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Fake hand in movement: visual motion cues from the rubber hand are processed for kinesthesia

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ABSTRACT

The feeling that a fake (e.g. rubber) hand belongs to a person's own body can be elicited by synchronously stroking the fake hand and the real hand, with the latter hidden from view. Here, we sought to determine whether visual motion signals from that incorporated rubber hand would provide relevant cues for sensing movement (i.e. kinesthesia). After 180 s of visuo-tactile synchronous or asynchronous stroking, the fake hand was moved along the lateral or the sagittal axis. After synchronous stroking, movement of the rubber hand induced illusory movement of the static (real) hand in the same direction; the illusion was slightly more frequent and more intense when the fake hand was moved along the sagittal axis. We therefore conclude that visual signals of motion originating from the rubber hand are integrated for kinesthesia by the central nervous system just as visual signals from the real hand are.

Keywords: rubber hand illusion, body representation, kinesthesia

1. INTRODUCTION

Body representations have rather flexible boundaries; the latter can stretch to include prostheses, avatars, tools and even fake (e.g. rubber) body segments (Abdulkarim & Ehrsson, 2016; Botvinick & Cohen, 1998; Cardinali, Brozzoli, & Farnè, 2009; de Vignemont & Farnè, 2010; Giroux et al., 2018; Guerraz, Breen, Pollidoro, Luyat, & Kavounoudias, 2018; Head & Holmes, 1911; Maravita & Iriki, 2004). Although the incorporation of non-living objects into the body representation is widely accepted, the extent of body plasticity remains an open question; it is not clear whether incorporated objects (i.e. fake limbs) are processed by the central nervous system in the same way as living arms and legs are (de Vignemont & Farnè, 2010). In a series of studies (including the present work), we have questioned whether visual signals originating from incorporated objects provide relevant cues for kinesthesia (i.e. the sense of one's own movement), just as visual signals originating from biological body segments themselves would.

A large body of literature data attests to the strong involvement of proprioception in kinesthesia (for a review, see Proske & Gandevia, 2018). However, as for most events with which humans are confronted, body movements rarely consist of a unimodal sensory signal. Indeed, the proprioceptive signal is often accompanied by other sensory signals, such as motor (Gandevia et al., 2006, Metral et al., 2013), tactile (Blanchard et al., 2011, Chancel et al., 2016) and visual signals. These various signals are then combined and integrated by the central nervous system, which generates a robust kinesthetic percept (Blanchard, Roll, Roll, & Kavounoudias, 2013; Chancel, Kavounoudias, & Guerraz, 2017; Ernst & Bulthoff, 2004; Maravita, Spence, & Driver, 2003; Proske & Gandevia, 2018). The fact that illusory body movements can nevertheless be evoked by visual manipulation confirms the involvement of vision in kinesthesia. In this context, the mirror illusion (evoked by the reflection of a person's moving hand in a mirror positioned in the sagittal axis) is particularly relevant. The “mirror hand” stands in for the unseen one, and its displacement gives an appearance of symmetrical, bimanual movements. The static, unseen hand (i.e. hidden behind the mirror) is perceived to move (Guerraz et al., 2012; Ramachandran & Altschuler, 2009). When the “mirror hand” is replaced by an avatar in a virtual reality mirror box display, the same kinesthetic mirror-like illusions are experienced (Giroux et al., 2018). These results indicate that visual motion signals originating from the incorporated avatar are, for the purposes of kinesthesia, integrated in the same way as visual signals originating from real (biological) body segments.

In the same vein, we recently showed that visual cues originating from a hand-held tool can be integrated by the central nervous system (Guerraz et al., 2018). Kinesthetic illusions were investigated by passively moving one arm (via a robotized manipulandum) and the tool (a rake), using the mirror paradigm. The reflected part was limited to the tool only, the arm only, or the two together. Illusory movements were experienced for the other (static) arm, hidden behind the mirror. The most striking finding was that the reflection of the moving tool alone was sufficient to induce consistent kinesthetic illusions in the arm hidden behind the mirror - at least when the participant held two similar tools (i.e. one in each hand).

Here, we investigated the kinesthetic impact of visual motion cues originating from a rubber hand incorporated in the body representation. In the rubber hand illusion (RHI), a feeling that a fake rubber hand belongs to a person's body is induced by repeated tactile stimulation (stroking) of one of the participant's hands, which is hidden from view. A (visible) fake hand placed in front of the participant is stroked at the same time. In this particular experimental set-up, there is a temporal match between the visual input (seeing a rubber hand being stroked) and the tactile input (feeling one’s real hand being stroked). This gives the participant the illusory feeling that the tactile stimuli originate from the rubber hand - as if the latter had sensed the stroking (Botvinick & Cohen, 1998; Ehrsson, Ehrsson, Spence, &

Passingham, 2004; Ehrsson, Holmes, & Passingham, 2005; Keizer, Smeets, Postma, van Elburg, & Dijkerman, 2014; Metral, Gonthier, Luyat, & Guerraz, 2017). Here, we induced the conventional RHI in our participants as described above and then moved the fake hand at a constant velocity of 4 mm/s for 5s. Participants were required to report whether they felt their hidden, static hand move when the fake one was moved by the experimenter. Avatars, tools and rubber hand incorporation might be different facets of a single phenomenon, each represented in the brain as if they were parts of the participant's own body (de Vignemont, 2011; de Vignemont & Farnè, 2010). This last point remains speculative, although our recent results prompted us to suggest that the visual properties of incorporated avatars and tools are represented as if they were parts of the body and used for kinesthesia. We hypothesized that in the present experiments, a movement of the incorporated fake hand would induce an illusory movement (i.e. kinesthetic illusion) of the biological hand in the same direction. The kinesthetic illusions were therefore expected to be more frequent and more intense in condition of synchronous visuo-tactile stroking than in condition of asynchronous stroking (considered to be a control condition in the pioneering study by Botvinick and Cohen (1998)).

As mentioned above, visual and proprioceptive signals are of prime importance for both localizing a body segment in space and perceiving its movements (Maravita et al., 2003). However, their respective involvements in the final percept can be direction-dependent, based on the intrinsic precision of these signals in different spatial directions (van Beers, Sittig, & Denier van der Gon, 1998; van Beers, Sitting, & Denier van der Gon, 1999). The latter researchers showed that visual targets are localized more precisely along the lateral axis than along the sagittal axis, whereas the reverse is true for proprioceptive targets (van Beers et al., 1998). Hence, in order to facilitate the emergence of illusory movements of the biological hand upon displacement of the rubber hand, the latter was displaced along the lateral axis (left to right) in our first experiment (hereafter “experiment 1”). In our second experiment (hereafter "experiment 2"), we repeated experiment 1 but moved the rubber hand along the lateral axis in half of the trials and along the sagittal axis in the other half. Considering the direction-dependent efficiency of visual and proprioceptive signals, we hypothesized that the illusory displacements of the biological hand would be more frequent and more intense when the rubber hand was moved along the lateral axis than we it was moved along the sagittal one.

2. METHODS

2.1 Participants

28 of the 32 participants who volunteered to participate in Experiment 1 were sensitive to the RHI (see pre-test) and therefore took part in the full experiment (27 females, mean ± SD = 21.4 ± 4.8 years). 24 of the 28 participants who volunteered to participate in Experiment 2 were sensitive to the RHI and took part in the full experiment (21 females, mean ± SD = 21.5 ± 2.3). None of the participants in Experiment 2 took part in Experiment 1. All but four participants were right-handed (as determined using the Edinburgh Inventory Test; Oldfield, 1971). None of them had a history of visual, proprioceptive or neuromuscular disease and all provided their prior, written, informed consent to participate. The Experiments were performed in accordance with the tenets of the declaration of Helsinki.

2.2 Material

The rubber hand set-up

Participants sat at a table with their hands positioned in front of them, palms face down. There were two marks on which to place the right and left index fingers. A life-sized rubber model of a right hand and wrist was placed on the table directly in front of them, between the two forearms. An opaque board (measuring 60 cm depth by 40 cm height) was positioned vertically and oriented parallel to the mid-sagittal axis. This set-up prevented the participants from viewing their right forearm. The opaque board created two compartments: one for the hidden right hand and one for the left hand and the rubber one (see Figure 1), the last two being visible. The index finger of the rubber hand and that of the participant's hidden right hand were both positioned at a distance of 10 cm from the opaque board and they were therefore separated by approximately 20 cm.

In the design of our study, the rubber hand could be moved both in the left-right or forward-backward directions. To this end, the rubber hand was fixed via two small rods to a motorized train and driven using a joystick. The train was positioned under the table on a linear track and was therefore not visible to the participant (see Figure 1). The motor used to move the train was a 'Low Noise Stepper Motor' coupled with rubber-belts. The rods on which the rubber hand was fixed could be moved through a slot made in the table allowing the train to move the rubber hand on top (see Figure 1) at a constant velocity of 4mm/s. This low speed was chosen because of the low sensitivity of proprioceptive receptors toward slow segment movements (Hall & Mccloskey, 1983) thus avoiding breaking the RHI.

Figure 1. Experimental set-up. The participant sat in front of a table, facing his left hand and the rubber hand. Participants wore a hairdresser's blouse to ensure that no gap were visible between the participants' body and the rubber hand. An opaque board occluded the right hand from his view. The motorized train positioned under the table could move the rubber hand in the lateral (as shown here) or the sagittal axis, according to the Experiment. The hidden right hand (but also the left one) was always static.

2.3. General Procedure

Pre-test: sensitivity to the rubber hand illusion (RHI)

All participants underwent a pre-test that consisted of evaluating whether or not they were sensitive to the prototypical rubber hand illusion. For this purpose, the participant sat in front of the rubber hand set-up with his hands positioned in front of him, palms down on the table. The experimenter synchronously stroked the visible rubber hand and the unseen biological right hand for 90s, with two identical soft brushes (the rubber hand remained static during the pre-test). Under this synchronous condition, the stroking movement was systematically from just above the knuckle toward the fingertips, with a frequency of approximately one stroke every 2s. The participant was instructed to keep his hand still, to look carefully at the rubber hand and to report verbally when he started to feel the RHI as described in the first three statements of the Embodiment Questionnaire (see EQ Botvinick & Cohen, 1998) that were stated to him before the experiment started: i) feeling the touch of the paintbrush in the location where they saw the rubber hand touched, ii) feeling a touch as if it was caused by contact between the paintbrush and the rubber hand, iii) feeling as though the rubber hand was their own hand. After the brushing period, each participant was asked to fill out all statements of the EQ (based on Botvinick & Cohen, 1998; Kammers, de Vignemont, Verhagen, & Dijkerman, 2009). The questionnaire assessed the subjective experience of illusion by rating nine statements (e.g. "I felt as if the rubber hand were my hand") on a ten-point Likert-scale ranging from one (*strongly disagree*) to ten (*strongly agree*). The first three statements specifically measure the experience of ownership of the rubber hand. The remaining statements were included as controls (according to Botvinick to Cohen 1998). Participants were considered sensitive to the RHI and therefore included in the experiment if they reported a subjective report of a RHI within the 90s brushing period and obtained a higher average score (> 0) for the first three items of the EQ than for the last six (questions 4 to 9). In addition to this inclusive pre-test, the participant's proprioceptive drift was measured. Before and after the brushing period, each participant closed his eyes and had to move his left index finger along a straight edge against the table, until it was judged in alignment with his right hidden finger. The difference between the two estimated positions was calculated as the proprioceptive drift (Botvinik and Cohen 1998).

Experiment: movement of the rubber hand

The participant sat in front of the rubber hand set-up with his hands positioned on either side of the opaque board. Then the initial stroking started, with both the rubber hand and the hidden right hand being stroked (using two brushes) at a frequency of ~ 0.5 Hz (one stimulation every 2s). Stroking was either synchronous or asynchronous. In the synchronous condition, the rubber hand and the participant's right hand were stimulated at the same time and the same location, following the agenda described in the "pre-test" (cf. section above). In the asynchronous condition, the stroking frequency was identical to that of the synchronous condition (one stimulation every 2 seconds), and constant between the participants. However, the stimulation pattern of the rubber hand and the hidden hand was spatially non-congruent and temporally asynchronous. In addition, speed and length of stroking between the rubber hand and the hidden hand varied randomly, and were therefore variable from trial to trial and from participant to participant (see Botvinick & Cohen 1998, Kammers et al., 2009). During the first 180s of stroking, the rubber hand remained static. After 150s the participant was required to answer verbally the first three statements of the EQ using a 10-points Likert-scale ranging from 1 (strongly disagree) to 10 (completely agree). The participant had to keep looking at the rubber hand while answering. After this initial stroking period and RHI evaluation, the rubber hand was moved at a constant velocity of 4mm/s for 5s (for a total displacement of 2cm) while the stroking stimulation continued (see Figure 2). As soon as the rubber hand displacement was over, the participant was required to mention out loud if he felt any movement of his hidden right hand. If so, he had to declare the direction and estimated intensity of the illusory movement. The direction could be left or right for the lateral axis (Experiment 1-2) and forward or backward for the sagittal axis (Experiment 2). The intensity of the illusory movement was appraised using a six-point self-rating scale, with zero indicating the absence of any sensation of movement, and one to five indicating respectively a very weak, weak, moderate, strong and very strong sensation of movement. Once the participant had finished reporting his feelings, the next trial began and the rubber hand was moved at the constant velocity of 4mm/s for 5s in the opposite direction (see below for a description of number of blocks and trials). As depicted in Figure 2 (solid black line), the rubber-hand was not returned to its original position between trials. In summary, after a stroking period of 180s while the rubber hand was static, the rubber hand was then moved with the direction alternating from left to right (Experiment 1 - 2) or from forward to backward (Experiment 2). It is important to note that in order to maintain the RHI, stroking wasn't stopped throughout the entire block of ten trials (see Figure 2). During the experiment, participants listened to soothing music (Marconi Union) through headphones. The headphone volume was set to a low value (4 with an I-phone5®) so that the participant could hear the experimenter but not the motorized device.

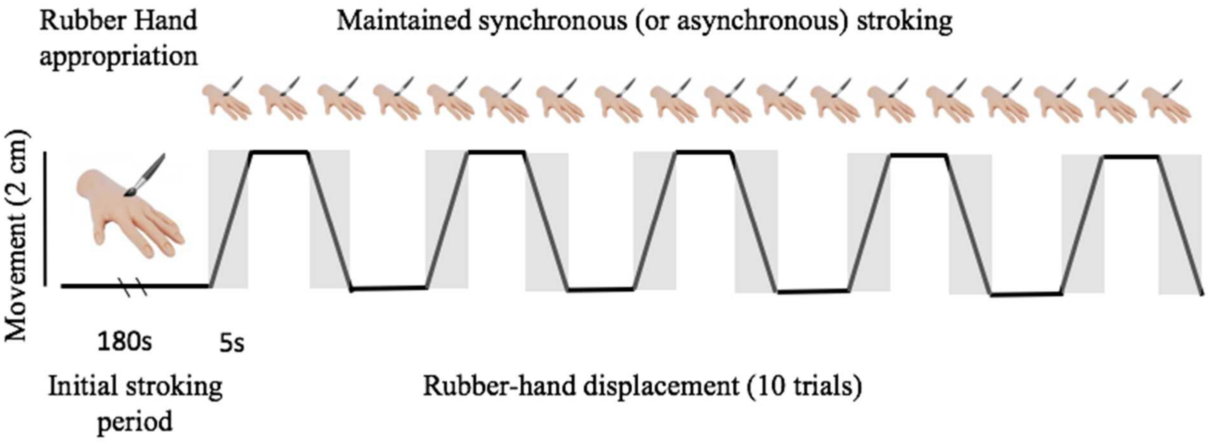

Figure 2. Illustration of a block of 10 trials. After 180s of synchronous or asynchronous visuo-tactile stimulation (only one type of stimulation per block), the rubber hand was moved in the lateral axis (from left to right: Experiment 1-2) and in the sagittal axis (forward and backward: Experiment 2). It must be noted that stroking never stop. Grey rectangles represent the rubber hand displacements, each of 5s duration. Within two grey rectangles was represented the period during which participants were required to report their subjective ratings (lasting from 5 to 15s). One block of trials lasted approximately 6'30 min. A rest period of 5min was given after each block of trials.

2.4. Experiment 1: lateral movement of the rubber hand

Movement of the rubber hand began after the initial stroking period of 180s. Experiment 1 consisted of four blocks of ten trials, with movement of the rubber hand in the lateral axis (right / left), with either synchronous (two blocks) or asynchronous stroking stimulation (two blocks). Thus, there were 20 trials with synchronous stimulation and 20 with asynchronous stimulation for a total of 40 trials per participant. The order of blocks was counterbalanced between participants.

2.5. Experiment 2: lateral versus sagittal displacements of the rubber hand

The displacements of the rubber hand began after the initial stroking period of 180s with either synchronous or asynchronous stimulation. In Experiment 2, the movement of the rubber hand could be either 1) in the lateral axis (the left / right) or 2) in the sagittal axis (backward / forward). Each block consisted in ten trials with the displacement of the rubber hand alternating in direction from trial to trial. The experiment was composed of two blocks with lateral displacements of the rubber hand (one block with synchronous stroking and one with asynchronous stroking) and two blocks with sagittal displacements (one block with synchronous stroking and one with asynchronous stroking). Overall, there were 40 trials per participant. The order of the axis (lateral versus sagittal) was counterbalanced between participants.

2.6. Statistical analysis

Correlations, pairwise comparisons t-tests and analysis of variance were assessed with Bayesian equivalent tests. Statistical analysis was performed using JASP software (JASP Team 2018, https://jasp-stats.org/)(See also Wagenmakers et al., 2018). Posterior probability distributions of the effect size (median Cohen's δ) were reported with their 95% credibility interval (CI 95%). Statistical evidence was reported using Bayes factors (BFs), BF_{10} for paired sample comparisons as well as for correlation analysis and BF_{incl} for ANOVAs denoting the level of evidence of the alternate hypothesis (non-signed difference), and the inclusion of a specific parameter in a model (ANOVA) respectively. The cut-off values defined by Jeffreys (1998) were used to interpret BFs. Considering that the kinesthetic illusion was measured with a subjective self-rating scale (ordinal data), statistics was performed on the median illusion intensity. Mean intensity was also provided in tables 1 and 2 for information. Raw data are available from https://figshare.com/s/a9c1d941b41a7f1a70e0.

3. RESULTS

3.1. Results of Experiment 1

3.1.1. Statistics from the RHI pre-test.

Among the 32 volunteers who agreed to participate in the experiment, 28 were sensitive to the RHI and were therefore included in Experiment 1. These 28 participants reported subjective feeling of RHI during the 90s stroking period and in each of them, the subjective rating based on the first three statements of the EQ after 90s was higher than that of the last six. Bayesian paired samples t-test showed extreme evidence (BF_{10} = 1.02e^{+11}, δ = 3.6, $CI_{95\%}$ [2.85, 4.50]) for a higher mean subjective rating based on the first three statements of the EQ (m = 7.33 ± 1.8) as compared to the last six (m = 2.43 ± 1.5). The median proprioceptive drift was positive (1.93 ± 3.27), that is, in the direction of the rubber hand. There was in some participants either no drift or a drift in the direction opposite to the rubber hand. Overall, nineteen of the participants (68%) of Experiment 1 had a proprioceptive drift in the direction of the rubber hand (positive drift) after the 90s of synchronous visuo-tactile stimulation. Bayesian one sample t-test showed moderate to strong evidence for a proprioceptive drift toward the rubber hand (BF_{10} = 9.35, δ = 0.54, $CI_{95\%}$ [0.16, 0.94]).

3.1.2. ***RHI*** and s***ynchronous versus asynchronous stimulation (initial stroking period).***

At the end of the initial stroking period (and for each block of trials), participant's RHI was evaluated using the first three statements of the EQ. The median subjective intensities of the RHI following the initial stroking period are reported in table 1. A Bayesian repeated sample t-test was performed to test differences between synchronous and asynchronous stroking. We found extreme evidence (BF_{10} = 4.4e^{+9}, δ = 3.2, $CI_{95\%}$ [2.51, 3.99]) to show that the median RHI in synchronous conditions (7.93 ± 2.46) was higher than in the asynchronous conditions (1.93, ± 1.65).

Table 1. *Descriptive statistics for both the RHI and kinesthetic illusion in Experiment 1*

Direction		Synchronous	Asynchronous
RHI	Median RHI	7.93 (2.46)	1.93 (1.65)

(Initial period)		Mean RHI	7.89 (1.76)	2.69 (1.74)
Kinesthetic Illusion	Right	Occurrence (%)	76.8 (37)	29.3 (38)
		Median intensity	2.71 (1.92)	0.77 (1.39)
		Mean intensity	2.79 (1.77)	0.90 (1.33)
	Left	Occurrence (%)	72.8 (38)	28.2 (35)
		Median intensity	2.46 (1.95)	0.73 (1.35)
		Mean intensity	2.59 (1.73)	0.85 (1.22)

Note. For the RHI, the subjective rating represents an agreement on a 10-point Likert scale from the first three statements of the EQ. For the kinesthetic mirror illusion, a subjective rating represents the intensity of movement felt on a self-rating scale from 0 to 5, with zero indicating the absence of any sensation of movement, and one to five indicating respectively a very weak, weak, moderate, strong and very strong sensation of movement. Statistical analysis have been performed on the median scores. Mean scores are given for information.

3.1.3. Kinesthetic illusion and synchronous versus asynchronous stroking

Results showed that following the initial stroking period, lateral movements of the rubber hand may evoke in participants, sensations of movement of the hidden biological hand (kinesthetic illusions). When it occurred, the illusory movement of the biological hand was always in the direction as that of the moving rubber hand. As seen in the following statistics, both the percentage occurrence and the intensity of kinesthetic illusions are closely linked to the synchrony-asynchrony of the stroking stimulation.

Percentage occurrence of the kinesthetic illusion*:* The percentage occurrences of the kinesthetic illusion induced by lateral displacement of the rubber hand, following either synchronous are asynchronous visuo-tactile stroking are reported in table 1. These data were submitted to a Bayesian repeated measures ANOVA with Synchrony and Direction as within-subject factors. The percentage of the kinesthetic illusion in the synchronous condition reached 75 % (± 37) when left and right displacements were pooled. It was 29 % (± 36) with asynchronous stroking. We found extreme evidence (BF_{incl} = 7.3e^{+12}, $\delta = 1.5$, $CI_{95\%}$ [0.88, 2.10]) to show that the percentage occurrence was higher in the synchronous as compared to asynchronous stroking. In contrast, there is moderate evidence for an absence of effect (H0) of both Direction (left vs right – BF_{incl} = 0.194, δ = 0.4, $CI_{95\%}$ [-0.09, 0.93]) and interaction between Synchrony and Direction (BF_{incl} = 0.201, δ = 0.28, $CI_{95\%}$ [-0.18, 0.78]).

Median subjective intensity of the kinesthetic illusion*:* The intensity of the kinesthetic illusion was measured by the use of a self-rating scale from 0 to 5, with zero indicating the absence of any sensation of movement, and one to five indicating respectively a very weak, weak, moderate, strong and very strong sensation of movement. All trials were considered for this analysis, including those in which no illusion was reported, therefore quoted with a "zero". Results of the Bayesian repeated measures ANOVA (Synchrony * Direction) showed that upon synchronous stroking, lateral movement of the rubber hand evoked a sensation of movement of the hidden biological hand, in the same direction as that of the moving rubber hand. The median intensity of the kinesthetic illusion in the synchronous condition reached 2.59 ± 1.9 (corresponding to a moderate illusion on our six-point (0 to 5) self-rating scale) when left and right displacements were pooled (see Figure 3). No, or very weak sensations of movement were reported in conditions of asynchronous stroking (*Me* = 0.75, ± 1.4). These data were submitted to a Bayesian repeated measures ANOVA. We found extreme evidence (BF_{incl} = $1.7e^{+11}$, δ = 1.37, $CI_{95\%}$ [0.777, 1.986]) to show that the median subjective intensity of the kinesthetic illusion was higher in the synchronous as compared to asynchronous stroking. In contrast, our data showed moderate evidence for an absence of effect (H0) of both the Direction (left vs right – BF_{incl} = 0.218, δ = 0.47, $CI_{95\%}$ [-0.010, 0.996]) and interaction Synchrony * Direction (BF_{incl} = 0.248, δ = 0.39, $CI_{95\%}$ [-0.081, 0.911]).

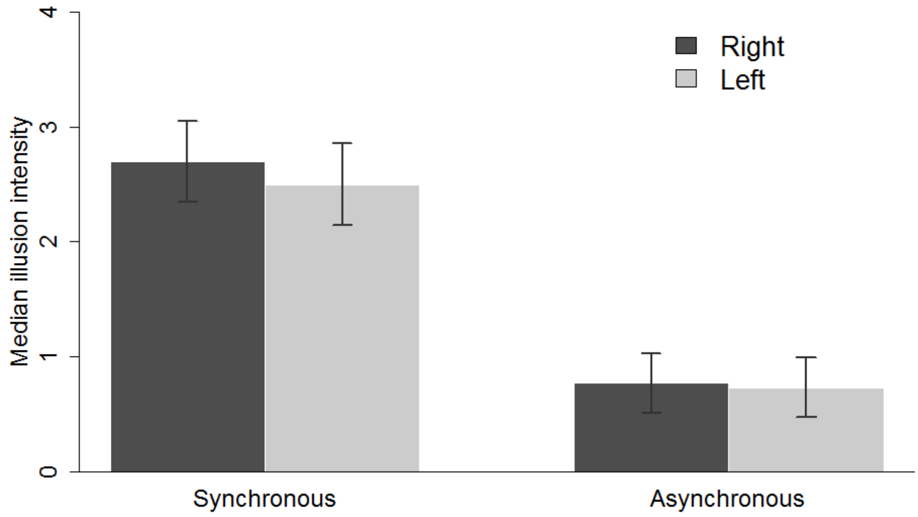

Figure 3. Median subjective intensity of the kinesthetic illusion (from 0 to 5, zero indicating the absence of any sensation of movement, and one to five indicating respectively a very weak, weak, moderate, strong and very strong sensation of movement) according to Synchrony (synchronous, asynchronous) and movement direction (right versus left) of the rubber hand. Arrows represent standard errors of the mean.

3.1.4. Relationship between the RHI and the kinesthetic illusion

The relationship between the median RHI and the kinesthetic illusion was evaluated by the use of the Bayesian equivalent of the Pearson correlation coefficient. Positive correlations were observed between the median RHI as measured after the initial synchronous stroking period and both the occurrence ($r = .57$, $BF_{10} = 26.7$, $CI_{95\%}$ [0.23; 0.76]) and median intensity ($r = .52$, $BF_{10} = 10.8$, $CI_{95\%}$ [0.17; 0.73]) of the kinesthetic illusion evoked by the displacement of the rubber hand (left and right combined).

3.2. Results of Experiment 2

3.2.1. Statistics from the RHI pre-test.

Of the 28 participants who volunteered to participate in Experiment 2, 24 were sensitive to the rubber illusion and were therefore included. In these 24 participants, the subjective rating based on the first three statements of the EQ was higher than that of the last six. Bayesian paired samples t-test showed extreme evidence (BF_{10} = 1.7e^{+6}, δ = 2.45, $CI_{95\%}$ [1.68, 3.36]) for a higher mean subjective ratings based on the first three statements of the EQ (7.27 ± 1.58) as compared to the last six (3.68 ± 1.59). Fourteen of them (58%) had proprioceptive drift in the direction of the rubber hand. Bayesian one sample t-test showed anecdotal evidence for a proprioceptive drift toward the rubber hand (1.27 cm ± 2.5; BF_{10} = 2.7, δ = 0.45, $CI_{95\%}$ [0.051, 0.883]). Finally, all participants felt a RHI during the 90s stroking period.

3.2.2. RHI and synchronous versus asynchronous stimulation (initial stroking period)

The median subjective intensity of the RHI following this initial stroking period was higher in the synchronous stroking condition (7.58 ± 1.7) than in the asynchronous one (2.58 ± 1.9) as confirmed by a Bayesian paired samples t-test comparison (BF_{10} = 1.4e^{+6}, δ = 2.42, $CI_{95\%}$ [1.68, 3.19]).

3.2.3. Kinesthetic illusion and synchronous versus asynchronous stroking

Results of Experiment 2 revealed that the kinesthetic illusion evoked in condition of synchronous stroking occurred when the rubber hand was moved in the lateral as well as in sagittal axis. No, or limited, sensation of movement were reported with asynchronous stroking.

Percentage occurrence of the kinesthetic illusion (see table 2)*:* These data were submitted to a Bayesian repeated measures ANOVA with Synchrony (synchronous versus asynchronous), Axis (lateral versus sagittal) and Direction (left vs right – forward vs backward) as within-subject factors. The percentage occurrence of the kinesthetic illusion when Axis and Directions were pooled was 66 % (±30.8) and 40 % (± 34.2) in conditions of synchronous and asynchronous stroking respectively. We found extreme evidence (BF_{incl} = 1.8e^{+9}, δ = 1.2, $CI_{95\%}$ [0.57, 1.86]) to show that the percentage occurrence was higher in the synchronous as compared to asynchronous stroking as a main effect. There was anecdotal statistical evidence regarding a main effect of Axis (lateral vs sagittal – BF_{incl} =1.6, $\delta = 0.52$, $CI_{95\%}$ [-0.01, 1.09]) and a strong evidence of an absence of a main effect of Direction (left vs right – forward vs backward – BF_{incl} =0.096, $\delta = 0.21$, $CI_{95\%}$ [-0.29, 0.73]). There was also moderate to strong evidence for an absence of any significant interaction between Synchrony, Axis and Direction.

Median subjective intensity of the kinesthetic illusion*:* Results showed that when lateral and sagittal axis were pooled, the median intensity of the kinesthetic illusion was higher when visuo-tactile stimulation was synchronous (2.09 ± 1.34, weak to moderate kinesthetic illusion on our six point self-rating scale) than asynchronous (0.77 ± 0.9, absent to very weak kinesthetic illusion) (see Figure 4). This was confirmed by the Bayesian ANOVA (Synchrony * Axis * Direction) that showed extreme evidence toward the inclusion of this factor (H1) (BF_{incl} = 9.3e^{+12}, $\delta = 1.6$, $CI_{95\%}$ [0.83, 2.24]). There was only moderate evidence toward the inclusion of Axis factor (BF_{incl} = 3.7, $\delta = 0.49$, $CI_{95\%}$ [-0.03, 1.06]). Indeed, when synchronous and direction conditions were pooled, the median intensity of the kinesthetic illusion tended to be lower when and rubbed hand was moved in the lateral direction (1.22, ± 0.9) than in the sagittal one (1.63 ± 0.9). There was strong evidence for an absence of effect of Direction (BF_{incl} = 0.101, $\delta = 0.004$, $CI_{95\%}$ [-0.52, 0.51]). There was also moderate to strong evidence for an absence of any significant interaction between Synchrony, Axis and Direction.

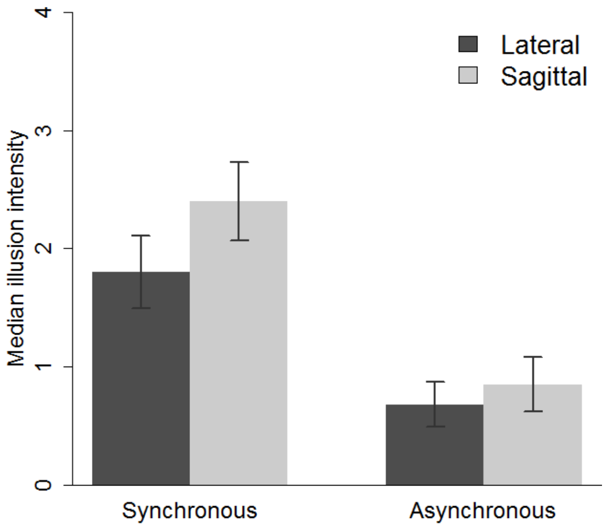

Figure 4. Median subjective intensity of the kinesthetic illusion (from 0 to 5, zero indicating the absence of any sensation of movement, and one to five indicating respectively a very weak, weak, moderate, strong and very strong sensation of movement) according to Synchrony (**s**ynchronous, **vs** asynchronous stroking) and Axis (lateral vs sagittal movement). Arrows represent standard errors of the mean.

Table 2. *Descriptive statistics for both the RHI and kinesthetic illusion in Experiment 2*

	Axis	Direction		Synchronous	Asynchronous
RHI (Initial period)			Median RHI	7.58 (1.77)	2.58 (1.95)
			Mean RHI	7.54 (1.72)	2.67 (1.89)
Kinesthetic illusion	Lateral	Right	Occurrence (%)	62.5 (38.8)	36.7 (37.1)
			Median intensity	1.75 (1.59)	0.54 (0.88)
			Mean intensity	1.88 (1.47)	0.80 (0.81)
		Left	Occurrence (%)	58.3 (40.8)	40.0 (39.1)
			Median intensity	1.79 (1.67)	0.83 (1.05)
			Mean intensity	1.81 (1.53)	0.86 (0.95)
	Sagittal	Forward	Occurrence (%)	69.2 (32.8)	43.3 (36.1)
			Median intensity	2.25 (1.70)	0.85 (1.24)
			Mean intensity	2.14 (1.50)	1.06 (1.14)
		Backward	Occurrence (%)	75.8 (32.8)	43.3 (39.8)
			Median intensity	2.58 (1.59)	0.85 (1.09)
			Mean intensity	2.43 (1.48)	1.06 (1.09)

Note. For the RHI, the subjective rating represents an agreement on a 10-point Likert scale from the first three statements of the EQ. For the kinesthetic mirror illusion, a subjective rating represents the intensity of movement felt on a self-rating scale from 0 to 5, with zero indicating the absence of any sensation of movement, and one to five indicating respectively a very weak, weak, moderate, strong and very strong sensation of movement.

3.2.4. Relationship between the RHI and the kinesthetic illusion

A positive correlation was observed between the subjective intensity of the RHI measured after the initial synchronous stroking period and both the occurrence (r = .61, BF_{10} = 28, $CI_{95\%}$ [0.25; 0.79]) and subjective intensity (r = .72, BF_{10} = 403, $CI_{95\%}$ [0.41; 0.86]) of the kinesthetic illusion evoked by the movement of the rubber hand (Axis and Direction conditions being pooled). Therefore, the more a participant was sensitive to the RHI, the more frequent and stronger the kinesthetic illusion (see Figure 5).

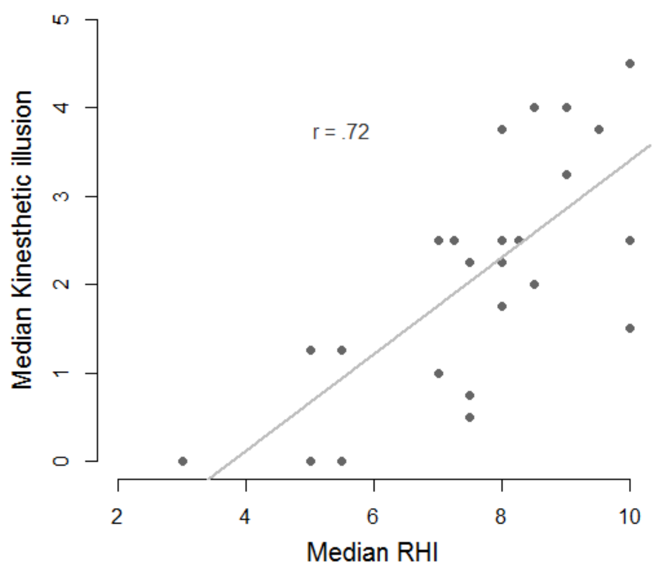

Figure 5. Relationship between the median RHI (x axis) and median kinesthetic illusion (y axis) in conditions of synchronous stroking stimulation.

4. DISCUSSION

A combination of synchronous visual and tactile stimuli (or visual and motor stimuli) is enough to prompt the self-attribution of a rubber hand by the central nervous system (Botvinick & Cohen, 1998; Costantini & Haggard, 2007; Dummer, Picot-Annand, Neal, & Moore, 2009). Here, we showed that movement of an incorporated rubber hand can induce an illusory movement (in the same direction) in the unseen biological hand. This kinesthetic illusion was observed in both Experiment 1 and Experiment 2. The results of Experiment 2 also revealed that the axis of the rubber hand motion does influence (albeit to a limited extent), the intensity of the kinesthetic illusion; the kinesthetic illusion was slightly more frequent and slightly more intense for sagittal displacements than for lateral displacements.

4.1. Processing of visual motion cues from incorporated objects.

The incorporation of avatars, tools and rubber hands into the body representation implies that some of the properties of these objects can be processed by the central nervous system in the same way as those originating from authentic (i.e. biological) body parts. Here, we focused on the visual properties of the incorporated objects in the context of kinesthesia, bearing in mind that a large body of literature data attests to the strong involvement of visual signals in the latter (Blanchard et al., 2013; Botvinick & Cohen, 1998; Ishihara & Kodaka, 2018; Kaneko et al., 2015; Ramachandran & Altschuler, 2009). We recently showed that visual motion signals originating from either an avatar of the participant’s arm or an incorporated tool provide relevant cues to update the body's representation, particularly the sense of movement (Giroux et al., 2018; Guerraz et al., 2018). Using the mirror paradigm, we demonstrated that reflection of the moving tool alone (without reflection of the arm holding the tool) in the mirror was sufficient to induce consistent kinesthetic illusions in the arm hidden behind the mirror (Guerraz et al., 2018). However, it must be noted that the illusion only occurred if the participant held two similar tools (i.e. one in each hand) - indicating that top-down processes are involved in the integration of visual-motion signals from the tool. On the same lines, we have shown that moving the arm of an embodied humanoid avatar (using immersive virtual reality) induces consistent kinesthetic illusions in the participant's biological arm, just as the vision of the biological arm itself would (Giroux et al., 2018). The present results are fully consistent with our previous findings, and reveal that visual motion signals from the incorporated rubber hand are processed by the central nervous system for kinesthesia. This does not imply that incorporated tools, avatars and rubber hands are all incorporated to the same extent. Indeed, as reported by de Vignemont (2010), there are important differences between the tool and the rubber hand phenomena. In contrast to the RHI, for example, the tool is rarely experienced as if it were a body part. However, the data as a whole show that once incorporation has occurred (and whatever the object), the central nervous system takes advantage of visual motion signals originating from the incorporated object for the purpose of kinesthesia.

4.2. The RHI and the kinesthetic illusion

The RHI is reported to be much more prevalent during synchronous visuo-tactile stimulation than during asynchronous stimulation (Botvinick & Cohen, 1998; Keizer et al., 2014; Newport, Pearce, & Preston, 2010). In their pioneering work, Botvinik and Cohen (1998) reported that a slightly asynchronous brushing of the two hands was associated with a much less prevalent illusion and a two-fold reduction in proprioceptive drift in the direction of the artificial hand. This was also true in our Experiments 1 and 2; the RHI (measured using the EQ) was three times more intense with synchronous stroking than with asynchronous stroking.

Synchronous visuo-tactile stimulation and the concomitant RHI also appear to be determinant factors in both the occurrence and intensity of the kinesthetic illusion. Indeed, when the RHI was limited or absent (such as in the asynchronous stroking condition), the kinesthetic illusion evoked by movement of the rubber hand was two to three time less intense than in the synchronous condition – even though the visual stimulation was similar in the two stroking conditions. This observation was also true for the prevalence of the kinesthetic illusion. Furthermore, a correlation analysis indicated that the greater the intensity of the RHI (as measured by the EQ), the stronger the kinesthetic illusion (*rho* = .45 and .69 in Experiments 1 and 2, respectively).

Looking at things in another way, the kinesthetic illusion induced by our present experimental set-up could be considered as an alternative measurement of rubber hand incorporation, relative to the classical EQ or to proprioceptive drift. However, it should be borne in mind that although proprioceptive drift (i.e. changes in the sense of position) and subjective rating (i.e. changes in limb ownership) are often used indifferently to measure the strength of the RHI, these two measures do not go "*hand in hand*" (Rohde et al 2011). Indeed, proprioceptive drift can be observed in the absence of ownership (as in the asynchronous visuo-tactile stroking condition) or even when the real hand is not stroked (i.e. with vision of the rubber hand only). This echoes some of our results regarding the kinesthetic illusion during asynchronous visuo-tactile stroking; we indeed observed kinesthetic illusions in the visuo-tactile asynchronous stroking condition in Experiments 1 and 2, even though they were much less frequent and less intense than in the synchronous condition. Consequently, body ownership may not go *"hand in hand"* with either proprioceptive drift or the kinesthetic illusion.

4.3. The rubber hand, kinesthetic illusions, and body representations

The integration of a rubber hand into the representation of one's body attests to the flexibility of the latter's boundaries (Abdulkarim & Ehrsson, 2016; Cardinali et al., 2009; de Vignemont

& Farnè, 2010; Maravita & Iriki, 2004). However, a distinction has been made between two types of body representation: the “body image” and the “body schema”. the body image is related to an internal mental representation of properties concerning one's body (such as its external appearance or its shape), and is primarily constructed from top-down factors such as perceptual experience, emotions, attitudes etc. (Gallagher & Cole, 1995; Newport, Pearce, & Preston, 2010). The body schema is related to a postural model that keeps track of limb position and has an important role in the control of action. The body schema is therefore a dynamic representation that is primarily updated by bottom-up sensory inputs (Gallagher, 1986; Paillard, 1999).

Models of body representation predict that the manipulation of sensory information (as happens in the RHI) can affect both the body image and body schema (see Pitron & de Vignemont, 2017 for a review). The fake hand replaces the biological hand or is considered to be an additional hand (see de Vignemont, 2010; Newport et al., 2010 for a discussion), and thus modifies the perception and appearance of the body by, for example, reducing body overestimation in patients with anorexia (conventionally classified as a body image disorder) (Keizer et al., 2014). However, Newport et al. (2010) and Kammers et al., (2009) have shown that synchronous visual and tactile stimulation affects not only the appearance of the person's body (i.e. the body image), but also the motor responses achieved with the biological hand (i.e. the body schema). The proprioceptive reaching and pointing responses in the rubber hand paradigm can also be dissociated from the visual capture of tactile location or from higher-order bodily sensations such as ownership (Snijders, Holmes, & Spence, 2007). Therefore, the RHI seems to induce distortions in both the body image and the body schema.

Kinesthesia is intimately linked to the body schema, since the former has a key role in the essential updating of the latter. Indeed, the kinesthetic system immediately informs the brain of changes in the configuration of body parts (Gallagher, 1986; Paillard, 1999). In this respect, the kinesthetic illusion evoked by the displacement of the rubber hand in our experiments highlights the intrinsic dynamic dimension of the incorporated rubber hand, which therefore shares the intrinsic dynamic dimensions of biological segment belonging to the body schema. These findings reinforce the hypothesis whereby the RHI has an impact on the body schema as well as on the body image.

4.4. Multisensory integration, action space, and the kinesthetic illusion along the lateral and sagittal axes

The central nervous system uses different sources of sensory information to localize the hand in space and to perceive its movements (Maravita et al., 2003). As far as localization is concerned, visual and proprioceptive signals have direction-dependent weightings that are based on the intrinsic precision of each signal (van Beers et al., 1998; van Beers et al., 1999). In the experiment described by van Beers et al. (1998), participants were seated at a table and had to perform proprioceptive or visual position-matching tasks. They were asked to match the position of a visual target (a dot) or a proprioceptive target (the right index finger) on the upper side of a table by touching the underside of the table with their unseen left hand. The visual target was localized more precisely along the lateral axis than along the sagittal axis, whereas the reverse was true for the proprioceptive target. In our paradigm, the movement of the rubber hand created incongruence between the visual movement of the incorporated rubber hand and the proprioceptive signals originating from the static biological hand. Considering the high accuracy of the proprioceptive signals whit respect to the sagittal axis, we hypothesized that the proprioceptive signals originating from the static biological hand would be more likely to counter the kinesthetic illusion evoked by the forward-backward movement of the incorporated rubber hand than kinesthetic illusion evoked by left-right movement. This rationale led us to prioritize movement of the rubber hand along the lateral axis in Experiment 1. However, results of Experiment 2 do not fit with our hypothesis since we observed moderate evidence for higher intensity of kinesthetic illusion for sagittal displacements of the rubber hand, relative to lateral displacements. The inclusion of a larger number of participants in Experiment 2 might have yielded more clear-cut results. Despite the potential lack of statistical power, these results clearly contradict our starting hypothesis. However, more precise proprioception along the lateral axis than along the sagittal axis (with the opposite for visual perception) might well be true for localization but might not be true for movement perception. This interpretation is rather speculative, although it is thought that perceptions of position and movement are processed separately by the central nervous system (McCloskey, 1973; Proske & Gandevia, 2009). However, another interpretation is possible. In contrast to the visual environment used by van Beers et al (1998), the visual environment used here was particularly rich; the rubber hand moved in a well-illuminated three dimensional environment. In this respect, the participant's vision provided unequivocal signals of movement. In contrast, the slow movement of the rubber hand (velocity: 4 mm/s) was rather close to the threshold for the proprioceptive detection of motion (Abdulkarim & Ehrsson, 2016; Hall & Mccloskey, 1983; Pickett & Konczak, 2009). In line with multisensory integration rules (Ernst & Bulthoff, 2004), the proprioceptive signals' low reliability in detecting such slow movements might led to them being underweighted and thus having a limited impact on the final percept. This contrasts with the high reliability of visual signals.

Multisensory integration also varies as a function of the action space. Recent data suggest that the RHI is more intense when the hand is in its usual action space (i.e. near the shoulder on the same body side). The intensity of our illusion might have depended on the rubber hand's position with regard to the body's midline and/or the position of the hidden hand. For example, Preston (2013) found that the RHI was less intense when the rubber hand was far from both the real hand and the trunk. On the same lines, it has been shown that proprioceptive drift decreases linearly as the hand is laterally moved away from the shoulder axis (Dempsey-Jones and colleagues, 2017). In our experiment, “left” and “forward” displacements correspond to movements away from both the body and the real hidden hand. Conversely, “right” and “backward” displacements correspond to movements towards the body and real hidden hand. In contrast to precedent studies, we did not find any effect of direction along either of the axes. The kinesthetic illusion experienced during a movement away from the body (left or forward) was similar to that experienced during movement towards the body (right or backward).

4.5. Proprioceptive drift and the rubber hand illusion

Participants were considered sensitive to the RHI and therefore included in Experiment 1 or 2 1) if they reported a subjective report of a RHI during the 90 seconds brushing period and 2) obtained a higher average score (> 0) for the first three items of the EQ (questions 1 to 3) than for the last six (questions 4 to 9). However, it must be noted that only 68% and 58% of the participants included in Experiment 1 and 2, respectively, showed, during the pre-test phase, a proprioceptive drift towards the rubber hand. The absence of proprioceptive drift could have been considered as an exclusion criterion since it often accompanies the feeling of ownership of the rubber hand. However, proprioceptive drift is labile, as Botvinick and Cohen (1998) had already shown, and it is not specific to the RHI since it can occur in the absence of RHI (see Rohde et al., 2011). This is what motivated our decision to include these particpants in our analyses. In all cases, we ensured that the statistical results of Experiment 1 and 2 were similar with or without these participants.

CONCLUSION

Using a modified version of the rubber hand paradigm, we showed for the first time that the movement of a rubber hand after synchronous visuo-tactile stroking, induces illusory movement (in the same direction) in the unseen static real hand. When considering our present results and our previous studies with avatars and tools (Giroux et al., 2018; Guerraz et al., 2018), we conclude that visual motion signals from incorporated non-living objects are integrated by the central nervous system for the purpose of kinesthesia.

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Conflicting interests

Neither of the authors has any conflicts of interests.

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Figure caption

Figure 1. Experimental set-up. The participant sat in front of a table, facing his left hand and the rubber hand. Participants wore a hairdresser's blouse to ensure that no gap were visible between the participants' body and the rubber hand. An opaque board occluded the right hand from his view. The motorized train positioned under the table could move the rubber hand in the lateral (as shown here) or the sagittal axis, according to the Experiment. The hidden right hand (but also the left one) was always static.

Figure 2. Illustration of a block of 10 trials. After 180s of synchronous or asynchronous visuo-tactile stimulation (only one type of stimulation per block), the rubber hand was moved in the lateral axis (from left to right: Experiment 1-2) and in the sagittal axis (forward and backward: Experiment 2). It must be noted that stroking never stop. Grey rectangles represent the rubber hand displacements, each of 5s duration. Within two grey rectangles was represented the period during which participants were required to report their subjective ratings (lasting from 5 to 10s). One block of trials lasted approximately 6'30 min. A rest period of 5min was given after each block of trials.

Figure 3. Median subjective intensity of the kinesthetic illusion (from 0 to 5, zero indicating the absence of any sensation of movement, and one to five indicating respectively a very weak, weak, moderate, strong and very strong sensation of movement) according to Synchrony (synchronous, asynchronous) and movement direction (right versus left) of the rubber hand. Arrows represent standard errors of the mean.

Figure 4. Median subjective intensity of the kinesthetic illusion (from 0 to 5, zero indicating the absence of any sensation of movement, and one to five indicating respectively a very weak, weak, moderate, strong and very strong sensation of movement) according to Synchrony (**s**ynchronous, **vs** asynchronous stroking) and Axis (lateral vs sagittal movement). Arrows represent standard errors of the mean.

Figure 5. Relationship between the median RHI (x axis) and median kinesthetic illusion (y axis) in conditions of synchronous stroking stimulation.

Supplementary material

Embodiment questionnaire from Botvinick and Cohen (1998)

Q1: It seemed as if I were feeling the touch of the paintbrush in the location where I saw the rubber hand touched.

Q2: It seemed as though the touch I felt was caused by the paintbrush touching the rubber hand.

Q3: I felt as if the rubber hand were my hand.

Q4: It felt as if my (real) hand were drifting towards the left (towards the rubber hand).

Q5: It seemed as if I might have more than one right hand or arm.

Q6: It seemed as if the touch I was feeling came from somewhere between my own hand and the rubber hand.

Q7: It felt as if my (real) hand were turning ‘rubbery’.

Q8: It appeared (visually) as if the rubber hand were drifting towards the right (towards my hand).

Q9: The rubber hand began to resemble my own (real) hand, in terms of shape, skin tone, freckles or some other visual feature.