Sleeping on the rubber-hand illusion: memory reactivation during sleep facilitates multisensory recalibration

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Abstract

Plasticity is essential in body perception so that physical changes in the body can be accommodated and assimilated. Multisensory integration of visual, auditory, tactile, and proprioceptive signals contributes both to conscious perception of the body's current state and to associated learning. However, much is unknown about how novel information is assimilated into body perception networks in the brain. Sleep-based consolidation can facilitate various types of learning via the reactivation of networks involved in prior encoding or through synaptic down-scaling. Sleep may likewise contribute to perceptual learning of bodily information by providing an optimal time for multisensory recalibration. Here we used methods for targeted memory re-activation (TMR) during slow-wave sleep (SWS) to examine the influence of sleep-based reactivation of experimentally induced alterations in body perception. The rubber-hand illusion (RHI) was induced with concomitant auditory stimulation in 24 healthy participants on 3 consecutive days. While each participant was sleeping in his or her own bed during intervening nights, electrophysiological detection of SWS prompted covert stimulation with either the sound heard during illusion induction, a counterbalanced novel sound, or neither. TMR systematically enhanced spatial recalibration of perceived hand location during subsequent inductions of the RHI. Illusory feelings of body ownership for the rubber hand also differed as a function of whether the novel or RHI-associated sound was played on the prior night. This evidence for sleep-based modulation of a body-perception illusion demonstrates that the recalibration of multisensory signals can be altered overnight to modify new learning of bodily representations. Sleep-based memory processing may thus constitute a fundamental component of body-image plasticity.

Key words: embodiment; slow-wave sleep; memory replay; consolidation; binding; multisensory integration

Introduction

The sense of embodiment is a central aspect of human consciousness. Throughout daily experience, internal models of the body constrain interpretations of sensory input in forming a coherent percept of the body's location, configuration, and spatial extent (Graziano and Botvinick, 2001; Tsakiris, 2010; Ivanenko *et al.*, 2011). Over a lifetime, these models must evolve to accommodate physical changes in the body due to growth

(Visser *et al.*, 1998; Ishak *et al.*, 2014), injury and medical intervention (Ramachandran and Hirstein, 1998; Dominici *et al.*, 2009), or biological events such as puberty (Rogol *et al.*, 2000) or pregnancy (Franchak and Adolph, 2013). Over shorter timescales, neural representations of the body strategically adapt to changing behavioral demands, such as tool use (Maravita and Iriki, 2004). These situationally optimized body representations are also learned and refined over time. However, much is unknown about how novel information about the body is acquired and maintained.

On the timescale of perception and action, a dynamic integration of visual, tactile, and proprioceptive information is fundamental to determining which parts of the sensory environment are identified as parts of the body (Blanke, 2012; Ehrsson, 2012). For example, in the rubber-hand illusion (RHI), viewing an artificial hand that is touched synchronously with tactile stimulation of one's own hand causes the artificial hand to be perceived as if part of one's own body (Botvinick and Cohen, 1998).

The RHI also induces a recalibration between the spatial alignment of visual and proprioceptive cues, resulting in a distortion of the perceived spatial location of the observer's real hand when not in view (Longo *et al.*, 2008). Multisensory recalibration is a general process in which the spatial or temporal alignment of auditory, visual, and tactile signals is updated to accommodate a spatial (Recanzone, 1998) or temporal (Van der Burg *et al.*, 2013) offset between the senses (for a review, see Chen and Vroomen, 2013). Recalibration occurs extremely quickly, within a short experimental session or even from one trial to the next (Wozny and Shams, 2011; Van der Burg *et al.*, 2013), and persists over time if there is no competing recalibration. In real-world contexts, temporal or spatial recalibration is typically extinguished shortly after training due to competing information from the environment. However, because the prolonged maintenance of visuo-proprioceptive recalibration is critical to tool-usage and body-image updating, a comprehensive understanding of how recalibrated representations are learned is needed, as are methods of selectively enhancing this learning.

One candidate mechanism that might contribute to the neural assimilation of recalibrated body representations is sleep-dependent memory consolidation. Sleep-dependent consolidation can facilitate both the selection of important information for storage (Fischer and Born, 2009; Wilhelm *et al.*, 2011) and the integration of novel information into existing neural representations (e.g., Tamminen *et al.*, 2010; Lewis and Durrant, 2011; Stickgold and Walker, 2013). Consolidation during sleep promotes long-term storage of valuable information by selectively reactivating networks that previously encoded important experiences (Diekelmann and Born, 2010; O'Neill *et al.*, 2010; Born and Wilhelm, 2011). Sleep may provide an optimal time for neural assimilation of bodily information because decreased bodily demands might reduce network interference between consolidation and ongoing body perception.

Targeted memory reactivation (TMR) using covert sound or odor cues during slow-wave sleep (SWS) can influence sleep-dependent consolidation by reactivating specific memories that may not have otherwise been selected for preferential processing (Oudiette and Paller, 2013). Auditory TMR can improve visuospatial learning (Rudoy *et al.*, 2009; Oudiette *et al.*, 2013; Creery *et al.*, 2015), verbal learning (Fuentemilla *et al.*, 2013; Schreiner and Rasch, 2015), unlearning of social bias (Hu *et al.*, 2015), and sensorimotor skill learning (Antony *et al.*, 2012), demonstrating a causal role for sleep-based reactivation in the consolidation of these types of information. Whereas body

perception may rely partially on visuospatial and sensorimotor processing similar to that known to be enhanced by TMR (Andersen, 1987; Graziano *et al.*, 1994), no research to date has directly examined the role of sleep-based reactivation in the implicit learning that subserves body perception.

We used auditory TMR to reactivate memories of multisensory recalibration induced by the RHI. If body perception changes are reactivated during sleep, then TMR might affect the extent to which they influence subsequent perception. On one hand, TMR might strengthen the RHI during subsequent inductions by facilitating the assimilation of RHI information into body perception networks. On the other hand, TMR might decrease illusion strength by stabilizing prior body representations (Honma *et al.*, 2014). If sleep is not relevant for learning with respect to body perception, then TMR would have no effect.

Methods

Participants

Twenty-four young healthy adults (mean age = 20.1 years; 18 females) were compensated for their participation (US$40). They reported no history of drug or alcohol abuse, and no neurological or psychiatric disorders. They all had normal sleep screening test results (Buysse *et al.*, 1989; Pittsburgh Sleep Quality Index; mean score = 4.11, SEM = 0.35). The Northwestern University Institutional Review Board approved the study protocol, and all participants provided written informed consent.

Procedure

Design

The RHI was induced once a day for three consecutive days. In each session, participants repeatedly indicated their subjective feeling of bodily ownership of the rubber hand and the perceived location of the stimulated hand while it was out of sight. In synchrony with illusion induction, one of two sounds was presented (counterbalanced across participants in each group). During the two intervening nights, participants were covertly presented with either the same sound that they heard during illusion induction, the other sound, or neither sound.

The procedure was designed to assess effects of TMR by comparing sleep cueing with sounds associated with RHI induction to sleep cueing with sounds not associated with RHI induction. Accordingly, equipment for sound presentation during sleep was set up in an identical way on all nights, but without participants knowing whether or not the RHI sound would be presented. They were merely told that sounds superimposed on white noise may play without their knowledge during deep sleep. We thus compared RHI effects on the day after sleep with the associated sound (TMR condition) to RHI effects on the day after sleep with the novel sound.

In a crossover design, participants were randomly assigned to the TMR-1 group or the TMR-2 group. In the former case, participants had TMR on the first night and novel-sound stimulation on the second night (n = 8, 6 females, mean age = 20.0). In the latter case, participants had novel-sound stimulation on the first night and TMR on the second night (n = 8, 6 females, mean age = 20.1). This contrast effectively dissociated TMR effects from possible effects of repeated stimulation. In order to observe the effects of repeated stimulation in the absence of any sound stimulation during sleep, we included an additional group (no-sound condition; n = 8, 6 females, mean age = 20.5).

RHI induction and measures

Figure 1 shows a schematic experimental setup. The participant sat at a table and placed his or her head on a chin rest that was adjusted to a comfortable height. The left hand was positioned so that the tip of the middle finger rested on a point marked on the table. The participant was asked to hold the hand still in this position. A standard artificial hand was placed to the right of the participant's left hand, with the wrist area wrapped in a towel that extended below the edge of the table, so that the artificial hand could conceivably be connected to the participant's body from the participant's point of view. The distance from the middle finger of the left hand to the middle finger of the rubber hand was 150 mm. A partition prevented the participant from viewing his or her own left hand from the position of the chin rest, and the partition was positioned at the midpoint between the real and rubber hands.

Participants were instructed to attend to the rubber hand throughout the RHI induction. The experimenter used two small paintbrushes to stroke the participant's hand and the rubber hand simultaneously and in synchrony with 150 repeated sounds. Two unusual sounds were created from frequency-modulated pure tones for this purpose (available as Supplementary Data). Each sound lasted 1 s and was presented with a 1-s inter-stimulus interval. Sound presentations (40 dB) were counterbalanced, such that one sound was used for half of the participants and the other sound for the remaining participants. Each time the sound played, a stroke was applied from the base of the middle finger to the tip of the middle finger.

Each session began and ended with a test of participants' perception of hand location. The right hand was used to indicate the perceived location of the middle finger of the left hand. The task was to draw a straight line under the desk (on a piece of paper affixed there) from the tip to the base of the finger while viewing the rubber hand. This provided a measure of the extent to which the perceived location of the left hand shifted toward the rubber hand, a feature of the RHI known as "proprioceptive drift."

Participants reported on subjective ownership of the rubber hand before RHI induction (immediately after the first hand-location test), and 10 additional times during 5-s breaks after every 15 sound-stroke stimulations. A visual analog scale was provided, with "no feeling" indicated at the left of a 100-mm-long horizontal line and "strong feeling" at the right. Participants used their right hands to draw a vertical mark on the line to indicate their subjective feeling of the extent to which the rubber hand seemed like part of their own bodies. Scores were calculated on a 100-point ownership scale where 0 represented "no feeling" and 100 represented "strong feeling."

Auditory stimulation during sleep

Participants received direct instructions and a demonstration of the electroencephalographic (EEG) recording methods, so that sleep monitoring could be carried out in the home. They brought home a sleep-monitoring system (Sheepdog Sciences, Inc.) that included a laptop computer equipped with sleep-monitoring hardware and software, some of which was adapted from the Zeo personal sleep system. The computer was set up near the bed, and the participant prepared for their own recordings just prior to sleep.

First, they cleaned an area on the forehead with an alcohol pad. Then, three sensors (single-use silver/silver-chloride electrode on a foam sticker) were snapped into a battery-powered wireless transmitter and filled with electrolyte (signa gel). The paper backing on each sensor was removed to reveal the
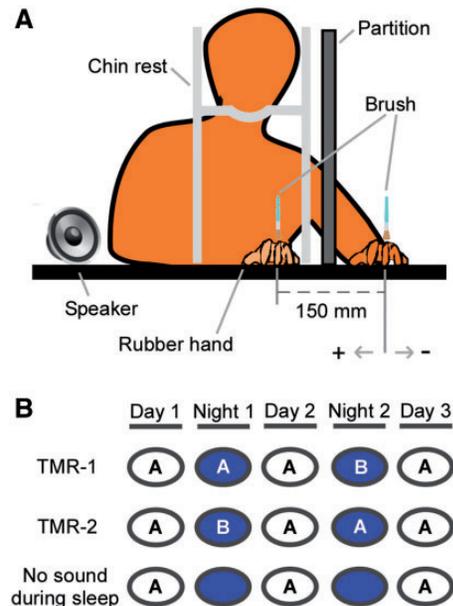

Figure 1. Experimental paradigm. (A) During the RHI-induction session, the participant's head was held stationary on a chin rest, the participant's left hand was obscured from view by a partition, and a realistic life-sized rubber left hand was placed 150 mm to the right of the participant's left hand. A speaker was placed on the table to the right of the participant. Two small paintbrushes were used to stroke the rubber hand and the left hand simultaneously. (B) In each experimental group, there was an RHI-induction session each day for 3 days. In the TMR-1 and TMR-2 groups, a sound was played during SWS on the first and second night, as depicted by the ovals (either the sound used during illusion induction, A, or the other sound, B). The third group received neither sound during sleep. See text for further details.

adhesive surface, and then the sensors were affixed on the forehead at locations corresponding roughly to three locations near Fpz of the international 10–20 system (one ground, one active, and one reference electrode). Single-channel EEG was transmitted wirelessly to a receiver connected to the computer, so that 30-s epochs could be classified based on time-domain and frequency-domain characteristics of the signal (Shambroom et al., 2012). Classification was achieved using an algorithm optimized via an artificial neural network trained to maximally reflect determinations made by a human sleep scorer using conventional guidelines for laboratory polysomnography (Rechtschaffen and Kales, 1968). Auditory stimuli were presented at 5-s intervals whenever the classification algorithm detected SWS. Therefore, the amount of auditory stimulation depended on the amount of SWS each night. However, there were no systematic differences in the amount of auditory stimulation during the TMR and novel sound conditions (see below).

Prior assessments have found moderate to high overall agreement between classification with the Zeo system and full polysomnography (Griessenberger et al., 2012; Shambroom et al., 2012; Tonetti et al., 2013; Cellini et al., 2015). Our procedures corresponded to those of the Zeo system except that we used electrolyte-filled electrodes in place of the Zeo dry electrodes. Importantly, the Zeo system has been found to be conservative in its detection of SWS (Griessenberger et al., 2012; Tonetti et al., 2013), and to score as SWS only 3–5% of epochs scored as
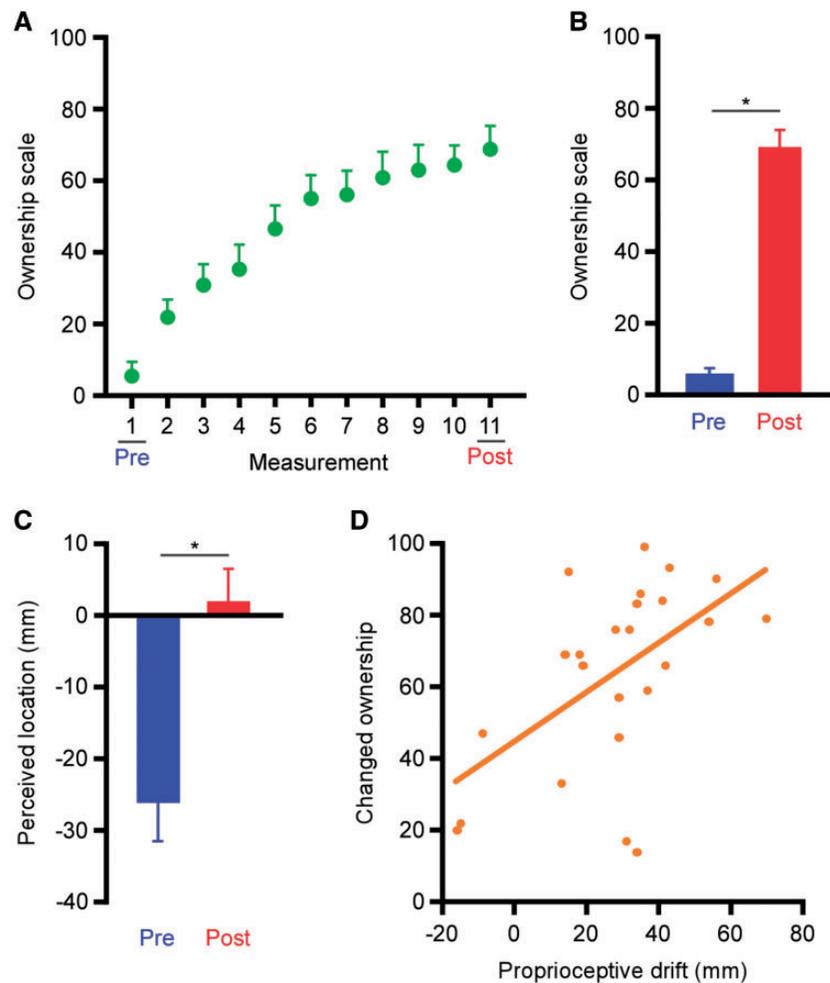
Figure 2. Successful RHI induction. (A) Ownership ratings showed little feeling of subjective ownership at measurement 1 (prior to RHI induction) and a steadily increasing feeling of subjective ownership over the course of RHI induction. (B) Comparison of ownership ratings between first and last measurements showed that subjective ownership increased after illusion induction. (C) Measures of perceived hand location demonstrated proprioceptive drift, in that the left hand was perceived to be closer to the rubber hand following RHI induction (0 denotes the actual location of the middle finger; negative values are locations farther from the rubber hand). (D) Changes in ownership ratings were positively correlated ($r = 0.549$) with proprioceptive drift. Error bars indicate standard error of the mean (SEM) and * indicates a significant difference between conditions ($P < 0.05$).

wakefulness by experts (Griessenberger *et al.*, 2012; Shambroom *et al.*, 2012). Therefore, it is unlikely that any observed effects of nighttime stimulation were due to unintentional stimulus presentation during wakefulness. In previous research using this system, its measure of overall SWS was found to predict retention for word pairs learned before sleep (Scullin, 2013), suggesting that it can successfully track the periods of sleep critical for memory reactivation during sleep.

Results

RHI on Day 1

Measures of subjective ownership and perceived hand location collected on Day 1 indicated that the RHI was successfully induced. Pooling across all participants, ownership ratings gradually increased with continued stimulation, as shown in Fig. 2A (one-way repeated-measures analysis of variance, RM-ANOVA: $F_{10, 230} = 44.870$, $P < 0.0001$; logarithmic regression: $R^2 = 0.992$, $F_{1, 9} = 1060.102$, $P < 0.0001$). Comparing the first and last ratings

revealed that ownership of the rubber hand increased dramatically after training (paired t test: $t_{23} = 11.952$, $P < 0.0001$; Fig. 2B). Perceived hand location also shifted toward the rubber hand after training, demonstrating proprioceptive drift ($t_{23} = 6.549$, $P < 0.0001$; Fig. 2C). Location ratings prior to RHI induction were not accurate, but rather averaged about 25 mm to the left of the actual location of the middle finger of the left hand (indicated by 0 mm on the location scale); yet, the perceived location of the left hand shifted to the right, in the direction of the rubber hand, following RHI induction.

To summarize these illusion-induced changes for subsequent analyses, we subtracted pre-stimulation scores from post-stimulation scores. On Day 1, changes in ownership ratings were correlated with the amount of proprioceptive drift across participants (Fig. 2D; Pearson's $r = 0.549$, $P = 0.005$).

RHI across the 3 days

To assess effects of repeated RHI induction without any sleep manipulation, we compared illusion-induced changes in perception in

the no-sound condition across the 3 days of testing. Proprioceptive drift decreased across days (one-way RM-ANOVA: $F_{2, 14} = 5.586$, $P = 0.016$; linear trend: $F_{1, 7} = 9.299$, $P = 0.019$) from a mean drift of 28.8 mm (within-subjects SEM = 3.1) on Day 1, to 19.8 mm (2.6) on Day 2, and to 12.0 mm (5.3) on Day 3. However, as shown in Fig. 3A, these decreases were accompanied by an overall shift in the perceived location of the hand toward the rubber hand across days (two-way RM-ANOVA; main effect of day: $F_{2, 14} = 3.868$, $P = 0.046$; linear trend: $F_{1, 7} = 5.044$, $P = 0.060$).

By contrast, illusion-induced changes in ownership ratings did not differ across days ($F_{2, 14} = 1.475$, $P = 0.262$). Further, as shown in Fig. 3B, there were no differences across days in overall ratings of perceived ownership ($F_{2, 14} = 0.230$, $P = 0.798$).

RHI enhanced by TMR

To assess effects of TMR on the RHI, we compared proprioceptive drift and ownership change scores after a night with TMR with associated-sound cues during sleep versus a night with novel-sound cues during sleep. Within-subject comparisons were possible because participants in the TMR-1 and TMR-2 groups received both conditions, either TMR first or TMR second in a crossover design. To ensure that within-subjects comparisons were appropriate, we first verified that there were no order effects (drift: $F_{1, 14} = 0.074$, $P = 0.790$; ownership: $F_{1, 14} = 0.035$, $P = 0.855$) or interactions between order and stimulation type (drift: $F_{1, 14} = 0.228$, $P = 0.640$; ownership: $F_{1, 14} = 0.094$, $P = 0.764$). To assess the effects of the sleep interventions with reference to a neutral baseline, we also compared the no-sound condition to the TMR and novel-sound conditions on Days 2 and 3. Separate comparisons were made for data from each day because collapsing across days would partially conflate between-subjects variance in the TMR groups with within-subjects variance across days in the no-sound group.

Figure 4 shows a summary of indices of proprioceptive drift and subjective ownership of the rubber hand in each condition (for daily scores for each treatment group, see below; Fig. 5). As shown in Fig. 4A, pairwise comparisons revealed enhanced proprioceptive drift in the TMR condition. Specifically, proprioceptive drift was larger for the TMR condition compared to the novel-sound condition ($t_{15} = 4.954$, $P = 0.0001$); larger for the TMR condition compared to the no-sound condition (Day 2: $t_{14} = 2.905$, $P = 0.012$; Day 3: $t_{14} = 2.888$, $P = 0.012$; unpaired t tests) and not different between the novel-sound condition and the no-sound condition (Day 2: $t_{14} = 1.507$, $P = 0.154$; Day 3: $t_{14} = 0.377$, $P = 0.711$).

Figure 4B shows that there was a greater ownership change from pre to post RHI induction in the TMR condition than in the novel sound condition ($t_{15} = 5.022$, $P < 0.0001$). TMR procedures thus systematically influenced results for this measure as for the proprioceptive drift measure. However, there were no significant differences between the TMR condition and the no-sound condition (Day 2: $t_{14} = 0.096$, $P = 0.925$; Day 3: $t_{14} = 0.780$, $P = 0.448$) or the novel-sound and no-sound conditions (Day 2: $t_{14} = 1.281$, $P = 0.221$; Day 3: $t_{14} = 1.778$, $P = 0.095$). Therefore, it is unclear whether the observed difference between the TMR and novel-sound conditions was due to a TMR-based increase in illusion strength, a decrease in illusion strength due to stimulation with novel sounds, or both.

To better discriminate between these interpretations, we compared subjects' changed ownership scores following each type of sleep stimulation to their scores on Day 1. This analysis was justified because we observed no differences in changed ownership scores across days due to repeated stimulation alone
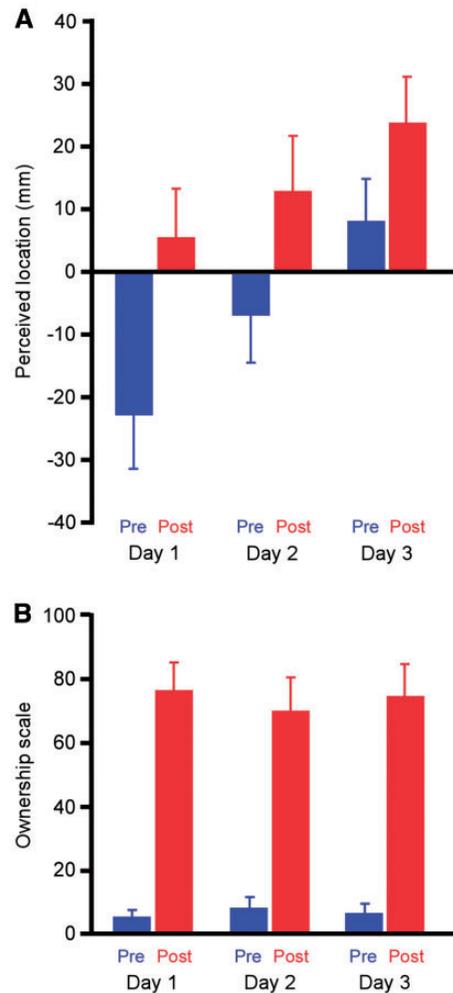

Figure 3. Behavioral performance for RHI across days, based on data from the condition in which no sounds were presented during sleep. (A) The illusion of proprioceptive drift was demonstrated each day, but there was also a steady shift across days toward locations closer to the rubber hand (more positive). (B) Subjective ownership of the rubber hand was similar across days, each day showing enhanced ownership following RHI induction. Error bars indicate standard error of the mean (SEM).

(Fig. 3A). However, a similar analysis would not be justified for proprioceptive drift because it would be contaminated by decreases in proprioceptive drift observed across days (Fig. 3B). Ownership changes were smaller following novel-sound stimulation (mean = 43.750) than they were on Day 1 (M = 60.313; $t_{15} = 2.800$, $P = 0.014$), which did not differ significantly from scores after TMR stimulation (M = 59.625; $t_{15} = 0.172$, $P = 0.866$). These results suggest that illusion-induced changes in ownership ratings decreased following sleep stimulation with novels sounds.

Prior to our sleep interventions, self-reported changes in ownership were found to correlate with proprioceptive drift scores across all subjects (Fig. 2D). To test whether the observed effects of sleep stimulation affected this correlation, we compared correlations on Day 1 (TMR-1 and TMR-2 subjects only, $n = 16$; $r = 0.542$, $P = 0.030$) with those observed after each type of stimulation. Changes in ownership were no longer correlated with proprioceptive drift after either novel-sound stimulation ($r = -0.311$, $P = 0.241$) or TMR ($r = -0.103$, $P = 0.704$). The correlation coefficient following novel-sound stimulation was
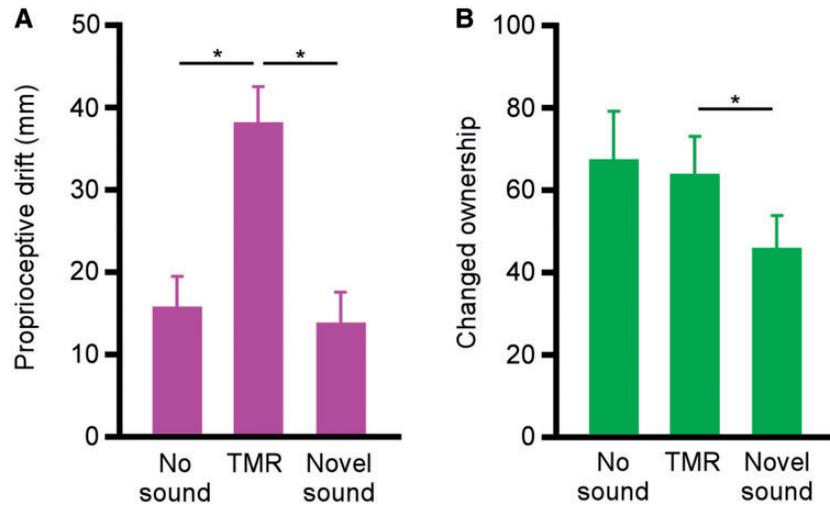
Figure 4. Effects of auditory stimulation during sleep on the RHI performed the next day. Stimulation-induced changes were apparent in (A) perceived hand location and (B) bodily ownership of the rubber hand. Error bars indicate the SEM and * indicates a significant difference between conditions ($P < 0.05$). Between-subject comparisons against the no-sound condition involved two separate statistical tests for Day 2 and Day 3 (see text). In those cases, the * indicates that both tests were significant. For the no-sound condition, the average and SEM across both Day 2 and 3 are shown for visualization purposes.
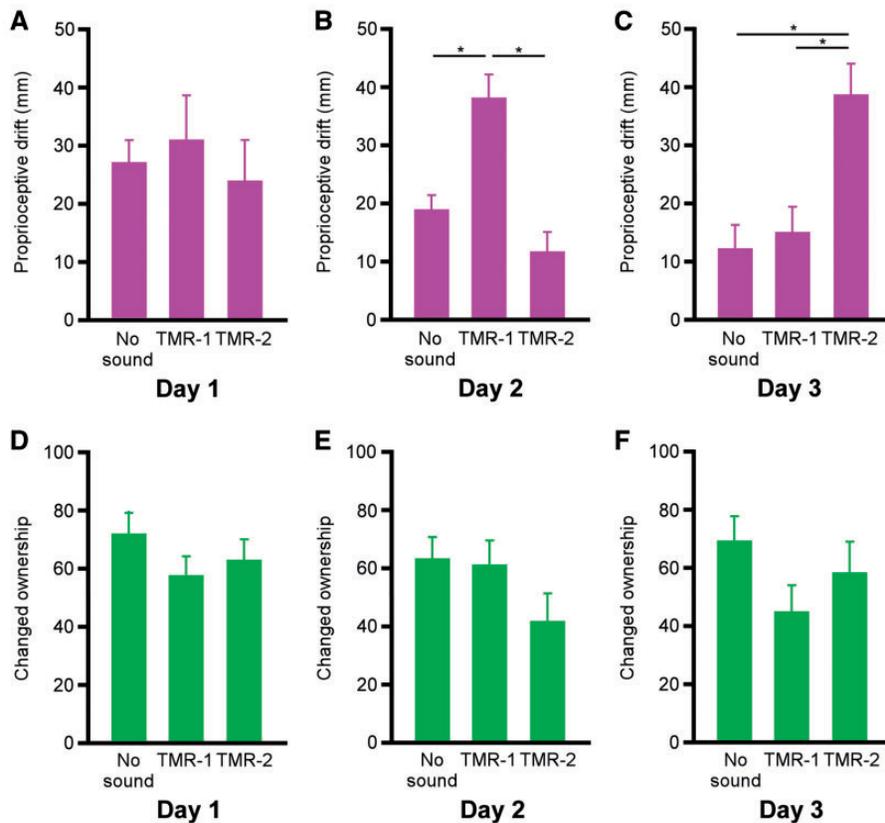

Figure 5. Results from all three groups shown separately for each day. The TMR-1 group received the TMR sound on the first night and the novel sound on the second night. The TMR-2 group received the novel sound on the first night and the TMR sound on the second night. Error bars indicate the SEM and * indicates a significant difference between conditions ($P < 0.05$).

significantly smaller than that found on Day 1 ($z = 2.648$, $P = 0.008$; two-tailed; approach described by Raghunathan et al., 1996). The difference between the Day 1 and post-TMR correlation coefficients was marginal ($z = 1.950$, $P = 0.051$). These results suggest that the positive correlation between the two

illusion metrics decreased following either type of overnight stimulation. By contrast, correlations within the no-sound group ($n = 8$) decreased gradually across days (Day 1: $r = 0.602$, $P = 0.114$; Day 2: $r = 0.440$, $P = 0.276$; Day 3: $r = 0.345$, $P = 0.403$) and did not differ significantly between days (Day 1 vs Day 2:

z = 0.364, P = 0.716; Day 1 vs Day 3: z = 0.535, P = 0.592). As would be expected, statistical power for these correlations was generally weaker than the correlation based on data pooled across all participants (Fig. 2D). Whereas the subgroup results provide only tentative evidence due to small sample size, they are consistent with the hypothesis that TMR and novel-sound stimulation affected the RHI in a measurement-specific manner that disrupted the correlation between proprioceptive drift and feeling of ownership.

Finally, correlations were calculated to determine whether the magnitude of any of the changes in the two tests across subjects were associated with the number of sounds administered during sleep the previous night (which would also reflect the amount of SWS). One significant correlation was found (Fig. 6), in that a greater amount of proprioceptive drift on the day after TMR was associated with a larger number of sounds administered (Pearson's $r_{14} = 0.498$, P = 0.049). Proprioceptive drift was not correlated with number of sounds in the novel-sound condition, and ownership was not correlated with number of sounds in either the TMR condition or the novel-sound condition (P values > 0.464). The number of sounds administered during sleep in the TMR condition ranged from 279 to 1225. A similar number of sounds was presented in the TMR condition (mean = 724, SEM = 65.1) and the novel-sound condition (mean = 695, SEM = 72.8; $t_{15} = 0.352$, P = 0.730). Given that the number of sounds delivered in this procedure corresponds closely to the amount of SWS detected, these results showed that amount of SWS did not differ between the TMR and novel-sound conditions.

Discussion

Auditory stimulation during sleep altered body perception in the RHI, as indexed by two standard measures. Both proprioceptive drift and the feeling of bodily ownership for the rubber hand were stronger after TMR during sleep than they were after sleep stimulation with a sound not associated with RHI induction. Because these two conditions were tightly matched in all ways except for the associative meaning of the sounds presented during sleep, these results provide intriguing evidence for a causal role of sleep-dependent reactivation in plasticity of body perception.

The experiment was particularly powerful due to within-subject comparisons in a crossover design with the tight experimental control of all relevant factors. Sixteen participants received TMR during SWS with the same sound used during induction of the RHI. Measures obtained on the day after TMR were compared to measures obtained on the day after a very similar sleep manipulation, except that the sound presented was not linked with the RHI. Yet, the order of conditions was counterbalanced, and the two sounds were counterbalanced across conditions such that the specific physical characteristics of the sounds could not produce any systematic effects with regard to the comparison between the TMR and novel-sound conditions.

We also included a separate group of participants who did not receive auditory stimulation during sleep, which provided baseline measures of the RHI across 3 days (Fig. 3). Across-group comparisons thus allowed us to assess whether observed effects were due to TMR-based reinforcement of the altered body representation or to disruption of that representation due to stimulation with an unassociated sound. Proprioceptive drift was significantly larger after TMR compared to the no-sound condition, suggesting that TMR reinforced prior visuo-
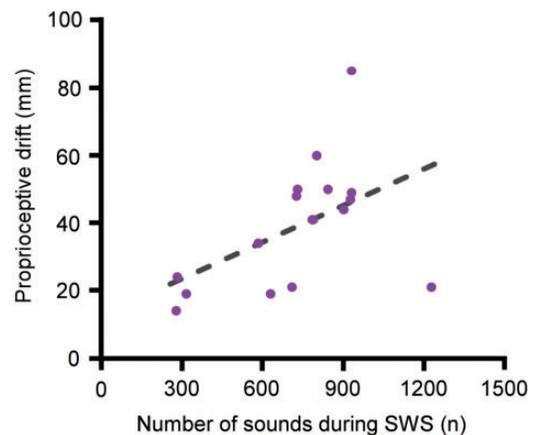

Figure 6. Correlation between proprioceptive drift and the number of sounds during SWS in the TMR condition (n = 16). Proprioceptive drift was positively correlated with the number of sounds during SWS.

proprioceptive recalibration. In contrast, illusion-induced changes in ownership were similar following TMR and in the no-sound condition. Rather, it appears that sleep stimulation with novel sounds weakened subsequent ownership induction. Thus, our results suggest that TMR with RHI-associated sounds increased subsequent proprioceptive drift in the RHI, while stimulation with unassociated sounds decreased the feeling of ownership for the rubber hand.

This dissociation may be partially attributable to a neural dissociation between the functional subsystems underlying each component of the illusion. The RHI and bodily self-attribution in general rely on a network of frontoparietal cortical areas that support distinct perceptual components of the experience of embodiment (Zeller et al., 2011). Whereas activity in posterior parietal cortex (PPC) is associated with the integration or reconciliation of multisensory information about body position, activity in ventral premotor cortex (PMv) is associated with the feeling of bodily ownership itself (Makin et al., 2008). For example, transcranial magnetic stimulation over the inferior parietal lobule prior to RHI induction disrupts proprioceptive drift while leaving feelings of bodily ownership unaffected (Kammers et al., 2008). By contrast, activity in PMv, but not in PPC, is correlated with the intensity of the feeling of ownership during the RHI (Ehrsson et al., 2004; Brozzoli et al., 2012) and full-body ownership illusions (Petkova et al., 2011). These independent functional associations between regional activation and perception possibly enable distinct changes in perceived ownership and visuo-proprioceptive calibration (e.g., Rohde et al., 2011).

Proprioceptive drift may have been uniquely susceptible to TMR-based enhancements because the same posterior parietal areas implicated in visuo-proprioceptive recalibration during the RHI also form a major hub of a posterior cortical-hippocampal network (Vann and Albasser, 2011; Ranganath and Ritchey, 2012), with functional and anatomical connectivity mediated by connections with retrosplenial and parahippocampal cortex (Mesulam et al., 1977; Cavada and Goldman-Rakic, 1989; Kahn et al., 2008). Because TMR is thought to strengthen particular memories by encouraging hippocampal-cortical dialogue with particular neural ensembles (Born and Wilhelm, 2011; Oudiette and Paller, 2013), the brain areas that are most

closely connected with the hippocampus may also be the most susceptible to TMR.

By contrast, hippocampal connections with the frontal lobe do not include connections to the PMv or associated frontal operculum (Schmahmann and Pandya, 2009). Whereas multisensory neurons in both the PPC and PMv likely integrated the simultaneous visual, tactile, and auditory information presented during RHI induction (Graziano *et al.*, 2004; Schlack *et al.*, 2005), auditory stimulation during sleep may have only been sufficient to reactivate this integrated representation across a relatively short pathway. During normal RHI stimulation, PPC activity is observed as soon as stimulation begins, whereas PMv activity only emerges later, when the illusion of bodily ownership emerges (Ehrsson *et al.*, 2004; Makin *et al.*, 2008). During sleep, auditory reactivation may have been sufficient to reproduce RHI-like PPC activity, but not to the point of bringing about the subsequent effects in PMv. Further research is needed to clarify which cortical areas may be most susceptible to TMR during sleep.

The negative effects of novel-sound stimulation on subsequent feelings of ownership most likely reflect disruption of spontaneously occurring sleep-dependent consolidation. Because the novel sounds would not have been associated with any competing body representation, it is unlikely that they weakened subsequent self-attribution toward the rubber hand by reinforcing an alternative body representation. Rather, it is more plausible that stimulation with novel sounds interrupted naturally occurring consolidation of the altered body representation by inducing consolidation of other arbitrarily associated memories. Importantly, there was no difference in the amount of SWS detected during the novel sound and associated sound conditions, suggesting that this effect was not due to interruptions of SWS.

Conclusions from this study must be made in the context of possible limitations. First, in lieu of traditional sleep staging based on full polysomnography, we used an automated system that classified sleep stages on the basis of signals recorded from a forehead montage. This system had the advantage of sleep taking place in each individual's normal sleeping environment, avoiding the downsides of a sleep laboratory, but with the disadvantage of lower-quality electrophysiological data. Given that prior assessments showed that 3–5% of epochs scored as wakefulness by experts were scored by this sort of system as SWS, it remains possible that some small percentage of the sounds presented to participants in our study could have been presented during wakefulness. Nevertheless, it is highly unlikely that a small number of sounds presented during wakefulness could have produced the observed effects. Second, our study, being exploratory in nature, suffered from a somewhat small sample size. Yet, the primary within-subjects effects of interest were large enough to be detected with high confidence. Still, replication and further investigation will prove valuable in validating this potentially promising line of research.

In total, our results suggest that auditory stimulation during sleep can modulate perceptual proclivity toward novel body representations. Sounds associated with the body representation evoked within a particular sensory context (i.e., RHI induction) increased the visuo-proprioceptive recalibration required to adapt to that sensory context when it was subsequently reinstated. This type of learning may reflect a process similar to the learning of body representations that are optimized for particular sensorimotor contexts, such as tool use. For example, monkeys that do not naturally use tools can learn over the course of weeks to integrate tools into neural representations of the body (Maravita and Iriki, 2004). In humans, this type of learning may contribute to the development of specialized body representations for more complex tasks, such as driving an automobile. Future research should examine whether TMR can accelerate or strengthen the learning of body representations that are optimized for particular sensorimotor skills. Based on our findings with the RHI, we speculate that memory reactivation during natural sleep is a fundamental contributor to this general type of body-image learning over the long term.

Data Availability

Data for this article are available on request.

Supplementary data

Supplementary data is available at *Neuroscience of Consciousness Journal* online.

Conflict of interest statement. None declared.

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