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Temporal limits on rubber hand illusion reflect individuals' temporal resolution in multisensory perception.

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Running title: The Temporal Binding Window and the Rubber Hand Illusion

1. Abstract

Synchronous, but not asynchronous, multisensory stimulation has been successfully employed to manipulate the experience of body ownership, as in the case of the rubber hand illusion. Hence, it has been assumed that the rubber hand illusion is bound by the same temporal rules as in multisensory integration. However, empirical evidence of a direct link between the temporal limits on the rubber hand illusion and those on multisensory integration is still lacking. Here we provide the first comprehensive evidence that individual susceptibility to the rubber hand illusion depends upon the individual temporal resolution in multisensory perception, as indexed by the temporal binding window. In particular, in two studies we showed that the degree of temporal asynchrony necessary to prevent the induction of the rubber hand illusion depends upon the individuals' sensitivity to perceiving asynchrony during visuo-tactile stimulation. That is, the larger the temporal binding window, as inferred from a simultaneity judgment task, the higher the level of asynchrony tolerated in the rubber hand illusion. Our results suggest that current neurocognitive models of body ownership can be enriched with a temporal dimension. **Moreover, our results suggest that the different aspects of body ownership operate over different time scales.**

Keywords: Rubber Hand Illusion; Multisensory Integration; Temporal Binding Window; Body Ownership; Simultaneity Judgment Task

2. Introduction

Body representation has been linked to the processing and integration of multisensory signals (for reviews: Blanke, 2012; Ehrsson, 2012). An outstanding example of the pivotal role played by multisensory mechanisms in body representation is the Rubber Hand Illusion (RHI; Blanke, 2012; Botvinick & Cohen, 1998; Ehrsson, 2012). This illusion is generated when temporally close visual and tactile events occur on a visible rubber hand and the hidden participant's hand. The typical procedure has a participant sit with a visible fake (rubber) hand in front of them and her real hand under a curtain (not visible) while an experimenter uses a pair of paintbrushes to simultaneously stroke the rubber hand and the hidden-real hand. The illusion typically elicits a feeling of "ownership" of the rubber hand. The RHI does not arise when visual and tactile stimuli are out of synchrony, with a stimulus offset larger than 300 ms (Bekrater-Bodmann et al., 2014; Shimada, Suzuki, Yoda, & Hayashi, 2014).

Based on this temporal constraint and evidence showing that RHI is associated with neural activity in multisensory brain areas (Blanke, 2012; Ehrsson, Holmes, & Passingham, 2005; Ehrsson, Spence, & Passingham, 2004; Ionta, Martuzzi, Salomon, & Blanke, 2014; Makin, Holmes, & Ehrsson, 2008; Tsakiris, Hesse, Boy, Haggard, & Fink, 2007), it has been assumed that RHI depends upon multisensory integration processes (Blanke, 2012; Ehrsson, 2012). Hence, temporal constraints of RHI would reflect those characterizing multisensory processing. Indeed, seminal studies in animals showed that multisensory integration is more likely to occur when the constituent unisensory stimuli arise synchronously or over a short temporal interval called temporal window of integration (or Temporal Binding Window, TBW; Colonius & Diederich, 2004; Vroomen & Keetels, 2010; Wallace & Stevenson, 2014). The most established paradigm used to study the multisensory temporal binding window is the simultaneity judgment task **(Vatakis & Spence, 2006)**, in which participants judge the perceived simultaneity (i.e., the synchrony) of paired stimuli.

Despite the common temporal features between multisensory integration and the RHI, there is no empirical data supporting the dependency of the RHI upon the temporal resolution of multisensory integration mechanisms.

Starting from this gap in the literature, we seek to provide the first comprehensive evidence linking individual susceptibility to the RHI to individual temporal resolution in multisensory perception (i.e., the TBW). Indeed, they are both characterized by marked interindividual differences (Asai, Mao, Sugimori, & Tanno, 2011; Stevenson, Zemtsov, & Wallace, 2012).

Previous researches have already shown that varying the Stimulus Onset Asynchrony (SOA) between the visual stimulus delivered on the rubber hand and the tactile stimulus delivered on the real hand has consequences on the strength of the RHI. For instance Shimada and colleagues (Shimada, Fukuda, & Hiraki, 2009) investigated delays up to 600 ms in steps of 100 ms. The authors found that illusion ratings were significantly higher for short delays, up to 300 msec. In the present study we do a step forward by formally associating sensitivity to the rubber hand illusion to temporal sensitivity in multisensory integration. Such a finding would foster new investigations into the temporal unfolding of body ownership, an issue largely neglected so far.

In order to achieve this, we measured participants' TBWs through the use of a simultaneity judgment task, employing visual and tactile stimuli. Next, in the same participants, and employing the same stimuli, we measured susceptibility to the RHI in the synchronous and asynchronous conditions. Importantly, in the asynchronous condition we individualized the amount of asynchrony (i.e. Stimulus Onset Asynchrony, SOA) between the visual and the tactile stimuli, based on the individuals' TBW. This means that the individuals' own TBW was used to establish the asynchrony between the visual stimulus delivered on the rubber hand and the tactile stimulus delivered on the participants' real hand. In more details, rather than using standard large asynchronies, as used in previous research (Tsakiris & Haggard, 2005) (usually up to 1000 ms), we selected, at the individual level, the SOA where the stimuli had 25% probability of being integrated. This allowed for direct coupling between the individual's temporal resolution in visuo-tactile multisensory integration and the temporal determinants by which touch can be attributed to a rubber hand. To this end, we used a new computer-controlled visuo-tactile stimulation for RHI. **This is a methodological aspect that deserves mention. Previous studies on the RHI have either used manual stroking of the real and the rubber hands (for a review see: Costantini, 2014) or have used virtual reality. Here, instead, visual stimuli consisted on a LED attached on the dorsal surface of the index finger of a realistic prosthetic hand, whilst the tactile stimulus consisted on a mechanical tapper attached on the dorsal surface of the participants' index finger. This experimental setup allows accurate timing in the stimulation while keeping the environment more ecological that the one that could be achieved in virtual reality.**

Based on the theoretical assumption of a dependency of the individual susceptibility to RHI upon the individual multisensory temporal binding window, our prediction was that even a small amount of asynchrony, but outside the individuals' TBW, is enough to prevent the experience of the RHI.

However, since we are using the individuals TBW to define the level of asynchrony to be used in the RHI, we cannot rule out a systematic bias that is inherent to this design. That is, it could be argued that individuals with a wide TBW are also more susceptible to the RHI based on a third, unaccounted for variable. In a second study we hope to buttress this by using a median spit method. That is, we recruited a new group of participants, and measured their TBW. Subsequently, we asked them to perform the RHI in the synchronous and asynchronous conditions. In this new study the level of asynchrony between the visual stimulus delivered on the rubber hand and the tactile stimulus delivered on the participants' hand corresponded to the median value of the TBW in the new sample. This procedure allowed us to use the same amount of asynchrony that was within the TBW of half the participants but outside the TBW of the others.

Again, based on the assumption of a dependency of the individual susceptibility to RHI upon the individual multisensory temporal binding window, we expect a difference between the synchronous and the asynchronous condition only in the latter group (where RHI is induced with a stimulus onset asynchrony greater than the individual temporal binding window).

3. Experiment 1

3.1. Participants

Thirty-seven participants (14 male, mean age = 21.2 years, SD = 6.2 years, range = 18–32 years) were included in the study. All procedures were approved by the Institute of Mental Health Research, University of Ottawa Review Board (REB N° 2014008). On the same day participants took part in two separate sessions. In the first session we measured the individuals' temporal binding window (via the simultaneity judgment task); in the second session we induced the RHI in synchronous and asynchronous conditions.

3.2. Simultaneity judgment task - Stimuli and Procedure

The experimental stimuli consisted of series of cross modal stimuli (1 visual and 1 tactile). Stimuli were delivered across hemispaces (1 tactile Left/1 visual Right or 1 visual Left/1 tactile Right). This was done to ensure that the spatial distribution of the stimuli in the SJ task resembled, as much as possible, the spatial distribution of visuo-tactile stimuli during the RHI. Stimuli were delivered sequentially with one of the following Stimulus Onset Asynchronies (SOA): ±350, ±200, ±120, ±70, ±40, ±25 ms. By convention, throughout the current article negative SOAs indicate a trial in which the visual stimulus was presented first, whereas a positive SOA indicates a trial in which the tactile stimulus was presented first. A total of 12 intervals were used, with 32 trials per **interval**. For balance, in half of the trials, left-sided stimuli preceded right-sided stimuli, and vice versa for the other half. The intertrial interval (ITI) ranged between 2000 and 3000 ms. The presentation of the stimuli was pseudo-randomized. Visual stimuli consisted of two red light-emitting diodes (LEDs; with a 0.5 cm diameter) fixed on a table and positioned at 4 cm Left and Right of a central fixation point (subtending 4° of visual angle, see figure 1) with a luminance of 0.48 lm. Visual stimuli lasted 30 ms.

Tactile stimuli were delivered by means of two miniature solenoid tappers (MSTC3; M & E Solve, www.me-solve.co.uk) attached to the dorsal surface of the middle fingers. The solenoids produced a supra-threshold vibrotactile stimulus oscillating at 100 Hz for a total duration of 30 ms.

Participants were seated in a dimly lit room with their corporeal midline aligned with a fixation point located 57 cm from the plane of their eyes, with their right and left index fingers resting on two response buttons located on a table. Each hand was in its homonymous hemispace, close to each LED (see figure 1). Participants were asked to focus on a fixation cross that was placed half way between the response buttons at all times.

Please insert figure 1 near here

The task was a simultaneity judgment, used to derive the TBW. In this task, participants were presented with a series of visuo-tactile stimuli at the above-defined SOAs. The participants were asked to report whether each presentation occurred at the same time (temporally synchronous) or not (asynchronous) by pressing a response button with the right or the left index finger, with the button representation (synchronous or asynchronous) being balanced across participants. The timing of the stimulation and participants' responses were controlled by a PC running psychtoolbox **(Brainard, 1997; Pelli, 1997)**.

3.3. Data Analysis

Responses from the simultaneity judgment task were used to calculate a TBW for each subject. First we calculated a rate of perceived synchrony with each SOA as the percentage of trials in a given condition in which the individual reported that the presentation was synchronous. According to previous studies (Stevenson & Wallace, 2010; Stevenson et al., 2012; Stevenson, Zemtsov, & Wallace, 2013), two psychometric best-fit sigmoid functions were then fit to the rates of perceived synchrony across SOAs one to the visual-first presentations and a second to the tactile first presentations. These best-fit sigmoid functions were calculated using the *glmfit* function in MATLAB. Following this first fit, the intersection of the left and right best-fit curve was used to estimate the point of subjective simultaneity (PSS) defined as the SOA at which the participant maximally responded "synchronous". Then in each participant we defined a temporal interval outside her TBW. This interval was defined as the SOA at which the left best-fit sigmoid (y-value) equaled a 25% rate of perceived synchrony. This latter interval was subsequently used during the induction procedure of the rubber hand illusion in the asynchronous condition.

3.4. Rubber Hand Illusion - Stimuli and Procedure

For the rubber hand manipulation we used a specially constructed multi-chambered wooden box. The box measured 100 cm in width, 20 cm in height and 40 cm in depth and was placed in a darkened room. The walls of the room were covered with a light-absorbing textile so to prevent any reflections on the top of the box that could serve as a landmark. On the top of the box was placed a two-way mirror, which prevented the subjects from seeing their hands during the experiment. A series of lights in the rubber hand chamber and the measuring chamber were used in combination with this two-way mirror in order to illuminate/de-illuminate the chambers when required, effectively concealing the contents of each chamber (see below).

Participants sat in front of a table with the right hand placed at a fixed point inside the box, while the left hand was left in their lap. **A right** rubber hand was placed in front of the subject's body midline. The participant's right hand and the rubber hand were aligned on the vertical axis and were positioned 20 cm from each other, with a wall between them to avoid any light over spilling into the actual hand chamber. Two lights were installed in the apparatus, one light was used to illuminate the rubber hand during the stimulation phase of each trial, and the other was used to illuminate a sliding ruler used to measure the proprioceptive drift, further described below. The experimenter turned on the light in the rubber hand chamber during the 2 minutes stimulation phase so that the participant could see the rubber hand.

Stimuli used to induce the rubber hand illusion were a white LED and one miniature solenoid tapper (MSTC3; M & E Solve). The LED was positioned on the dorsal surface of the right index finger of the rubber hand. The light lasted 30 ms. The solenoid was attached to the dorsal surface of the right index finger of the participant's hand. The solenoids produced a supra-threshold vibrotactile stimulus oscillating at 100 Hz for a total duration of 30 ms. To increase the congruence between the felt and seen stimuli (Ward, Mensah, & Junemann, 2015), a dummy solenoid was attached to the dorsal surface of the right index finger of the rubber hand. Participants wore headphones to muffle the noise of the tapper. Each participant completed 2 RHI blocks, one in the synchronous condition and one in the asynchronous condition, each lasting 2 minutes. Block order was counterbalanced across participants.

The illusion was measured using a standard questionnaire (Botvinick & Cohen, 1998), adapted to fit **the specific procedures of this study** (see table 1), and the proprioceptive drift (Costantini & Haggard, 2007; Tsakiris & Haggard, 2005). The questionnaire consisted of 9 statements regarding the participant's experience on a 7-point Likert scale ranging from 1 to 7, with 1 corresponding to 'fully disagree' and 7 corresponding to ‘fully agree’. Items 1–3 captured the proper RHI experience, while items 4–9 served as controls for task compliance and suggestibility. **In agreement with previous studies (e.g. Abdulkarim & Ehrsson, 2016), for** the data analysis we computed a RHI index, defined as the difference between the mean score of the three illusion statements (Items 1–3) and the mean score of the six control statements (Items 4–9).

Please insert table 1 near here

The proprioceptive drift was used as **an implicit measure** of the illusion as previous studies have shown a shift in the perceived position of the subject’s hand toward the rubber hand during the RHI (Botvinick & Cohen, 1998; Costantini & Haggard, 2007; Tsakiris & Haggard, 2005).

A ruler with the numbers printed in reverse was supported between two poles 20 cm above the box. When illuminated from above, the mirrored surface of the box allowed for the numbers to be reflected in their proper orientation and they appeared at the same gaze depth as the rubber hand.

Participants were asked: “Using this ruler, where is your index finger”? They responded by verbally reporting a number on the ruler. They were instructed to judge the position of their finger by projecting a parasagittal line from the center of their index finger to the ruler. During the judgments, there was no tactile stimulation, and participants were prevented from seeing the rubber **and the real hands** or any other landmarks on the work surface, by switching off the lights under the two-way mirror. The participants were also cautioned not to move their hand during the stimulation phase, nor during the judgment phase. The experimenter monitored this closely. The ruler was always placed with a different random offset for each judgment to prevent participants from memorizing and repeating responses given in previous **conditions**. The experimenter would record the offset position and deduct that from the reported position, yielding the perceived finger position both before (baseline) and after (drift) **the induction period of each experimental condition**. The difference between the baseline and drift estimations represents the change in perceived hand position due to the stimulation, and was taken as a quantitative measure of RHI. A brief rest period followed each condition, during which participants filled in the 9-statements questionnaire. To prevent transfer of the illusion across conditions, the participants were encouraged to move their hand and body between conditions.

4. Results

4.1. Determining the temporal binding window (Simultaneity judgment task)

Data were normally distributed (Shapiro-Wilks, $p > 0.05$). Table 2 shows the the individuals' TBW and the relative measures of goodness of fit. Two participants were discarded, as their response distribution did not fit to the sigmoid function ($R^2 < 0.6$). The delays equating a 25% rate of perceived synchrony (outside the TBW: the OUT condition) ranged from 103 ms to 311 ms. On average it was 211 ms (SD 59.9 ms, See Figure 2).

Please insert figure 2 near here

4.2. Rubber Hand Illusion - questionnaire

Data violated the assumptions for normality (Shapiro-Wilks, $p < 0.05$). Wilcoxon rank tests are reported. **As we implemented a new procedure to induce the RHI, using a LED on the rubber hand and a mechanical tapper on the participants' hand, we firstly tested whether such induction procedure was effective in producing a reliable illusion. To this aim we tested whether mean rating to**

illusion statements were significantly different from the ‘‘neither agree/disagree’’ response (i.e. central point in the Likert scale). Illusion ratings after synchronous stimulation (Median(SD): 1.5(1.18)) was significantly higher than the central point (Wilcoxon test: $p<0.001$). Hence, we can safely infer that we induced the RHI. Importantly, when comparing the synchronous and the asynchronous conditions (i.e. 25% rate of perceive synchrony) we found that participants experienced a significantly stronger RHI following the synchronous (median(SD) = 1.5(1.18)) compared to the asynchronous condition (median(SD) = 0.8(1.35); $z_{(35)} = 2.38$; $p = 0.017$; Monte Carlo simulation as implemented in SPSS v.20 [0.013 0.018], Figure 3).

4.3. Rubber Hand Illusion – Proprioceptive Drift

Data violated the assumptions for normality (Shapiro-Wilks, $p < 0.05$). Wilcoxon rank tests are reported. Participants showed **a similar** proprioceptive drift in the synchronous and the asynchronous condition ($z_{(35)} = 2.5$; $p = 0.7$). **Importantly, both values were statistically higher than zero (Synchronous: median(SD) = 1(3.0); Asynchronous: median(SD) = 1(3.0); ps < 0.05), meaning that, as for subjective reports, we can safely infer that we induced the RHI.**

Please insert figure 3 near here

5. Experiment 2

5.1. Participants

Forty naïve participants (14 male, mean age = 21.2 years, SD = 6.2 years, range = 18–32 years) were included in the study. All procedures were approved by the Institute of Mental Health Research, University of Ottawa Review Board (REB N° 2014008). Participants took part in two separate sessions on different days. In the first session we measured the individuals' TBW (via the simultaneity judgment task); in the second session we induced the RHI in synchronous and asynchronous conditions.

5.2. Stimuli and Procedure

For both the SJ task and the RHI illusion the stimuli were the same as those used in the first experiment. The only difference between the two studies was the way we established the level of asynchrony to be used during the RHI. In this study the level of asynchrony was established as follows: We first measured and computed the individuals' TBW in the entire sample. Then, using a median split method, the group of 40 participants was split into two groups: wide TBW (wTBW) and narrow TBW (nTBW).

The median value used to split our sample in two subgroups, namely wide and narrow TBW, was subsequently used as Stimulus Onset Asynchrony, during the asynchronous condition of the RHI.

6. Results

6.1. Determining the temporal binding window (Simultaneity judgment task)

The procedure used to calculate the TBW was the same used in the previous study. One participant was discarded, as their response distribution did not fit to the sigmoid function ($R^2 < 0.6$). Data were normally distributed (Shapiro-Wilks, $p > 0.05$). Table 2 shows the individuals' TBW and the relative measures of goodness of fit. On average the width of the TBW was 196 ms (SD = 47 ms), See Figure 4). The median value of the TBW was 176 ms.

Please insert table 2 and figure 4 near here

6.2. Rubber Hand Illusion – questionnaire

Data on the proprioceptive drift are not reported in this study, as they did not produce significant results in study 1. Data violated the assumptions for normality (Shapiro-Wilks, $p < 0.05$). Wilcoxon rank tests are reported. Participants assigned to the narrow TBW group experienced a more pronounced RHI following synchronous stimulation **(median = 1.2(1.45)) compared to asynchronous stimulation (median = 0(1.49); $z_{(19)} = 2.53$; $p = 0.01$; Monte Carlo simulation as implemented in SPSS v.20 [0.006 0.011]). Conversely (and as predicted), participants assigned to the wide TBW group experienced a similar illusion in the synchronous (median = 0.5(1.20)) and asynchronous condition (median = 1(1.11); $z_{(19)} = 0.88$; $p = 0.38$) conditions. The illusion in the synchronous condition did not differ between the two groups ($z = -1.14$; $p = 0.25$), while in the asynchronous condition it was significant only using a one-tail test ($z = -1.68$; $p = 0.047$).**

Please insert figure 5 near here

7. Discussion

We tested the hypothesis that temporal limits of the RHI reflect individuals' temporal resolution in multisensory perception. Our main finding pertains to the fact that very short delays, yet outside the individuals' temporal binding window, were enough to significantly reduce the rubber hand illusion, as reported by the participants, but had no impact on proprioceptive drift. **Indeed, the proprioceptive drift was significantly different from zero in both the synchronous and the asynchronous conditions.**

The RHI depends upon the temporal structure of visual information arising from the observed touch and the temporal structure of the felt touch (e.g. Tsakiris & Haggard, 2005). When the two sources of information are congruent, that is simultaneous, the rubber hand illusion is experienced. Conversely, when the two sources of information are incongruent, usually in the range of 500-1000 ms, the RHI is dramatically reduced if not entirely abolished. Here we show that even very short delays (on average: 211 ms in the first study) are enough to prevent the subjective illusion provided that the amount of asynchrony is defined at the subject level according to her temporal sensitivity. This finding was supported by the second study where the level of asynchrony was outside the TBW in half of the participants and inside the TBW of the other half (on average 176 ms).

The only systematic attempt to manipulate the amount of asynchrony between the visual and the tactile stimuli during the RHI was done by Shimada and colleagues (Shimada et al., 2009). In this study, they investigated delays up to 600 ms in steps of 100 ms. The authors found that the subjective ratings of the illusion and the proprioceptive drift were significantly higher for short delays, up to 300 msec. Despite the fact that Shimada and colleagues (Shimada et al., 2009) used fixed, rather than individualized levels of asynchrony, their results are well in accordance with the ones obtained here in our two studies. This claim is supported by the observation that, in Shimada's results, the longer delays were characterized by higher variability in RHI effects (See: Shimada et al., 2009), figure 3). This suggests that although on average participants did not experience the illusion with longer delays, some still did. Based on our results, especially the second study, we postulate that the high variability at longer delays in Shimada's results may be related to the interindividual differences in width of the TBW. In other words, the participants who still reported the illusion with longer delays may have had a wider TBW then those who did not report the RHI.

In general, the multisensory processing of stimuli forms the building blocks upon which perceptual and cognitive representations are created (Stevenson et al., 2012). Such a framework predicts that interindividual differences in multisensory processes have a profound effect on many aspects of our mental life (Stevenson et al., 2012). Our data enrich this theoretical framework by showing that susceptibility to the RHI, and ultimately body representation, is explained, at least in part, by the individuals' sensitivity to the temporal offset of multisensory stimuli.

How can we account for the lack of sensitivity of the proprioceptive drift to small temporal asynchronies? The RHI is thought to be the product of the three-way interaction between vision, touch and proprioception. However, these systems are markedly different in terms of temporal resolution. For instance, visual, auditory and tactile stimuli are usually processed in less than 100 ms (Bacon-Mace, Mace, Fabre-Thorpe, & Thorpe, 2005; Hari & Forss, 1999; Vroomen & Keetels, 2010). A different, much slower time scale should be used, however, when investigating the temporal resolution of the proprioceptive system. Although investigations on the temporal resolution of the proprioceptive system are sparse (Fuentes, Gomi, & Haggard, 2012; Shimada, Hiraki, & Oda, 2005; Shimada, Qi, & Hiraki, 2010), it seems that its temporal acuity is longer than those of the other sensory modalities. Fuentes and colleagues (Fuentes et al., 2012) used tendon vibration illusions to study the temporal properties of signals contributing to position sense. They found that, in the case of **illusory movements produced by tendon vibration**, delays below 300 ms are unlikely to be detected by muscle spindles. In another study Shimada and colleagues (Shimada et al., 2010) asked participants to judge whether observed hand movements were delayed with respect to the felt movement. The results showed that the discrimination threshold of visual feedback delay was, on average, 230 ms. These results suggest that the delays we used were outside the visuo-tactile temporal window of integration, but yet within the visuo-proprioceptive (Balslev, Nielsen, Lund, Law, & Paulson, 2006; Balslev, Nielsen, Paulson, & Law, 2005) temporal window of integration.

Possibly one may argue that the above-described studies are all related to movement or direct stimulation of the muscles. Hence, they cannot apply to our study, as no movement was allowed. However, the sense of position is contributed also by other information, including vision. For instance, Graziano and colleagues (Graziano, 1999; Graziano, Cooke, & Taylor, 2000) recorded the response of visuo-tactile neurons to visual stimuli approaching the hand, with respect to systematic changes in the static position of the monkey's arm (proprioceptive manipulation). Results revealed that neurons with visual receptive fields anchored to the tactile receptive fields showed a shift in their response with the hand when it was moved. Interestingly, they also showed that when an artificial monkey's hand was placed above the monkey's static hand (which was now hidden from view), and the position of the visible artificial hand was manipulated, some of the visual responses shifted with the artificial hand to its new position. According to the authors, results suggest that visual information is exploited by the brain to encode the position of sense. Similar findings have been reported in humans using functional magnetic resonance (Makin et al., 2008).

Our findings may also account for the dissociation sometimes observed between proprioceptive drift and subjective report of the RHI. Since the first description, the proprioceptive drift has been used as a proxy of the incorporation of the rubber hand. Recently, however, its relation to the subjective ratings of the illusion has been questioned (Holle, McLatchie, Maurer, & Ward, 2011; Keizer, Smeets, Postma, van

Elburg, & Dijkerman, 2014; Rohde, Di Luca, & Ernst, 2011). **Our data suggest that visuo-tactile and visuo-proprioceptive integration, in the context of the RHI, are bounded by different temporal rules, and they are differently sensitive to asynchronies. According to an influential model of body ownership (Makin et al., 2008), visuotactile synchrony provides positive feedback on existing processes of visuo-proprioceptive integration. That is, visuo-tactile synchrony produces the recalibration of the sense of position observed during the rubber hand illusion. Rohde et al. (2011) extended this view by suggesting that, conversely, asynchronous stroking deteriorates visuo-proprioceptive integration. Following this reasoning it can be argued that proprioceptive drift is directly related to the multisensory integration between touch-vision. However, multisensory integration occurs only when visuo-tactile stimuli are presented simultaneously.**

If our hypothesis is correct, our results have the potential to enrich current neurocognitive models of body ownership (Botvinick & Cohen, 1998; Makin et al., 2008; Tsakiris, 2010). One such model has been proposed by Tsakiris (Tsakiris, 2010). According to his model, the RHI arises from an interaction between current multisensory input and internal models of the body. In particular, three critical comparisons are predicted. In the first comparison, the visual form of the viewed object is compared against a pre-existing body model that contains a reference description of the visual, anatomical and structural properties of the body (Costantini & Haggard, 2007; Tsakiris, Carpenter, James, & Fotopoulou, 2010; Tsakiris, Costantini, & Haggard, 2008; Tsakiris & Haggard, 2005). The second critical comparison takes place between the current state of the body and the postural and anatomical features of the body-part that is to be experienced as mine (visuo-proprioceptive comparison). The third comparison is between the current sensory inputs, that is, between the vision of touch and the felt touch (visuo-tactile comparison). The temporal organization of these three comparisons is yet unclear. Our findings, which specifically refer to the last two comparisons, suggest that they operate on different temporal scales, as a consequence of the different temporal properties of the stimuli they process.

Enriching current neurocognitive models of body ownership with a temporal dimension would allow investigating the temporal structure of their neural underpinnings according to more recent understanding of brain functioning (Kiebel, Daunizeau, & Friston, 2008). Thus, it would allow going beyond the mere description of brain regions involved in the RHI.

For instance, our proposal fits with the hypothesis that neural activity, as well as behaviour, operates over multiple time scales (Chandrasekaran, Trubanova, Stillittano, Caplier, & Ghazanfar, 2009). According to Kiebel and colleagues (Kiebel et al., 2008): "brain function can be understood in terms of a hierarchy of temporal scales at which representations of the environment evolve. The lowest level of this hierarchy corresponds to fast fluctuations associated with sensory processing, whereas the highest levels encode slow contextual changes in the environment, under which faster representations unfold". In our case, the lowest level would correspond to the comparison between current sensory input, the highest level would correspond to the comparison between the visual form of the viewed object, in this case the rubber hand, and the pre-existing internal body model. Finally, the comparison between the current state of the body and the postural and anatomical features of the observed body-part would lie in between.

As organisms, we are continuously exposed to a flow of sensory information featured with particular time constants, durations, and repetition rates. It is thought that our brain exploits temporal organization in the sensory information stream to optimize behaviour (Chandrasekaran et al., 2009; Kiebel et al., 2008; Northoff, 2014). Visual, tactile and proprioceptive information are featured with different temporal structures (so-called "natural statistics"), so it is quite plausible that the above-described comparisons operate over different temporal scales.

Our results prompt interesting future investigations on the rubber hand illusion and ultimately body ownership, for instance (i) is the susceptibility of the rubber hand illusion related to the temporal structure of brain activity? (ii) does the susceptibility to the rubber hand illusion change if we experimentally manipulate the visuo-tactile TBW? Future investigations should attempt to answer these questions. And, if the response is affirmative one may think to overwrite participants' sense of body ownership by altering either the temporal structure of brain activity using neurophysiological techniques, or the TBW by using perceptual training (Powers, Hillock, & Wallace, 2009). This is not without consequences, especially in all the clinical conditions in which the representation of the body is altered, including, but not limited to, schizophrenia (Peled, Pressman, Geva, & Modai, 2003; Peled, Ritsner, Hirschmann, Geva, & Modai, 2000; Thakkar, Nichols, McIntosh, & Park, 2011), eating disorders (Eshkevari, Rieger, Longo, Haggard, & Treasure, 2012, 2013; Mussap & Salton, 2006), and body identity disorder (van Dijk et al., 2013). For instance, research has shown that, compared to healthy controls, individuals with schizophrenia require a longer time period between two stimuli to successfully identify them as two distinct stimuli (a wider temporal binding window; Foucher, Lacambre, Pham, Giersch, & Elliott, 2007). Due to this dysfunction, the body may be experienced as fragmented, incoherent and anxiety provoking. If perceptual training indeed can impact, that is, improve the TBW then perhaps this can be developed into a tool that could ultimately yield a decrease in clinical symptoms.

8. References

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Table 1: Questionnaire Statements used in the RHI Experiment. **Bold indicates illusion statements. The original statements were modified to fit the specific procedures of this study.**

Table 2: Temporal Binding Window of the individual subjects and goodness-of-fit (R^2) of the sigmoid distribution of responses. Asterisks indicate excluded participants.

Figure 1: Panel A: Experimental setup in the SJ task. A) Response buttons; B) Light Emitting Diodes; C) Tappers. Panel B) Experimental setup in the RHI.

Figure 2: Individuals' TBWs (grey lines) and group averaged TBW (Black line) **in study 1**

Figure 3: Box-plot representing the median RHI index **(Panel A) and the proprioceptive drift (Panel B)** in the synchronous and asynchronous conditions **(Study 1)**. Circles represent the individual subjects. Vertical bars represent standard deviations.

Figure 4: Individuals' TBWs (grey lines) and group averaged TBW (Black line) **in study 2.**

Figure 5: Box-plot representing the median RHI index in the synchronous and asynchronous conditions for the narrow and the wide TBW groups **(Experiment 2)**. Circles represent the individual subjects. Vertical bars represent standard deviations.