Title: Having a live huntsman spider on a rubber hand does not modulate the rubber-hand illusion in a top-down manner.

Running title: Rubber hand illusion under threat.

Authors: Philippe A. Chouinard1*, Rachel Stewart1

1 Department of Psychology and Counselling, School of Psychology and Public Health, La Trobe University, Melbourne, Victoria, Australia.

* Corresponding author:

Philippe A. Chouinard, Ph.D.
Senior Lecturer of Psychology
Applied Science 2 Building, Room 3.15
La Trobe University, Bendigo Campus
Bendigo, Victoria, 3550, Australia
Telephone: +61 3 5444 7028
E-mail: p.chouinard@latrobe.edu.au
The rubber-hand illusion is an illusion where a person embodies a rubber hand as if it were their own. After embodiment, many studies have threatened the false hand and measured physiological responses to the threat for the purposes of verification. For the first time, we tested if embodiment of the false hand could be modulated with a fearful stimulus already present prior to the elicitation of the illusion. This was done by having a live huntsman spider placed on top of the false hand for the entire duration of testing. We also examined if the procedure could change implicit attitudes towards spiders. The results revealed that the embodiment of the false hand with the fearful stimulus on top of it occurred as strongly as when the latter was not there, suggesting that the top-down processing of fearful stimuli is not strong enough to influence bottom-up processes. However, implicit attitudes towards spiders did not change.

**Keywords**

Rubber hand illusion
Multisensory integration
Body representation
Body ownership
Fearful stimulus
Implicit association test
Spider
Introduction

The rubber-hand illusion (RHI) pertains to an experimentally induced experience of owning a rubber hand. Botvinick and Cohen (1998) provided the first demonstration of the illusion. The authors obscured the vision of their participants’ real hand behind a screen while they positioned a rubber version of a false hand in front of them in plain sight. The experimenters stroked both the real and false hands concurrently with paintbrushes. After a brief period, the participants began to experience ownership of the false hand. Since then, the illusion has been used as a tool in investigations of bodily consciousness and theories to explain the illusion have evolved. The interplay between bottom-up and top-down processes is considered an important element to explain the illusion – regardless whether the theory is based on a Bayesian framework (Apps & Tsakiris, 2014; Kilteni, Maselli, Kording, & Slater, 2015), underscores the importance of agency (Braun et al., 2018) or affordances (Aymerich-Franch & Ganesh, 2016), or is based on a neurocognitive model (Serino et al., 2013; Tsakiris, 2010). The nature of this interplay has been debated since its inception and remains an important avenue for investigation.

According to a recent review, the two most common methods for measuring the strength of the illusion are subjective self-reports as assessed by questionnaires and measures of the perceived position of the hand (Riemer, Trojan, Beauchamp, & Fuchs, 2019). The original RHI study by Botvinick and Cohen (1998) used both approaches. In keeping with tradition and current convention, both approaches were used in the present investigation. For the first, experiences about ownership of the false hand was scored along a Likert scale. For the second, participants indicated with the other hand where they perceive their hidden hand to be located in space.
Some studies threaten the false hand and measure physiological responses to the threat to confirm the presence of the illusion (Riemer et al., 2019). For example, Armel and Ramachandran (2003) recorded skin conductance while bending the fingers of the false hand into painful positions. The skin conductance response correlated with levels of ownership as determined by a questionnaire. Other studies have since utilised a variety of threats while measuring skin conductance to verify the embodiment of the false hand, including an attack with a hammer (Llorens et al., 2017), an approaching needle stab (Ehrsson, Wiech, Weiskopf, Dolan, & Passingham, 2007), a stab with a knife (Hägni et al., 2008), and the breaking of the fingers (Bashford & Mehring, 2016). Constraints on the nature of the threat have also been investigated. For effectiveness, the threat needs to be plausible and salient (Zhang & Hommel, 2016) and capable of inducing distress (Ma & Hommel, 2013).

However, what is not known is whether the strength of the illusion differs when the threat is already present prior to the induction of the illusion. Answering this question could shed further light on the interplay between bottom-up and top-down processing. In particular, this study aims to examine top-down modulation that is specifically related to the ongoing processing of a fearful stimulus on the false hand.

To test this possibility, the present study examined if the RHI can be modulated with a living huntsman spider (*heteropoda venatoria*) on top of the false hand. A spider seemed like a good choice. Due to evolutionary pressures, spiders capture and hold attention, modulate emotional states, and influence goal-directed actions (Bertini, Grasso, & Ladavas, 2016; Öhman, Flykt, & Esteves, 2001; Okon-Singer, Pessoa, & Shackman, 2015). Importantly, their detection is quick and known to be mediated preconsciously by the phylogenetically older colliculus-pulvinar-amygdala pathway (Bertini et al., 2016). This quick pass could, in theory, provide ample opportunities to allow for subsequent top-down influences on the processing of information by other sensory pathways, such as tactile information from the hand and visual
information processed by the slower geniculate-striate pathway, as well as on the integration of multiple sensory channels.

A secondary question was if people’s implicit attitudes might change after experiencing a RHI with a spider, which is of clinical interest for the treatment of arachnophobia. The current treatment of choice for arachnophobia is exposure therapy, which involves multiple sessions of a gradual exposure to real spiders (Eaton, Bienvenu, & Miloyan, 2018). The RHI could provide an effective treatment option by means of embodied exposure. Embodied exposure offers the advantage of making it possible to expose the fearful stimulus to a degree that would not be possible otherwise. Namely, it would allow better control for interrupting the experience at any given moment, which is an important consideration for exposing fearful stimuli to phobic patients. In addition, it offers better protection against the intrinsic dangers associated with real exposure, such as a spider bite.

A relevant example highlighting the effectiveness of embodied exposure in the treatment of phobia is a study by Freeman et al. (2018). The study consisted of a randomised control trial comparing the use of immersive virtual reality versus usual care in the treatment of acrophobia, which is the fear of heights. In the virtual-reality treatment, the participants embodied an avatar and were exposed to various fearful situations graded in difficulty with the assistance of a virtual coach. The results demonstrated that the treatment effects were better than typical interventions delivered face-to-face with a therapist.

Past studies demonstrate an association between the embodiment of a false body part and altered subconscious attitudes towards other kinds of stimuli. For instance, the incorporation of a dark-skinned hand by Caucasians was shown to accompany improved implicit attitudes towards non-Caucasians (Farmer, Maister, & Tsakiris, 2014; Maister, Sebanz, Knoblich, & Tsakiris, 2013; Maister, Slater, Sanchez-Vives, & Tsakiris, 2015) using the implicit association test (IAT) (Greenwald, McGhee, & Schwartz, 1998; Greenwald, Nosek, & Banaji, 2003). The
IAT is designed to measure implicit attitudes and is widely used for investigating biases in racial groups, gender, sexuality, age, and religion (Brownstein, Madva, & Gawronski, 2019). The present investigation also uses the IAT.

Historically, theoretical explanations for the RHI have always considered the extent to which bottom-up and top-down processing account for the illusion. In terms of bottom-up processing, the original RHI study by Botvinick and Cohen (1998) attributed the illusion to the intermodal integration of vision, touch, and proprioception. The authors arrived at this conclusion because embodiment of the false hand, as measured by a questionnaire, was negligible unless brush strokes between the two hands were synchronous. The visual input of seeing the false hand brushed had to temporally match the tactile input received from feeling the real hand being brushed. Further studies also demonstrated that the synchronicity between what is seen and felt is an essential requirement (Ehrsson, Spence, & Passingham, 2004; Shimada, Suzuki, Yoda, & Hayashi, 2014; Tsakiris & Haggard, 2005). Conspicuous discrepancies in sensory input between modalities prevents the illusion from occurring (Riemer et al., 2019). While the original Botvinick and Cohen study (1998) deemed visuo-somatosensory integration as necessary to generate the RHI, subsequent research has demonstrated that a purely bottom-up explanation cannot account for the illusion (Ide, 2013; Kammers, Longo, Tsakiris, Dijkerman, & Haggard, 2009; Lloyd, 2007; Riemer et al., 2014; Tsakiris, Carpenter, James, & Fotopoulou, 2010; Zhang & Hommel, 2016).

An integral part of the debate was the question of whether objects that do not resemble body parts can also be embodied. In support of a purely bottom-up explanation, Armel and Ramachandran (2003) found that participants could embody a table in place of their hand when stroked in synchrony with the real hand. Armel and Ramachandran (2003) suggested that any object can be embodied as the result of bottom-up processing and that the illusion was cognitively impenetrable. A lifetime of experience knowing that a table could not possibly
replace a hand did not prevent the RHI from occurring. However, these assertions are now weakened by the following subsequent accepted notions and observations. First, embodiment and sense of ownership are now considered to be two different illusory experiences that are mediated by separate mechanisms (Kilteni et al., 2015) – the former being a more general illusory experience that does not necessarily include the latter. Second, Hohwy & Paton (2010) demonstrated that participants can embody an object that does not resemble a body part, specifically a cardboard box, only if they had just experienced the RHI immediately before – suggesting a transference effect of some kind. The original study by Armel and Ramachandran (2003) did not counterbalance the order of conditions. All participants underwent the more traditional RHI before they moved onto the table condition. Third, the embodiment of objects that do not resemble body parts have not been reproduced in most studies (Ide, 2013; Kammers et al., 2009; Lloyd, 2007; Riemer et al., 2014; Tsakiris et al., 2010; Zhang & Hommel, 2016), which further undermines Armel and Ramachandran’s assertions.

For instance, Zhang and Hommel (2016) were unable to demonstrate the embodiment of a cat’s claw for a hand. In a different study, Tsakiris et al. (2010) tested if participants could embody either a block of wood, a rubber hand, or different objects that varied between the two at different gradations. In doing so, they tested for: 1) a bottom-up hypothesis in which all stimuli, regardless the degree to which they looked like a hand, would elicit an illusion, 2) a proportional hypothesis in which the strength of the illusion would increase as the objects became more human-like, and 3) a body-model hypothesis whereby only the object that matched the stimulated body part would be successfully incorporated as part of the self. Only the third hypothesis was supported, suggesting a strong influence of top-down input. Similarly, Ide (2013) found a reduction in illusion strength when the false hand was rotated outside of what is biomechanically possible. Lloyd (2007) derived similar findings when the false hand was placed outside of peripersonal space. In addition, other studies have found that participants
will only embody a finger if both the real and false fingers being stroked (Kammers et al., 2009; Riemer et al., 2014) or moved (Riemer et al., 2014) corresponded to the same digit. A mismatch in digits eliminates the strength of the illusion (Kammers et al., 2009; Riemer et al., 2014).

These studies suggest that ownership of an object can only occur if it matches an internal representation of a body part (Costantini & Haggard, 2007; Tsakiris & Haggard, 2005). In this sense, top-down processing appears to set constraints on what is possible in the embodiment of these objects. However, there appears to be some flexibility. For instance, the manipulation of skin colour (Farmer, Tajadura-Jimenez, & Tsakiris, 2012), enlargement of hand size (Pavani & Zampini, 2007), and variations in hand length, width, and luminance (Longo, Schuur, Kammers, Tsakiris, & Haggard, 2009) do not interfere with the RHI. In fact, changes in skin colour can improve implicit attitudes towards a different race (Farmer et al., 2014; Maister et al., 2013; Maister et al., 2015). Nevertheless, these variations must remain anatomically consistent with what is possible for a human hand. Previous studies have also considered other top-down effects. Hägni et al. (2008) found a stronger embodiment of a virtual arm in participants who were asked to actively imagine taking ownership of one compared to those who only passively looked at it. Similarly, motivation towards wanting to experience the illusion has been shown to increase its strength (Litwin, Denkiewicz, & Raczaszek-Leonardi, 2016).

We hypothesised that our experiments would reveal top-down modulation related to the processing of a fearful stimulus placed on top of the false hand. Today, the consensus seems to be that bottom-up and top-down processes interact in some fashion to generate the RHI (Apps & Tsakiris, 2014; Kilteni et al., 2015; Lewis & Lloyd, 2010; Liepelt, Dolk, & Hommel, 2017; Longo, Schuur, Kammers, Tsakiris, & Haggard, 2008; Tsakiris & Haggard, 2005). Yet how one might experience the RHI when a fearful stimulus, like a spider, is already present on
the false hand represents an aspect of this interaction that has never been examined before. Seeing a spider on the false hand could provide top-down signals to modulate the RHI. These signals would most likely reflect implicit processing given that the presence of spiders can be detected before conscious awareness via the colliculus-pulvinar-amygdala pathway (Bertini et al., 2016). Regarding altering implicit attitudes, we hypothesised that participants would be more amenable to spiders after the RHI. The prediction was based on the therapeutic value of embodied exposure to fearful situations (Freeman et al., 2018).

Methods

Study design

A between-subjects design was employed such that participants experienced only one of three conditions. We chose a between-subjects design, as opposed to a within-subjects design, to mitigate response biases (Firestone & Scholl, 2016), which can be pronounced in RHI experiments to the point that proper counterbalancing is unable to manage these effects (Farmer et al., 2014; Litwin et al., 2016; Llobera, Sanchez-Vives, & Slater, 2013; Maister et al., 2013; Tsakiris et al., 2010; Zhang & Hommel, 2016). We expand further on our choice of design in the Discussion. A real spider on the false hand with synchronous movement between the real and false hands (real spider, synchronous condition: RSs) served as the experimental condition of interest. Two other conditions served as control conditions. They consisted of a toy spider with synchronous movement between the hands (toy spider, synchronous condition: TSs) and a toy spider with asynchronous movement between the hands (toy spider, asynchronous condition: TSa). The comparison between the real and toy spiders with synchronous movement allowed us to isolate the effects of the fearful stimulus while the comparison between the toy
spider with and without synchronous movements allowed us to quantify the magnitude of the RHI when the fearful stimulus was absent. Thus, a full-factorial design with a fourth condition with a real spider with asynchronous movement, although more elegant, was not necessary. Our three conditions still allowed us to isolate the contributions of the fearful stimulus and synchronous movements, which was an important consideration given we did not want to handle the real spider more than what was necessary. The real spider consisted of a living mature golden huntsman spider purchased from Minibeast Wildlife in Kuranda, Queensland, Australia (https://www.minibeastwildlife.com.au) (Fig. 1A). The toy spider was made of plastic and had googly eyes (Fig. 1B). The googly eyes were added to minimise fear as much as possible. The order of tasks performed in the testing session is listed in Table 1.

Participants

Our sample consisted of 26 male and 25 female participants with an age span of 19 to 38 years ($M = 23.02, SD = 5.16$). They were right handed, as confirmed by the 10-item Edinburgh Handedness Inventory questionnaire (Oldfield, 1971), reported to have normal or corrected to normal vision, and reported to be in good physical and mental health. Potential candidates who considered themselves likely to react strongly to aversive stimuli were advised not to participate. The RSs condition consisted of 11 males and 6 females ($M = 23.29, SD = 5.64$) between 19 to 38 years of age. The TSs condition consisted of 9 males and 8 females ($M = 22.47, SD = 3.84$) between 19 to 35 years of age. The TSa condition consisted of 6 males and 11 females ($M = 23.29, SD = 6.02$) between 19 to 38 years of age. Participants were randomly allocated to one of the three conditions. As one should expect from a random allocation, there were no differences in gender distribution between conditions ($X^2 = 2.98, p = .225$). Participants provided written informed consent prior to participation. All procedures were
approved by the Human Ethics Committee of La Trobe University in accordance with the Declaration of Helsinki. As advised by La Trobe University’s Animal Ethics Committee, a formal review was not required for spiders according to the Australian Code for the Care and Use of Animals for Scientific Purposes (National Health and Medical Research Council, 2013) and the Victoria Prevention of Cruelty to Animals Act (1986).

**Implicit Association Test (IAT)**

Questionnaires and other tests based on perceptual decision making require conscious introspection. As such, demand and responses biases can never be eliminated entirely using these instruments. In contrast, measuring implicit attitudes reflect involuntary appraisals outside of conscious awareness and are therefore not influenced by these types of biases (Greenwald & Banaji, 1995). The implicit association test (IAT), devised by Greenwald, McGhee, and Schwartz (1998), compares reaction times to visual stimuli traditionally associated with a particular valence, with reaction times to an oppositional valence. Unconscious preference to one pairing is detected through faster reaction times via button pressing. The test was included in the present investigation to assess whether the ownership of a false hand with a spider on top might influence implicit attitudes towards spiders.

The IAT was programmed in E-Prime 3.0 (Psychology Software Tools, Sharpsburg, PA, USA) and carried out on a Dell Precision Tower 3420 desktop computer with a 23-inch Dell display monitor (Dell Technologies, Round Rock, Texas, USA). The monitor had a resolution of 1920 x 1080 and a refresh rate of 60 Hz. Key presses were recorded on a Cedrus Response Pad model RB-840 (Cedrus Corporations, San Pedro, USA). The participant’s head was supported with a chin rest that was adjustable in height. Viewing distance was 57 cm. The test was modelled on the one developed by Effting, Salemink, Verschuere, and Beckers (2016).
The stimuli comprised of eight images of spiders and eight images of flowers. Eight positive (freedom, peace, pleasure, lucky, sunrise, family, happy, laughter) and eight negative (accident, grief, poison, hatred, pollute, ugly, rotten, evil) words were selected from a list by Greenwald, McGhee and Schwartz (1998) based on a study carried out by Bellezza, Greenwald, and Banaji (1986) that established norms of pleasantness for words in American undergraduate students. The order of blocks for the IAT is listed in Table 2.

Practice Block 1 acquainted the participant with the correct key responses to the pictures. The left and right keys were used to indicate when a picture of a flower and spider appeared, respectively. Practice Block 2 acquainted the participant with the correct key responses to the words. The left and right keys were used to indicate when positive and negative words appeared, respectively. Practice Block 3 and Test Block 4 displayed either a picture or a word. In these blocks, either a picture of a flower or a positive word required a left key response while either a picture of a spider or a negative word required a right key response. Practice Block 5 accustomed the participant with a different response key mapping for the pictures presented in the remaining blocks. The left key now corresponded to a picture of a spider while the right key now corresponded to a picture of a flower. In Practice Block 6 and Test Block 7, either a picture or a word was presented and the participants pressed the left key for either a picture of spider or a positive word and the right key for either a picture of a flower or a negative word.

In Practice Blocks 1, 2 and 5, each image or word was presented twice, and accuracy feedback was provided following each response. In Practice Blocks 3 and 6, each image and word were presented twice. Test Blocks 4 and 7 presented each image and word four times. The stimuli were presented in the centre of the computer monitor and remained there until a response was made. The order of images and words was randomised in each block. Each block
was introduced by a set of written instructions presented on the computer screen. Participants were instructed to respond to the stimuli as quickly and accurately as possible.

Two identical IAT’s were carried out for each participant – one prior to the RHI induction and one immediately after induction.

**RHI apparatus**

An apparatus, like the one designed by Kalckert and Ehrsson (2012), was constructed (Fig. 1C). The apparatus contained the participant’s right hand and a false right hand above it, which the participant saw through a one-way mirror. The index finger for both the false and real hands were attached by a lever system, which the experimenter could move either synchronously or asynchronously. Participants did not actively move their real hand. A passive as opposed to an active paradigm was chosen for logistical reasons. First, we were concerned that participants with the real spider would not want to move their hand as much as those with the toy spider. Second, there was always the possibility that a participant could harm the real spider if they were permitted to control hand movements, either voluntarily or involuntarily. Having the experimenter move the real and false hands allowed us to better control movement and ensure the real spider’s welfare. The apparatus measured 36 cm x 36 cm x 30 cm. Both the false and real hands wore rubber gloves. The false hand was enclosed in a Perspex box, which was designed to contain the huntsman spider on top of the false hand and ensure it did not interfere with movements of the false hand’s index finger. A black cloth was draped over the participant’s shoulders and the adjacent edge of the testing apparatus to help foster a connection between the participant and the false hand. The one-way mirror over the false hand became see through when an interior light inside was turned on. This enabled the experimenter to control the visibility of the false hand. There was no way for us to control the real spider’s mobility.
inside the apparatus. Hence, movement between the real spider, who could move, and the toy spider, which remained stationary, was not controlled. Nonetheless, as we elaborate in the Discussion, the real spider remained largely immobile during the experiment. Thus, the degree of movement was somewhat matched between spiders.

*Drift measurements*

Alongside the feeling of ownership of the false hand, previous studies have also demonstrated a perceived shift in the position of the real hand towards the false one (Kalckert & Ehrsson, 2012; Ma & Hommel, 2015; Tsakiris et al., 2010). For this reason, a clipboard with graph paper was fixed to the outer surface of the apparatus on the participant’s left side, enabling the participant to indicate the perceived vertical positioning of the real hand. Prior to the RHI induction, the participant was asked to close their eyes and indicate the perceived height of their right hand at that moment with their left index finger. The experimenter marked this position on the graph paper attached to the clipboard. This same procedure was repeated after the RHI induction. In this instance, the participant was asked to indicate where they had felt their real hand was positioned during the induction phase of the experiment. Drift was calculated as the difference between the two measurements.

*RHI induction*

The induction phase of the experiment began with the experimenter instructing the participant that they would soon see a false hand and that they had to focus their attention on it for five minutes. Consulting the literature revealed that the bulk of previous RHI studies varied their induction phases from 1 to 10 minutes and that a five minute duration is appropriate to allow
for sufficient time to both induce and experience the illusion (Riemer et al., 2019). The experimenter then turned on the light inside the apparatus, which allowed the participant to see the false hand through the one-way mirror. The experimenter then commenced movement of the connected fingers either synchronously (to induce the illusion) or asynchronously (as to not induce the illusion). After five minutes, the interior light was turned off, which ended the induction phase of the experiment.

Post-illusion questionnaires

Participants completed two questionnaires at the end of the testing session. The first measured ownership and consisted of 8 items from Kalckert and Ehrsson (2012) (Table 3). The questions were initially sourced from the original RHI study by Botvinick and Cohen (1998) and a principle components analysis carried out by Longo et al. (2008). Participants responded to statements on a Likert scale ranging from “-3” for “totally disagree” to “+3” for “totally agree” with “0” in between as “uncertain”. Four plausible ownership statements (e.g. “I felt as if I was looking at my own hand”) and four control statements (e.g. “I felt as if my real hand were turning rubbery”) were presented to the participant. As others have done before us, we considered an average rating of +1 or more on the ownership statements as an indication of ownership of the false hand (Kalckert & Ehrsson, 2012). In addition, we asked participants one last question (“What level of threat did you experience regarding the stimuli in the study?”) to measure their subjective level of perceived threat (Fernandes et al., 2013). Responses to items on this question were collected on a Likert scale ranging from “-3” for “very low” to “+3” for “very high” with “0” in between as “uncertain”. For each participant, we calculated an average score for both the ownership and control questions on the ownership questionnaire and tabulated their response to the threat question.
Preparing the IAT data for analyses

We processed the IAT data using a scoring algorithm developed and validated by Greenwald, Nosek & Banaji (2003). The reader should consult this paper for further details regarding the validity of the procedures and further justification for each of the different steps described below. We used reaction times (in ms) from Test Blocks 4 and 7 as well as Practice Blocks 3 and 6. The rational for including the Practice Blocks is based on Greenwald et al. (2003) reporting a stronger correlation with explicit self-report measures when Practice Blocks were included with Test Blocks than when only Test Blocks were included. All trials with reaction times over 10,000 ms were excluded, leading to the elimination of two trials from the overall data set. In addition, response times for incorrect trials were replaced with the participant’s mean reaction time plus an additional 600 ms.

The difference in reaction times between blocks with incongruent (i.e. when spiders and positive words mapped onto one key while flowers and negative words mapped onto a different key) and congruent (i.e. when spiders and negative words mapped onto one key and flowers and positive words mapped onto a different key) response mappings provided an index of implicit attitudes, with greater differences denoting a preference for flowers over spiders. With this in mind, two difference scores were then computed per participant: 1) a difference score between mean response times between Practice Blocks 6 (with incongruent response mappings) and 3 (with congruent response mappings), and 2) a difference score between Test Blocks 7 (with incongruent response mappings) and 4 (with congruent response mappings). Each of these difference scores were then divided by their pooled standard deviation and a final measure (D) was obtained by averaging the two resultant scores. Greenwald et al (2003) termed this measure D because of its similarity with Cohen’s d (Cohen, 1988). For each participant, a
D score was obtained before (D1) and after (D2) RHI induction. A change in implicit attitudes towards spiders (ΔD) was also calculated by subtracting D2 from D1, which was then used for statistical analyses. A positive ΔD score denotes improved implicit feelings towards spiders. Treatment of the data using the Greenwald et al. (2003) scoring algorithm led to no participants being excluded from the analysis.

**Statistical analyses**

All data were analysed using IBM SPSS Statistics for Windows, Version 25.0 (IBM Corporation; Armonk, New York, USA), JASP software version 0.86 (University of Amsterdam, Amsterdam, The Netherlands), and GraphPad Prism version 8 (La Jolla, CA, USA). Both null hypothesis statistical testing (NHST) and Bayesian approaches were used to analyse the data. For the former, all reported p values represent corrected values for multiple comparisons unless specified otherwise. Significance was established at an alpha level of 0.05. For the latter, all reported Bayes factors (BF\textsubscript{10}) represent the likelihood that the data support the alternative relative to the null hypothesis as a ratio between the two. We considered a BF\textsubscript{10} value of 3 or above as substantial evidence in favour of the alternative hypothesis and values of 0.33 or less as substantial evidence in favour of the null hypothesis (Jeffreys, 1961). The Bayesian approach allowed us to determine if a different statistical approach might converge with the more traditional NHST approach, which would provide more confidence in the findings and draw more definite inferences from null results.

To examine the results from the ownership questionnaire, ANOVA with Treatment Group (RSs vs. TSs vs. TSa) as a between-subject factor and Question Category (Ownership vs. Control) as a within-subject factor was performed. To examine drift, changes in IAT scores, and threat scores, ANOVA with Treatment Group (RSs vs. TSs vs. TSa) as a between-subject
factor were performed. For NHST, post-hoc Bonferroni multiple comparison tests were used to examine differences between conditions. Corrections for multiple comparisons were performed at the family level. Partial eta-squares ($\eta^2_p$) and Cohen’s $d$ are reported. The default specifications for priors in JASP were used when performing the analyses using a Bayesian approach (ANOVA: the r scales were set at 0.5 and 1.0 for fixed and random effects, respectively; t-tests: the Cauchy scale was set at 0.707). There was no need to correct for multiple comparisons for Bayes Factors given that they do not reflect probabilities (Gelman, Hill, & Yajima, 2012). Descriptions for any additional analyses performed are described in the Results.

**Results**

*Ownership questionnaire*

ANOVA revealed a main effect of Question Category ($F_{(1,48)} = 62.28, p < .001, \eta^2_p = .56, BF_{10} > 1,000$), a main effect of Treatment Group ($F_{(2,48)} = 10.86, p < .001, \eta^2_p = .31, BF_{10} = 45.2$), and an interaction between the two factors ($F_{(2,48)} = 11.38, p < .001, \eta^2_p = .32, BF_{10} = 314.7$). Examination of this interaction revealed higher scores for the ownership than the control questions in the RSs ($t_{(16)} = 6.74, p < .001, d = 1.64, BF_{10} > 1,000$) and TSs ($t_{(16)} = 5.02, p < .001, d = 1.22, BF_{10} = 230.4$) groups but not in the TSa group ($t_{(16)} = 1.04, p = .947, d = 0.25, BF_{10} = 0.396$) (Fig. 2A). The interaction was also driven by group differences in ownership but not control questions. Ownership scores were higher in the RSs ($t_{(32)} = 5.51, p < .001, d = 1.89, BF_{10} > 1,000$) and TSs ($t_{(32)} = 4.07, p < .001, d = 1.40, BF_{10} = 86.5$) compared to the TSa group (Fig. 2A). The difference in ownership scores between the RSs and TSs groups was
insignificant ($t_{(32)} = 1.23, p = .796, d = 0.39, BF_{10} = 0.539$) (Fig. 2A). Control score means were negative across all groups and group differences did not reach significance for the control questions (all $t_{(32)} < 1.51, d < 0.52, p > .428, BF_{10} < 0.779$). In line with earlier studies using similar questions, we considered an average rating of +1 or more on the ownership questions as an indication of ownership of the rubber hand (Kalckert & Ehrsson, 2012). Thirteen of the 17 participants (76%) experienced ownership in the RSs group, nine (53%) in the TSs group, and one (6%) in the TSa group. Descriptive statistics are listed in Table 3.

Drift

ANOVA indicated a main effect of Treatment Group ($F_{(2,48)} = 5.88, p = .005, \eta^2_p = .20, BF_{10} = 8.8$). Pairwise comparisons between the groups revealed higher drift scores in the RSs compared to the TSa ($t_{(32)} = 3.19, p < .001, d = 1.09, BF_{10} = 12.2$) but not the TSs ($t_{(32)} = 0.12, p > .999, d = 0.04, BF_{10} = 0.331$) group (Fig. 2B). Higher drift scores were also observed for the TSs relative to the TSa group ($t_{(32)} = 3.09, p = .012, d = 1.06, BF_{10} = 10.0$) (Fig. 2B). Drift scores in both synchronous groups were greater than zero ($t_{(16)} = 5.64, RSs: p < .001, d = 1.37, BF_{10} = 687.9; t_{(16)} = 5.58, TSs: p < .001, d = 1.35, BF_{10} = 625.3$) as determined by one-sample t-tests. This was also the case for the TSa condition using the Bayesian ($BF_{10} = 3.2$) but not the NHST ($t_{(16)} = 2.60, p = .058, d = 0.63$) approach. Descriptive statistics are listed in Table 3.

Change in IAT scores

Classical ANOVA did not reveal a main effect of Treatment Group ($F_{(2,48)} = 0.56, p = .572, \eta^2_p = .38$) while the Bayesian ANOVA provided substantial support in favour of the null
hypothesis ($BF_{10} = 0.226$). Taken together, we can infer that there were no differences between groups (Fig. 2C). Descriptive statistics are listed in Table 3.

**Threat scores**

ANOVA indicated a main effect of Treatment Group ($F_{(2,48)} = 14.98$, $p < .001$, $\eta^2_p = .38$, $BF_{10} > 1,000$). Pairwise comparisons between the groups revealed higher threat scores in the RSs compared to the TSs ($t_{(32)} = 4.24$, $p < .001$, $d = 1.45$, $BF_{10} = 131.0$) and TSa ($t_{(32)} = 3.81$, $p < .001$, $d = 1.31$, $BF_{10} = 47.1$) groups (Fig. 2D). The difference in threat scores between the TSs and TSa groups was insignificant ($t_{(32)} = 0.64$, $p > .999$, $d = 0.16$, $BF_{10} = 0.359$) (Fig. 2D). As a reminder, only participants in the RSs condition were exposed to the fearful stimulus in the form of a live huntsman spider while participants in the remaining conditions were exposed to a toy spider. Therefore, the real spider proved to be more threatening than the plastic one in relative terms. The threat was not as high as we had hoped. Eight of the 17 exposed to the huntsman spider reported certain threat with responses greater than zero (uncertain threat) as did one participant in the TSa condition. Descriptive statistics are listed in Table 3.

**Discussion**

This study aimed to determine if a living huntsman spider on top of a rubber hand might influence the RHI in a top-down manner. The results indicate that this was not the case. Ownership of the rubber hand was as strong in the real spider (RSs) compared to the toy spider (TSs) conditions, indicating that the bottom-up effects of the illusion were not affected by the top-down effects of the fearful stimulus. A secondary question assessed if experiencing ownership of a rubber hand with the real spider might change implicit attitudes towards them.
Exposure to the real spider did not change implicit attitudes. The ensuing discussion will expand on these key findings and how they relate to theory. The discussion will then cover methodological considerations and clinical implications.

**Key findings and how they relate to theory**

We were successful at inducing a RHI. This was evidenced by a stronger sense of ownership of the false hand as determined by the ownership questionnaire and a stronger proprioceptive drift of the real hand towards the false one in conditions when movements between the two hands were synchronous compared to when they were not. Both these measures are frequently used in RHI studies to confirm the presence of the illusion (Kalckert & Ehrsson, 2012; Ma & Hommel, 2015; Riemer et al., 2019; Tsakiris et al., 2010). The induction of a RHI while the false hand had a real spider on top of it has never been tested before. However, some studies have examined the illusion under other kinds of aversive situations, such as the embodiment of an injured false hand (Giummarra, Georgiou-Karistianis, Verdejo-Garcia, & Gibson, 2015; Osumi, Imai, Ueta, Nobusako, & Morioka, 2014) and during the anticipation of an electric shock (Riemer, Bublatzky, Trojan, & Alpers, 2015). These studies demonstrate that participants can still experience the RHI. Furthermore, the enfacement illusion (a similar illusion whereby the synchronous stroking of a participant’s face and the face of another person seen in a mirror causes a perceptual change in self-identification) is not interrupted when the latter expresses fearful and angry expressions (Beck, Cardini, Ladavas, & Bertini, 2015). Thus, this study adds to this previous work that one can still take ownership of an external object or stimulus in unpleasant situations.

For the purposes of this study, it was necessary to determine the effectiveness of the huntsman spider as a threat (Ma & Hommel, 2013; Zhang & Hommel, 2016). The threat
questionnaire confirmed that participants felt relatively more threatened in the presence of this spider than the fake one. It is unlikely that this difference was driven by suggestion given that the control questions on the ownership questionnaire did not yield any evidence that the participants’ answers to the questions were influenced by suggestion. Even with this elevated threat, the participants still embodied the false hand to the same degree as they did when the threat was not present. This has implications for understanding the mechanisms of the RHI. The RHI was induced in the conditions in which there were synchronous but not asynchronous movements between the real and false hands, which confirms the importance of bottom-up processing. Yet top-down processing of the huntsman spider on top of the false hand did not influence the RHI, which suggests that the illusion is not influenced by the ongoing processing of a fearful stimulus.

Another key finding was the lack of change in implicit attitudes towards spiders in participants who were exposed to the real spider. This finding contrasts with previous studies demonstrating improved racial attitudes in Caucasians towards people with dark skin after experiencing ownership of a rubber hand of a dark colour (Farmer et al., 2014; Maister et al., 2013; Maister et al., 2015). This may relate to the following fundamental difference between the two scenarios. Implicit attitudes are measured for an object that is physically separated from the embodied one in the first case (i.e. participants are not embodying the spider but rather the false hand where it sits) while implicit attitudes are measured for a characteristic of the actual embodied object in the second case.

Current theories place an important role in the interplay between bottom-up and top-down processes, including those that are based on a Bayesian framework (Apps & Tsakiris, 2014; Kilteni et al., 2015), those that underscore the importance of agency (Braun et al., 2018) and affordances (Aymerich-Franch & Ganesh, 2016), and those that are based on a neurocognitive model (Serino et al., 2013; Tsakiris, 2010). These theories differ in the nature
of this interaction, which remains unclear. It is difficult to infer how our study informs theories that underscore the importance of agency (Braun et al., 2018) and affordances (Aymerich-Franch & Ganesh, 2016) given we did not measure these constructs, nor did we have participants actively move their hand. Future work could expand on our preliminary experiments by having participants actively move their hand and acquiring measures of agency. Our study also does not address the neural substrates that underlie the RHI given we did not use brain mapping techniques. However, we can say a few things about how our findings might relate to Bayesian explanations of the RHI.

Namely, we think that the present results are difficult to reconcile within a Bayesian framework (Apps & Tsakiris, 2014; Kilteni et al., 2015). Bayesian explanations posit that our perception of hand ownership arises from weighing the likelihood that a particular hand is ours based on previous experience and incoming sensory information. Experiencing ownership of the false hand occurs when the brain processes visual information of the false hand moving as if it were the real hand based on the proprioceptive and tactile signals it receives from the latter. Consequently, the false and real hands are processed as a single object given that there is a high probability that congruent signals from three different sensory modalities originate from the same source. So far, this fits well within a Bayesian framework. However, it is highly unlikely that a huntsman spider would remain stationary on a person’s hand for five minutes or that a person would allow this to happen in the real world. Yet participants in this study still experienced a RHI under this improbable context, which is counterintuitive under a Bayesian framework.

Methodological considerations
There are six methodological considerations we wish to raise. First, within-subjects design are often preferable in psychological research because they offer more power. Nonetheless, they are not always the best choice for RHI studies (Farmer et al., 2014; Litwin et al., 2016; Llobera et al., 2013; Maister et al., 2013; Tsakiris et al., 2010; Zhang & Hommel, 2016). Our primary motivation for choosing a between-subjects design was to mitigate response biases (Firestone & Scholl, 2016). It is conceivable that if a participant was exposed to both the real and toy spiders then they might deduce that the purpose of the experiment was to determine if the real spider could affect the illusion. This deduction might then cause them to exaggerate or understate their responses of embodiment of the false hand, depending on what kind of spider was on top of it.

Second, power was not an issue given the significant results we report with NHST, the convergence of support for the alternative hypotheses with Bayesian statistics, and the affirmation of the null hypotheses with Bayesian statistics. Furthermore, we provide effect sizes for all results. These effect sizes were large for significant results and small for insignificant results. In many instances, the Bayesian statistics affirmed the null hypothesis for the latter. This convergence among the different tests would not have happened had we lacked power. Other steps were taken to further mitigate experimental biases. Participants were randomly allocated to one of the three conditions. This ensured that differences between conditions could not be explained by differences in the composition of participants. In addition, all participants received the same instructions and underwent the same procedures with the exception of what type of spider they saw on the false hand and how the real hand moved relative to the false one.

Third, our huntsman spider remained largely immobile inside the apparatus. This immobility was good in some ways but not in other ways. On the one hand, one could say that the degree of movement by the real and toy spiders was somewhat matched, and therefore any
differences arising from their presence cannot be explained by differences in seeing more movement in one relative to the other.¹ On the other hand, the lack of movement by the real spider may have diminished its apparent threat if one considers that the saliency of a threat is amplified by movement (Carretié et al., 2009). Furthermore, many Australians are familiar with the behaviour of the huntsman spider. They are known for being harmless and remaining stationary for long periods of time, waiting for small prey to pass them by before they pounce and attack it. Seeing a contained and immobile huntsman may not have induced the same level of fear as we had originally hoped. Perhaps had we chosen a spider that was more animate and known to be dangerous to Australians, such as the redback spider or the Sydney funnel-web spider, our participants would have felt more threatened. Perhaps more fear could have been obtained in a sample from a different culture that is less familiar with the huntsman spider. Future work could investigate these possibilities. Nonetheless, it is important to underscore that participants did feel relatively more threatened by the real spider than the fake one – allowing us to draw some inferences about the effects of threat. For participants exposed to the toy spider, the mean score on the threat question was close to minus 3 (very low threat) and the vast majority of participants (33/34) reported feeling no threat. This represents a substantial and significant decrease in threat levels.

Fourth, which is related to the third consideration, is the possibility that our sample was not sufficiently scared of spiders in general to see a change in implicit attitudes and that these changes could have been more easily demonstrated in a population with arachnophobia. Indeed, for ethical consideration, we advised all potential candidates that they should not participate in our study if they considered themselves likely to react strongly to aversive

¹ Interestingly, in the few cases where the real spider did move, participants reported after the testing session that they could feel the spider move on their real hand.
stimuli. In doing so, we could have introduced a selection bias that favoured participants who react less strongly to aversive stimuli, including spiders. Fernandes et al. (2013) allege that the relevance of threat from an individual’s perspective is important in shaping behaviour and implicit attitudes. Research demonstrates that people who fear spiders will respond to them more strongly than those who do not – even when they are not consciously aware of their presence (de Jong, van den Hout, Rietbroek, & Huijding, 2003). Our participants were extracted from the general population, advised not to participate in the study if they were likely to react strongly to aversive stimuli, and consequently may not have been sufficiently scared of spiders prior to the RHI to have demonstrated altered implicit attitudes afterwards. Indeed, while participants exposed to the real spider scored considerably higher on the threat question, their mean score was close to zero (uncertain threat) and slightly less than the majority (8 / 17) of them reported feeling a certain threat to it.

Fifth is the possible impact of the sensory conflict associated with the lack of tactile cues from either the real or toy spiders. The importance of maintaining similar sensory input between visual and somatosensory modalities has been known since the first RHI study (Botvinick & Cohen, 1998). It is possible that not having a spider on the real hand in addition to the one on the false hand may have diminished the strength of the illusion. However, this was not feasible to do with the real spider for ethical considerations. It is also unclear how one could ensure simultaneous movements between spiders on the real and false hands when they occur. Nonetheless, the effect sizes reported in this paper for the synchronous conditions were still large, indicating that this fifth consideration had little impact in our ability to find differences between conditions.

Sixth is the lack of physiological confirmation of embodiment, such as measuring heartrate or skin conductance in response to another threat that suddenly appears (Armel & Ramachandran, 2003; Ehrsson et al., 2007; Ma & Hommel, 2013). We were unable to do this
for practical reasons. The real spider was on top of the false hand and both were inside a Perspex box – making it physically impossible for us to suddenly impose another threat on the false hand for the purposes of measuring a physiological response. In retrospect, physiological measures could have been used differently to confirm differences in the levels of threat to the real compared to the toy spider. For example, the recording of heart rate and skin conductance could have assessed activation of the sympathetic nervous system. It would have also been interesting to assess whether these measures might correlate with the onset of the RHI. Future work could explore these possibilities. However, we have no reason to question the validity of how we quantified threat. This has previously been validated elsewhere (Fernandes et al., 2013).

Clinical implications

In our study, implicit attitudes towards spiders did not change after exposure. However, as discussed earlier, a different outcome may arise in people who have arachnophobia. With this in mind, our paradigm could be useful in the treatment of arachnophobia if it can be demonstrated that the paradigm can change implicit attitudes in this population. The current treatment of choice for arachnophobia is exposure therapy, which involves multiple sessions of a gradual exposure to spiders (Eaton et al., 2018). Virtual reality is being developed for this purpose, which has led to promising results (Carlin, Hoffman, & Weghorst, 1997; Garcia-Palacios, Hoffman, Carlin, Furness, & Botella, 2002). However, virtual reality is expensive. In comparison, our apparatus was constructed at a fraction of the cost of a virtual reality system. Given our participants experienced a RHI with a live huntsman spider to the same extent as a fake one, future treatments could be developed where clients with arachnophobia begin exposure with a fake spider followed by exposure to a relatively immobile living spider.
followed by exposure to a more animate spider. Indeed, having a RHI that does not diminish with threat would be beneficial for this purpose. Future work could investigate the possibility of testing our RHI paradigm in people with arachnophobia and seeing if the paradigm might improve their implicit attitudes towards spiders.

Closing remarks

Our study aimed to determine if the RHI can be influenced with a live huntsman spider on top of the false hand, and if so, whether implicit attitudes towards spiders can change. Prior studies have first induced the RHI and then followed this with the introduction of a threat for the purposes of verifying embodiment of the rubber hand. Our study is unique in that the fearful stimulus was introduced prior to the induction of the RHI. The results demonstrate that the illusion did not differ between the presence of a real compared to a toy spider. Ownership and drift scores reveal that any top-down effects were not enough to influence the bottom-up processing of the illusion. Additionally, the results demonstrated that implicit attitudes towards spiders did not change.

Acknowledgements

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Conflicts of interest

The authors have no conflicts of interest to declare.
Fig. 1. Apparatus. A: In this photo, the huntsman spider is shown on the false hand. The false hand was placed in Perspex box to contain the spider. B: In this photo, the toy spider is shown on the false hand. The toy spider was purposely made to look silly to minimise threat. C: In this photo, the participant (the male in the background) is watching the index finger of a false hand move through a one-way mirror while the experimenter (the female in the foreground) is controlling movement of both the real and false hands using a lever system. The false hand (not shown) is above the real hand (shown). Both hands are wearing rubber gloves. The lever system could be adjusted to move the index finger of both hands either synchronously or asynchronously. The individuals in this figure have provided written consent to publish their picture.
Fig. 2. Comparisons between treatment groups. A: Means and standard errors for the ownership (grey) and control (pink) questions for each group (RSs: Real Spider Synchronous; TSs: Toy Spider Synchronous; TSa: Toy Spider Asynchronous). B: Means and standard errors for drift for each group. The groups are shown in blue (RSs), orange (TSs), and green (TSa). Drift was measured in centimetres. C: Means and standard errors for the $\Delta D$ scores on the IAT test. D: Means and standard errors for threat scores. Asterisks (*) denote significant differences ($p < .05$) after corrections were made for multiple comparisons using the Bonferroni method at the family level.
Table 1: Sequence of the experimental procedure.

<table>
<thead>
<tr>
<th>Step</th>
<th>Action</th>
<th>Measurement</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Completion of pre-experimental questionnaires</td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>Participant performs IAT</td>
<td>Initial IAT</td>
</tr>
<tr>
<td>3</td>
<td>Place right hand in rubber glove</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Insert hand in lower shelf of testing box</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Finger inserted into ring connected to false finger</td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>Inner chamber lights off</td>
<td>Initial drift measurement</td>
</tr>
<tr>
<td></td>
<td>Estimate vertical position of real hand</td>
<td></td>
</tr>
<tr>
<td>5</td>
<td>Inner chamber light on, allows view of false hand</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Experimenter moves connected fingers</td>
<td></td>
</tr>
<tr>
<td>6</td>
<td>Inner chamber lights off</td>
<td>Final drift measurement</td>
</tr>
<tr>
<td></td>
<td>Repeat vertical estimation of position of real hand</td>
<td></td>
</tr>
<tr>
<td>7</td>
<td>Detach from RHI apparatus</td>
<td>Final IAT</td>
</tr>
<tr>
<td></td>
<td>Participant performs IAT</td>
<td></td>
</tr>
<tr>
<td>8</td>
<td>Completion of final questionnaires</td>
<td>Ownership and threat questionnaires</td>
</tr>
</tbody>
</table>
Table 2: Procedure of blocks in the spider versus flower IAT.

<table>
<thead>
<tr>
<th>Block</th>
<th>Number of trials</th>
<th>Function</th>
<th>Item assigned to left key response</th>
<th>Item assigned to right key response</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>32</td>
<td>Practice</td>
<td>Flower images</td>
<td>Spider images</td>
</tr>
<tr>
<td>2</td>
<td>32</td>
<td>Practice</td>
<td>Positive words</td>
<td>Negative words</td>
</tr>
<tr>
<td>3</td>
<td>32</td>
<td>Practice</td>
<td>Flower image + positive words</td>
<td>Spider images + negative words</td>
</tr>
<tr>
<td>4</td>
<td>64</td>
<td>Test</td>
<td>Flower image + positive words</td>
<td>Spider images + negative words</td>
</tr>
<tr>
<td>5</td>
<td>32</td>
<td>Practice</td>
<td>Spider images</td>
<td>Flower images</td>
</tr>
<tr>
<td>6</td>
<td>32</td>
<td>Practice</td>
<td>Spider images + positive words</td>
<td>Flower images + negative words</td>
</tr>
<tr>
<td>7</td>
<td>64</td>
<td>Test</td>
<td>Spider images + positive words</td>
<td>Flower images + negative words</td>
</tr>
</tbody>
</table>
Table 3: Ownership questionnaire.

<table>
<thead>
<tr>
<th>Statement</th>
<th>Category</th>
</tr>
</thead>
<tbody>
<tr>
<td>Q1  I felt as if I was looking at my own hand</td>
<td>Ownership</td>
</tr>
<tr>
<td>Q2  I felt as if the rubber hand was part of my body</td>
<td>Ownership</td>
</tr>
<tr>
<td>Q3  It seemed as if I were sensing the movement of my finger in the</td>
<td>Ownership</td>
</tr>
<tr>
<td>location where the rubber finger moved</td>
<td></td>
</tr>
<tr>
<td>Q4  I felt as if the rubber hand was my hand</td>
<td>Ownership</td>
</tr>
<tr>
<td>Q5  I felt as if my real hand were turning rubbery</td>
<td>Control</td>
</tr>
<tr>
<td>Q6  It seems as if I had more than one right hand</td>
<td>Control</td>
</tr>
<tr>
<td>Q7  It appeared as if the rubber hand were drifting towards my real</td>
<td>Control</td>
</tr>
<tr>
<td>hand</td>
<td></td>
</tr>
<tr>
<td>Q8  It felt as if I had no longer a right hand, as if my right hand had</td>
<td>Control</td>
</tr>
<tr>
<td>disappeared</td>
<td></td>
</tr>
</tbody>
</table>
Table 4: Descriptive statistics for the different dependent variables (n = 17 per condition)

<table>
<thead>
<tr>
<th>Ownership Scores</th>
<th>Control Scores</th>
<th>Drift</th>
<th>Change in IAT Scores</th>
<th>Threat Scores</th>
</tr>
</thead>
<tbody>
<tr>
<td>RSs</td>
<td>TSs</td>
<td>TSa</td>
<td>RSs</td>
<td>TSs</td>
</tr>
<tr>
<td>M</td>
<td>1.12</td>
<td>0.40</td>
<td>-1.96</td>
<td>-1.71</td>
</tr>
<tr>
<td>SD</td>
<td>1.80</td>
<td>1.91</td>
<td>1.43</td>
<td>1.18</td>
</tr>
</tbody>
</table>

Abbreviations: Real Spider, Synchronous (RSs); Toy Spider, Synchronous (TSs); Toy Spider, Asynchronous (TSa).
References


Hohwy, J., & Paton, B. (2010). Explaining away the body: experiences of supernaturally caused touch and touch on non-hand objects within the rubber hand illusion. *PloS one, 5*(2), e9416. doi:10.1371/journal.pone.0009416


