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Crossmodal congruency measures of lateral distance effects on the rubber hand illusion

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Abstract

Body ownership for an artificial hand and the perceived position of one's own hand can be manipulated in the so-called rubber hand illusion. To induce this illusion, typically an artificial hand is placed next to the participant's body and stroked in synchrony with the real hand, which is hidden from view. Our first aim was to test if the crossmodal congruency task could be used to obtain a measure for the strength of body ownership in the rubber hand illusion. In this speeded location discrimination task participants responded to tactile targets presented to their index or middle finger, while trying to ignore irrelevant visual distracters placed on the artificial hand either on the congruent finger or on the incongruent finger. The difference between performance on congruent and incongruent trials (crossmodal congruency effect, CCE) indicates the amount of multisensory interactions between tactile targets and visual distracters. In order to investigate if changes in body ownership influence the CCE, we manipulated ownership for an artificial hand by synchronous and asynchronous stroking before the crossmodal congruency task (blocked design) in Experiment 1 and during the crossmodal congruency task (interleaved trial-by-trial design) in Experiment 2. Modulations of the CCE by ownership for an artificial hand were apparent in the interleaved trial-by-trial design. These findings suggest that the CCE can be used as an objective measure for body ownership. Secondly, we tested the hypothesis that the lateral spatial distance between the real hand and artificial hand limits the rubber hand illusion. We found no lateral spatial limits for the rubber hand illusion created by synchronous stroking within reaching distances. In conclusion, the sense of ownership seems to be related to modulations of multisensory interactions possibly through peripersonal space mechanisms, and these modulations do not appear to be limited by an increase in distance between artificial hand and real hand.

Keywords: Rubber Hand Illusion; Crossmodal Congruency Task; Body-Part Ownership; Body Ownership; Peripersonal Space

1. Introduction

Walking along a busy street, our bodies are surrounded by many different objects and other human bodies. In order to coordinate our bodily movements and sensory experiences while interacting in such a complex environment, it is important to identify the current position of our body-parts and which body-parts belong to us. The existence of a sense for body-part ownership in addition to a sense for body-part position seems surprising. However, interestingly there are examples of disturbed body ownership (see Moseley et al., 2008 for a list). One such example is somatoparaphrenia - a monothematic delusion where body ownership for a part of the body is denied and which can occur in patients after stroke (see (Vallar & Ronchi, 2009) for a review).

The perceived position of our arms relies on the integration of proprioceptive, visual and auditory information (Lackner & DiZio, 2000). This multisensory integration uses positional information from each modality, weighted differently depending on the given situation (van Beers, Wolpert, & Haggard, 2002). To specify the influence of each modality on position coding, in several studies spatial differences between visual and proprioceptive information were introduced using, for example, prisms, mirrors, and artificial hands (Graziano, Cooke, & Taylor, 2000; Holmes, Snijders, & Spence, 2006; Mon-Williams, Wann, Jenkinson, & Rushton, 1997). In the study by Holmes and colleagues (2006) participants were asked to perform reaching movements with their left hand which was placed behind a mirror and could not be seen. Just before a reaching movement, participants saw the mirrored reflection of their own right hand, of an artificial right hand, or of a wooden block. The visual image was projected to a position in space different from the covered left hand, thus creating a conflict between visual and proprioceptive information. The authors found that the felt hand position prior to reaching movements was biased towards the visual information when a hand was seen (real or artificial) as compared to a wooden block or a misaligned rotated artificial hand. This suggests that the position of a hand is encoded relative to what is felt *and* what is seen which can lead to errors if ‘misleading’ visual information is given.

What can contribute to the resolution of these conflicts and determine where one's own arms and hands are perceived? One possibility is that additional multisensory input is used to determine perceived hand position and perceived hand ownership. This possibility has been investigated using the so-called "rubber hand illusion" (Botvinick & Cohen, 1998). Again, a spatial difference between visual and proprioceptive information is introduced by placing an artificial rubber hand in front of the participant while the participant's real hand is hidden from view. Both hands are now stroked with brushes simultaneously. When asked after the brushing most participants report the perceived position of the real hand (i.e., what is felt) to be closer to the artificial hand (i.e., what is seen) (Botvinick & Cohen, 1998; Tsakiris & Haggard, 2005). Importantly, this drift in perceived position depends on the simultaneity of the prior multisensory input: For synchronous brushing larger position drifts were found as compared to asynchronous stroking. Note that to date it is has not been resolved whether synchronous brushing increases position drift, or asynchronous brushing decreases position drift, or both. Many participants also report the subjective experience that the felt touch of the brush is located where the seen artificial hand is touched and that the felt touch is caused by the brush touching the artificial hand. Furthermore, many participants also feel as if the artificial hand is their own hand. It therefore seems that the synchronicity of tactile and visual input produced by objects touching the hand can further modulate the multisensory integration for hand position together with changes in the perceived localisation of touch and the sense of body ownership. However, the multisensory and/or sensory-motor processes involved still need to be explained.

Neurons that are specialized in the encoding of multisensory information concerning body-parts have been studied in the monkey brain. Electrophysiological studies suggest that multisensory information regarding hand position modulates cortical activity in parietal and frontal brain areas (Graziano, 1999; Graziano et al., 2000). Furthermore, in some parietal and frontal brain areas a multisensory map of space around a body-part in a body-part-centred frame of reference is encoded in addition to a representation of body-part position; for example, in the ventral intraparietal area (VIP) and the premotor cortex (or more precisely the polysensory zone in the precentral gyrus) in the monkey brain (see Graziano & Cooke, 2006 for a review). Some neurons in these areas have visual receptive fields that cover the area around the body-part and move with the body-part when it changes position. These multisensory neurons thus map the near space around body-parts which is known as “peripersonal space” (Rizzolatti, Fadiga, Fogassi, & Gallese, 1997).

In humans, brain areas have been identified that are specialized in the representation of visual stimuli within peripersonal space around the arm. In a functional magnetic resonance imaging (fMRI) study tactile activation *and* significant differences in visual activation for the visual appearance of a ball appearing near versus far from the participant’s hand have been found in the anterior intraparietal sulcus (IPS) and premotor cortex (Makin, Holmes, & Zohary, 2007). Interestingly, very similar areas have been related to the conditions that may lead to illusory ownership for an artificial rubber hand and the reported feelings of body-part ownership itself in human fMRI studies (Ehrsson, Holmes, & Passingham, 2005; Ehrsson, Spence, & Passingham, 2004; Ehrsson, Wiech, Weiskopf, Dolan, & Passingham, 2007). Based on the above studies, common mechanisms have been suggested to play a role in the representation of body-part position, body-part ownership, and peripersonal space (Ehrsson et al., 2004; Lloyd, 2007; Makin, Holmes, & Ehrsson, 2008). In this present study, we investigated two questions regarding the rubber hand illusion that are related to these aspects of body representation.

Crossmodal Congruency Effect as a Measure of the Rubber Hand Illusion

Our first aim for the present study was to obtain an objective measure of changes of body ownership in the rubber hand illusion. Many previous studies have used rating scales, position judgements, or skin conductance responses to measure the differences in illusion strength (Armel & Ramachandran, 2003; Botvinick & Cohen, 1998; Lloyd, 2007; Longo, Schuur, Kammers, Tsakiris, & Haggard, 2008b; Tsakiris & Haggard, 2005). We tested if the crossmodal congruency task might be used to obtain an indirect measure of the rubber hand illusion which is probably less susceptible to observer and experimenter biases. The crossmodal congruency task is a speeded location discrimination task for which for example tactile targets as well as visual distracters are presented to one of two different locations on the hand (see Spence, Pavani, Maravita, & Holmes, 2004; Spence, Pavani, Maravita, & Holmes, 2008, for reviews). The location of target and distracter can be congruent (same finger) or incongruent (different finger). The difference in performance between incongruent and congruent trials, known as the crossmodal congruency effect (CCE), specifies the influence of the visual distracter on discriminating the tactile target and thus indicates multisensory interaction. Importantly, the CCE is modulated by the distance between the tactile and visual stimuli: Visual stimuli near the body-part receiving tactile stimuli lead to a larger CCE compared with more distant visual stimuli. Thus, the task can be used to investigate multisensory interactions with respect to peripersonal space in humans.

This task has been used to obtain an online measure for changes in 'global body self-consciousness' (Aspell, Lenggenhager, & Blanke, 2009). Participants saw their own back from 2 m behind. In a 'synchronous' condition the backs of the participants were brushed and participants could see the brushing on their own backs. In an 'asynchronous' condition a delay was introduced between felt and seen brushing. In the synchronous condition (but not in the asynchronous condition), participants reported experiencing that the felt touch was in the location where the seen body was touched, that the 'virtual body' was their own body, and a significant drift of perceived body position towards the seen body. Furthermore, an adapted version of the crossmodal congruency task was used in which tactile targets and visual distracters were attached to the upper back. CCEs for stimuli presented on the same side of the back were larger in a condition in which changes in 'global body self-consciousness' were induced by synchronous stroking, compared with the asynchronous stroking condition.

Findings from a previous study conducted by Pavani, Spence, and Driver (2000) suggest that the amount of CCE and the strength of ownership for an artificial body-part are also related (see also (Walton & Spence, 2004), for related findings). The authors investigated the effect of conflicting visual and proprioceptive information regarding arm position on multisensory interactions in peripersonal space as measured by the CCE. Participants received tactile targets to their covered real hands, while visual distracters were placed next to artificial hands that were positioned above the real hands. Pavani and colleagues found that the presence of artificial hands next to visual distracters led to an increased CCE compared with the absence of artificial hands or misaligned rotated artificial hands; this occurred only for visual and tactile stimuli presented on the same side of space (on/near the same hand). The authors argued that the tactile targets are perceived closer to the visual distracters when artificial hands are present and aligned with the position of the participants' own hands. Although no brushing was used in this study to induce the rubber hand illusion, participants experienced the rubber hand illusion more (but overall, not very strongly) when aligned artificial hands were present and the individual vividness ratings for the illusion correlated with increase in CCE when the artificial hands were present. In other words, there seems to be a link between the reported sense of ownership and changes in CCE and thus multisensory interactions. However, it is not clear from these data if a sense of ownership for an artificial hand is only caused (to some extent) by multisensory stimuli in the crossmodal congruency task or if ownership can also modulate multisensory interactions as measured by the crossmodal congruency task.

In order to investigate this issue and in contrast to the study by Pavani and colleagues (2000), we manipulated the strength of the illusory sense of ownership for an artificial hand prior to measuring the CCE. To this end, for each participant the synchronicity of brushing was manipulated in different conditions: synchronous versus asynchronous brushing which leads to more versus less reported ownership. If the CCE can be modulated by ownership it should be larger in the synchronous stroking condition.

Spatial Limits of the Rubber Hand Illusion

Our second aim was to explore the possibility for a spatial limit for body ownership. Based on the finding that the visual receptive fields of neurons in monkeys coding for peripersonal space are limited to space near the body-part, a spatial limit has been suggested for the rubber hand illusion (Lloyd, 2007). For the majority of bimodal neurons in VIP and premotor cortex this limit was between a few centimetres up to 20-35 cm (Colby, Duhamel, & Goldberg, 1993; Fogassi et al., 1996; Graziano, Hu, & Gross, 1997). However, as noted by Graziano (2006) more distant space was also represented by a few studied neurons in both cortical areas.

The hypothesis regarding the existence of a spatial limit for the rubber hand illusion has been put to test in two previous behavioural studies. In both studies however, the manipulation of distance was confounded with other factors that might influence the illusion strength. First, Armel and Ramachandran (2003, Experiment 3) manipulated the spatial distance for an artificial hand using one condition with an arm of normal length and a second condition in which the arm's length was extended forwards by 0.91 m. They found that the extended arm condition was less effective in inducing the rubber hand illusion than the normal length condition. Although the authors argued that they manipulated the location of the artificial hand, in fact this was confounded with the plausibility of visual appearance, as the longer extended hand was less realistic looking and body-like than the short hand. Importantly, the illusion of ownership is different when the visually presented object does not look body-like (Experiment 2, (Armel & Ramachandran, 2003; Tsakiris & Haggard, 2005). Armel and Ramachandran (2003) emphasised the fact that the illusion was also present for non-body-like objects to argue that the rubber hand illusion is primarily based on bottom-up detection of synchronicities. In contrast, Tsakiris and Haggard (2005) emphasised the difference between non-body-like objects and the rubber hand and argue for an account in which the rubber hand illusion is modulated by pre-existing body representations in a top-down fashion. Nevertheless, in both cases the illusion of ownership is modulated by visual plausibility and thus arguably in the above study where arms of different length were used, the change in visual plausibility that the object is body-like and not the change in distance led to a reduced illusion. In the second study on the influence of distance on the rubber hand illusion, Lloyd (2007) manipulated the lateral distance between the participant’s real hand and the artificial hand. Using six steps spanning 17.5 to 67.5 cm she found a significant non-linear decay of the illusion. Furthermore, the illusion was reduced significantly compared with the closest distance when the artificial hand was placed 27.5 cm away from the participant’s hand. The illusion strength was quantified by subjective ratings regarding the question “*It seemed as though the touch I felt was caused by the experimenter touching the rubber hand*”. Agreement or disagreement with this statement could be influenced by the distance manipulation per se, as the closer the hands are the more likely participants could have responded positively to the statement. More importantly, the distance manipulation was confounded with rotational differences (this was also noted by (Makin et al., 2008)). That is, with the aim of maintaining anatomical plausibility, the artificial hand was more rotated the further it was positioned away from the real hand. It has been found that the rubber hand illusion can be modulated by rotational differences between the hands (Costantini & Haggard, 2007; Pavani, Spence, & Driver, 2000; Tsakiris & Haggard, 2005). Also in Holmes et al. (2006) proprioceptive reaching errors were affected by rubber-hand rotation, despite no illusion of ownership. Thus, the rotational changes of the seen artificial hand and not the lateral distance could have resulted in significant decay of the illusion in Lloyd's study. In sum, in both studies that have investigated the spatial limit hypothesis for the rubber hand illusion, the manipulations of distance were confounded with changes in visual plausibility or rotation.

The present study was designed to explore changes in the rubber hand illusion due to different lateral distances between rubber hand and real hand without confounding changes in visual plausibility or rotation. If there is a spatial limit on the rubber hand illusion, we would expect distance modulations for the strength of the rubber hand illusion as measured using CCEs as well as using subjective rating scales.

2. Experiment 1

2.1. Methods

2.1.1. Participants

Twenty-four participants (15 female; 20 right-handed; mean age 26.5 years, age range 18-49 years, standard error of the mean [SEM] 2.2 years) took part in the first experiment. All participants had no previous experience with the rubber hand illusion, had normal or corrected-to-normal vision, and no known tactile deficits for their hands. The experiment was split into two sessions that took place 7 days apart (except for 2 participants for whom this gap was 12 and 13 days respectively). Participants received course credit or $15 per hour. All participants gave their informed consent to participate prior to the start of the first experimental session. The experiment was conducted in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki and was approved by the Macquarie University Ethics Review Committee (Human Research).

2.1.2. Apparatus, Experimental Design and Procedure

A box was used which contained a rubber hand, a (covered or uncovered) mirror (see Figure 1a and 1b), tactile vibrators and light emitting diodes (LEDs). The floor of the box was covered with a checkerboard pattern; all other parts were covered with black cloth. We used a checkerboard pattern for the flooring of the box (instead of, e.g., black flooring) to support the estimation of visual spatial distance. A realistic looking right or left prosthetic rubber hand was placed inside the box (Otto Bock Australia Pty Ltd). The size of the hand was chosen to be close to the average size of an adult human hand (Garrett, 1971). Two round paintbrushes (diameter about 1 cm) were used for brushing the index finger of the participant's real hand and the rubber hand or the checkerboard. The chair was adjusted so that the participant's shoulders were above the top of the box in order to ensure that they could comfortably view the apparatus.

---- Figure 1 near here ----

The study by Lloyd (2007) implies that the illusion is reduced for 27.5 cm and beyond relative to a closer position of 17.5 cm. We were interested to investigate this finding without rotational changes of the hands using distances that were close (17.5 cm and smaller) and distant (27.5 cm and larger) for which Lloyd's data predicted a significant difference. Two distance conditions were implemented: Overlying and Distant. For the Overlying condition the mirror-reflection of a right rubber hand was projected onto the (hidden) participant's left hand which was placed to the left of the body midline (see Figure 1a) (similar to methods used in, e.g., (Gallace & Spence, 2005; Longo, Cardozo, & Haggard, 2008a; Soto-Faraco, Ronald, & Spence, 2004). The veridical distance between the index fingers of the rubber hand and the real hand amounted to 30 cm; however, the perceived distance was 0 cm. In the Distant condition the mirror was covered with a black cloth and placed between the rubber hand and the participant's real hand (see Figure 1b). The distance between the index fingers of the rubber hand and the real hand was 30 cm. The (perceived) location of the rubber hand as well as the visual information regarding hand size and location was constant for both conditions. For both distances the strength of the rubber hand illusion was manipulated by participants performing three different illusion condition blocks: 1) the seen rubber hand (RH) and the hidden real hand were brushed synchronously (RH–Synchronous); 2) the hands were brushed asynchronously (RH-Asynchronous); and 3) in a control condition there was no rubber hand present (No RH-Synchronous). In this control condition the hidden real hand and the visible checkerboard floor of the box were brushed synchronously. The checkerboard was brushed in the position normally corresponding with the index finger of the rubber hand.

Participants might form hypotheses regarding their experience of the rubber hand illusion with respect to different distances. In order to minimize such direct comparisons and thus any influence on subjective responses, the illusion conditions for each distance were performed in two sessions separated by at least a week (for half of the participants the Overlying session was performed first). The order of the illusion condition blocks (RH-Synchronous; RH-Asynchronous; No RH-Synchronous) for each distance was counterbalanced across participants.

As a further control condition, we also implemented a condition in which both visual and tactile stimuli were presented on the participant's real hand without the presence of a rubber hand. This condition was always conducted in the very first block of the first session and the last block of the second session. However, we found order effects for the CCE: The magnitude of the effect declined across sessions as well as increased within a session (see also Spence et al., 2008). These changes could be explained by practice and fatigue effects. As the order for this Participant's Hand condition was not counterbalanced with the other conditions none of the results for the Participant's Hand condition will be reported.

The procedure for each block was consistent across different distances and illusion conditions. Each illusion condition block started with 2.5 min stroking. The brush strokes were short and were repeated every 4 s. In the asynchronous condition a delay of about 2 s was used between the stroke onsets. The experimenter listened to a pre-recorded sound file with 100 ms sounds every 4 s in order to control the timing for the brushing as much as possible. After the first brushing phase participants performed 72 trials of the crossmodal congruency task (duration ~ 2.5 min) followed by brushing. Altogether, each block in Experiment 1 was ~15 min long and consisted of three intervals with brushing and three intervals with the crossmodal congruency task (216 trials altogether).

Crossmodal Congruency Task

A unimanual version of the crossmodal congruency task was implemented with stimuli on the index finger and middle finger of the left hand. Two small speakers (40 mm, 100mW, 8Ω) with a round vibrating surface (9 mm diameter) delivered the vibrotactile stimuli. For visual stimuli presentation two LEDs (yellow, diameter 5 mm) were used. Vibrotactile and visual stimuli were controlled with the experimental control software Presentation (Neurobehavioural Systems, www.neurobs.com). The speakers were placed into fixed sockets that were mounted in different positions on the checkerboard surface. The centre of the distal phalanx of the participant's left index and middle finger was positioned on the vibrating surfaces of the two speakers. Another pair of dummy speakers was placed under the fingers of the rubber hand so that the apparatus visually simulated the setup for the real hands. The LEDs were mounted on a stand and placed above the vibrotactile device. A red fixation dot was attached between the LEDs.

The crossmodal congruency task included go-trials that required a response and no-go-trials in which participants were instructed to withhold their response. Go-trials consisted of one vibrotactile target stimulus and one visual distracter stimulus that were presented simultaneously. Vibrotactile target stimuli consisted of three 200 Hz vibrations each lasting 50 ms, with 50 ms intervals in between. Visual distracter stimuli were three 50 ms long illuminations of the LEDs with 50 ms intervals in between. Both vibrotactile and visual stimuli were suprathreshold. In congruent trials both stimuli occurred on the same finger. In incongruent trials the vibrotactile stimulus was presented to index or middle finger while the visual stimulus was presented to the other finger (middle or index finger respectively). A no-go-trial consisted of a vibrotactile stimulus on the index or middle finger and the illumination of both LEDs. These trials were included to monitor whether participants actually looked at the lights in different conditions and did not, for example, close their eyes. Each trial for the crossmodal congruency task began with stimulus onset. A response was recorded until 2 s after the stimulus finished, and ended the trial. Feedback was given in case of false alarms (on no-go-trials), absent responses or incorrect responses (on go-trials) whereby both lights illuminated for 1 s. The subsequent stimulus was always presented after a random interval between 900 ms to 1100 ms. All participants used their right index and middle finger to respond. The response mapping for index/middle finger tactile targets on left hand was either index/middle or middle/index finger on right response hand. This was counterbalanced across participants.

Participants were instructed to fixate their eyes on the red dot between the LEDs. They were asked to discriminate the location of the vibrotactile targets as quickly and as accurately as possible, while ignoring the position of the visual distracters as much as possible. Furthermore, they were instructed to withhold their response when both LEDs were illuminated.

Each illusion condition block consisted of 216 trials: 96 congruent and 96 incongruent go-trials (half of those stimuli to the index finger and half to the middle finger); and 24 no-go-trials. The stimuli were presented in randomized order for segments of 36 trials (16 congruent, 16 incongruent go-trials, 4 no-go-trials). Six such segments were used, two after each brushing period.

In order to block the sound associated with the vibrotactile stimuli, participants wore headphones through which white noise was played during the crossmodal congruency task and during finger brushing.

Two training blocks each with 36 stimuli (16 congruent and 16 incongruent go-trials, 4 no-go-trials) were conducted in the beginning of the first session and one such training block was conducted in the beginning of the second session. Both vibrotactile and visual stimuli were presented on the participant’s real hand. In cases where participants responded more than once on no-go-trials or required more training, one or two more training blocks were conducted.

Rating Scales

To quantify the subjective experience of the rubber hand illusion, two questionnaires with 10 rating scales followed by two open questions were given to the participants at the very end of each block. In one version participants were asked to report their experience during brushing and in the other version during the task. To minimize any order effects half of the participants always answered the brushing version first and half the task version. The 10 rating scales were chosen from previous studies (Botvinick & Cohen, 1998; Ehrsson et al., 2004; Holmes et al., 2006). First, eight questions presented in random order were to be rated using a scale from 1 (strongly disagree) to 10 (strongly agree) (see S1 for supplementary material). In two further questions presented in random order participants were asked to rate the vividness (*"Please indicate how realistic the feeling was that the rubber hand is your hand.")* from 1 (not very realistic) to 10 (very realistic), as well as the duration of the illusion (*"Please indicate how much of the time the feeling that the rubber hand is your hand was present.")* from 1 (never) to 10 (the whole time). The open questions were *"Is there anything else you perceived, felt or thought in this block?"* and *"Other comments?"* For the No RH-synchronous condition the term 'rubber hand' was replaced by 'checkerboard'. Participants read an example of the questionnaire before the very first experimental block in order to become familiar with it.

Position Judgement

Participants were asked to judge the position of their index finger at the beginning (pre-test) and the end of each block (post-test). They viewed a number line in a mirror that was placed above the setup to cover any view of the rubber hand or checkerboard (Tsakiris & Haggard, 2005). The number line was attached 30 cm above the mirror in order to be projected at the same gaze depth as the participants' hands. Participants were asked to judge the position of their real index finger by mentally projecting a straight line from the centre of the finger tip to the number line. A random number onset was used each time the perceived position of the index finger was measured (4 different onsets used). After the pre-test the mirror was removed so that participants could view the setup and the experimenter started with the first stroking phase. After the last phase in which participants performed the crossmodal congruency task the mirror was again moved to be above the setup for the post-test.

Onset Measure

In order to measure the onset of the illusion, participants were asked to press a mouse button during each stroking period whenever they first had the feeling that the rubber hand or the checkerboard was their own hand. They were also told that this may or may not happen and may differ in different conditions and also be of different strengths.

The whole experiment lasted four hours (two hours each session) with an extra 30 minutes for explanation and training in the first session.

2.1.3. Statistical Analysis

Repeated measures 2x3 ANOVAs were conducted for CCE and position judgement data comprising the factors Illusion Condition (RH-Synchronous, RH-Asynchronous, No RH-Synchronous) and Distance (Overlying, Distant). Greenhouse-Geisser adjustments for non-sphericity were applied. Two-tailed Student's t-tests were used for post-hoc paired comparisons. An alpha-level of .05 was used to indicate significant statistical differences. Two-tailed paired non-parametric Wilcoxon Signed-Rank Tests were used for rating scale data to test for differences due to the distance manipulation for each illusion condition separately. The Bonferroni criterion was used to adjust *p*-values for multiple comparisons.

3. Results Experiment 1

3.1. Crossmodal Congruency Task

Trials with an incorrect response or a reaction time (RT) faster than 200 ms and slower than 1800 ms were discarded from the RT analysis (0.46 % of trials).

For an average of 8.9% no-go-trials false alarms were recorded. No significant differences were found between distances and illusion conditions with respect to the false alarm rate.

---- Figure 2 near here ----

Figure 2 depicts the CCE (i.e., performance on incongruent minus congruent trials) for RT and percentage error rate (%E) (for table of values see S2 supplementary material).

As can be seen in Figure 2 for both distances the CCEs were larger in the RH-Synchronous and RH-Asynchronous condition compared to when no rubber hand was present. In fact, a main effect for Illusion Condition was found for both CCE-RT, $F(1,23)=10.22$, $p<.001$, and CCE-%E, $F(1,23)=4.61$, $p<.05$. Paired comparisons between the mean CCEs across both distances for RH-Synchronous, RH-Asynchronous and No RH-Synchronous conditions revealed significant differences between the conditions when a rubber hand was present and the condition when no rubber hand was present: For CCE-RT: RH-Synchronous (*M*=131 ms, SEM=21) – No RH-Synchronous (*M*=100 ms, SEM=17), $t(23)=3.20$, $p<.01$; RH-Asynchronous (*M*=134 ms, SEM=20) – No RH-Synchronous, $t(23)=4.87$, $p<.0001$; For CCE-%E: RH-Synchronous (*M*=18.0, SEM=3.4) – No RH-Synchronous (*M*=13.6, SEM=2.4), there was a trend with $t(23)=2.05$, $p<.06$; RH-Asynchronous (*M*=18.8, SEM=3.5) – No RH-Synchronous, $t(23)=2.66$, $p<.05$. However, for the comparison RH-Synchronous versus RH-Asynchronous, no significant differences in CCE were found, either for RT, $t(23)=0.39$, $p=0.70$, or for %E, $t(23)=0.63$, $p=0.53$. This indicates that during both conditions similar illusion strengths are created during the task period unmediated by the synchrony of prior stroking.

Furthermore, when comparing CCEs for different distances, they were very similar for all illusion conditions. Neither a statistically significant main effect for Distance nor a significant interaction with Illusion Condition were found (all Fs<1).

In Experiment 1, we only brushed the index finger. A previous study found local differences with respect to illusion strength, with reduced illusion strength for a non-brushed finger (Tsakiris, Prabhu, & Haggard, 2006). To explore possible differences between the different fingers, ANOVAs for both RT and %E data were conducted with the factors Finger (index, middle), Illusion Condition and Distance. No significant main effect or interactions were found involving the factor Finger. This is a further indication that the CCE was unmediated by the synchrony of prior stroking.

3.2. Rating Scales

Only some participants gave comments to the open questions, so we do not report a detailed analysis here. In order to reduce the rating scales to a smaller set of orthogonal components we first performed a principal components analysis (PCA) with an orthogonal varimax rotation for the mean responses to the eight rating scales across all conditions and versions of the questionnaire. Vividness and Duration scales were not included. We identified three components (Ownership, Location-Cause, and Real Hand) which we interpreted and named according to their component loadings for individual scales (results for the PCA can be found in S1 supplementary material). The first two components are very similar to those reported in a previous study with a similar sample size and number of rating scales (Longo et al., 2008a). The authors also found a third component with an eigenvalue less than 1 and for which the item about the hand "turning rubbery" had a high loading. We also found this third component and found that the "Rubbery" scale as well as the rating scale regarding not being able to move one's own hand loaded high on this component (note that this "Not Move Own Hand" rating scale was not included in Longo, Cardozo et al., 2008). Hence, we concluded that this component might be meaningful and related to the sensation in the real hand. Another previous study conducted with 27 rating scales and 130 participants found more components, which is to be expected as more items were included into the PCA (Longo et al., 2008b). However, the authors found two subcomponents for "Embodiment of rubber hand" namely "Ownership" and "Location" which again seem to be similar to the first two factors found for the present data.

In order to obtain individual scores for each condition and component, the mean for the rating scales that correlated highly with this component (component loading > 0.6) was computed. For example, for the component Ownership we computed the mean of the scales "My Hand", "Rubber Hand Resembles" and "Move Rubber Hand". The results for the three components and the Vividness and Duration rating scales are depicted in Figure 3.

---- Figure 3 near here ----

Interestingly, as can be seen in Figure 3 for the asynchronous illusion condition the medians for ratings are larger in the task condition compared with the brushing condition, whereas for synchronous stroking with or without a rubber hand the medians are larger in the brushing condition. This indicates that the crossmodal congruency task itself can lead to the rubber hand illusion, which seems to be weaker than during synchronous stroking and stronger than during asynchronous stroking.

In order to investigate specifically differences between Overlying and Distant, Wilcoxon Signed-Rank Tests for all six pairs (e.g., RH-Synchronous – Brushing – Overlying and RH-Synchronous – Brushing – Distant) for each component as well as the Vividness and Duration rating scales were conducted. We found no significant differences for any comparison between Overlying and Distant conditions.

3.3. Position Judgement

We analysed pre-test position judgements and found that they differed with respect to illusion conditions, $F(1,23)=4.64$, $p<.05$. The values were generally larger when a rubber hand was present. Although participants could not see any hand during the judgement, they were perhaps influenced by the instruction we gave that they will see a rubber hand or no rubber hand in the next block. Hence, we subtracted the mean pre-test value across all illusion conditions for each distance from the post-test value for each condition to obtain a measure for the drift in perceived position towards the rubber hand. None of the position drifts of the Overlying conditions differed significantly from zero: RH-Synchronous $M=0.90$ cm (SEM=0.43), RH-Asynchronous $M=-0.31$ cm (SEM=0.56), No RH-Synchronous $M=0.60$ cm (SEM=0.60); all position drifts in the Distant conditions were significantly different from zero: RH-Synchronous $M=6.61$ cm (SEM=1.20), $t(23)=5.53$, $p<.0001$, RH-Asynchronous $M=6.40$ cm (SEM=0.90), $t(23)=7.10$, $p<.0001$; No RH-Synchronous $M=3.38$ cm (SEM=0.92), $t(23)=3.66$, $p<.01$. Furthermore, significant main effects for both Illusion Condition, $F(1,23)=4.29$, $p<.05$, and Distance, $F(2,46)=29.47$, $p<.001$, and as well as for their interaction, $F(2,46)=5.5$, $p<.05$, were found. For the Distant condition, the mean proprioceptive drift after synchronous brushing was larger when a rubber hand was present, compared to a checkerboard only. This replicates previous findings on the modulation of the rubber hand illusion by visual appearance (Tsakiris & Haggard, 2005). However, Tsakiris and Haggard (2005) who used a similar method to measure perceived hand position found on average a proprioceptive drift that was close to zero when synchronously stroking a non-hand like object. The blocks for each condition in our study took 15 min in total, which is long relative to Tsakiris and Haggard (2005) who stroked for 4 min. This increase in time could have induced an illusion of ownership even in the no hand condition; the questionnaire data do not support this explanation, however, as participants on average disagreed when asked about their subjective experience regarding the illusion. Alternatively, we think that perceived proprioceptive drifts are generally increased the further the real hand is placed away from the stroked object and/or the body midline. An increase of position bias has previously been shown for increasing distances between visual and proprioceptive information regarding arm position in reaching studies using mirrors (Holmes, Crozier, & Spence, 2004; Holmes et al., 2006; Holmes & Spence, 2005). We found on average 6.61 cm proprioceptive drift when the rubber hand was stroked synchronously for the 30 cm distance condition. In contrast, Tsakiris and Haggard (2005) found generally smaller proprioceptive drifts for this condition (below 3 cm in Experiment 1). They used 17.5 cm difference between real hand and artificial hand which was aligned with the participant's body midline (n.b. this is comparable to our finding in Experiment 2 where the proprioceptive drift is 2.69 cm in the synchronous rubber hand condition when 15 cm was used). In order to partly correct for this issue we subtracted the proprioceptive drift in the no rubber hand condition from the synchronous and asynchronous rubber hand conditions. This amounted to 3.23 cm (SEM=1.39) for the synchronous rubber hand condition and 3.02 cm (SEM=0.88) for the asynchronous rubber hand condition. These values are again comparable with previous studies (Tsakiris & Haggard, 2005; Tsakiris et al., 2006). Furthermore, we also calculated the proprioceptive drift as a proportion of distance. This amounted to 0.22 in the synchronous rubber hand condition, 0.21 in the asynchronous rubber hand condition and 0.11 in the no rubber hand condition.

With or without these corrections for distance, the data show a similar drift after the RH-Synchronous and RH-Asynchronous illusion condition for a large distance. In line with the results from the crossmodal congruency task and the rating scales, this suggests that the rubber hand illusion is created during the task period. Not surprisingly, the amount of perceived position drift differs between different distances: There is no significant drift when hands are overlying, whereas significant drifts towards the rubber hand were found in distant conditions when a rubber hand was present. In the overlying condition, although a rubber hand illusion is induced, the perceived position of the participant's hand does not seem to drift towards the rubber hand because the rubber hand is actually perceived in the same position as the real hand. Therefore, the position drift cannot be used to compare illusion strengths between different distance conditions.

The onset data for the illusion were very unreliable as many participants did not understand the task until they actually experienced the rubber hand illusion or they forgot to press the button at the time the illusion started. For this reason, none of these data are reported and onset data were not obtained in Experiment 2.

4. Discussion Experiment 1

In agreement with the study conducted by Pavani and colleagues (2000), a difference in CCE was found between conditions when an artificial rubber hand was present compared with when it was absent and only the checkerboard flooring of the box was visible. However, the CCE was not modulated by the synchronicity of prior stroking—no difference between synchronous and asynchronous stroking was found when the artificial hand was present. This pattern of results indicates that the CCE can be modulated by the visual presence of an artificial hand near the visual stimuli, but not by changes in illusory sense of ownership for an artificial hand due to manipulation of the synchronicity of multisensory input. An alternative explanation however is that the crossmodal congruency task itself generates the rubber hand illusion independently of the synchronicity of prior stroking. The task actually includes multisensory stimuli that are always synchronized in time and in half of the trials also appear on the same finger. Our subjective data are in line with this explanation as the ratings for the illusion were larger during the task compared with those for asynchronous brushing. Furthermore, the position drift which was measured after the crossmodal congruency task did not differ between synchronous and asynchronous conditions for larger distances. Aspell et al. (2009) studied changes in the CCE during changes in bodily self-consciousness with respect to the whole body. They found no difference in CCE between synchronous and asynchronous stroking conditions when visual and tactile stimuli for the crossmodal congruency task were presented in close temporal contiguity (SOA=33ms). When, however, the visual and tactile stimuli for the task were presented further apart (SOA=233ms) prior stroking significantly affected the CCE. In other words, experiencing visual and tactile stimuli close in time might itself lead to some illusion irrespective of prior stroking. In the study by Pavani et al. (2000), some participants also experienced the rubber hand illusion to some extent after performing the crossmodal congruency task without any stroking and when the hands were aligned. Although on average participants did not agree about experiencing the illusion, the mean ratings were larger in the condition when the hands were aligned compared to when they were misaligned. The use of simple lights and vibrations thus seems sufficient to induce or modulate the illusion to some extent. Very simple computer-controlled stimuli (visual movements of a stick and vibrations) have also been used to modulate body representation in a previous event-related potentials study (Press, Heyes, Haggard, & Eimer, 2008). This could be an important means of stimulation in future study, as these stimuli can be better controlled compared with brush strokes. In sum, we propose that the crossmodal congruency task itself resets the strength of ownership in the rubber hand illusion independently of the type of prior stroking. Therefore, we cannot answer the question if ownership during the rubber hand illusion has an effect on task performance. To study the influence of the synchronicity of prior stroking and in order to rule out such a complete resetting of ownership during the task, we used a design in Experiment 2 whereby we delivered brush strokes prior to every trial. Trial-by-trial stroking has also been used by Aspell et al. (2009).

5. Experiment 2

5.1. Methods

5.1.1. Participants

Twenty-four new participants took part in Experiment 2 (15 female; 20 right-handed; mean age 20.8 years, age range 18-27 years, SEM 0.4 years). All participants were naïve with respect to the rubber hand illusion, had normal or corrected-to-normal vision, and did not report any tactile deficits for their hands. The study was conducted in two sessions that took place 7 days apart (except for 1 participant for whom this gap was 10 days). Participants received $15 per hour. Each participant gave his or her informed consent to participate prior to the start of the first experimental session. The experiment was conducted in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki and approved by the Macquarie University Ethics Review Committee (Human Research).

5.1.2. Apparatus, Experimental Design and Procedure

The apparatus and stimuli were identical to those used in Experiment 1 with a few exceptions. A possible limitation in Experiment 1 was that we used a mirror in the Overlying condition and no mirror in the Distant condition. The use of a mirror itself could reduce the visual plausibility of the artificial hand and thus reduce the strength of the rubber hand illusion. Such a possible reduction could then lead to a similar modulation of illusion strength as does a distance manipulation, hence making both conditions very similar. In order to control for this possibility, in Experiment 2 no mirror was used. To manipulate the distance between the hands a closer and a larger distance was used. The distance between the hands was 15 cm for the Close condition and 45 cm for the Distant condition (also see Figures 1c and 1d). The position of the seen rubber hand was the same for both distance conditions. Hence, the visual information regarding the hand was kept constant, whereas the proprioceptive information regarding the real hand differed. To obscure the distance between the rubber hand and the participant’s real hand a piece of cardboard covered in black cloth was used. This time larger flat paintbrushes (6 cm wide) were used in order to simultaneously brush both index and middle finger. Before each crossmodal congruency trial the hands were brushed once. The brushing time (asynchronous or synchronous) was signalled via an auditory signal to the headphones of the experimenter. The auditory signal consisted of two 100 ms sounds separated by 200 ms. In the asynchronous condition the experimenter aimed to brush one hand during the first sound (the rubber hand or real hand) and then the other during the second sound (the real hand or the rubber hand). The order in which hand real or rubber hands were brushed first was counterbalanced across participants. During the synchronous condition the experimenter brushed both hands during the second sound.

Crossmodal Congruency Task

We were interested if the illusion strength generated by trial-by-trial brushing influenced performance in the crossmodal congruency task. Hence, with the aim of reducing the potential for the crossmodal congruency task to generate the rubber hand illusion, the synchronicity of the stimuli in the task was reduced and vibrotactile stimuli started with a delay of 150 ms after the visual stimuli. In order to keep the stimuli more consistent across time no feedback was given and a response did not end a trial. Stimuli started after a random interval of 1500-1700 ms after the brushing and responses were recorded until 2 s after the stimulus onset. Instructions and training for the crossmodal congruency task were as in Experiment 1.

Rating Scales

Only one questionnaire was given after each block as there were no separate brushing and task periods. Two versions for Questions 1 and 2 were used. One version asked about the touch of the brush (Location – Brush; Cause – Brush) and the other version about the touch of the tactile device (Location – Vibration; Cause – Vibration); this resulted in 12 rating scales (see S3 in supplementary material).

Position Judgement

This aspect was the same as in Experiment 1.

5.1.4. Statistical Analysis

Statistical analyses were conducted as in described for Experiment 1. The Distance factor now included the levels Close versus Distant.

6. Results Experiment 2

6.1. Crossmodal Congruency Task

Trials with an incorrect response or RT faster than 200 ms or slower than 1800 ms were discarded from the RT analysis (0.3 % of trials).

For an average of 5.27% false alarms were recorded for no-go-trials. No significant differences were found between distances and illusion conditions with respect to the false alarm rate.

---- Figure 4 near here ----

Figure 4 shows the CCEs for RT and %E (for table of values see S4 supplementary material). We found a significant main effect for Illusion Condition for both CCE-RT, $F(1,23)=14.39$, $p<.0001$, and CCE-%E, $F(1,23)=12.29$, $p<.001$. Consistent with Experiment 1 significant differences for the mean CCEs across both distances were found between RH-Synchronous, CCE-RT M=128 ms (SEM=12), CCE-%E M=17.1 (SEM=3.4), and No RH-Synchronous, CCE-RT M=90 ms (SEM=11), $t(23)=5.33$, $p<.0001$, CCE-%E M=9.1 (SEM=2.0), $t(23)=4.2$, $p<.001$, as well as between RH-Asynchronous, CCE-RT M=115 ms (SEM=12), CCE-%E M=12.7 (SEM=2.8), and No RH-Synchronous conditions, for CCE-RT, $t(23)=3.1$, $p<.01$, for CCE-%E, $t(23)=2.48$, $p<.05$. In contrast to Experiment 1, we now found significant differences for CCEs between synchronous and asynchronous brushing: for CCE-RT, $t(23)=2.1$, $p<.05$, and for CCE-%E, $t(23)=3.02$, $p<.01$.

A significant main effect for Distance was found for CCE-RT, $F(2,46)=9.38$, $p<.01$, which did not reach significance for the error data, $F(2,46)=1.69$,$p=0.21$. Post-hoc comparisons between distances for CCE-RT were significant only for the RH-Asynchronous illusion condition, $t(23)=2.86$, $p<.01$, with RH-Synchronous $t(23)=1.44$, $p=0.16$, and a trend for No RH-Synchronous, $t(23)=1.84$, $p<.08$. In sum, we found that CCEs after trial-by-trial brushing differed significantly for different distances only when the input was more asynchronous. Across distances, the CCEs were modulated by the synchronicity of prior stroking. This modulation was most prominent however for a large distance between rubber hand and real hand.

6.2. Rating Scales

A PCA with orthogonal varimax rotation for the mean responses to the ten rating scales across all conditions was conducted. Again, the Vividness and Duration items were not included.

The components from Experiment 1 were confirmed except that the eigenvalues for two components were less than 1 (results for the PCA can be found in S3 supplementary material). We nevertheless interpreted all three components as meaningful because the component structure was very similar to the one found in Experiment 1. With one exception: the rating scale “More Hands” now had a component loading >0.6 for the first component. The means for individual scores for the three components and the Vividness and Duration item are depicted in Figure 5.

---- Figure 5 near here ----

To examine differences between Close and Distant, Wilcoxon Signed-Rank Tests for all six pairs (e.g., RH-Synchronous – Brushing – Close and RH-Synchronous – Brushing – Distant) for each component and the Vividness and Duration item were conducted. We found significant differences regarding the subjective experience for the RH-Asynchronous illusion condition between a smaller and a greater distance for the Ownership component, Close *Mdn*=5.13, Distant *Mdn*=4.00; z=2.75, p<.05, for the Location-Cause component, Close *Mdn*=5.17, Distant *Mdn*=4.10, z=2.49, p<.05, and the Duration item, Close *Mdn*=5.30, Distant Mdn=3.00, z=2.73, p<.05, as well as a trend for significance for the Real Hand component, Close *Mdn*=6.00, Distant *Mdn*=4.50, z=2.33, p<.06. Consistent with the findings for the crossmodal congruency task, this indicates that synchronous stroking as well as the absence of a rubber hand leads to similar illusion strengths for different distances between rubber hand and real hand. If, however, the multisensory input is more asynchronous then lateral spatial distance matters.

6.3. Position Judgement

First, we conducted t-tests to investigate if position drifts are significantly different from zero. For the Close distance we found a significant position drift for the synchronous condition, M=2.69 cm (SEM=0.85), $t(23)=3.18$, $p<.05$, and a trend for the asynchronous condition, M=1.99 cm (SEM=0.76), $t(23)=2.62$, $p<.10$; position drifts for all illusion conditions for the Distant were significantly different from zero: RH-Synchronous M=6.39 cm (SEM=1.00), $t(23)=6.39$, $p<.0001$, RH-Asynchronous M=3.62 cm (SEM=0.85), $t(23)=4.24$, $p<.01$, No RH-Synchronous M=3.28 cm (SEM=0.78), $t(23)=4.22$, $p<.01$. Significant main effects were found for both Illusion Condition, $F(1,23)=7.11$, $p<.01$, and Distance, $F(2,46)=34.09$, $p<.00001$. Across both distances, significant differences were found between the RH-Synchronous and RH-Asynchronous condition, $t(23)= 2.9$, $p<.01$, and between the RH-Synchronous and No RH-Synchronous condition, $t(23)=3.2$, $p<.01$. Not surprisingly, when a larger distance was used the position drifts were greater compared with when the rubber hand and the real hand were close. Proprioceptive drifts are generally increased the further the real hand is placed away from the stroked object and/or the body midline (Holmes et al., 2004; Holmes et al., 2006; Holmes & Spence, 2005). In order to partly correct for this issue, we subtracted the proprioceptive drift in the no rubber hand condition from the synchronous and asynchronous rubber hand conditions. This amounted for the close condition to 2.25 cm (SEM=0.98) for the synchronous condition and 1.54 cm (SEM=0.98) for the asynchronous condition. For the distant condition we calculated 3.10 cm (SEM=1.30) for the synchronous rubber hand condition and 0.33 cm (SEM=0.99) for the asynchronous rubber hand condition. We also calculated the proprioceptive drift as proportion of distance. This amounted to 0.18 (SEM=0.06) in the synchronous rubber hand condition, 0.13 (*SEM*=0.05) in the asynchronous rubber hand condition and 0.03 (*SEM*=0.03) in the no rubber hand condition for the close condition. For the distant condition, we calculated 0.14 (*SEM*=0.02) in the synchronous rubber hand condition, 0.08 (*SEM*=0.02) in the asynchronous rubber hand condition and 0.07 (*SEM*=0.02) in the no rubber hand condition. We conducted ANOVAs using the corrected values and found again significant main effects for Illusion Condition, both $Fs(1,23)>5$, both $ps<.05$, but not for Distance, both $Fs<1$. As can be seen from these values and consistent with the results from the crossmodal congruency task and the rating scales, both corrected (and non-corrected) values for the asynchronous condition are more similar to the synchronous condition when the displacement between the real and rubber hand was small; indeed, they are not significantly different for corrected and non-corrected values, $t(23)=0.78$, $p=0.44$. However, for a large distance, the corrected position drift in the asynchronous condition was close to zero and significantly different from the synchronous condition for corrected and uncorrected measures, $t(23)= 2.6$, $p<.05$.

7. Discussion Experiment 2

We found in Experiment 1 that the crossmodal congruency task itself led to changes in rubber hand illusion irrespective of a prior interval of stroking. Accordingly, in Experiment 2 we stroked prior to every trial in order to investigate the effect of stroking synchronicity on multisensory interactions. Due to practical issues, however, we had to perform other changes in the experimental and stimuli design. In order to deliver the brush strokes between the crossmodal congruency trials we reduced the asynchrony between strokes from about 2000 ms in Experiment 1 to about 300 ms in Experiment 2. In both experiments, the second stroke began after the first was finished. With the aim of reducing the potential for the crossmodal congruency task to generate the rubber hand illusion, the synchronicity of the stimuli in the task was reduced and the vibrotactile stimuli started with a delay of 150 ms after the visual stimuli. In order to apply comparable stimulation to the index and middle fingers we brushed both fingers in Experiment 2. Furthermore, to make stimuli more consistent across time and conditions, no feedback was given and a response did not end a trial. The use of a mirror versus no mirror in Experiment 1 might be a possible confounding factor for the distance manipulation. Hence, we did not use a mirror in Experiment 2. In order to have again a 30 cm difference between distances, we now implemented a 15 cm and 45 cm difference between the participant's real hand and the artificial hand. Because of these changes, we interpret the findings from the two present experiments separately as it is not easy to make direct comparisons between them for any measures.

In this experiment, an increase of the rubber hand illusion due to synchronous stroking was associated with an increase in CCE, whereas a decrease in the rubber hand illusion due to asynchronous stroking was associated with a decrease in CCE.

This indicates that multisensory interactions, as measured by the CCE, can be modulated by the synchronicity of input and illusory ownership for an artificial hand.

Data from the crossmodal congruency task, rating scales and corrected position drifts indicate that there was no significant modulation of illusion strength for different distances between artificial hand and real hand when the multisensory input was synchronous. However, a significant reduction in illusion strength with increased distance between hands was found for prior asynchronous brush stroking. Thus, the synchronicity of multisensory input affected the rubber hand illusion and the multisensory interactions differently, depending on the distance between the hands. The closer the hands were, the less important it appears that the input was synchronous, whereas the further the hands were apart, the more the multisensory input synchronicity played a role.

8. General Discussion

We investigated if the crossmodal congruency task can be used to obtain an objective measure of body ownership in the rubber hand illusion and if the rubber hand illusion is limited by spatial distance between artificial hand and real hand.

Crossmodal Congruency Effect as a Measure of the Rubber Hand Illusion

We studied if the illusory sense of ownership for a rubber hand modulates visual-tactile interactions. A crossmodal congruency task was implemented and ownership for an artificial hand was manipulated by prior brush stroking. In Experiment 2, we provide evidence that manipulation of ownership for an artificial hand using synchronous versus asynchronous stroking before every crossmodal congruency trial modulated the CCE. We also found that synchronous stroking compared with asynchronous stroking resulted overall in an increased subjective experience of the illusion and position drift. Previously, the illusory sense of ownership for an artificial hand due to brush stroking has been proposed to modulate unimodal somatosensory processing (Longo et al., 2008a). On the basis of our data, we suggest that the CCE is modulated by changes in body ownership and that the crossmodal congruency task can be used to obtain an objective measure of changes in body-part ownership.

Furthermore, our data implies bidirectional influences between multisensory processing and body ownership in the rubber hand illusion: multisensory stimulation generates body ownership for a seen artificial hand and multisensory interactions can be modified by body ownership.

According to a recently proposed model for the mechanisms involved in the rubber hand illusion, body-part ownership could modulate multisensory interactions on the basis of peripersonal space mechanisms. Makin et al. (2008) propose that integrated information for hand position from both visual input from the seen artificial hand and proprioceptive input from the hidden real hand are encoded in the IPS and premotor cortex. Proprioceptive information for hand position is weighted context-dependently and it is assumed that it is weighted less when the hands are stationary than when the hands are moving. The result is that the representation of hand position is partially shifted towards the artificial hand and space around the artificial hand is encoded as part of peripersonal space. Thus, information regarding the seen and felt touch is thought to activate the same bimodal peripersonal space neurons and the felt touch is remapped into the reference frame of the seen artificial hand. This leads to the illusion that the touch is located on the artificial hand and to an illusory sense of ownership for the artificial hand. The sense of ownership for the seen artificial hand is thought to further increase the weight of visual information. Thus the sense of ownership is proposed to lead to a further spatial shift of the representation of arm position towards the seen artificial hand. This is supported by the common finding that a perceptual proprioceptive drift accompanies the rubber hand illusion (Botvinick & Cohen, 1998; Tsakiris & Haggard, 2005). The proposed further shift due to ownership could increase multisensory integration due to a further remapping of bimodal peripersonal space neurons. Thus ownership could modify perceptual integration per se, possibly mediated through changes in the location of visual receptive fields in peripersonal space neurons. The sense of ownership could therefore be related to a change in spatial representation of peripersonal space. As has been demonstrated using the rubber hand illusion, synchronous multisensory input may lead to changes of body ownership which furthermore may contribute to the processing of multisensory information with respect to one’s own body.

Interestingly, tool use has also been demonstrated to modify multisensory interactions as measured by the CCE (Maravita, Spence, Kennett, & Driver, 2002). In fact, it has been suggested that the visual receptive fields of bimodal neurons representing peripersonal space might be extended to incorporate the tool after use (Iriki, Tanaka, & Iwamura, 1996; Maravita & Iriki, 2004). However, an alternative explanation has been proposed and supported by several studies: Tool use may lead to a shift of spatial attention, resulting in enhanced processing of visual stimuli near the tool (Holmes, Sanabria, Calvert, & Spence, 2007; Holmes & Spence, 2004; Holmes, Spence, Hansen, Mackay, & Calvert, 2008; Yue, Bischof, Zhou, Spence, & Roder, 2008). In principle, spatial shifts of visual attention could also explain the effects we found for the crossmodal congruency task with respect to ownership. In this sense, ownership could be related to an allocation of visual attention towards a seen body-part, thereby enhancing the processing of visual stimuli nearby. These attentional modulations could be dependent on peripersonal space mechanisms: Graziano and Cooke (2006) proposed that frontal and parietal peripersonal space neurons could "participate...in the general allocation of attention to objects near the body" (p. 2632). Further behavioural and imaging studies are needed to explore the relationship between peripersonal space mechanisms and allocation of attention with respect to body ownership.

Spence et al. (2008) discuss evidence that in addition to actual integration of visual and tactile stimuli (spatial ventriloquism) a more important factor that may contribute to the CCE is the difference in response selection conflict generated by congruent versus incongruent stimuli. The idea is that visual distracters can prime correct or incorrect responses especially when close to the target, and thus lead to changes in a crossmodal congruency effect. Furthermore, a third and most likely much smaller factor that may affect the magnitude of the CCE is exogenous spatial attentional cuing. In Experiment 2 the distractor was presented 150 ms before the target and response selection conflicts as well as attentional cuing effects are thought to influence the CCE the more the distractor information is delivered before the target is presented (Shore, Barnes, & Spence, 2006). It is thus possible that a manipulation of ownership by stroking may affect the degree of response priming and attentional cuing in addition to or without changes in multisensory integration. These changes in turn could possibly be mediated by visual attention and/or peripersonal mechanisms.

Spatial Limits of the Rubber Hand Illusion

In two experiments we manipulated the distance between an artificial hand and real hand and measured the strength of the rubber hand illusion using subjective and objective measures. The rubber hand and the participant’s hand always had the same rotational orientation. We did not find any significant differences in illusion strength between the distances implemented in Experiment 1. However, this might be due to the fact that a mirror was used in one condition, but not in the other. In Experiment 2 no mirror was used and the visual information regarding the rubber hand was exactly the same in both conditions. We think that the results from Experiment 1 have important practical implications for future studies, namely that using a mirror to reflect an image into exactly the same spatial position as the hidden real hand does not increase the rubber hand illusion compared with the typical setup in which a spatial distance is present between the hands. However, for theoretical discussion on physical limits of the rubber hand illusion the mirror confound might be important thus in the following we will mainly consider the results from Experiment 2.

In Experiment 2, we did not find any significant differences for illusion strength between the implemented distances when both hands were stroked synchronously. This was the case for both the CCE as an objective measure as well as for subjective rating scale data. We would like to argue that lateral distance can be ‘overcome’ in the rubber hand illusion—for both distances a similar remapping of peripersonal space towards the seen rubber hand could be possible after synchronous stimulation.

The question then remains as to why rotational position changes affect the illusion, whereas lateral position changes do not? One possibility could be that the proprocioceptive information for rotational displacement is stronger as compared to lateral displacement. In line with the model by Makin and collegues (2008), due to relatively weak proprioceptive information for lateral displacement, similar shifts of the representation for hand position could thus be possible for different distances. As a result, for small as well as larger distances, the space around the artificial hand can be encoded as part of peripersonal space and the rubber hand illusion can be generated.

Surprisingly, we found a modulation due to distance for asynchronous prior stroking for both objective and subjective measures. In fact, for close distances the illusion strength was more similar between synchronous and asynchronous stroking. This pattern of results was supported by data from the crossmodal congruency task, rating scales and position judgement. These results are in contrast to previous studies using relatively close distances where significant differences between synchronous and asynchronous stroking were found (Tsakiris & Haggard, 2005; Tsakiris et al., 2006). However, in the interleaved design we used, some of the input in the asynchronous conditions is close to synchronous, because participants perceived multisensory stimuli that occurred very close in time. These stimuli are likely to be able to generate the rubber hand illusion to some extent. We would like to suggest: The more synchronous the multisensory input the less important distance is, as was seen in the synchronous condition. Conversely, the more temporal conflict there is with regard to the multisensory input, the more the distance and thus conflict regarding arm position matters for the strength of ownership. It thus seems that the factors lateral distance and synchronicity interact in their influence on body ownership and possibly peripersonal space mechanisms. When the artificial hand is seen close, peripersonal space mechanisms could be activated independently of the synchronicity, whereas when there is a large distance only synchronous input could lead to changes in the representation of peripersonal space.

Another interaction for two factors influencing the strength of body ownership, namely amount of movement and synchronicity, was found by Tsakiris et al. (2006). In this study the video projection of the participant's hand was presented 15 cm away from the hidden participant’s hand. The strength of the ‘video hand illusion’ was measured with proprioceptive judgements in three conditions: stroking only, active movement, and passive movement. Furthermore, for all three conditions the synchronicity between felt and seen information was manipulated. For synchronous input both were fairly synchronous whereas for asynchronous stimulation a temporal delay was introduced. While the proprioceptive drifts for synchronous stimuli were very similar for all three conditions, larger proprioceptive drifts for passive and active finger movement compared to stroking only were found for asynchronous input (Tsakiris et al., 2006, Table 1). In other words, on average the movement manipulation made a difference only when the input was asynchronous, similar to the distance manipulation in our study. It thus seems important to study how different modulators interact in order to understand how our brain is able to identify the current position of our body-parts and which body-parts belong to us.

The rubber hand was placed near the body midline and close to the body in our experiment—thus it was placed within reaching distance. Furthermore, close and distant positions for the hands were confounded with the fact that the real hand was close to the body midline versus far away from the body midline. In order to rule out possible confounds due to this setup, further tests need to be conducted in which the artificial hand is placed further away from the body without rotating it while keeping the position of the hidden real hand constant. This way, distances that are out of reach could also be investigated. However, these studies have to be designed carefully; when placing the seen artificial hand further away from the real hand visual information regarding the artificial hand cannot be kept constant.

Conclusion

We demonstrated that the crossmodal congruency task can be modulated by body-part ownership for an artificial rubber hand. Thus the crossmodal congruency task can be used as a method to study multisensory interactions with respect to the rubber hand illusion and body-part ownership. Disturbances of multisensory processes and/or sensory-motor processes have been suggested to play a role in disturbances in body and body-part ownership in brain damaged patients (Lopez, Halje, & Blanke, 2008; Vallar & Ronchi, 2009) and the crossmodal congruency task could be a tool to investigate these possibilities. Furthermore, in contrast to previous studies we did not find a spatial limit for the rubber hand illusion. We suggest that the sense of ownership leads to modifications in the representation of peripersonal space. The space for which these modifications may occur does not seem to be limited at least with respect to the space near the body. Future studies are needed that investigate possible limits on the illusion for larger distances away from the body.

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Figure Captions

Figure 1.

Experimental setup used in Experiment 1 (Figure 1a and 1b) and in Experiment 2 (Figure 1c and 1d). 1a and 1c depict the positions of the rubber hand and real hand for the Overlying/Close condition and 1b and 1d depict the position of the rubber hand and real hand for the Distant condition.

Figure 2.

Mean Crossmodal Congruency Effects (CCEs; performance on incongruent trials minus performance on congruent trials) for Experiment 1. Bars represent RT CCEs and Lines Error CCEs. Error bars indicate one standard error.

Figure 3.

Medians for rating scale items components (3a), and Vividness and Duration scales (3b) for Experiment 1. Error bars indicate the interquartile range.

Figure 4.

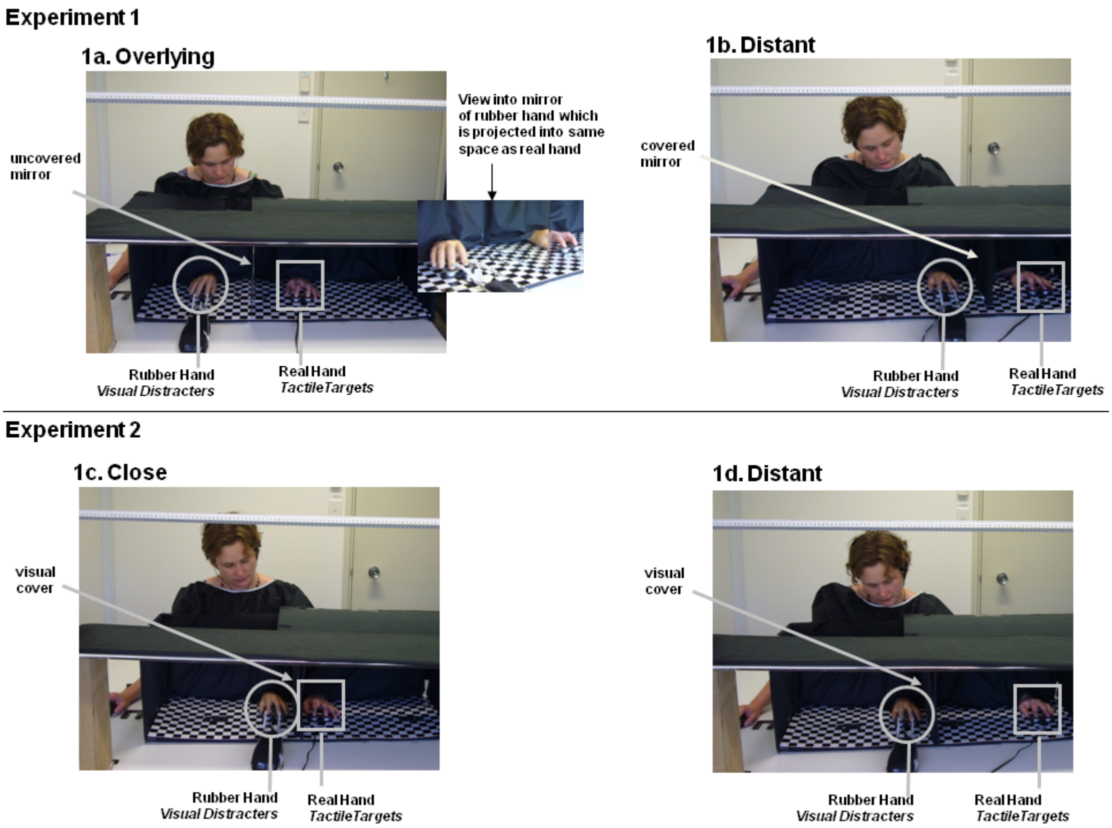
Mean Crossmodal Congruency Effects (CCEs; performance on incongruent trials minus performance on congruent trials) for Experiment 2. Bars represent RT CCEs and Lines Error CCEs. Error bars indicate one standard error.

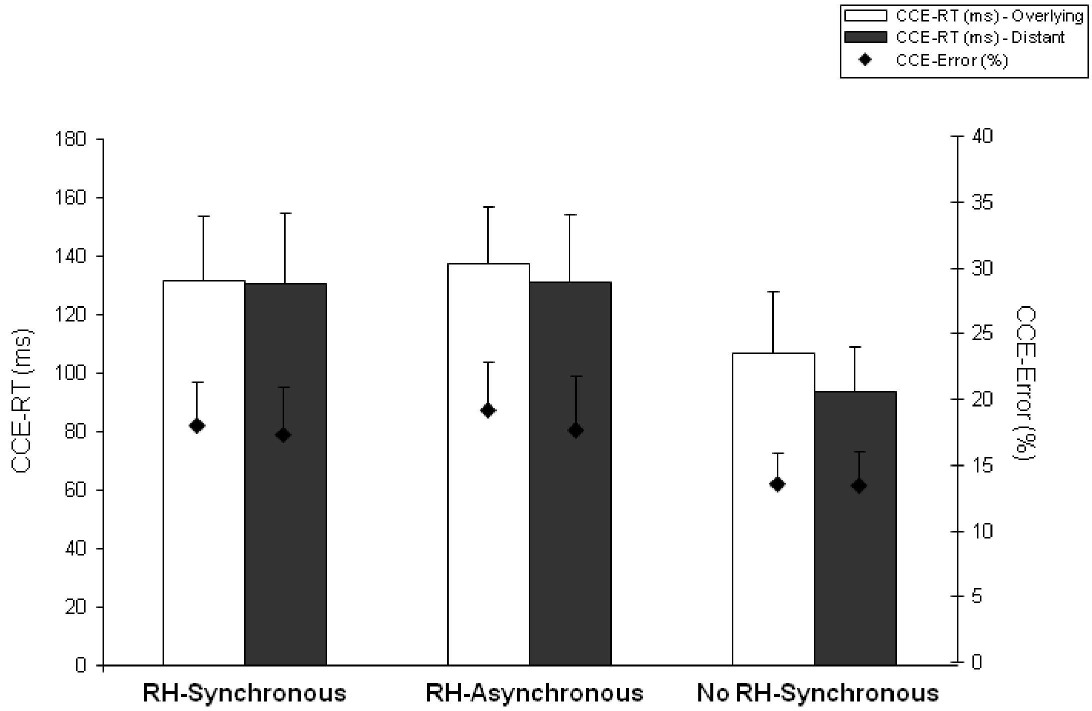
(*) $p<.06$; * $p<.05$

Figure 5.

Medians for rating scale items components (5a), and Vividness and Duration scales (5b) for Experiment 2. Error bars indicate the interquartile range.

(*) $p<.06$; * $p<.05$


Experiment 1
1a. Overlying
uncovered mirror
View into mirror of rubber hand which is projected into same space as real hand
Rubber Hand
Visual Distracters
Real Hand
Tactile Targets
1b. Distant
covered mirror
Rubber Hand
Visual Distracters
Real Hand
Tactile Targets
Experiment 2
1c. Close
visual cover
Rubber Hand
Visual Distracters
Real Hand
Tactile Targets
1d. Distant
visual cover
Rubber Hand
Visual Distracters
Real Hand
Tactile Targets


CCE-RT (ms) - Overlying
CCE-RT (ms) - Distant
CCE-Error (%)
CCE-RT (ms)
CCE-Error (%)
180
160
140
120
100
80
60
40
20
0
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35
30
25
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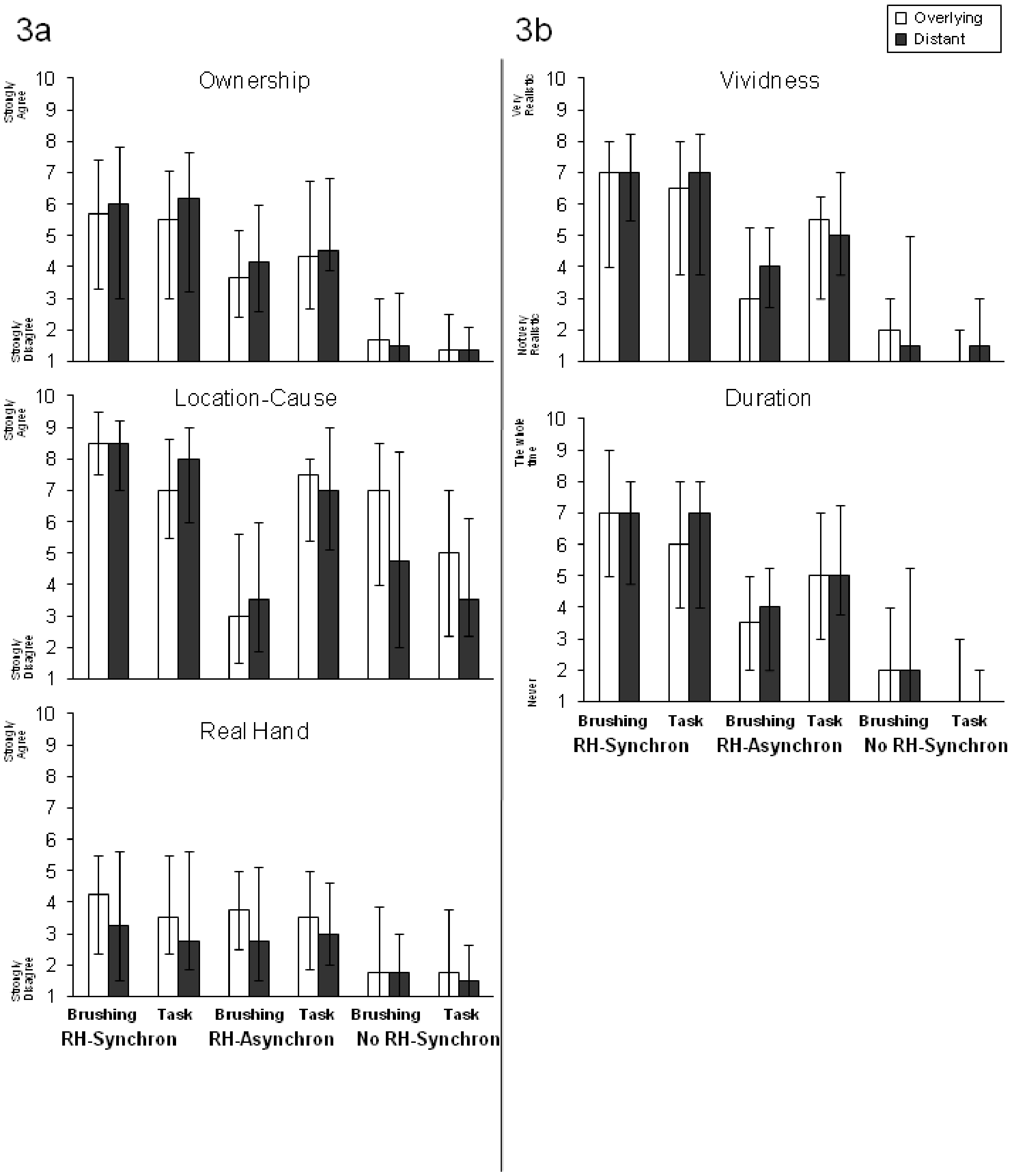
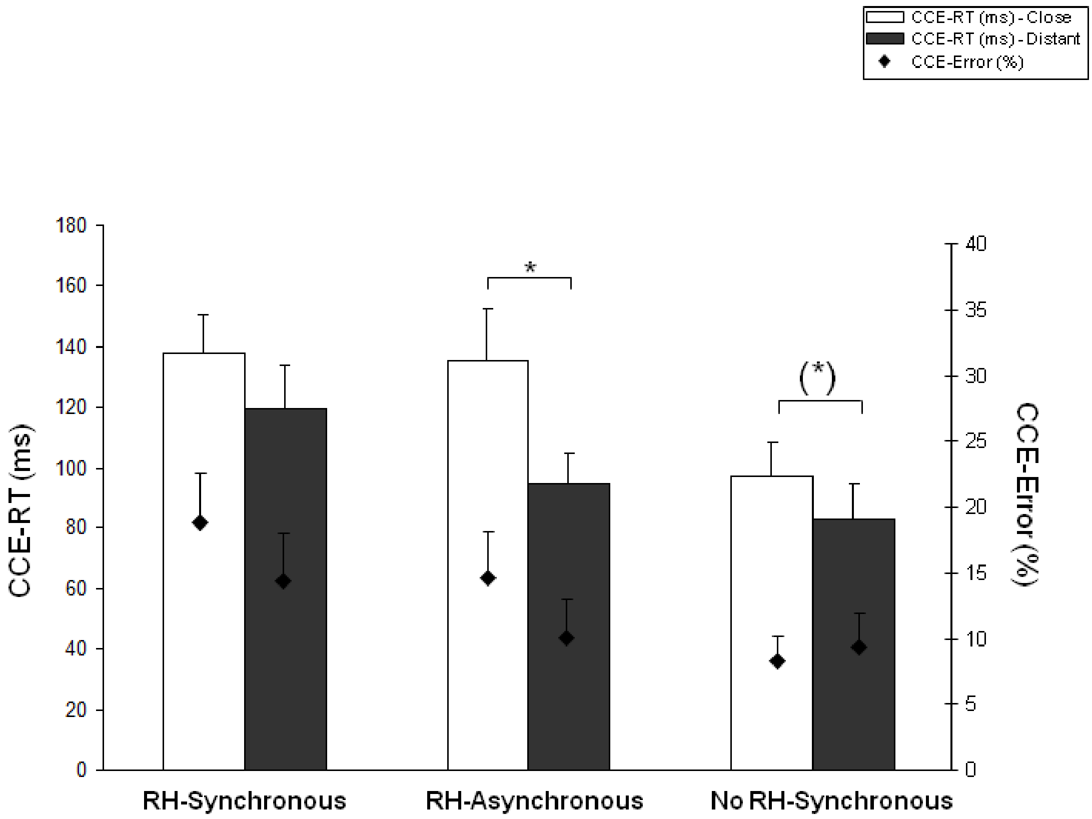
5
0
RH-Synchronous
RH-Asynchronous
No RH-Synchronous

Figure 2.


3a
3b
Overlying
Distant
Ownership
Location-Cause
Real Hand
Vividness
Duration
Strongly Agree
Strongly Disagree
Very Realistic
Not very Realistic
The whole time
Never
10
9
8
7
6
5
4
3
2
1
Brushing
Task
RH-Synchron
RH-Asynchron
No RH-Synchron


CCE-RT (ms) - Close
CCE-RT (ms) - Distant
CCE-Error (%)
CCE-RT (ms)
CCE-Error (%)
180
160
140
120
100
80
60
40
20
0
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35
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25
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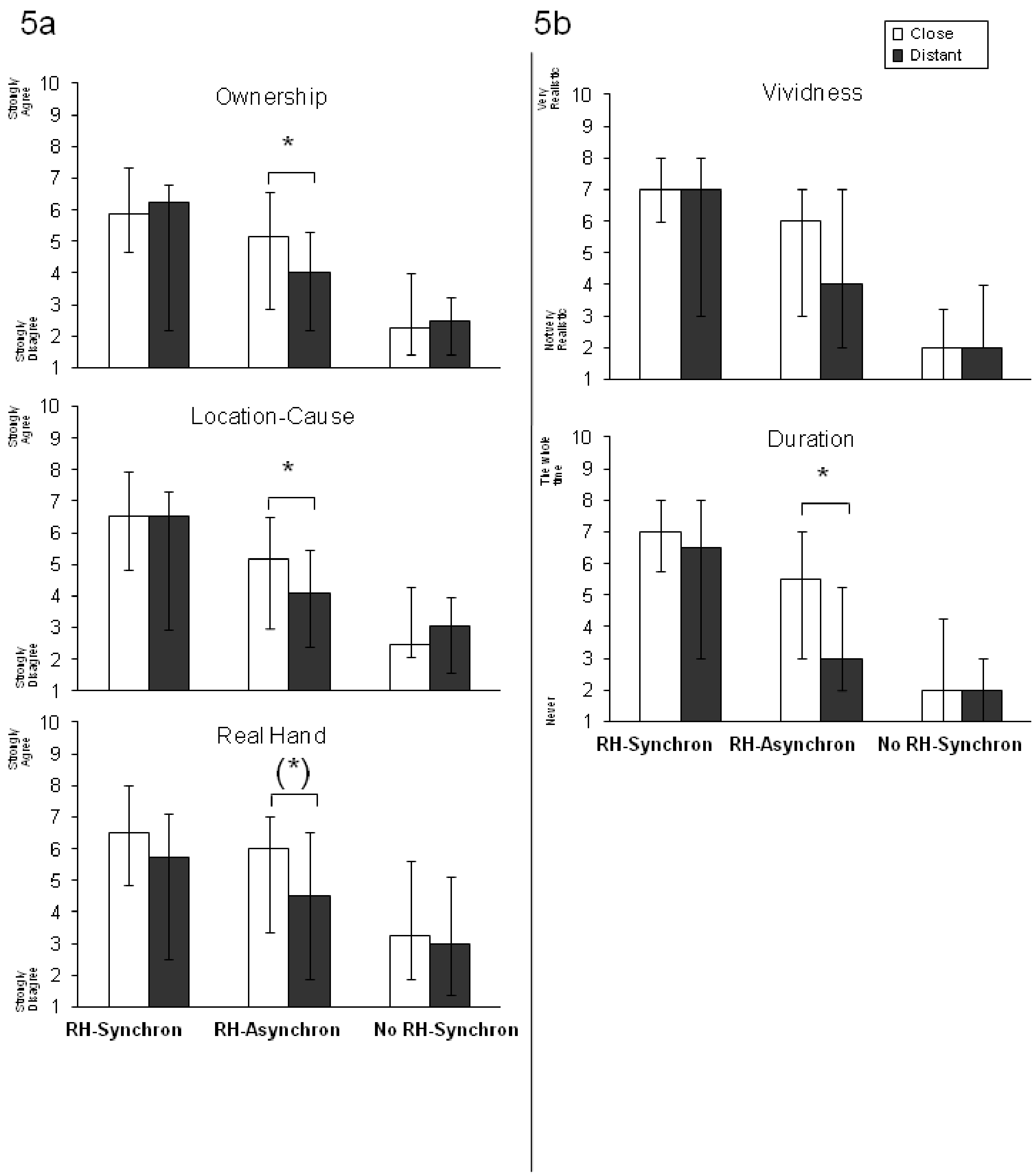
*
(*)
RH-Synchronous
RH-Asynchronous
No RH-Synchronous

Figure 4.


5a
5b
Close
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Ownership
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Location-Cause
*
Real Hand
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Vividness
Duration
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Strongly Agree
Strongly Disagree
Very Realistic
Not very Realistic
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RH-Asynchron
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