=0.50$; illusion median $=1.50$, IQR $=2.00$; control median $=-1.33$, IQR $=3.50$; *passive:* $Z=2.37$, $p=.02$, $r=0.36$; illusion median $=.67$, IQR $=2.83$; control median $=-1.17$, IQR $=2.83$). In turn, in *asynchronous* condition the significant difference was observed only in *visuotactile* RHI ($Z=2.76$, $p=.006$, $r=0.47$; illusion median = − 0.83 IQR = 4.33; control median = − 2.33, IQR = 3.00), but not in *active* ($Z = 1.44$, $p = .15$; illusion median = − 1.33, IQR = 3.50; control median = − 2.00, IQR = 2.83) or *passive* ($Z = 0.82$, $p = .41$; illusion median = − 2.00, IQR = 2.33; control median = − 2.50, IQR = 1.83). As in the group of pianists, the ratings in illusion statements in *synchronous* condition did not differ significantly between the three types of RHI: *visuotactile* vs *active* RHI: $Z = 0.95$, $p = .34$; *visuotactile* vs *passive* RHI: $Z = 2.07$, $p = .04$ (N.S. after Bonferroni correction; alpha level: $p = .017$); *active* vs *passive* RHI ($Z = 1.63$, $p = .10$).

In summary, pianists experienced significantly less ownership of the fake hand in *active* and *passive* RHI, but not in *visuotactile* RHI in synchronous condition. Within-group analysis showed the same pattern of differences between illusion and control statements within *synchronous* and *asynchronous* condition in each type of the RHI in the two groups of participants. However, in the group of pianists, the median ratings in illusion statements were negative in all experimental conditions, while in the control group they were positive in *synchronous* condition in all types of RHI. These results suggest that pianists did not experience subjective ownership of the fake hand, while the control group embodied the fake hand in all types of the illusion.

Discussion

In present study, we aimed at investigating the role of movements in the construction of body ownership. In order to answer this question, we examined whether, and to what extent, long-term motor practice affects the sense of body ownership measured by the RHI. Specifically, we experimentally manipulated the sense of body ownership with three different types of stimulation (visuotactile, active movements and passive movements) in expert pianists and a control group of people without any experience in playing musical instruments. Then, we compared different indices of the illusion (proprioceptive drift and ownership questionnaire) between groups. We predicted that pianists would experience less (or none) embodiment in any type of the RHI and that the illusory effects would be even lower in the condition of active movements.

The first prediction was confirmed, since the pianists were significantly less susceptible to the RHI of any type. Specifically, while they did not differ significantly from the control participants in the accuracy of pre-stimulation proprioceptive judgments (i.e., there was no a priori difference), after the stimulation phase, pianists had significantly less proprioceptive drift in the *visuotactile* and *active* RHI, and lower ratings of ownership of the fake hand in the *active* and *passive* RHI. Crucially, within-group analysis showed that pianists did not experience either subjective ownership of the fake hand (i.e., they had negative scores in the questionnaire), or the proprioceptive drift in any type of the RHI. On the contrary, the control participants presented the typical RHI pattern in all types of RHI: in the condition of synchronous stimulation, the perceived location of their own hand shifted towards the fake hand (proprioceptive drift), and the participants agreed with the ownership questionnaire statements that described different aspects of illusory ownership [consistently with previous data (Kalckert & Ehrsson, 2014)]. Contrary to our second prediction, however, pianists did not present any significant differences in the proprioceptive drift or the subjective ownership between the three types of the RHI, and neither did the control group. In case of the control group, such absence of differences is consistent with the previous studies that used the same RHI procedure (Kalckert & Ehrsson, 2012, 2014). In turn, the pianists did show a trend for lower subjective ownership ratings in the *active* RHI, although it was not significant.

In the rest of the discussion, we will argue that these results might be explained as due to the long-term motor practice in pianists. This, in turn, would support the view that movements per se contribute to the coherence of body ownership (Burin et al., 2015; Burin, Pyasik, et al., 2017; Fiorio et al., 2011; Tidoni, Grisoni, Liuzza, & Aglioti, 2014). Broadly speaking, any kind of prolonged and regular motor practice automatically increases the amount and the variety of motor-related afferent and efferent signals to the body. As regards pianists, these perceptual and motor changes are represented by anatomo-functional plastic changes in the brain for both somatosensory (Schulz, Ross, & Pantev, 2003) and motor (Gaser & Schlaug, 2003; Vaquero et al., 2016) cortex regions, and increased functional connectivity in multisensory and motor cortices (Luo et al., 2012). One study that addressed motor and somatosensory functions in expert pianists (Hosoda & Furuya, 2016) showed that more precise motor control had a positive covariation with higher somatosensory acuity. Here we argue that this increase of motor-related afferent and efferent signals affects body ownership as follows. As stated above, in normal circumstances, the rubber hand illusion emerges because vision overcomes touch and proprioception—a pattern consistent with a visual dominance over touch (Hartcher-O'Brien, Gallace, Krings, Koppen, & Spence, 2008). Specifically, when visual and tactile stimuli are presented simultaneously, control participants typically respond only to the visual component of the bimodal stimuli and fail to recognize the tactile one (Hartcher-O'Brien et al., 2008). Furthermore, this dominance becomes even stronger when the visual stimuli are presented on the body, and it remains present not only for one's own body parts but also for a congruently located fake hand (Hartcher-O'Brien, Levitan, & Spence, 2010). Accordingly, the absence of the illusion in pianists would follow a decrease of such dominance. Indeed, the musical skills of expert pianists require many years of motor training with constant presence of kinesthetic/tactile signals, without a corresponding increase of visual signals. Hence, the higher weight given to kinesthesis and touch would prevent the visual information from dominating (therefore not allowing the fake hand to be embodied). In fact, in pianists, the proprioceptive drift (which relies on the perceived location of participant's real hand) was almost equal to zero in all types of the RHI in the condition of synchronous stimulation.

Our results are not trivial, but rather consistent with previous studies. Indeed, hemiplegic patients showed absence of RHI effects for the healthy hand, suggesting that the increased use of the healthy hand provided more motor-related signals, which enhanced body ownership (Burin et al., 2015). On the contrary, for the immobile plegic hand the illusory effects were significantly stronger than in healthy participants. Similar results were observed in healthy participants after a week of mechanical limb immobilization. After such period, the RHI effects were stronger for immobilized hand and weaker for the non-immobilized hand (Burin, Garbarini, et al., 2017). To sum up, the RHI effects seem to be absent or decreased in any condition of increased amount of movements and motor-related signals.

It is worth emphasizing that our interpretation should be taken cautiously and alternatives need to be considered. Firstly, one might argue that the absence of RHI in pianists might be a consequence of better hand proprioception per se. Although our results cannot entirely rule out such interpretation, together with the existing literature, they suggest that it is rather unlikely. Indeed, a more accurate hand perception would have caused pianists to differ from the control participants in proprioceptive judgments before the stimulation. Since this did not happen in any condition, our data are more compatible with a different susceptibility to the illusion, rather than with possible pre-existing differences. Specifically, after seeing the touches to the fake hand (or the movements of its finger) synchronously with feeling the touches on their own hand (or the movements of their own finger), pianists did not feel any changes in the perceived location of their hand; therefore, their proprioception was not affected by the synchronous visual information. At the subjective level, this resulted in the absence of illusory ownership of the fake hand. Such interpretation is also supported by the fact that populations with superior proprioception but without specific motor training of the hands [advanced yoga practitioners (David, Fiori, & Aglioti, 2014) and people that practiced Tai Chi (Kerr, Agrawal, & Nayak, 2016)] did not present modulations in the RHI. Furthermore, the nature of piano practice itself suggests that pianists' superior somatosensory functions (Ragert, Schmidt, Altenmüller, & Dinse, 2004; Schulz et al., 2003) are more likely to be related to the practice rather than to the pre-existing proprioceptive sensitivity (e.g., Hosoda & Furuya, 2016). In addition, it is known that the development of expert musical skills and the level of expertise strongly depend primarily on the amount of deliberate practice and related additional factors, such as motivation, rather than innate skills and "talent" (Ericsson, 2014; Ericsson, Krampe, & Tesch-Römer, 1993; Lehmann, 1997). Therefore, although it might be difficult to separate the input of motor and sensory signals in piano practice, our results support the idea that sensory signals alone do not account for the observed absence of the RHI in pianists. One might also argue that the pianists could have been less susceptible to the RHI because they were more familiar with and accustomed to the hand posture and movements of the RHI setup and procedure, compared to the control group. While this might be a contributing factor, it also does not account for the main results because, as described above, the pianists were not more accurate in pre-stimulation proprioceptive judgments.

Taken together, our results suggest that, despite the complex interaction of motor and somatosensory functions in piano practice, long-term motor training contributes to the construction of body ownership by providing additional motor-related afferent and efferent signals included in the multisensory integration. This conclusion is strongly consistent with the fact that humans interact with the environment through the actions of their physical bodies (Gallese & Sinigaglia, 2010). Indeed, our own body allows to translate desires and goals into effects in the external world (Head & Holmes, 1911). To extend our results, future studies might focus on exploring this topic within a more cause-and-effect approach between variables (e.g., comparing different indices of body ownership before and after short-term non-musical motor training). Alternatively, body ownership might be further explored in other highly skilled individuals (e.g., dancers or athletes); in this case, it would be possible to investigate ownership of the whole body, rather than of the hands, in a virtual environment [virtual body illusion (Lenggenhager, Tadi, Metzinger, & Blanke, 2007)].

Compliance with ethical standards

Ethical approval All procedures performed in studies involving human participants were in accordance with the ethical standards of the institutional and/or national research committee and with the 1964 Helsinki declaration and its later amendments or comparable ethical standards.

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