Illusory body-ownership entails automatic compensative movement: for the unified representation between body and action

Tomohisa Asai

Introduction

Awareness of one’s own body is fundamental for self-consciousness or for the sense of self. Body-ownership is referred to as the feeling that the body I inhabit is “my own” (Tsakiris 2010). Intuitively speaking, the sense of body-ownership is essential for the self as it constitutes the physical boundary between the self and the environment. However, recent studies have shown that the sense of body-ownership is quite plastic in spite of our intuition. Because the sense of ownership of one’s body may be realized through multimodal integration, particularly in the sensory interactions between vision and somatosensation (Kennett et al. 2001; Ladavas and Serino 2010; Taylor-Clarke et al. 2002), it could be susceptible to illusions. The rubber hand illusion (RHI) provides evidence that multisensory signals interact with body representations to generate a sense of self (Botvinick and Cohen 1998). Watching a rubber hand being stroked synchronously with one’s own unseen hand for a short time causes the observers to subjectively or explicitly attribute the rubber hand to their own body, to aver that it “feels like its my hand.”

An interesting observation in the RHI is that the observers’ sense of their own hand’s location drifts toward the external proxy hand. The rubber hand illusion (RHI) provides evidence that multisensory signals interact with body representations to generate a sense of self (Botvinick and Cohen 1998). Watching a rubber hand being stroked synchronously with one’s own unseen hand for a short time causes the observers to subjectively or explicitly attribute the rubber hand to their own body, to aver that it “feels like its my hand.”

Abstract

The sense of body-ownership involves the integration of vision and somatosensation. In the rubber hand illusion (RHI), watching a rubber hand being stroked for a short time synchronously as one’s own unseen hand is also stroked causes the observers to attribute the rubber hand to their own body. The RHI may elicit proprioceptive drift: The observers’ sense of their own hand’s location drifts toward the external proxy hand. The current experiments examined the possibility of observing, not the proprioceptive drift, but the actual drift “movement” during RHI induction. The participants’ hand, located on horizontally movable board, tended to move toward the rubber hand only while they observed synchronous visuo-tactile stimulation. Furthermore, even when the participants’ hand was located on a fixed, unmovable board (that is, the conventional RHI paradigm), participants automatically administered the force toward the rubber hand. These findings suggest that since awareness of our own body and action are fundamental to self-consciousness, these components of “minimal self” are closely related and integrated into “one agent” with a unified awareness of the body and action.

Keywords

Body · Action · Proprioceptive drift · Movement · Self-consciousness · Embodiment
not to agency (Longo et al. 2008). This suggests that, aside from the background mechanism, illusory body-ownership unnecessarily entails proprioceptive drift but might not be related to the sense of action or to the motor system. On the other hand, one study has suggested that it is only during the synchronous stimulation that the arm is rotating, concluding that “the sensory illusion is somehow recruiting the motor system” (Slater et al. 2008).

One possible mechanism of proprioceptive drift that I intend to show in this paper is related to the cross-referenced relationship between the body and action. When we do some action, the motor command should be calculated on the basis of the current state of the body to achieve the desired state (Wolpert 1997; Wolpert et al. 1995; Newport et al. 2010). In turn, once the action is done, its sensory feedback contributes to recalibrate the body state (Tajadura-Jimenez et al. 2012; Tsakiris et al. 2006). Given this inseparable relationship between the body and action, it is reasonable to suspect the role of the motor system behind the proprioceptive drift in the RHI. It is possible that the proprioceptive drift is a compensative process when localization mismatch is detected between the actual hand location (the location from which the actual proprioceptive feedback is coming) and the location of the sense of body. It is hypothesized that in this situation, the actual hand location should be adjusted to the location of the target to which we attribute the sense of body-ownership; this might be the proprioceptive drift. In other words, if the participants’ hand is free to move, we should observe not the proprioceptive drift, but the actual drift movement toward the rubber hand to compensate for the mismatch in hand localization. Here, I show the compensative automatic movement in the RHI. This motor compensation for the illusory body-ownership indicates the essential interaction between the body and action for the unified representation of the embodied self (Tsakiris et al. 2007).

Experiment 1

Method

Participants

Twenty-six university students (11 females, 15 males, average age of 19.12) participated in this experiment, but one male was excluded from the following analysis because of his excessive and uncoordinated movements during the induction phase (see below). All participants reported normal or corrected-to-normal vision, hearing, and somatosensation and no neurological abnormalities. The experiment was conducted in accordance with the Declaration of Helsinki.

Procedure

We followed the standard RHI procedure (e.g., Botvinick and Cohen 1998) except that the spatial location of the participants’ target hand (left hand in the current study) was movable during the induction phase (Fig. 1). Participants sat at a table across from the experimenter with their arms resting on the table. Participants put their left hand on a foam polystyrene board (length = 20 cm, width = 18 cm, height = 2 cm) with a handprint affixed to a horizontally movable slider (R25-320L, Pultonchain, Saitama, Japan). When movability was unnecessary, this slider was locked. A standing screen was positioned beside the left arm to hide it from the participant’s view, and a life-sized rubber model of a left hand and arm was placed on the table directly in front of the subject. The participant sat with eyes fixed on the artificial hand while two small paintbrushes were used to stroke the rubber hand and the participant’s hidden hand. A proprioceptive location judgment was obtained by having the participants adjust the arrowhead of a digital slide caliper, which was laid across the hollow pedestal, to the corresponding location using their right hand. But in Exp. 2, the movable board was fixed to a force gauge, so that board was no longer movable in this situation (almost same as the conventional RHI setup).
directly in front of the subject. The participant sat with eyes fixed on the artificial hand while two small paintbrushes were used to stroke the rubber hand and the participant’s hidden hand. The stroking was manually delivered by the experimenter at 1 Hz in time with metronomic beats that only the experimenter could hear. The initial distance between the participant’s left hand and the rubber hand was 17.5 cm. The slider was locked at this point.

The experiment consisted of three blocks: synchronous stroking, asynchronous stroking (alternative stroking between both hands), and a control condition (the stroking was delivered only on the rubber hand). The order was counterbalanced across the participants. A pretest proprioceptive location judgment was obtained by asking the participants, with their eyes open, to adjust the arrowhead of a digital slide caliper to where they felt the tip of their middle finger with their eyes open, to adjust the arrowhead of a digital slide caliper to where they felt the tip of their middle finger. Location judgment was made in the same manner as the pretest. Following this proprioceptive judgment, the RHI questionnaire was administered, which contained 16 items (e.g., Botvinick and Cohen 1998) was administered, which was modified for the current experiment. Participants were asked to indicate the extent of their agreement or disagreement with each item on a seven-point Likert scale (ranging from −3 to +3): (1) “It seemed as if my real hand were absorbed by the rubber hand.” (2) “It felt as if my (real) hand was turning ‘rubbery’.” (3) “I felt as if my (real) hand was drifting toward the left (toward my hand).” (4) “It appeared (visually) as if the rubber hand were drifting toward the left (toward my hand).” (5) “The rubber hand began to resemble my own (real) hand, in terms of shape, skin tone, freckles, or some other visual feature.” (6) “It seemed as if my real hand and the rubber hand were integrated into one gradually.” (7) “It seemed as if I had more than one left hand.” (8) “It seemed as if my real hand were drifting toward the right (toward the rubber hand).” (9) “It felt as if my (real) hand was turning ‘rubbery’.” (10) “It seemed as if my (real) hand were drifting toward the right (toward the rubber hand).” (11) “The rubber hand began to resemble my own (real) hand, in terms of shape, skin tone, freckles, or some other visual feature.” (12) “It seemed as if my real hand and the rubber hand were integrated into one gradually.”

Three experimental indices were obtained from this procedure. RHI questionnaire scores provide the subjective measure of the RHI. Proprioceptive drifts were the distances between the participants’ reported pretest and posttest locations, which provide the objective measure of the conventional RHI (Botvinick and Cohen 1998). Drift movements were the distances between the participants’ actual pre- and post-hand (or the board) locations. Positive values of drift movement or proprioceptive drift mean that the participants’ actual hand location or perception of their hand position drifted toward the proxy hand after the induction phase (rightward in the current experiment). It was hypothesized that if the conventional proprioceptive drift is a proxy of actual drift movement, the current results should show not the proprioceptive drift, but the drift movement only under the synchronous stroking condition.

Results and discussion

Repeated measures using an analysis of variance with condition (synchronous, asynchronous, and control) as the within-subject independent variable and drift movement as the dependent variable (i.e., an one-way ANOVA) revealed that the main effect of the condition was statistically significant \[F(2, 48) = 5.23, p = 0.001; \text{Fig. 2a}\] but that it was not significant in the same one-way ANOVA for the proprioceptive drift \[F(2, 48) = 1.95, p = 0.154; \text{Fig. 2b}\]. The perception of the hand location drifted toward the rubber hand regardless of the condition, but there was no difference among conditions. Maybe this was because participants’ hands were moveable (they agreed with Q2: “It was difficult to keep my left hand immobile during the stimulation,” compared with other control items) and rightward drifts were natural in terms of the anatomical structure of the left arm (e.g., Wann and Ibrahim 1992) (see also the results of Exp. 2). To be sure that there was no difference among conditions in the proprioceptive drift, another measure of proprioceptive drift was calculated. The conventional proprioceptive drift (proprioceptive drift A) is defined as just the distance between the participants’ reported pretest and posttest locations, because their actual hand location is the same between the tests (participant’s hand is unmovable). In contrast, the new measure of proprioceptive drift (proprioceptive drift B) is the difference in localization error (the distance between the actual location and reported...
one) between the tests since the actual pretest and posttest locations were not the same (see Supplementary Fig. S1). However, even in this new measure, there was no statistical difference in the proprioceptive drift (see Supplementary Fig. S2).

Regarding drift movement, a multiple comparison using Ryan’s method (generally speaking, the most powerful in statistical power among the commonly used multiple comparison methods, Kirk 1995) revealed significant differences between synchronous and asynchronous conditions and between synchronous and control conditions (ps < 0.05). Participants’ actual hand location drifted toward the rubber hand during the synchronous stimulation even though they were instructed to relax their hand on the slider. This phenomenon could be interpreted as the automatic compensative movement in the RHI since we can see in what follows that participants felt illusory body-ownership of the proxy hand from the results of the questionnaire.

The questionnaire score as the dependent variable was analyzed using an ANOVA with condition (synchronous, asynchronous, and control) and item (12 questionnaire items) as the within-subject independent variables. This two-way ANOVA revealed a significant interaction [F(22, 528) = 6.79, p < 0.001], a main effect of condition [F(2, 48) = 39.08, p < 0.001] and a main effect of item [F(11, 264) = 16.02, p < 0.001] (Fig. 2c). A multiple comparison of the main effect of conditions using Ryan’s method revealed significant differences between synchronous and asynchronous conditions, between synchronous and control conditions, and between asynchronous and control conditions (ps < 0.05). Furthermore, significant differences between synchronous and asynchronous conditions (multiple comparison of the simple main effect of conditions) were observed for Q1, 3, 5, and 12 (ps < 0.05). The illusory sensory “location” (Q1 and Q5) and “ownership” of the rubber hand (Q3 and Q12) are typical subjective feelings caused by the RHI (Longo et al. 2008). Though participants’ hands were movable in the current experiment, their reports are typical ones seen in the classic RHI. They did not report the sense of actual drift (Q4 or Q10) even under the synchronous condition in comparison with that under the asynchronous condition (see below for the correlation analysis).

First of all, participants felt illusory body-ownership of the proxy hand subjectively. The questionnaire scores were generally enhanced under the synchronous condition. We would expect the proprioceptive drift if subjective ownership of the rubber hand is felt in the conventional RHI. However, in the current experiment, where the only difference was that participants’ hands were movable, the proprioceptive drift was not observed. Instead, participants’ actual hand locations drifted toward the rubber hand during the synchronous stimulation even though they were instructed to relax their hand on the slider. To investigate the direct relationship between drift movement and subjective feeling, Pearson’s product-moment correlation coefficients between the proprioceptive drift and the score of each item on the questionnaire were calculated (Table 1). The analysis revealed that drift movement under the synchronous condition was positively correlated with items 2, 3, 4, and 7 (ps < 0.05), while drift movement under asynchronous or control conditions was not, except for the combination between the asynchronous condition and Q7. These items are related to the subjective sense of “drift movements” (Q2, 4, and 7) as well as to the typical sense of “illusory ownership” over the rubber hand (Q3).
The drift movements should suggest that if the spatial difference between the perception of the hand location and the target of body-ownership is detected, the body automatically tries to compensate for and reduce that mismatch by moving. Since the body and action have a cross-referenced relationship, they cannot be independent of each other (Tsakiris et al. 2007). When the hand cannot move, instead of actual movement, the hand might only be perceived to drift toward the rubber hand, where the motor command is given, and then the brain expects the movement and its sensory feedback: This might be the proprioceptive drift.

The current experiment showed the congruency between subjective and objective indexes of not the proprioceptive drift but of the drift movement in the RHI, indicating that illusory body-ownership entails automatic compensatory movement. However, this congruency might also be the problem, because participants might have known the purpose of the experiment through the questionnaire. Or this drift movement might be observed only under the current setup: The movable situation could cause a top-down indication of drift movement. Indeed, even under the control condition, participants’ hands slightly moved toward the rubber hand. This problem was tackled in the second experiment, where the conventional RHI setup was delivered (the participants’ hands were no longer mobile) but the unconsciously applied force (leftward or rightward) was recorded during the induction as a function of actual drift movement. In this situation, participants had no idea that they could move their hand.

**Experiment 2**

**Method**

Thirty university students (19 females, 11 males, average age of 18.6) participated in this experiment. The basic procedure was almost the same as in Exp. 1 except that the movable board was fixed to a force gauge (FGJN-2, NIDEC-SHIMPO CORPORATION, Kyoto, Japan) (Fig. 1) so that board was no longer movable. Even if participants tried to move their hand rightward or leftward, the board would not move, but the applied force was recorded. The sampling rate was 1 Hz.

Participants were randomly divided into two groups: Near and Far groups. The distance between their left hand and the rubber hand was 17.5 cm (the same distance as in Exp. 1) for the Near group; it was 35 cm for the Far group. The spatial location of the rubber hand was fixed for both groups. These two groups were needed for the “between–control” condition as well as for the “within–control” condition in the RHI. Previous studies suggested that proprioceptive drift is observed not under the asynchronous but under the synchronous condition, and the current study examined this as a within factor. On the other hand, even under the synchronous condition, there are some constraints in the RHI. One is the anatomical constraint (See Tsakiris 2010 for a review). For example, if the distance between the actual hand and rubber hand is too large (>30 cm), the RHI would decay (Lloyd 2007). Accordingly, we can expect to observe the proprioceptive drift in the Near group but not in the Far group. This is the between factor in the current experiment. I hypothesized that the proprioceptive drift would be observed only under the synchronous condition and only in the Near group. Furthermore, if the proprioceptive drift is the proxy of actual drift movement as Exp. 1 suggested, we would see the corresponding force instead of the actual movement only under this condition.

**Results and discussion**

Repeated measures using an analysis of variance with condition (synchronous, asynchronous, and control) as the within-subject independent variable, group (Far and Near...
groups) as the between-subject independent variable, and the proprioceptive drift as the dependent variable (i.e., two-way ANOVA) revealed that the interaction was significant \[ F(2, 56) = 8.73, p < 0.001 \] and the main effect of the condition was statistically significant \[ F(2, 56) = 7.18, p < 0.001; \text{Fig. 3a} \]. The simple main effect of condition was significant only in the Near group \[ F(2, 56) = 15.48, p < 0.001 \], and then the multiple comparison using Ryan’s method revealed significant differences between synchronous and asynchronous conditions, between synchronous and control conditions, and between asynchronous and control conditions \( ps < 0.05 \). These results are consistent with previous studies that suggested that the proprioceptive drift should be elicited only under the synchronous stroking condition and also only for the closer rubber hand (Lloyd 2007).

Figure 4 shows the time course of the unconsciously applied force, which was down-sampled every 30 s with averaging. The positive values mean the rightward (toward the rubber hand) force, and the negative ones mean the leftward force. Since the applied force in the control condition was different between the two groups (maybe because of the difference in arm position) and there was not any trend in the time course, the subtracted force values were calculated, on the basis of the control condition, for asynchronous/synchronous conditions over a period of 180 s (Fig. 3b). A two-way ANOVA with condition (synchronous and asynchronous) as the within-subject independent variable, group (Far and Near groups) as the between-subject independent variable, and the applied force level as the dependent variable revealed that the interaction was
significant \( [F(1, 28) = 10.78, p = 0.003] \). The simple main effect of condition was significant only in the Near group \( [F(1, 28) = 7.93, p = 0.009] \), and the simple main effect of group was significant only under the synchronous condition \( [F(1, 56) = 5.17, p = 0.027] \). The synchronous condition only in the Near group elicited the proprioceptive drift and also entailed the unconsciously applied force toward the rubber hand as hypothesized.

Figure 3c shows the differences in questionnaire scores for the two groups, but only for the synchronous condition for simplification (see Supplementary Fig. S3 for full results). A two-way ANOVA with group (Far and Near groups) as the between-subject independent variable, item (12 questionnaire items) as the within-subject independent variable, and the questionnaire score under the synchronous condition as the dependent variable revealed that the interaction was not significant \( [F(11, 308) = 0.903, p = 0.54] \). When a \( t \) test was applied for each item, a significant difference was observed only for item 3 (“I felt as if the rubber hand was my hand”). Though this subjective feeling is the most typical impression for the RHI (sense of “illusory ownership” over the rubber hand), the subjective feelings were not so different between the two groups compared with the results for proprioceptive drift or for the applied force. In particular, there was no difference for items related to the sense of drift movement (Q2, 4, and 7) that were correlated with actual drift movement in Exp. 1. This result is consistent with previous studies. Some papers have suggested a significant correlation between proprioceptive drift values and the subjective sense of drift (e.g., Asai et al. 2011), but Longo et al. (2008) suggested that the subjective sense of “movement” (that is, drift) has a marginal effect, whereas the sense of “embodiment of the rubber hand” is, as a whole, related to proprioceptive displacement in the classic RHI.

Taken together, even when participants did not feel the subjective sense of drift movement, the synchronous stimulation entailed the unconsciously applied force toward the rubber hand as well as the proprioceptive drift in the Near group. This result indicates that even in the classic RHI setup, where participants’ hands are not movable and they do not have any a priori information about potential movements, they administered the force toward the rubber hand implicitly only under the illusional condition (i.e., synchronous stroking between the closely located rubber hand and the actual hand), possibly causing the proprioceptive drift.

Finally, the direct relationship between the force level and proprioceptive drift was examined for all data in Exp. 2 where the conditions and groups were collapsed (Fig. 5). Pearson’s product-moment correlation coefficients between them were statistically significant \( (r = 0.22, p = 0.038) \). This significance was still kept when a nonparametric test was conducted (Spearman’s \( \rho = 0.21, p = 0.048 \)), indicating no outlier effect. When participants reported stronger proprioceptive drift, stronger applied force level was recorded. This is because the body and action have a cross-referenced relationship, and if the sense of body-ownership is recalibrated, the motor system should be adjusted for this. Since the correlation between them is not so strong, I cannot say that the hand movement and proprioceptive drift are in a completely compensatory relationship. What I can say from the current results is that one factor in the proprioceptive drift is the motor compensation of the detected localization error. In what follows, I discuss this relationship in terms of the sense of self.

**General discussion**

The present study suggests that illusory body-ownership for the proxy hand entails automatic compensative movements toward it. Experiment 1, where the participants’ hand was located on a horizontally movable board, showed that participants tended to move their hand automatically toward the rubber hand only while they observed synchronous visuo-tactile stimulation; That is, there was actual drift movement toward the proxy. Furthermore, Exp. 2 showed that even when the participants’ hand was located on a fixed, unmovable board (the conventional RHI paradigm), participants automatically administered force toward the rubber hand, indicating automatically administered force, as a function of drift movement, in the direction of the proxy. On the other hand, proprioceptive drift was observed in Exp. 2, but not in Exp. 1, because when the participants’ hands actually moved, their sense of hand location did not...
have to be captured, indicating that the proprioceptive drift might be a substitute for automatic compensative movement when the hand is immovable.

This interaction between the body and action should not be surprising (e.g., Asai et al. 2012). Intuitively or theoretically, multimodal body representation (i.e., body-ownership) is achieved first and then contributes to the awareness of action (i.e., agency) (Schwabe and Blanke 2007). When we do some action, motor commands for the desired action are computed inversely on the basis of the current body state (Wolpert 1997). Therefore, when the sense of hand location drifts toward the proxy, the following reaching trajectory is affected (Newport et al. 2010). On the other hand, awareness of one’s own action, without body representation, could capture the hard-wired sense of body-ownership. Once the action is done, its sensory feedback contributes to recalibrate the body state (Tajadura-Jimenez et al. 2012; Tsakiris et al. 2006). A good example is the active version of the RHI where the participants’ perception of their hand (finger) location has been shown to drift toward proxy movements after they have observed movements synchronous with those of their own hand for a while (Tsakiris et al. 2006). These studies suggest that the body and action must be linked intrinsically in terms of self-awareness because there can be only one “I” (Tsakiris et al. 2007).

The proprioceptive drift might be the by-product not of embodiment of the rubber hand (Longo et al. 2008), but of drift movement that is by definition related to the motor system (Slater et al. 2008). The sense of actual hand position is always available through muscle spindles, and contacting the surface like in the current setup improves the accuracy of the judgment of its position (e.g., Rao and Gordon 2001). Even if so, this sense could be visually captured under the RHI. In this situation, sensory-based implicit hand location (bottom-up location) is in conflict with the location of a rubber hand to which we explicitly attribute our own body-ownership (top-down location). When compared between somatosensory and vision, visual information seems to be preferred and to override somatosensory information at least when it comes to localization. That is why our localization drifts toward the rubber hand. The important point here is that even in this situation, muscle spindles are still sending information regarding the location and the localization conflict should therefore always be calculated. Participants do not report the location of the rubber hand, but a location midway between it and their actual hand, indicating that somatosensation still exists (could be weakened though, Moseley et al. 2008) or that visual capture was not perfect. The felt position might be determined by maximum-likelihood estimation (White et al. 2011) because the two sensory events are perceived as a single underlying cause (Körding et al. 2007). In line with this, some previous studies suggested that people with high (or low) sensitivity to their body state are less (or more) susceptible to RHI (e.g., Asai et al. 2011; Tsakiris et al. 2011). The question that I tackled in the current study is how our brain resolves this detected localization conflict in an RHI situation. The actual drift movement maybe one possible solution when the hand is movable as the current study shows. Another might be the proprioceptive drift when the hand is immovable. Therefore, when the actual drift movement is possible, proprioceptive drift is no longer necessary (Exp. 1). In the strict sense, however, we are still unsure whether the proprioceptive drift and drift movement are in a compensatory relationship (in other words, proprioceptive drift could just be a substitute when drift movement is unavailable) since the correlation between the force level and proprioceptive drift was not so strong in Exp. 2. Instead, proprioceptive drift and drift movement might be independent solutions, not alternative ones, for resolving localization conflict. Further study should reconsider what the proprioceptive drift is and why it is necessary.

Body representation includes “body schema” for action as well as “body image” for perception, which are separately embodied (Preston and Newport 2011). This study also suggests that the RHI recalibrates the body schema as well as the body image. These findings suggest that since awareness of our own body and action are fundamental to self-consciousness, these components of the “minimal self” (Gallagher 2000) are closely related and are integrated into “one agent” with a unified awareness of the body and action.

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