Published in final edited form as:
Conscious Cogn. 2015 December ; 37: 71–82. doi:10.1016/j.concog.2015.08.011.

The Influence of Embodiment on Multisensory Integration using the Mirror Box Illusion

Jared Medina, Ph.D.[1,2], **Priya Khurana**[3], and **H. Branch Coslett, M.D.**[2]

[1]Department of Psychology, University of Delaware

[2]Department of Neurology, Center for Cognitive Neuroscience, University of Pennsylvania

[3]Department of Psychology, Haverford College

Abstract

We examined the relationship between subcomponents of embodiment and multisensory integration using a mirror box illusion. The participants' left hand was positioned against the mirror, while their right hidden hand was positioned 12″, 6″, or 0″ from the mirror – creating a conflict between visual and proprioceptive estimates of limb position in some conditions. After synchronous tapping, asynchronous tapping, or no movement of both hands, participants gave position estimates for the hidden limb and filled out a brief embodiment questionnaire. We found a relationship between different subcomponents of embodiment and illusory displacement towards the visual estimate. Illusory visual displacement was positively correlated with feelings of deafference in the asynchronous and no movement conditions, whereas it was positive correlated with ratings of visual capture and limb ownership in the synchronous and no movement conditions. These results provide evidence for dissociable contributions of different aspects of embodiment to multisensory integration.

Keywords

embodiment; multisensory integration; mirror box; deafference; body representation; ownership

1. Introduction

In representing body position, information from different primary senses are integrated, resulting in a single estimate of limb position. To determine the mechanisms by which multisensory information is integrated, various researchers have studied how the brain resolves discrepancies between senses. For example, viewing a limb while wearing prism glasses with a mild (10–20 degree) lateral displacement introduces a difference between visual and proprioceptive information regarding limb position. After viewing for a short

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Corresponding author and address: Jared Medina, University of Delaware, 105 The Green, Room 108, Newark, DE 19716, Phone: 302-831-8724, Fax: 302-831-3645, jmedina@psych.udel.edu.

period of time, individuals will feel as if their limb is in the same location as the shifted visual image ("visual capture", Hay, Pick, & Ikeda, 1965; Tastevin, 1937; Welch & Warren, 1980), providing initial evidence for a strong weighting of visual information in multisensory integration.

Studies of multisensory integration have elegantly shown that the contributions of vision and proprioception to position estimates are weighted based on the relative spatial precision of each input (Ernst & Bulthoff, 2004; van Beers, Sittig, & Denier van der Gon, 1999b; van Beers, Wolpert, & Haggard, 2002). However, there is another factor that may influence weighting processes in multisensory integration - our sense of **embodiment**. Here, embodiment refers to the subjective experience of having one's own body. Longo and colleagues (2008) attempted to identify different aspects of embodiment using the rubber hand illusion (Botvinick & Cohen, 1998). In the rubber hand illusion, simultaneous stroking of the participant's own hidden hand and a viewed rubber hand results in the rubber hand feeling like their own hand, thus embodying the rubber hand in some manner. Using a principal components analysis (PCA) on questionnaire responses to different aspects of the rubber hand illusion, Longo and colleagues found four major components for the rubber hand illusion during the synchronous stroking condition – embodiment of the rubber hand, loss of their own hand, movement, and affect. The embodiment component further dissociated into three subcomponents; ownership (the sense that the rubber hand was part of one's own body), location (the sense that the rubber hand was in the same location as one's own hand) and agency (the sense of control over the rubber hand). This study provided a starting point for further examinations of embodiment and its relationship to cognitive and phenomenological processes.

Interestingly, our sense of embodiment can be altered by multisensory conflict. In the previous study, Longo and colleagues (2008) also analyzed questionnaire responses during asynchronous stroking in the rubber hand illusion. Although this is often considered as simply a control condition for the synchronous stroking condition, asynchronous stroking is not neutral as it creates multisensory incongruence between visual and tactile inputs. Along with the factors previously reported for synchronous stroking, the principal components analysis for asynchronous stroking discovered an additional component – **deafference**. This component included responses in which participants reported that their real hand felt numb, less vivid, and had a "pins and needles" sensation.

Similar sensations have been reported during multisensory incongruence in the mirror box illusion (Ramachandran, Rogers-Ramachandran, & Stewart, 1992). In a typical mirror box experiment, a mirror is placed perpendicular to the trunk midline of the individual (in the sagittal plane), with one limb on each side of the mirror. When viewed by the participant, the reflection of the left arm in the mirror looks like the participant's right arm, as the visual image is in the typical space where the right hand would be, and has the same chirality as the participant's own right hand. However, since the participant does not actually see his/her own hidden limb, the experimenter can manipulate the congruence between visual and proprioceptive information to examine multisensory integration. When both the hidden limb and viewed reflection are moved congruently, there is a strong sense of ownership and visual capture. However, introducing incongruencies between visual information (from the reflected limb) and proprioception and motor information (from the hidden limb) can result in a variety of abnormal sensations. For example, McCabe and colleagues (2005) asked participants to make bimanual movements (flexion and extension of the forearm or lower leg, coordinated or out of phase) with the limbs separated by either a whiteboard or a mirror. When participants made out-of-phase movements while viewing the mirrored limb, creating a strong intersensory mismatch between visual and proprioceptive/motor information, participants reported various sensory phenomena in the hidden limb, including tingling sensations, weight changes in the hidden limb, a perceived decrease in hidden limb temperature, and (in some cases) perception of an additional limb (see also Fink et al., 1999; Foell, Bekrater-Bodmann, McCabe, & Flor, 2013; Jackson & Zangwill, 1952; Tajadura-Jimenez, Longo, Coleman, & Tsakiris, 2012; Wasaka & Kakigi, 2012). In both the rubber hand and mirror box illusions, multisensory incongruence regarding the body leads to changes in the subjective experience of one’s own body.

In this study, we examined the relationship between measures of embodiment and estimates of limb position while manipulating multisensory conflict using a mirror box paradigm similar to one used by Holmes and colleagues (Holmes, Crozier, & Spence, 2004; Holmes & Spence, 2005b). In a series of experiments, they instructed participants to reach to unseen targets while manipulating the spatial congruency between the mirror reflection and the actual position of their right hand, and found that reach endpoints were biased by the viewed position of the hand. They examined the effect of multisensory congruence on limb position estimates by measuring reach endpoints after synchronous movement of both hands (bimanual, in phase tapping of each index finger), no hand movement, and asynchronous out of phase tapping of both hands (Holmes, Snijders, & Spence, 2006; Experiment 4). They found that the visual bias was strongest in the synchronous condition, followed by the no movement condition, with the asynchronous condition resulting in the least visual bias. These results provided evidence that increased multisensory congruence leads to stronger weighting of visual information in limb position estimates. However, along with altering multisensory congruence, synchronous movement may also result in changes in feelings of embodiment towards the mirrored hand, which may also influence multisensory integration processes.

To examine the role of embodiment in multisensory integration, we also asked participants to tap both hands synchronously (increased sense of ownership), asynchronously (increased sense of deafference), or to make no movements in a mirror box, manipulating the spatial discrepancy between viewed and actual limb position. First, we examined whether differences in multisensory congruence influenced the relative weighting of visual or proprioceptive information in position estimation. Consistent with previous findings (Holmes et al., 2006), we predicted that the temporal congruence across modalities in the synchronous tapping condition would lead to more effective visual capture and result in increased bias towards the perceived visual position of the limb, whereas decreased temporal synchrony in the asynchronous tapping condition would result in more bias towards the proprioceptive estimate. Second, extensive variance has been observed across individuals in visual capture (Welch & Warren, 1980). We examined whether differences in measures of embodiment across individuals predict the effectiveness of visual capture in the mirror box illusion. As each movement condition has the same multisensory congruence across individuals, we predicted that differences in position estimates across individuals are tied to their own subjective sense of embodiment during the illusion. Therefore, we examined the relationship between subjective responses on an embodiment questionnaire and objective estimates of limb position within each movement condition.

2. Materials and Methods

2.1. Participants

Sixty-nine individuals (27 male, 42 female) participated in this study conducted at the University of Delaware and the University of Pennsylvania. All were right-handed (self-report), native English speakers between the ages of 18 and 30. Participants signed informed consent forms and received either $10 in payment (University of Pennsylvania) or credit for an Introductory Psychology class (University of Delaware).

2.2. Apparatus

Participants were tested using a modified mirror box (see Figure 1). This mirror box consisted of a 91.4 cm (36″) long × 40.6cm (16″) deep flat wooden board with a 40.6cm (16″) deep × 30.5cm (12″) tall acrylic mirror mounted in the center. A black curtain hung right of the mirror, perpendicular to the near side of the mirror, so that the participant could not see his/her right hand and forearm. A meter stick, viewable during the experiment, was suspended 33.0 cm (13″) above the base of the apparatus and perpendicular to the mirror. Participants had their right hand positioned either against the mirror itself or against an unseen wood block with an acrylic mirror attached to the end. The wood block was either 15.24 cm (6″) or 30.48 cm (12″ – see Figure 1) long. To limit visual information regarding actual arm position, a black cloak was draped over the right upper arm obscuring it from view. During the no mirror condition, a thin black cloth was tightly draped onto the large mirror; in order to maintain consistency between the tactile input from the viewed and hidden hand, a cloth was also wrapped on the small mirrors attached to the wood blocks.

2.3. Procedure

Mirror condition—At the beginning of each trial, the participant was asked to close his/her eyes while the experimenter positioned the index fingertip of their left hand against the mirror (see Figure 1). The participant's right hand was positioned in the same configuration either directly against the mirror (0″ condition), or against wooden blocks with mirror surfaces that were 6″ or 12″ from the mirror. The participant then opened his/her eyes and was instructed to focus on the reflection of their left hand in the mirror. In the no-movement condition, the participant maintained the same position (with the fingertip pressed against the mirror) and was instructed to focus on the reflected hand for 60 seconds. In both movement conditions, the participant was instructed to tap both fingers to a 170 Hz rhythm, provided by a metronome program. Tapping was either synchronous, with both index fingers tapping simultaneously; or asynchronous, with the left and right index fingers alternating with the beat. In all conditions, after 60 seconds elapsed the participant was asked to look up at the ruler stick and verbally report the perceived position (in mm) of their right index fingertip. After providing this finger position estimate, the experimenter removed the participant's hands from the mirror box and asked him/her to immediately fill out an embodiment questionnaire. The questions were modified from Longo et al. (2008) and chosen to measure specific aspects of the participant's subjective experience in the illusion. The questions were related to *location* of their own hand ("It felt as though my index fingers were making contact with each other", "It seemed like my right hand was in the same *location* as the hand in the mirror"), *ownership* of the hand in the mirror ("It felt as though the hand in the mirror was *my* right hand"), *deafference* ("It seemed like I couldn't really tell where my right hand was", "I had the sensation that my right hand was numb"), *agency* ("I felt like I was in control of the hand in the mirror"), and *affect* ("I found this experience interesting", "I found this experience enjoyable"). Participants responded as to whether they agreed or disagreed with each statement using a visual analog scale. Each experiment consisted of 9 trials in a 3 (movement) × 3 (hidden hand position) design, with trials presented in a random order. Forty-five participants were tested in this condition.

No mirror condition—The design was the same as the mirror condition, except for two differences. First, instead of instructing participants to focus on the reflection of their left hand, they were instead told to focus on the black surface in place of the mirror. Second, as some of the entries in the embodiment questionnaire directly referenced the hand in the mirror, we modified the questionnaire by eliminating one irrelevant question and changing two other questions to reference the right hand, not the hand in the mirror (see Appendix). Twenty-four participants were tested in the no mirror condition.

We used split-plot ANOVAs to examine the influence of movement, hand viewing, and hand position on limb position estimates (3.1) and questionnaire responses (3.3). We also used questionnaire responses in a principal components analysis to identify embodiment factors in our dataset (3.2). Finally, we used multiple regressions to examine the relationship between limb position estimates and questionnaire responses (3.4).

3. Results

3.1. Limb position estimation

We first examined the effects of viewing the mirrored hand, position of the right (hidden) hand and movement on estimates of limb position (see Figure 2). We used limb displacement, quantified as the difference between actual right hand position and the reported position of the right hand, as our dependent variable. Positive values denote a bias towards the central mirror, with negative values denoting a bias away from the mirror. We then ran a fixed-effect, split-plot ANOVA, with movement (synchronous, asynchronous, and no) and hand position (0″6″ and 12″ from the central mirror) as within-subject factors, and view (mirror, no mirror) as a between-subjects factor. When assumptions of sphericity were violated, Greenhouse-Geisser corrections were used.

First, we found a main effect of hand position. As expected, there was an increase in bias towards the central mirror as the right hand was positioned farther from the mirror, $F(1.31, 88.0) = 74.7$, $p < .001$. All pairwise comparisons between the hand position conditions (0″, 6″, and 12″) were significant ($ps < .001$). There was also a main effect of movement, $F(2,134) = 14.6$, $p < .001$. Overall, participants demonstrated the most displacement towards the mirror in the synchronous condition (+44.5mm), followed with less in the no movement condition (+36.3mm) and the least in the asynchronous condition (+24.8mm). All pairwise comparisons were significant (ps < .025). Importantly, there was a main effect of view, F(1, 67) = 55.5, p < .001, with a substantial bias in perceived limb locations towards the participant's left hand when seeing the mirror reflection (+68.3mm) compared to virtually no bias without the mirror (+2.1mm).

Given the effect that viewing the mirror reflected hand has on illusory visual displacement, the next question is whether the amount of illusory visual displacement due to the mirror reflection was influenced by other factors. We found a significant hand position by view interaction, F(1.31, 88.0) = 21.2, p < .001). Here, we report illusory visual displacement due to viewing the mirror reflected hand (i.e., displacement in the mirror condition minus displacement in the no mirror condition, positive denotes more illusory displacement). There was significantly more illusory displacement towards the mirror in the 12″ condition (+103.4 mm) compared to the 6″ (+80.9 mm) and 0″ (−14.5 mm) conditions (0″ vs. 12″, p > .001; 0″ vs. 6″, p > .001; 6″ vs. 12″, p = .046; all pairwise comparisons using paired t-tests). There was also a movement by view interaction, F(2,134) = 8.45, p < .001, as the amount of illusory displacement due to the mirror was largest in the synchronous condition (+81.5 mm) compared to the no movement (+65.8 mm) and asynchronous (+51.3 mm) conditions. All pairwise comparisons were significant (ps < .013). The three-way hand position by movement by view interaction was marginally significant, F(2.52, 168.95) = 2.40, p = .080. Furthermore, we were specifically interested in whether there was an effect of the perceived visual position of the hand on estimates of limb position, even in conditions in which multisensory binding is least likely (asynchronous tapping). Therefore, we compared the mean amount of illusory displacement for asynchronous tapping (6″ and 12″ conditions) in the mirror condition versus the no mirror condition, and found significantly more displacement in the mirror versus no mirror condition, t(65.2) = 6.93, p > .001.

In summary, these results demonstrate that a) visual information showing the right hand touching the mirror had a strong effect on reported limb position, even when the actual right hand is 12″ from the mirror and b) that this illusory shift in perceived limb location is greatest with increased multisensory congruence. The most illusory displacement is observed during synchronous tapping (with congruence across vision, touch, proprioception, and efferent outflow). In the no movement condition, with no contribution from efferent outflow along with decreased information from touch and proprioception, there is decreased illusory displacement. In the asynchronous condition, in which visual information actively conflicts with information about the actual hand from proprioception, touch, and motor outflow, there is the least illusory displacement. However, note that there is still substantial illusory displacement in the asynchronous condition with the mirror versus without a mirror, demonstrating the influence of visual information in estimating limb position, even in conditions with clear multisensory conflict.

3.2. Principal components analysis

Along with objective measures of limb position, we also collected subjective measures of embodiment via questionnaire responses during the experiment. Before examining the relationship between subjective measures of embodiment and objective measures of limb displacement, we first used factor analyses to examine if different ratings of embodiment correlated with one another, and if these correlations reflected discrete measures of embodiment consistent with other studies (e.g. Longo et al., 2008). Separate principal components analyses with varimax orthogonal rotation were performed separately for each movement condition on trials with a mirror (see Table 1). For all PCAs, Bartlett's Test of Sphericity (a measure of sampling adequacy) was significant ($p > .001$ for all PCAs). We also present a second measure, the Kaiser-Meyer-Olkin Measure of Sampling Adequacy (KMO). For the synchronous condition (KMO = .697), three components were extracted that accounted for 70.8% of the variance. The first factor (32.7% of variance) consisted of the ratings of location, ownership and agency, with a second factor (22.8%) composed of ratings of affect, and a third (15.3%) for ratings of deafference. For the no movement condition (KMO = .740), three similar components were extracted that accounted for 70.6% of the variance. The first factor (30.7% of variance) consisted of location and ownership ratings. The second factor (23.6%) consisted of ratings of affect and agency, with the third factor (16.3%) again being ratings of deafference. In the asynchronous movement condition (KMO = .592), there were four extracted components that accounted for 80.7% of the variance. The first component (27.0%) was composed of location and ownership ratings. The second component (22.8%) consisted of affective ratings, with the third component (17.2%) again composed of deafference responses. Interestingly, in the asynchronous condition a new factor emerged which consisted solely of responses regarding perceived agency (13.7%).

3.3. Influence of experimental conditions on questionnaire measures

Next, we examined the relationship between the experimental factors (mirror reflection, movement type, actual hand position) on ratings of embodiment, using separate mixed design ANOVAs for different subtypes of embodiment. For each ANOVA, movement (synchronous, asynchronous, and none) and hand position (0″, 6″ and 12″ from the central mirror) were within-subject factors, and view (mirror, no mirror) was a between-subjects factor. In selecting our dependent variables, preliminary analyses revealed very high correlations (< .7) between ratings for questions on ownership and location, and these questions always reduced to the same factor in all of our principal components analyses. To reduce collinearity, we combined the average ratings on questions of ownership and location into a single independent variable (ownership/location). For each ANOVA, we used the mean questionnaire responses for each of our four categories (ownership/location, agency, deafference, and affect; see Appendix) as our dependent variables. As one question on perceived limb ownership was not presented to the no mirror group, that question was not included in our analyses.

For ratings of perceived location (see Figure 3a), we found a significant main effect of movement type, $F(2,134) = 45.6$, $p < .001$, as individuals agreed most with statements that their hidden hand was closest to the mirror and their own hand in the synchronous condition (54.7%), followed by the no movement condition (46.6%) and the asynchronous condition (32.0%). All pairwise comparisons between conditions were significant ($ps < .001$). There was also a main effect of hand position, $F(2,134) = 82.6$, $p < .001$, as participants agreed most with statements in the 0″ condition (64.5%) versus the 6″ condition (39.4%) and the 12″ (29.6%) conditions. All pairwise comparisons were significant ($ps < .001$). Furthermore, there was a main effect of mirror view, F(1,67) = 27.1, p < .001, as participants agreed more with statements regarding limb location in the mirror condition (54.6%) versus the no mirror condition (34.4%). Importantly, there was a significant interaction between mirror view and movement type, F(2,134) = 32.0, p < .001. When reporting interactions that involve the mirror view condition, here and elsewhere in section 3.3., we will report the change in rating in the mirror condition versus the no mirror condition, with positive denoting an increase in agreement with statements. In the asynchronous condition, there was a small decrease in limb location ratings (−2.1%). However, viewing their reflected hand in the mirror resulted in a substantial increase in location ratings in both the no movement (+30.5%) and synchronous movement (+32.0%) conditions. Post-hoc tests showed a significant difference comparing both the no movement and synchronous movement conditions to the asynchronous movement condition (ps < .001), with no significant difference comparing no movement to synchronous movement (p = .97). Along with these results, there was also an interaction between hand position and mirror viewing, F(2,134) = 4.12, p = .018. Participants reported the largest increase in subjective location ratings due to mirror viewing in the 6″ condition (+29.2%), followed by significantly less increase in the 0″ (+13.8%) and 12″ conditions (+17.7%). In post-hoc analyses, there was significantly higher ratings of limb location in the mirror condition in the 6″ condition only (ps < .007). No other comparisons were significant. Overall, these subjective reports of limb localization reflect the objective reports reported earlier – with mirror viewing resulting in higher subjective ratings of limb location in the synchronous and no movement conditions compared to the asynchronous movement condition.

Next, we examined whether there was a relationship between other subjective measures of embodiment and our experimental conditions. Using subjective measures of deafference as our dependent variable (see Figure 3), we found a significant main effect of hand position, F(2,134) = 29.4, p < .001), with the highest ratings of deafference observed in the 6″ condition (36.1%), followed by the 12″ (33.2%) and 0″ (22.8%) conditions (all pairwise comparisons significant at p < .04). Although there were higher ratings of deafference in the mirror view group (34.0%) versus the no mirror view group (27.3%), this difference was only marginally significant (p = .079). No other comparisons for ratings of deafference were significant.

For ratings of agency (see Figure 3c), we found a main effect of mirror viewing, F(1,67) = 4.70, p = .034, with higher ratings in the mirror condition (70.9%) compared to the no mirror condition (59.5%). Next, there was a main effect of hand position, F(2,134) = 5.06, p = .009, as participants felt the most agency when the actual hand was positioned closest to the mirror (0″, 69.2%; 6″, 64.9%, 12″, 61.6%; pairwise comparisons only significant for 0″ versus 12″, p = .007). There was also a main effect of movement type, F(2,134) = 14.4, p < .001, with the most agency reported in the synchronous condition (71.0%) followed by the no movement condition (68.5%) and the asynchronous condition (56.1%; all pairwise comparisons except no movement versus asynchronous were significant). Finally, there was a significant movement type by mirror view interaction, F(2,134) = 15.2, p < .001. Participants in the mirror view condition reported a small increase in agency ratings compared to those in the no mirror condition (+6.3%) in the synchronous movement condition. However, the opposite pattern was found in the no movement (−14.5%) and asynchronous movement conditions (−26.1%), as in these conditions participants reported higher ratings of agency in the no mirror condition. No other comparisons were significant.

Finally, for ratings of affect (see Figure 3d), there was a main effect of movement type, F(2,134) = 8.5, p = .001, as people enjoyed synchronous tapping (63.8%) more than no movement (59.6%) or asynchronous tapping (57.4%). Participants in the mirror group (65.5%) enjoyed the task more than the no mirror group (55.1%), though this comparison was only marginally significant, F(1,67) = 3.72, p = .058). Finally, there were significant mirror group by hand position, F(2,134) = 3.51, p = .033, and mirror group by movement type, F(2,134) = 3.32, p = .039, interactions. Participants demonstrated the greatest increase in affect due to the mirror when the hands were closest (0″, +13.5%; 6″, +11.2%, 12″, +6.4%) and as synchrony increased (synchronous, +13.8%; no movement, +11.5%, asynchronous, +5.9%).

3.4 Relating measures of embodiment to illusory displacement

Our first analyses (3.1) demonstrated a clear effect of movement type on localization judgments in the mirror condition. However, within each movement condition, there was substantial variability in participants' localization judgments and embodiment ratings. As multisensory congruence for matched conditions is very similar across individuals, the observed variability in localization judgments may be related to participants' varying sense of embodiment. Therefore, we ran separate multiple linear regressions for each movement condition to examine whether subjective self-report measures for different sub-types of embodiment could predict the magnitude of illusory displacement. As we were interested in the relationship between illusory displacement and measures of embodiment, we only examined individuals in the mirror group and conditions that can lead to illusory displacement (6″ and 12″ conditions). In each regression, the dependent variable was relative illusory displacement (i.e. actual distance from hand to mirror minus distance from perceived hand position to mirror, divided by actual distance from hand to mirror) with 1 being a completely illusory percept, and 0 being a completely veridical percept. Our regressors were the average ratings of ownership/location, deafference, affect, and agency. Note that past studies have used the orthogonal component scores as regressors (e.g. Longo et al., 2008). We note that the relative contributions of each question rating to the component scores differs in each condition, making comparisons across conditions difficult. Therefore, we used the PCA analyses to reduce the number of factors (addressing potential collinearity problems), but used the same regressors across analyses to facilitate comparison across movement conditions.

Embodiment ratings significantly predicted illusory displacement in all three movement conditions (synchronous, F(4,85) = 9.86, p < .001, r^2 = .317; no movement, F(4,85) = 18.3, p < .001, r^2 = .462; asynchronous, F(4,85) = 3.74, p = .007, r^2 = .150). Examining individual factors, the ownership/location rating significantly predicted illusory displacement in the synchronous (β = .581, t(85) = 4.693, p < .001) and no movement (β = .602, t(85) = 5.482, p < .001) conditions, but did not predict illusory displacement in the asynchronous condition (β = .162, t(85) = 1.084, p = .281). Deafference significantly predicted illusory displacement in the no movement (β = .348, t(85) = 2.680, p = .009) and asynchronous conditions (β = .

370, t(85) = 2.655, p = .009), with higher deafference ratings predicting more illusory displacement. However, there was no relationship between deafference and illusory displacement in the synchronous condition (β = .137, t(85) = .892, p = .375). Finally, lower ratings of agency marginally predicted increased illusory displacement, found only in the asynchronous condition (β = −.156, t(85) = −1.939, p = .056).

4. Discussion

In our study, we used a mirror box to manipulate multisensory congruence and participants' sense of embodiment, examining the relationship between these factors and the perceived position of the hands. First, we found that increased visuomotor congruence (e.g. synchronous tapping) resulted in more bias towards the seen position of the hand compared to conditions with decreased visuomotor congruence. Second, we found that changes in visuomotor congruence also influenced participants' sense of embodiment. Finally, and most importantly, we found a direct relationship between perceived illusory displacement of the visual image of the hand and subjective measures of embodiment. First, increased feelings of limb ownership and location predicted bias towards the visual position in the synchronous and no movement conditions, but not the asynchronous condition. Second, a greater sense of deafference also predicted bias towards the visual estimate – but only in the no movement and asynchronous condition. We discuss these results below.

4.1. Embodiment and multisensory integration

Traditionally, the factors thought to influence multisensory binding for the body are the relative precision of the inputs from each modality, and/or cognitive and attentional factors (Kelso, Cook, Olson, & Epstein, 1975; Warren & Schmitt, 1978). However, in studies of multisensory integration in which the manipulations are the same across individuals, substantial inter-individual variance has been observed (McDonnell & Duffett, 1972; Pick, Warren, & Hay, 1969). In our experiment, we also observed substantial variability across individuals in illusory visual displacement, with some participants experiencing near complete visual capture (even with their hand 12″ away from the visually-defined position), while others experienced minimal capture and based their limb position estimate primarily on proprioceptive feedback. We found that the variance in illusory visual displacement is, in part, related to subjective feelings of embodiment. Our study provides novel evidence for a direct relationship between subjective aspects of embodiment and objective measures of limb location. We report two major findings regarding this relationship: increased feelings of *deafference* correlated with more illusory displacement in the no movement and asynchronous conditions, whereas increased feelings of *ownership* of the mirror reflection of the limb correlated with more illusory displacement in the synchronous and no movement conditions.

First, we found that an increased sense of deafference was strongly correlated with increased illusory visual displacement in the no movement and asynchronous tapping conditions. Why would feelings of deafference predict a more robust visual illusion? We propose that intersensory conflict caused by the asynchronous input from vision versus other senses (proprioception, touch, efference copy) results in deafferentation – i.e. a dampening of tactile and proprioceptive inputs. In similar studies which have created intersensory conflict with the body, self-reports often describe the feelings with terms (e.g. “pins and needles”, “tingling sensation”, McCabe et al., 2005) that are similar to those experienced after temporary deafferentation. In a related mirror box study in which participants viewed finger movements while the hidden hand was passive, Romano and colleagues (2013) found decreased kinesthetic sensitivity for the hidden hand, also consistent with our account. When integrating position information from multiple modalities, the contributions of position estimates for each modality are dynamically weighted based on the precision of the specific input. For example, Ernst and Banks (2002) asked participants to make judgments regarding the height of a felt ridge while seeing a distorted visual image of the ridge. Importantly, the quality of the visual input was actively manipulated by increasing the noise in the visual image. They found that the relative weighting of visual information in the multisensory estimate was based on the quality of the visual input, with more bias towards the visual estimate with less noisy visual inputs (see also Alais & Burr, 2004 for a similar example with vision and audition). In our study, we find that feelings of deafference are significantly correlated with increased illusory visual displacement. One possibility is that a reduction in tactile/proprioceptive sensitivity caused by the proposed gating mechanism creates a noisier input from touch/proprioception, resulting in more bias towards the visual estimate. Unfortunately, we do not have any data regarding whether tactile and/or proprioceptive sensitivity decreases with an increased sense of deafference. However, we note that some low-level changes in early somatosensory ERP components have been observed in related illusions. Dieguez and colleagues (2009) had participants press their left hand against someone else’s right hand, and instructed the participant to stroke the index finger of both pressed hands (synchronously or asynchronously) with the participant’s right hand. Participants reported numbness in their left hand in the synchronous condition only, possibly caused by confusion regarding ownership of the other person’s hand. The authors recorded somatosensory evoked potentials (SEPs) during this illusion, and found an enhanced N20 component during synchronous stroking compared to other conditions. Importantly, this enhanced N20 component has also been observed during actual temporary deafferentation from local anesthesia (Tinazzi et al., 1997), suggesting that changes in perceived embodiment may influence somatosensory perception. Future research will be necessary to examine the influence of different aspects of embodiment on somatosensory perception.

Second, we found a relationship between the ratings of ownership/location of the reflected limb and increased illusory displacement towards the visual image. One possibility is that an increased sense of ownership is a direct product of strong visual capture. During mirror tapping, participants (informally) described two states – at first, a sense of seeing their hand in one position while feeling their hand in another position. Next, participants stated that their felt hand would “shift” or “bind” onto the visual image, resulting in feeling a unitary limb. We propose that this “binding” across senses then leads to strong feelings of ownership of this now unitary limb – leading to a highly correlated relationship between ratings of limb ownership/location and illusory displacement. On this interpretation, a sense of ownership is a result of the effectiveness of visual capture and is not a causal factor (e.g. increased ownership of the limb results in more illusory displacement). If so, the variability across individuals in illusory visual displacement may be caused by factors other than a sense of ownership (e.g. higher visual acuity, poorer proprioception, better temporal coupling in the synchronous condition). However, a second possibility is that stronger feelings of ownership of the mirrored limb lead to increased illusory displacement. Our results, while demonstrating a relationship between subjective embodiment ratings and illusory displacement, cannot speak to whether visual capture causes a sense of ownership, vice versa, or both. Future work will be necessary to examine this question.

Our results reflect findings using the rubber hand illusion (Longo et al., 2008), in which proprioceptive drift towards the viewed rubber hand during synchronous stroking was strongly correlated with ratings of ownership and location of the rubber hand. We note that in Longo et al. (2008), questions about feelings of ownership over the rubber limb and the perceived location of the rubber hand dissociated into different subcomponents. However, in our study, we found that ratings of location and ownership of the reflected hand were highly correlated and did not dissociate in any of our PCAs. If a sense of ownership is a by-product of strong visual capture in the mirror box illusion, then a strong correlation between ratings of location and ownership would be expected. However, since ratings of the perceived ownership and location of their limb are highly correlated, it is difficult to tease apart the relationship between the amount of illusory visual displacement and these aspects of embodiment (location and ownership). Given the relatively small sample size in our PCA analysis, it is also possible that location and ownership would be separable with more subjects and/or questions.

4.2. The influence of action and temporal congruence on position estimates

First, we found the most illusory displacement in the synchronous tapping condition, followed by the no movement condition, with the least illusory displacement in the asynchronous tapping condition, consistent with similar findings examining the effect of tapping on reach endpoints (Holmes et al., 2006). We note that previous research on visuomotor congruence examined endpoints at the end of a movement, whereas our study examines the immediate changes caused by visuomotor integration on position estimates. Furthermore, consistent with multisensory integration in other domains (e.g. the ventriloquist effect), we found that the perceived position of the hand was more strongly influenced by the visual position estimate when there was increased multisensory congruence (synchronous condition). These results are generally consistent with the temporal rule of multisensory integration (Meredith, Nemitz, & Stein, 1987), in which inputs from different modalities are integrated if they are temporally coincident. This bias towards the visual, as opposed to the proprioceptive estimate, of limb position is likely due to the higher spatial precision of this modality. We find the most illusory displacement towards the visual estimate in conditions with the most temporal synchrony, consistent with the temporal rule. However, temporal congruency is not the only factor in biasing limb position estimates.

Multisensory estimates of limb position are optimally integrated, such that information from different modalities is weighted based on the relative precision of each input (Ernst & Bulthoff, 2004; van Beers, Sittig, & Denier van der Gon, 1996, 1999a; van Beers et al., 2002). Limb position estimates are more accurate during active versus passive movements, likely due to contributions from proprioception and efferent information (Chokron, Colliot, Atzeni, Bartolomeo, & Ohlmann, 2004; Paillard & Brouchon, 1968; van Beers et al., 2002; Welch, Widawski, Harrington, & Warren, 1979). In conditions with no movement, the proprioceptive estimate of the limb degrades over time (Brown, Rosenbaum, & Sainburg, 2003; Wann & Ibrahim, 1992) resulting in a greater reliance on visual information (Holmes & Spence, 2005a). We found more displacement towards the visual estimate in the no movement condition versus the asynchronous condition. Increased proprioceptive weighting during movement may also contribute to the increase in bias towards the actual hand position in the asynchronous condition versus the no movement condition.

Furthermore, we note that even in the asynchronous tapping condition, participants experienced their limb as closer to the mirror when viewing a reflection of it touching the mirror, compared to asynchronous tapping without viewing the mirror reflection. This bias occurs even in the face of strong evidence – temporal asynchrony between visual estimates on the one hand and feedback from touch, proprioception, and efference copy on the other hand – that the visual information is not reliable. In classic studies of visual capture (see Welch & Warren, 1980 for a review), there is a strong influence of visual information on the proprioceptive estimate of limb position even when there is no movement. Furthermore, seeing the mirror reflection of an active moving hand in the same position as a hidden passive hand increases motor evoked potentials, somatosensory evoked potentials, and lateralized readiness potentials for the hidden, passive hand (Funase, Tabira, Higashi, Liang, & Kasai, 2007; Garry, Loftus, & Summers, 2005; Touzalin-Chretien, Ehrler, & Dufour, 2010) We note that even in the asynchronous condition with the mirror, there is still some crossmodal congruence across modalities, including limb size and limb orientation. Given an individual’s lifetime of experience seeing and feeling their limbs in the same location, we propose that simply having a realistically sized and oriented limb within peripersonal space (Lloyd, 2007) is enough to create a strong, automatic bias towards the visual estimate.

4.3. Embodiment ratings, multisensory congruence, and limb position across participants

Participants demonstrated substantially higher ratings of location/ownership with the mirror in the synchronous and no movement conditions, consistent with the increased illusory displacement in those conditions. Furthermore, participants reported the highest ratings of location/ownership during mirror tapping in the 6″ condition compared to the 12″ condition, consistent with the illusion being more effective when there is a smaller spatial discrepancy between the viewed and felt hand. Furthermore, mirror viewing during asynchronous tapping resulted in a decreased sense of agency. As agency is thought to be based on congruence between predicted and observed sensory states (Farrer & Frith, 2002; Sato & Yasuda, 2005), the mismatch caused by the discrepant visual information likely leads to a decrease in agency in the asynchronous, mirror tapping condition.

Finally, we expected that the mismatch between vision and other senses in the incongruent condition would result in a greater sense of deafference when compared to the synchronous condition. However, we found no effect of movement condition on deafference at the group level. In our experiment, participants are instructed to view relatively precise movements for 60 seconds (e.g. finger tapping) compared to the more gross arm and hand movements made in other asynchronous conditions using a mirror box (Fink et al., 1999; McCabe et al., 2005;

Foell et al., 2013). One possibility is that slight differences in tapping rates between the two hands, even during bimanual tapping, created enough incongruence to cause some deafference in the synchronous condition.

5. Conclusions

Our results provide evidence for a relationship between specific aspects of embodiment influence multisensory spatial integration. We found that an increased sense of deafference during asynchronous tapping resulted in more illusory displacement towards the visual image. This provides evidence for increased weighting of visual input during deafference, possibly reflecting gating mechanisms that decrease somatosensory inputs during intersensory conflict. We also found that an increased sense of ownership of the limb was correlated with more illusory displacement towards vision in conditions without multisensory asynchrony. These results provide evidence that specific subcomponents of subjective embodiment measures identified in previous research are linked to more objective measures of multisensory integration.

Acknowledgments

The authors would like to thank Emily Baumert, Samuel Cason, Aline Szenczy, and Megan Ziegler for their assistance. This work was supported by NIH Grant R01NS048130.

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Appendix

Questions on both the mirror and no mirror questionnaires

1. It felt as though my index fingers were making contact with each other. (Location)
2. It seemed like I couldn’t really tell where my right hand was. (Deafference)
3. I had the sensation that my right hand was numb. (Deafference)
4. I found this experience interesting. (Affect)
5. I found this experience enjoyable. (Affect)

Questions that differed on the mirror and no mirror questionnaires [mirror questionnaire wording in brackets first, followed by no mirror questionnaire wording]

6. It felt like I was in control of [the hand in the mirror/my right hand.] (Agency)
7. It seemed like my right hand [was in the same location as the hand in/was against] the mirror. (Location)

Question on the mirror questionnaire only

8. It felt as though the hand in the mirror was *my* right hand. (Ownership)

Highlights

- We examine the relationship between multisensory integration and embodiment.
- We created a conflict between visual and proprioceptive feedback with a mirror box.
- Illusory visual displacement was correlated with dissociable embodiment subtypes.
- Illusion strength positively correlated with ownership after synchronous movement.
- Illusion strength positive correlated with deafference after asynchronous movement.

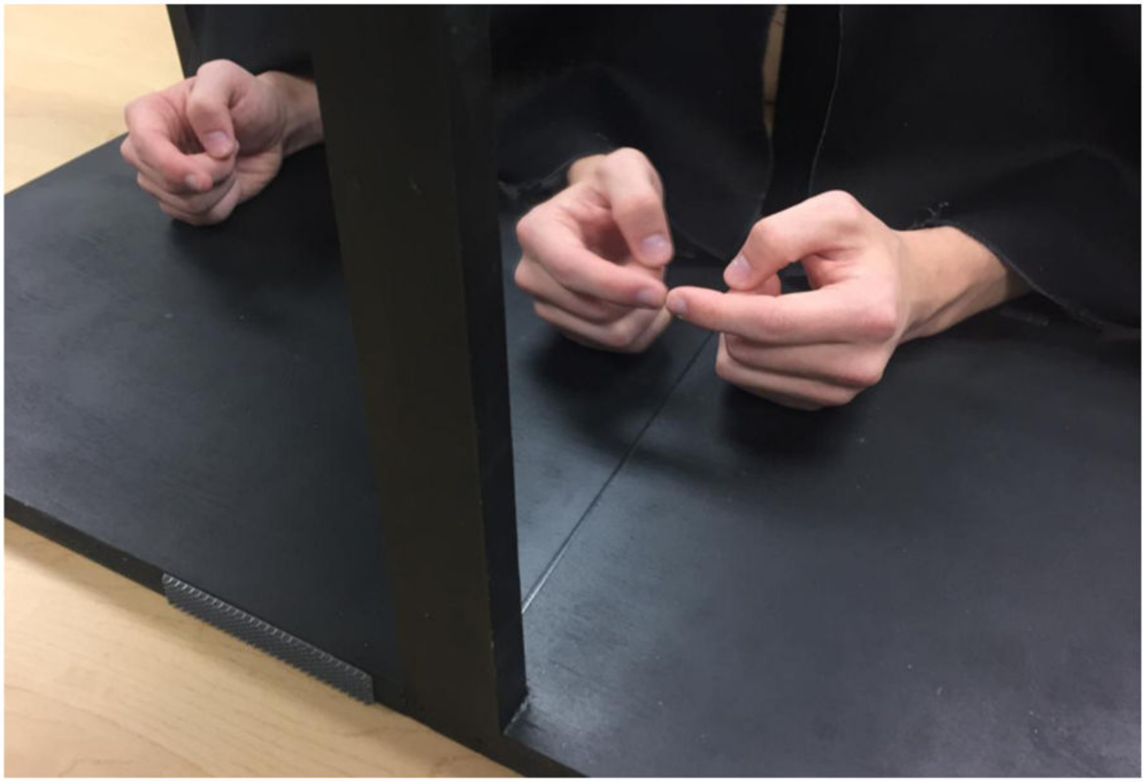

Figure 1.

Mirror box apparatus showing the viewed left hand and its reflection, with the hidden right hand 12″ from the mirror. In the actual experiment, the hidden right hand is touching a small acrylic mirror mounted to a wood block (not shown here).

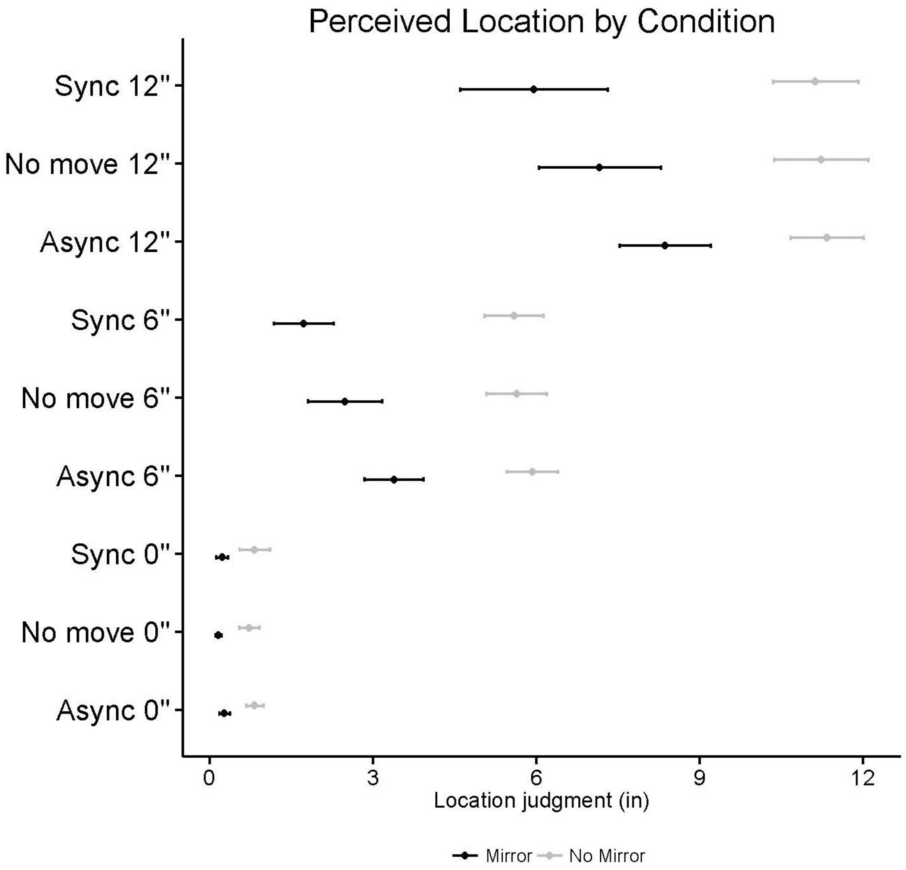

Figure 2.

Perceived hand position (in inches) in each of the nine conditions with (black) and without (grey) the mirror. Each plot shows the mean (diamond), and 95% confidence interval (bars). The visually defined hand position is at 0″ (touching the mirror) for all conditions.

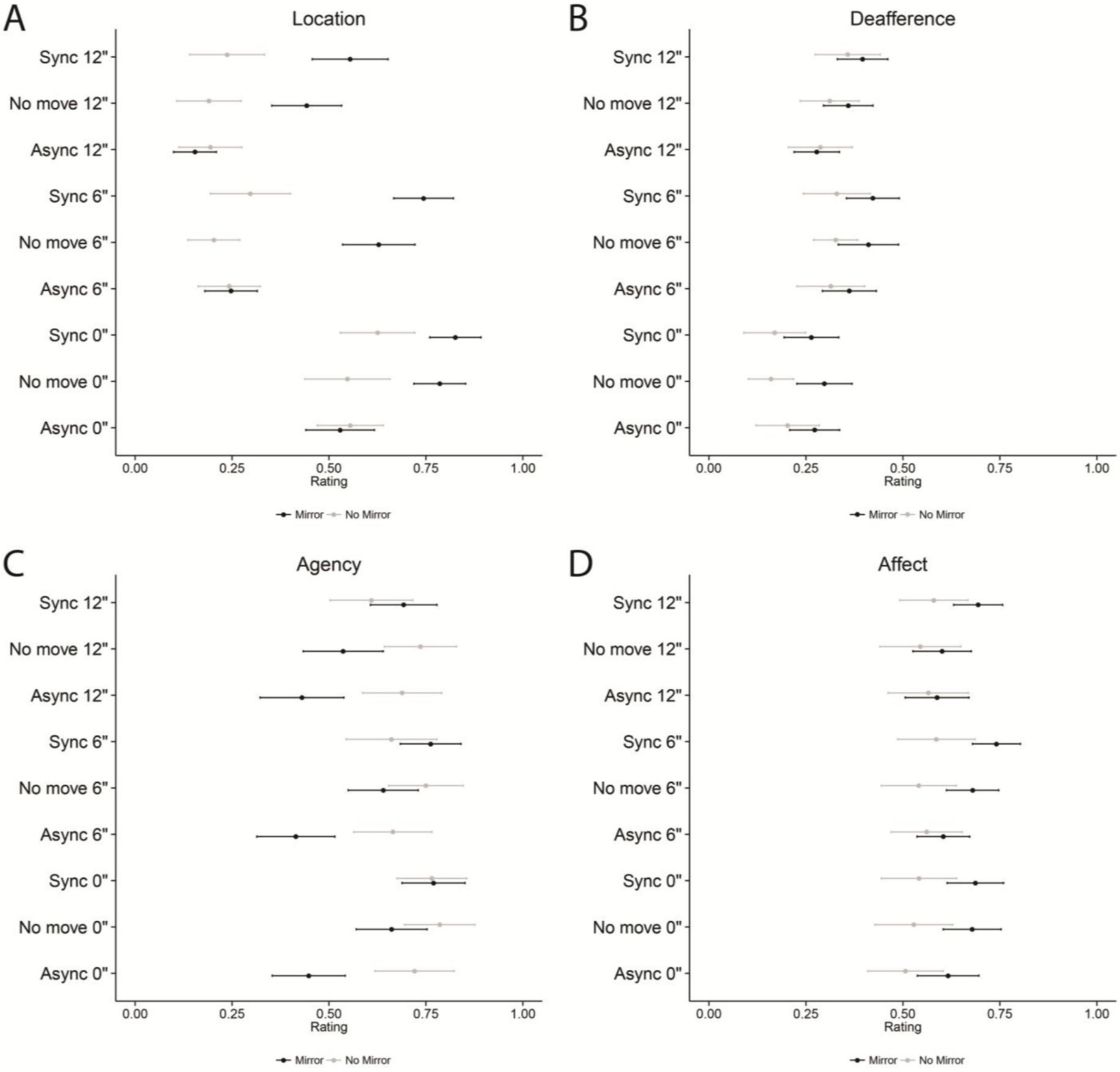

Figure 3.

Dot plots showing the mean questionnaire ratings for the four average measures of embodiment in the mirror (black) and no mirror (grey) conditions. Means (diamond) and 95% confidence intervals are shown.

Table 1

Principal Components Analyses

Movement condition	Synchronous			No Movement		
Factor	**1**	**2**	**3**	**1**	**2**	**3**
Location/Ownership						
It felt as though my index fingers were making contact with each other.	0.877			0.865		
It seemed like my right hand was in the same *location* as the hand in the mirror.	0.863			0.873		
It felt as though the hand in the mirror was *my* right hand.	0.902			0.9		
Affect						
I found this experience interesting.		0.903			0.839	
I found this experience enjoyable.		0.914			0.887	
Deafference						
It seemed like I couldn't really tell where my right hand was.			0.798			0.751
I had the sensation that my right hand was numb.			0.729			0.771
Agency						
It felt like I was in control of the hand in the mirror.	0.504				0.519	

Component loadings from the principal components analyses for the three conditions.

Component loadings less than .5 are not shown.