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

Marcello Costantini[1,2], Jeffrey Robinson[3], Daniele Migliorati[2], Brunella Donno[2], Francesca Ferri[1] & Georg Northoff[3]

1 Centre for Brain Science, Department of Psychology, University of Essex, Colchester, UK

[2] Department of Neuroscience and Clinical Sciences, University "G. d'Annunzio", Chieti, Italy

[3] Mind, Brain Imaging and Neuroethics, University of Ottawa Institute of Mental Health Research, Ottawa, ON, Canada

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 open the doors to investigations of body ownership, which take into account recent models of brain functioning suggesting that the brain operates over multiple 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) in front of them with their 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. However, 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 susceptibility to 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 Temporal Binding Window, 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 the subjective ratings of the illusion and the proprioceptive drift 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 detail, 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 during the simultaneity judgment task. This allowed for direct coupling between the individual's temporal precision 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 rubber hand illusion 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 dorsal surface of the index finger of a realistic prosthetic hand, while 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 split 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 TBWs in the new sample. This procedure allowed us to use the same level of asynchrony that was within the TBW of half the participants (wide TBW group, wTBW) but outside the TBW of the others (narrow TBW group, nTBW).

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 nTBW group (where RHI was 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 SOA. 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 (thus subtending 4° of visual angle, see figure 1) with a luminance of 0.48 lm. Visual stimuli lasted 30 ms.

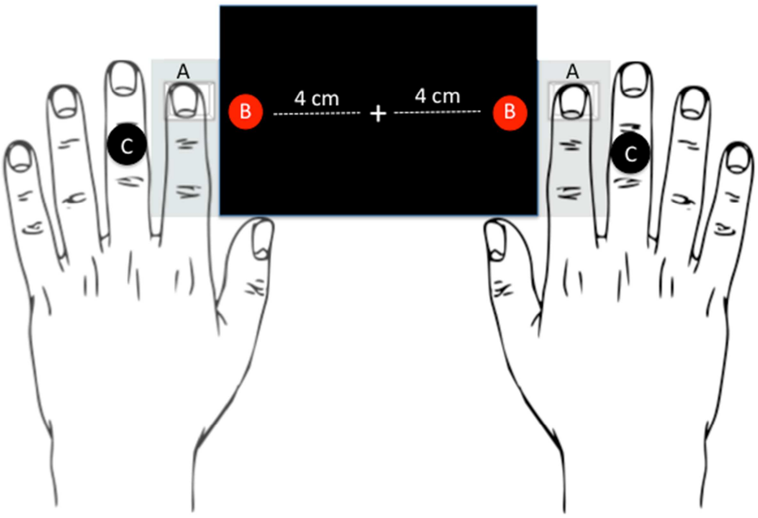

Figure 1: Experimental setup in the SJ task. A) Response buttons; B) Light Emitting Diodes; C) Tappers

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.

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; Kleiner et al, 2007).

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 their 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 reflection 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, www.me-solve.co.uk). The LED was positioned on 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) 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'. The original statements were modified to fit the purposes of this study (table 1). 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).

During the experiment there were times when:
1. it seemed like I was feeling the touch in the location where I saw the rubber hand being lit.
2. it seemed like the touch I felt was caused by the light on the Rubber

Hand.

3. **it seemed like the rubber hand was my hand.**
4. it seemed like my hand was moving towards the rubber hand.
5. it seemed like I had three hands.
6. it seemed as if the touch I was feeling came from somewhere between my own hand and the rubber hand.
7. it seemed like my own hand became rubbery.
8. it seemed like the rubber hand was moving towards my hand.
9. it seemed like the rubber hand began to resemble my real hand.

Table 1: Questionnaire Statements used in the RHI Experiment. The original statements were modified to fit the purposes of this study.

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 chopstick 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, not 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 on 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 (Botvinick & Cohen, 1998). 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)

The temporal binding window (TBW) was calculated for each participant on the basis of their simultaneity judgment responses. Data were normally distributed (Shapiro-Wilks, $p > 0.05$). Table 2 shows the parameters of 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).

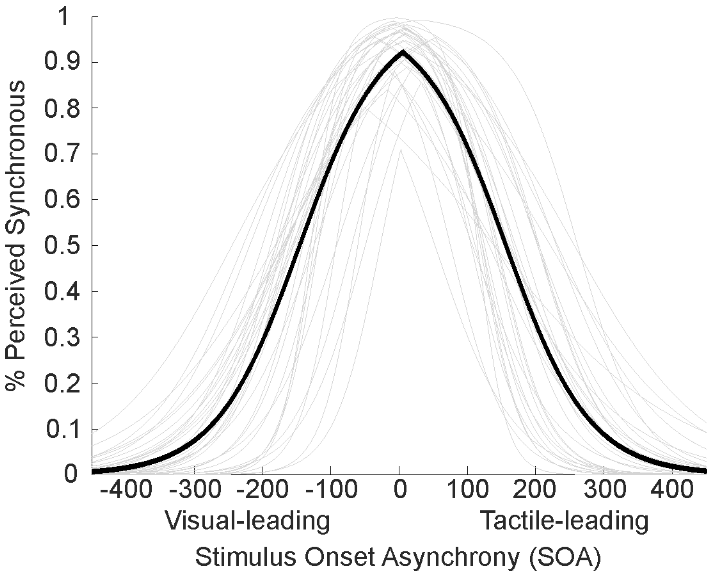

Figure 2: Individuals' TBWs (grey lines) and group averaged TBW (Black line)

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 rubber hand illusion, using LEDs on the rubber hand and a mechanical tapper on the participants' hand, we firstly tested whether such induction procedure was effective in producing a rubber hand 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 rating after synchronous stimulation (Median(SD): 1.5(1.18)) was significantly higher than the central point Wilcoxon test: $p<0.001$). Hence, we can say successfully that we induced the rubber hand illusion. Importantly, when comparing the synchronous and the asynchronous stimulation 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).

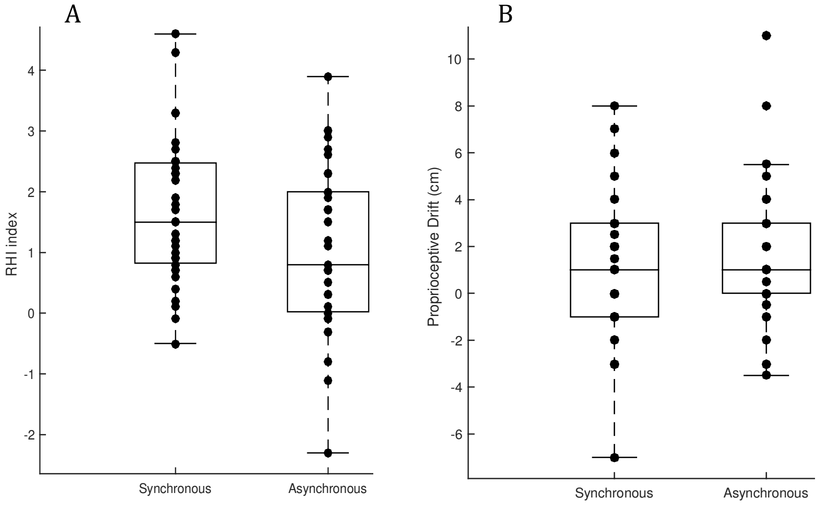

Figure 3: Box-plot representing the median RHI index (Panel A) and the proprioceptive drift (Panel B) in the synchronous and asynchronous conditions (Study 1). Circles represent the individual subjects. Vertical bars represent standard deviations.

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, the new procedure was effective in inducing the RHI.

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' temporal binding window (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 rubber hand illusion. 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 parameters of 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 3). The median value of the TBW was 176 ms.

	Experiment 1	**Experiment 2**

Participant	**TBW**	**R^2**	**TBW**	**R^2**
1	65	0.6	**76**	**0.58**
2	80	0.7	153	0.7
3	105	0.7	150	0.8
4	96	0.7	163	0.8
5	191	0.7	174	0.8
6	61	0.8	336	0.9
7	124	0.8	360	0.9
8	120	0.8	100	0.9
9	129	0.8	136	0.9
10	163	0.8	249	0.9
11	162	0.8	58	0.9
12	207	0.8	337	0.9
13	200	0.9	121	0.9
14	146	0.9	194	0.9
15	172	0.9	120	0.9
16	128	0.9	252	0.9
17	127	0.9	365	0.9
18	181	0.9	128	1.0
19	56	0.9	259	1.0
20	123	0.9	266	1.0
21	174	0.9	112	1.0
22	141	0.9	133	1.0
23	161	0.9	200	1.0
24	228	0.9	141	1.0
25	223	0.9	142	1.0
26	150	0.9	153	1.0
27	188	0.9	182	1.0
28	184	0.9	313	1.0
29	119	0.9	130	1.0
30	171	1.0	161	1.0
31	187	1.0	170	1.0
32	177	1.0	172	1.0
33	168	1.0	184	1.0
34	245	1.0	206	1.0
35	186	1.0	214	1.0
36	**200**	**0.4**	261	1.0
37	**184**	**0.5**	304	1.0
38			234	1.0
39			234	1.0

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

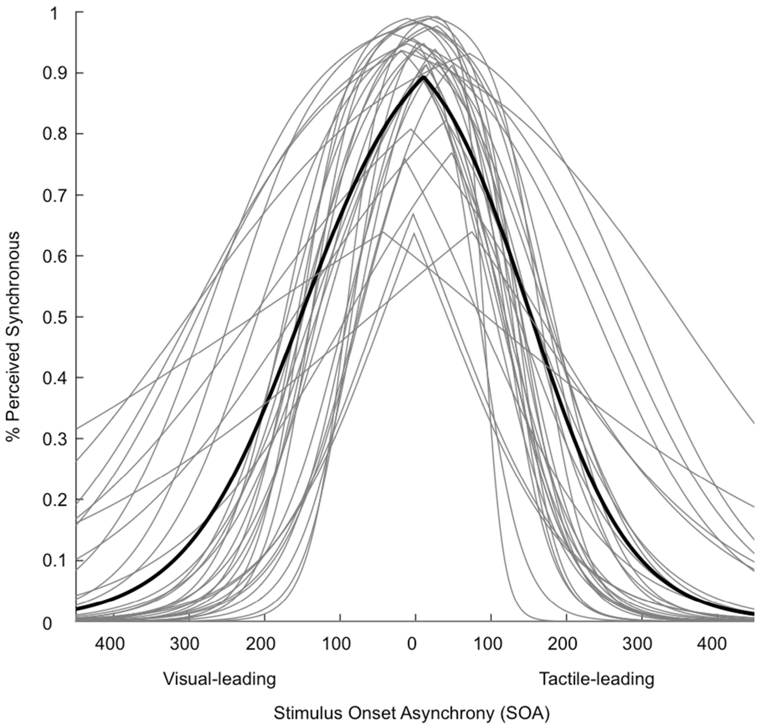

Figure 4: Individuals' TBWs (grey lines) and group averaged TBW (Black line) in study 2.

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 did not differ between the two groups (U mann-whitney: 152; p = 0.40).

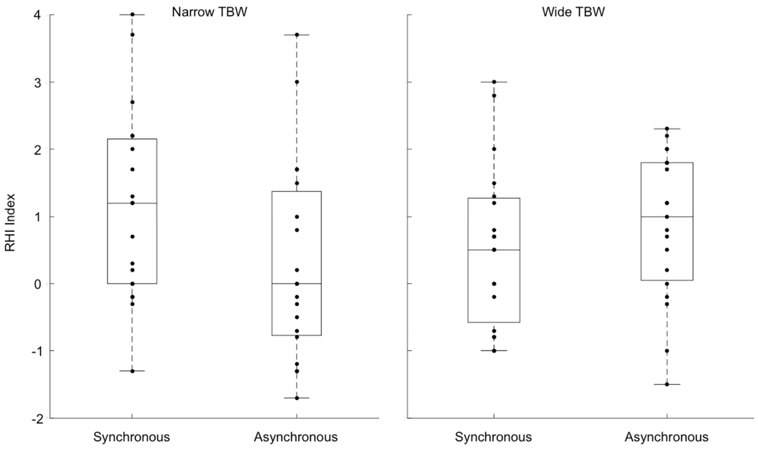

Figure 5: Box-plot representing the median RHI index in the synchronous and asynchronous conditions for the narrow and the wide TBW groups (Experiment 2). Circles represent the individual subjects. Vertical bars represent standard deviations.

7. Discussion

We tested the hypothesis that temporal limits of the rubber hand illusion 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 condition.

The rubber hand illusion 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 their temporal sensitivity. This finding was supported by the second study where the level of asynchrony was the same, but fell 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 rubber hand illusion 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 in both experiments? The rubber hand illusion 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 papers 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 can be 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, visuotactile 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 rubber hand illusion 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).

8. References

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