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Full-Body Ownership Illusion Elicited by Visuo-Vestibular Integration

Nora Preuss and H. Henrik Ehrsson
Karolinska Institutet

Vestibular signals allow us to maintain balance and orient ourselves in space. However, the possible contribution of the vestibular sense to the perception of the body as one's own (body ownership) remains poorly understood. The aim of the present study was to investigate how vestibular information contributes to the experience of body ownership using multisensory integration. We conducted 3 studies using a "full-body ownership illusion" induced by virtual reality technology and galvanic vestibular stimulation (GVS); the latter is a technique that allows for the selective stimulation of vestibular afferents. Participants wearing head-mounted displays saw a mannequin's body that was performing a slow swinging movement from a first-person perspective. At the same time, participants were exposed to GVS that elicited vestibular sensations of swinging whole-body movements in the corresponding direction. Perceived ownership of the seen body was measured using questionnaire ratings and skin-conductance responses to a knife threat toward the mannequin. We demonstrated that when participants were exposed to congruent visuo-vestibular information, they perceived a stronger ownership of the mannequin's body compared with when they were exposed to unimodal visual and vestibular conditions or an incongruent visuo-vestibular condition. The findings show that visuo-vestibular congruency is sufficient to increase the feeling of illusory body ownership of a mannequin's body.

Public Significance Statement
The study elucidates the important role that the balance system exerts on the perception of the body as one's own. When participants see a mannequin's body rotating in one direction and simultaneously feel a motion sensation in the same direction induced through electrical stimulation of their vestibular nerve, they experience stronger ownership of the mannequin's body.

Keywords: body ownership, multisensory integration, vestibular system, vestibular cognition, galvanic vestibular stimulation

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The perception of our own body as part of the self and distinct from all other objects in the external environment is a fundamental aspect of the human conscious experience. Over the last two decades, research in cognitive neuroscience has begun to shed light on how we come to sense ownership of our body through the dynamic integration of sensory signals from different sensory modalities (Blanke, Slater, & Serino, 2015; Botvinick & Cohen, 1998; Ehrsson, 2007, 2012; Ehrsson, Spence, & Passingham, 2004; Tsakiris & Haggard, 2005). However, the potential involvement of the vestibular sense—or our so-called "sense of balance"—in this process has only recently attracted the interest of scientists in the field (see below). The vestibular sense provides us with a gravitational frame of reference that allows us to move our body in space. It is particularly relevant for encoding head and body position and, therefore, contributes to spatial aspects of bodily awareness (Lenggenhager & Lopez, 2015; Pfeiffer, Serino, & Blanke, 2014). Although this ability seems to be highly relevant for us, the question of whether and how vestibular information contributes to the feeling of body ownership through multisensory integration mechanisms remains to be answered.

Recent experimental studies have used so-called "ownership illusions" in order to investigate the perceptual basis of body ownership and bodily awareness. During these illusions, participants develop a feeling of ownership of the artificial limbs (e.g., the rubber hand illusion, Botvinick & Cohen, 1998) and alien bodies (Petkova & Ehrsson, 2008) and attribute them to the bodily self (Ehrsson, 2012). In the original full-body ownership illusion paradigm, the participant wears a head-mounted display and looks at a mannequin's body from a first-person perspective (Petkova & Ehrsson, 2008). Congruent touches are then applied to the participant's real body and the mannequin's body. The temporal and spatial synchrony of the touches leads to an illusory ownership of the mannequin's body that is subjectively reported by the participant using questionnaire-based rating scales and can also be measured using implicit methods, such as skin-conductance re-

Nora Preuss and H. Henrik Ehrsson, Department of Neuroscience, Karolinska Institutet.

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Correspondence concerning this article should be addressed to Nora Preuss, Department of Neuroscience, Karolinska, Institutet, Tomtebodavägen 16, 17165 Stockholm, Sweden. E-mail: nora.preuss@ki.se

sponses (SCR) induced by threatening the mannequin's body with a knife. Previous studies came to the conclusion that ownership in the above described paradigm is the result of multisensory integration and depends on the first-person perspective and human-like shape of the body, in addition to visuo-tactile synchrony (Petkova & Ehrsson, 2008; Petkova, Khoshnevis, & Ehrsson, 2011).

The first evidence for vestibular contributions to bodily awareness came from clinical studies showing, for example, that vestibular stimulation helps to temporarily ameliorate disorders that affect the body representation such as somatoparaphrenia (Bisiach, Rusconi, & Vallar, 1991) or hemianesthesia (Bottini et al., 2005; Vallar, Bottini, Rusconi, & Sterzi, 1993; Vallar, Sterzi, Bottini, Cappa, & Rusconi, 1990). Furthermore, vestibular stimulation has shown the ability to restore phantom limb perception (André, Martinet, Paysant, Beis, & Le Chapelain, 2001; Le Chapelain, Beis, Paysant, & André, 2001). More recent experimental studies have started to investigate how the vestibular system contributes to body representation and body ownership (for a review, see Ferrè & Haggard, 2016). Such studies in healthy participants reported effects of vestibular stimulation on somatosensory perception as well as localization of the hand and nociception (Ferrè, Bottini, & Haggard, 2011; Ferrè, Day, Bottini, & Haggard, 2013; Ferrè, Haggard, Bottini, & Iannetti, 2015; Ferrè, Sedda, Gandola, & Bottini, 2011; Ferrè, Vagnoni, & Haggard, 2013; Ferrè, Walther, & Haggard, 2015; Lopez, Schreyer, Preuss, & Mast, 2012). However, the effect of vestibular stimulation on the rubber hand illusion—the most commonly used model system of body ownership—is not clear. Lopez, Lenggenhager, and Blanke (2010) combined galvanic vestibular stimulation (GVS) with the rubber hand illusion and reported that left, but not right, GVS increased the illusion ratings for limb ownership compared with a no stimulation condition. However, they did not find any significant effect of GVS stimulation on the objective measure of the illusion, the so-called "proprioceptive drift" (the change in perceived hand position toward the rubber hand). In contrast, Ferrè, Berlot, and Haggard (2015) reported that left-anodal galvanic vestibular stimulation decreased the strength of the rubber hand illusion as measured with the proprioceptive drift. Thus, these studies suggest a modulatory effect of vestibular stimulation on the visuo-tactile-proprioceptive integration mechanisms responsible for the rubber hand illusion.

Although the abovementioned studies show a general contribution of the vestibular sense to body awareness, these studies do not demonstrate a direct involvement of the vestibular sense in triggering a body ownership illusion. The aim of the present study was to therefore elucidate whether vestibular sensory information contributes to the feeling of body ownership through multisensory integration mechanisms. The specific research question was whether congruent visuo-vestibular information is sufficient to increase an illusory sensation of ownership of an entire body. We developed a paradigm to induce visuo-vestibular congruency without actually moving the participants using galvanic vestibular stimulation (GVS). In Experiment 1, participants were lying on a bed with their head tilted forward by ~45 degrees while they saw a mannequin's body from a first-person perspective. Visual cues stimulated slow rotations of the mannequin's body that appeared as if the body was gently swinging from left to right, back and forth (clockwise and counterclockwise rotation around the roll axis). At the same time, participants were exposed to GVS in order to elicit a vestibular sensation of the whole-body rotating in the corresponding direction. GVS involves placing two electrodes on the mastoids behind participants' ears. A weak current is then applied, affecting the activity of the efferent vestibular nerve (for a review, see Utz, Dimova, Oppenländer, & Kerkhoff, 2010). Depending on the polarization of the electrodes and the frequency of the current, participants experience being pulled to one side (DC) or a swinging movement (AC). We applied an AC and hypothesized that congruent visuo-vestibular information would lead to a stronger illusory ownership of the mannequin's body compared with two control conditions with the identical visual only or vestibular only motion stimulation. In Experiment 2, we compared the congruent visuo-vestibular condition (same as in Experiment 1) with a control condition with identical visual information and noise GVS. We expected stronger illusory body ownership in the congruent visuo-vestibular condition than in the noise control condition. In Experiment 3, we compared a congruent visuo-vestibular condition with an incongruent visuo-vestibular condition. In both conditions, the participant saw a mannequin's body from a first-person perspective making brief "swinging" movements toward the left side (counterclockwise rotation around the roll axis). A vestibular stimulation that generated a similar sensation of swinging toward the left was applied synchronously with the visual stimuli in the congruent condition, whereas a temporally delayed GVS stimulation was applied in the incongruent condition. Again, we expected stronger illusory body ownership in the congruent condition. In support of the above predictions, our results showed that visuo-vestibular congruency induced illusory ownership of the mannequin's body.

Experiment 1

The aim of the first experiment was to examine whether congruent bimodal visual and vestibular information is sufficient to elicit an illusory feeling of ownership over a mannequin's body.

Method

Participants. Thirty-three volunteers participated in the first experiment (mean age = 26.38 years, *SD* = 5.98, 21 female). All participants had normal or corrected to normal vision and gave written informed consent prior to participation. The experimental procedure was approved by the Regional Ethics Review Board of Stockholm.

Galvanic vestibular stimulation. Participants were exposed to GVS using a DC stimulator (neuroCon GmbH, Illmenau, Germany). The current applied was adjusted individually as participants differ in vestibular as well as pain sensitivity (median = 1.4 mA, M = 1.5 mA, SD = 0.35). The size of the rubber electrodes and electrode sponges was 3 × 3 cm (9 cm^2). Sponges were soaked in a sodium chloride solution (B. Braun Melsungen AG, Germany) before being attached behind participants' ears. The anode was placed on the left mastoid, and the cathode was placed on the right mastoid. Participants were first exposed to a current with a sinusoidal waveform (peak to peak 1.4 mA, offset 0 mA, frequency 0.5 Hz). As described by Wardman, Taylor, and Fitzpatrick (2003), participants usually report a movement toward the anode, hence to the left side (see also Day, Cauquil, Bartolomei, Pastor, & Lyon, 1997). After the first pulse, the current reverses its direction, inducing a perceived motion to the right. Hence, our GVS stimulation protocol induced a "hammock-like" (or swinging-like) motion sensation in the roll and yaw planes. Participants were instructed to verbally describe their perceived sensation and mimic the perceived motion with their right hand. Given their reported sensation, the current was then increased in increments of 0.5 mA or decreased until the participants reported a feeling as if they were swinging from left to right, back and forth (swinging-like), and the stimulation was not experienced as painful or uncomfortable. The participants were told that their sensation of motion direction and pace should be clear and that they should not experience any discomfort or pain.

Stimuli and apparatus. A three-dimensional (3D) image video of a male mannequin's body lying on a bed (1PP) was prerecorded using two identical cameras placed side-by-side (CamOne Infinity HD, resolution 1,920 × 1,080, ACME the game company GmbH, Germany) and a green screen setup. The life-size mannequin wore blue jeans and a yellow t-shirt to make it look more natural (Schmalzl & Ehrsson, 2011). Previous studies have shown that gender identity is not an important factor for perceiving ownership and that females can also perceive a male body as their own (Petkova & Ehrsson, 2008; Slater, Spanlang, Sanchez-Vives, & Blanke, 2010). The body stimulus (body lying on bed) and background (room) were recorded separately. The video material was processed using Finalcut Pro X (Apple). To induce a 3D perception of the visual scene, the pictures of the left and right cameras were placed side-by-side (1,920 × 1,080). A visual motion sensation was induced by sustained 6°/s oscillations of the background stimulus (clockwise and counterclockwise) in the roll plane, which induced a "hammock-like" self-motion sensation when presented in a large visual field. The 6°/s oscillation rate was determined in pilot experiments in order to match the vestibular motion sensation as closely as possible. The movement was performed with a frequency of 0.5 Hz (the same frequency as the vestibular stimulation). In the following article, we will refer to "visual motion of the body stimulus," although, in fact, the background was moving (and not the body stimulus). The video and GVS pulses were matched using a customized program that triggered the start of the GVS at a specific time point. The trigger pulse was sent at the same time as when the visual motion started in the congruent condition. Participants were instructed to lie as still as possible on the bed, and the experimenter observed that the participants complied with this instruction. A demonstration of the video material is included as online supplementary material.

Procedure. During the experiment, participants were lying on a bed with their head tilted forward in the pitch direction (approx. 45°). Pillows were taped to the bed to ensure that all participants had the same head position. Video stimuli were presented using a head-mounted display (HMD, Oculus Rift 2, http://www.oculusvr.com/). Participants were allowed to watch the video freely, and eye position and fixation point was not controlled for. Participants were exposed to three different conditions in a randomized and counterbalanced order: (a) Congruent visuo-vestibular stimulation was induced using a computerized signal that triggered the start of the vestibular stimulation simultaneously with the start of the visual motion of the body stimulus ("congruent"). The directions of the seen and felt whole-body rotations were the same in this condition. (b) In one control condition, participants only saw the visual motion of the body stimulus (identical to the congruent condition), and they were not exposed to GVS ("visual only"). (c) In a second control condition, the body stimulus remained stable, but participants were exposed to GVS (identical to the congruent condition; "vestibular only"). Each condition lasted for 3:45 min. These procedures and the length of the conditions were determined in pilot experiments in order to maximize the illusion induction during congruent visuo-vestibular stimulation. The participants in the present study were not made familiar with the conditions beforehand. They were instructed that they *might* feel motion (induced through the GVS device) and that they *might* see a visual motion of the mannequin's body. Illusory ownership of the mannequin's body was measured using questionnaires (subjective measurement) administered after each condition and SCR induced by threatening the mannequin's body with a knife (objective measurement; see below). Participants filled out a paper questionnaire that consisted of five statements concerning the illusion (S1 and S2) and control questions (S3–S5; see Table 1). Statements were rated on a 7-point Likert scale ranging from −3 (*strongly disagree*) to +3 (*strongly agree*), with 0 indicating *neither agree nor disagree*. Participants filled out the questionnaire after each condition. A stabbing knife threat toward the abdomen of the mannequin was applied three times during each condition (after 1 min, 1:50 min, and 2:40 min) for a duration of 2 s each time (see Figure 1). Hence, a total of nine SCRs were recorded.

Analysis. All data were analyzed using the statistical software package R. Alpha was set at 5% in all tests, and additionally, Bayes factors (BFs) are reported. The BF indicates to what extent the data supports one hypothesis (H_1, the alternative hypothesis) over another hypothesis (H_0, in this case, the null hypothesis). A BF of 8, for example, would mean that the observed data are eight times more likely to have occurred under H_1 than H_0 (Lee & Wagenmakers, 2013). A BF of 1 indicates that the data does not provide evidence for either H_1 or for H_0. A BF between 1 and 3 is termed "anecdotal evidence," based on a classification scheme by Jeffreys (1961, Appendix B). The advantages of Bayesian hypothesis testing are that the BF can also be used to collect evidence of the absence of an effect (supporting the null hypothesis) and that data collection can be stopped or continued depending on whether the accumulated evidence is sufficiently conclusive (Lee & Wagenmakers, 2013).

Questionnaire data. Questionnaire data were analyzed using a Wilcoxon signed-ranks test. Additionally, BFs were calculated for each comparison using the BayesFactor package 0.9.12 for R. The scale parameter of the prior on the effect size was set to the default value of $\sqrt{2}/2$. The Illusion Statements 1–2 were tested as one-sided, as we had a strong hypothesis that congruent stimulation would increase the perceived full-body ownership illusion and

Table 1
Illusory Ownership Questionnaire

Statement: During the experiment. . .	Type
S1. . . . it felt as if I was looking at my body.	Illusion
S2. . . . the body motion I saw was the motion I felt.	Illusion
S3. . . . I felt as if I had two bodies.	Illusion control
S4. . . . I felt as if my body was turning "plastic".	Illusion control
S5. . . . I felt dizzy.	Dizziness control

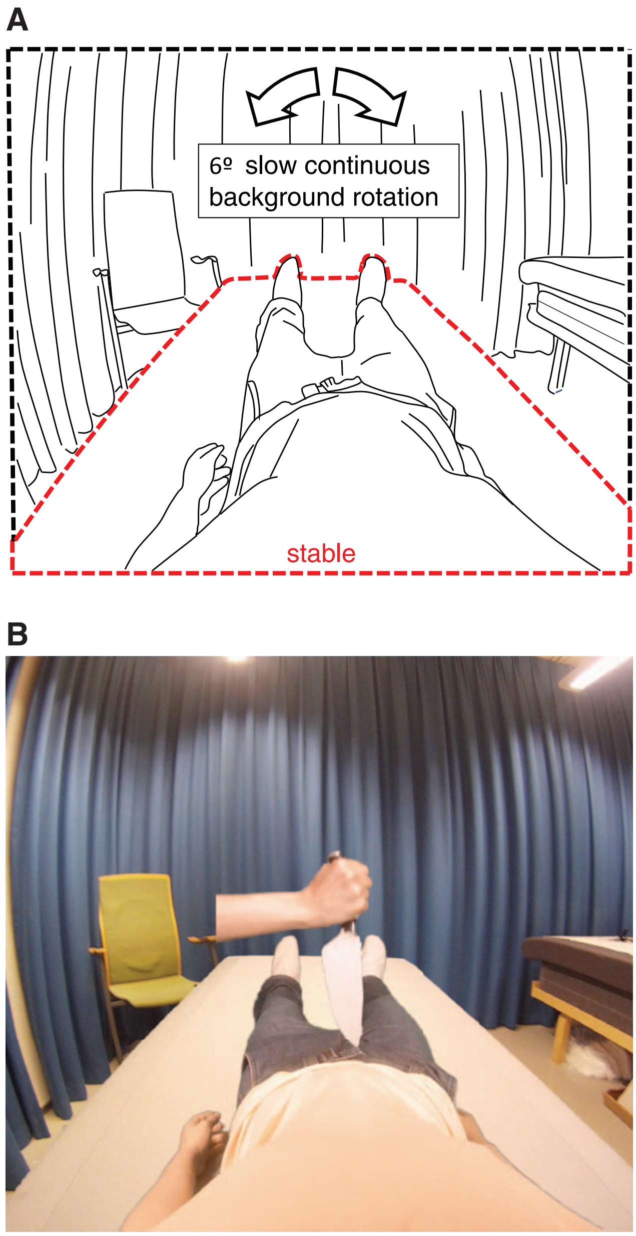

Figure 1. Illustration and picture of the 3D image material. (A) Participants saw a mannequin lying on the bed from a first-person perspective. The background of the image underwent a continuous 6° rotation along the longitudinal axis (clockwise and counterclockwise), inducing a sensation of self-motion in the participants. (B) Skin conductance in response to a physical threat—a hand holding a knife stabbing the belly of the mannequin's body from above—served as an objective proxy of ownership.

would be judged to be more congruent than the control conditions. All other control statements were tested as two-sided.

SCR data analysis. SCR data were range-corrected in order to correct for interindividual variance (Dawson, Schell, & Filion, 2007; Lykken, Rose, Luther, & Maley, 1966). Prior to the start of the first experimental block, the minimum and maximum SCRs of each participant were measured. Participants were instructed to take a deep breath and then hold the air for 2 s. Each data point was then expressed as a proportional value of the range of the maximum and minimum SCRs according to the following formula: SCR in mmho $= (SCR_{measured\_max} - SCR_{measured\_min}) / (SCR_{max} - SCR_{min}$; Lykken et al., 1966). $SCR_{max} - SCR_{min}$ refers to the peak-to-peak measurement of the breathing response, whereas $SCR_{measured\_max} - SCR_{measured\_min}$ refers to the peak-to-peak response of one trial. The SCR magnitude was analyzed using a Wilcoxon signed-ranks test, which includes all SCRs, including zeros. However, an increase in SCR magnitude can be caused by either a stronger response or by a higher response frequency (Prokasy & Kumpfer, 1973). Therefore, we separately analyzed both SCR amplitude, which only included positive responses (nonzeros) and SCR frequency, which describes the mere emergence of a response (recommended by Dawson et al., 2007). A response was considered to be positive when the peak-to-peak value was equal to or larger than 0.01 mmho.

The SCR was expected to decrease with increasing number of trials. SCR amplitude and frequency were therefore analyzed using mixed effect models that also included the number of knife threats ("repetition") as a predictor. The major advantage of the mixed model approach was that repetition could be used as a continuous predictor instead of considering it as categorical, which allowed us to model a regression line for repetition. Furthermore, mixed effects models are more flexible, as they do not require the same number of observations per subject or prior averaging of data. SCR amplitude and frequency were set as dependent variables that were predicted by "repetition," "condition," and "interaction" (fixed effects). The most useful model (which we will refer to as the "best model") was selected using a stepwise model selection (Seltman, 2012). "Repetition" was entered as the first predictor, followed by "condition" and the interaction between both. A random intercept per subject was included as a random effect. SCR amplitude data were continuous, positive and right-skewed; therefore, we used a gamma mixed effects model. The binary SCR frequency data were analyzed using a logistic mixed effects model (Seltman, 2012). Likelihood ratio tests were performed to test the overall influence of the predictors on the dependent variables. Further details about the estimated parameters of the respective models that provided the best model fit are reported as online supplementary material. The "congruent" condition and the first knife threat ("repetition" = 1) were used as reference categories. The SCR data of six participants had to be excluded from the SCR analysis, as these participants did not show any SCRs, including the breathing response (remaining total: 27 participants).

Relationship between subjective and objective illusion measurements. Linear regression models with condition differences concerning the illusion ratings (S1 and S2) as a predictor and condition differences concerning the SCR magnitude as the dependent variable were calculated in order to investigate how subjective illusion ratings corresponds to the objective measurement. In line with previously published studies, S1 and S2 were averaged in order to obtain a single value that captured the overall strength of the illusion (Guterstam, Björnsdotter, Gentile, & Ehrsson, 2015; Kalckert & Ehrsson, 2014; van der Hoort & Ehrsson, 2016). We consider S2 to be part of the illusion statement as it captures the perceived perceptual fusion of information, which we think is an important component of the overall ownership illusion experience. In a complementary analysis we also analyzed the relationship between the ownership statement S1 and SCR magnitude separately (figures are provided as online supplementary material). The hypothesis was tested as one-sided as we expected the relationship between subjective and objective measurements to be positive. BFs were computed using the Savage-Dickey density ratio using Stan (Stan Development Team, 2014) and the logspline package for R (Kooperberg & Kooperberg, 2013). The prior effect size was defined to be half-Cauchy distributed, and the scale parameter was set to $\sqrt{2}/2$. Further model details are available as supplementary information.

Results

The results of the questionnaire ratings are illustrated in Figure 2. The illusion statements were rated significantly more positively than the control statements (W = 528, $p < .001$, BF >100). Overall, participants rated the illusion experience to be higher in the visuo-vestibular congruent condition compared to the visual only (W = 397, $p < .001$, BF >100) and vestibular only (W = 381, $p < .001$, BF >100) conditions. There was no difference in terms of overall illusion perception when comparing the visual only to the vestibular only condition (W = 258, p = .1, BF = 0.62). Both illusion rating scores (S1 and S2) were significantly higher in the congruent visuo-vestibular condition compared to the visual only (S1: W = 201, p = .014, BF = 5; S2: W = 298, p = .002, BF = 15) and the vestibular only (S1: W = 137, p = .004, BF = 16.6; S2: W = 371, p = .0001, BF >100) conditions. Further results are summarized in Table 2. Dizziness ratings (S5) were relatively weak and differed between the congruent and visual only conditions (W = 236, p = .003, BF = 20.7) but not between the congruent and vestibular only conditions (W = 93, p = .663, BF = 0.2). There were no significant differences between the conditions in control questions S3 and S4 ($p > .05$). The BF = 0.21 revealed moderate evidence supporting the null hypothesis in S3.

Analysis of the SCR frequency using a logistic mixed model revealed a significant improvement of the model when adding the predictors repetition (χ^2 = 33, df = 1, $p < .001$), condition (χ^2 = 20.17, df = 2, $p < .001$), and the interaction (χ^2 = 9.88, df = 2, p = .007; Figure 3A). In terms of the condition-specific differences, the SCR frequency in the congruent condition did not decrease with an increase in the number of trials (β = −0.18, z = −1.11, p = .27), whereas it was significantly decreased in the visual only condition (β = −0.7 z = −2.83, p = .005; Figure 3A; see also online supplementary material). Analysis of the SCR amplitude revealed a significant effect of repetition (χ^2 = 24.1, df = 1, $p < .001$; "best model;" Figure 3B). None of the other predictors had a significant effect ($p > .41$; Figure 3B). A Wilcoxon signed-ranks test of SCR magnitude (combining both SCR frequency and amplitude) did not reveal a significant difference between the congruent and visual only conditions (W = 204, p = .14, BF = 0.56) or between the congruent and vestibular only conditions (W = 129, p = .22, BF = 0.38).

Interestingly, the linear regression between the questionnaire's illusion ratings and the SCR magnitude revealed a significant relationship for both comparisons (see Figure 4): congruent versus visual only (β = 0.1, t = 2.72, p = .005, BF = 8) and congruent versus vestibular only (β = 0.1, t = 2.18, p = .02, BF = 3). This means that higher illusion ratings were associated with greater SCR magnitude, both when comparing the congruent condition to the visual only condition and when contrasting the congruent condition with the vestibular only condition. Examining the linear regression between SCR magnitude and ownership statement S1 separately revealed a significant relationship when comparing congruent versus visual only (β = 0.09, t = 2.63, p = .01, BF = 11), but not when comparing congruent versus vestibular only (β = 0.03, t = 1.17, p = .25, BF = 0.7).

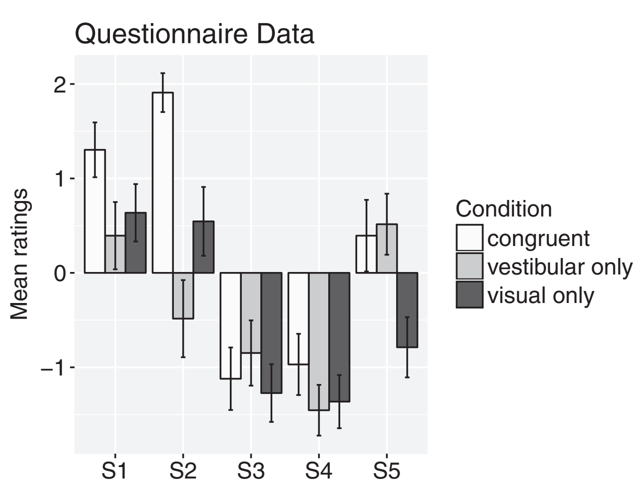

Figure 2. Results of the questionnaire data in Experiment 1. Mean ratings (from −3 to +3) and standard error of the mean are depicted for illustration purposes and to increase comparability of the results with previous studies.

Summary

The aim of Experiment 1 was to investigate whether congruent visual and vestibular motion stimulation is sufficient to elicit illusory body ownership over a mannequin's body and whether illusory body ownership is elicited more strongly under this congruent stimulation compared with unimodal control conditions. Participants reported a stronger illusion perception during the congruent bimodal condition compared to both control conditions with unimodal stimulation. Moreover, there was a significant effect of condition on SCR frequency, and this effect was primarily driven by more frequent SCRs in the congruent condition compared with the visual only condition, a difference that increased with the number of trials. More importantly, we found a significant relationship between the strength of the illusion and magnitude of the threat-evoked SCR. This means that the stronger the participants experienced the illusion, the greater the SCR magnitude was, and the weaker they experienced the illusion, the weaker the SCR magnitude was. To summarize, the results of the present study provide evidence that visuo-vestibular congruency is sufficient to elicit an illusory sense of body ownership and that such ownership sensations triggered by bimodal stimulation are significantly stronger than those reported during unimodal stimulation conditions.

Experiment 2

The results of Experiment 1 showed that congruent bimodal visuo-vestibular stimulation induced a significantly stronger sense of body ownership than unimodal (visual or vestibular) stimula-

Table 2
Results of the Wilcoxon Signed-Rank Test in Experiment 1 for Each Statement With Bayes Factors Reported

Statement	Type	Condition	*W*	*p*	BF
S1	Illusion	Congruent vs. visual only	201	.007**	5
S2	Illusion		298	.001**	61
S3	Illusion control		66.5	.728	.21
S4	Illusion control		112	.089	.85
S5	Dizziness control		236	.003**	20.7
S1	Illusion	Congruent vs. vestibular only	137	.002**	16.1
S2	Illusion		371	<.001***	>100
S3	Illusion control		41.5	.507	.25
S4	Illusion control		143	.05	1.1
S5	Dizziness control		93	.664	.2
S1	Illusion	Visual only vs. vestibular only	109	.58	.35
S2	Illusion		245.5	.08	1.65
S3	Illusion control		49	.335	.33
S4	Illusion control		85	.698	.2
S5	Dizziness control		23	.002**	30

** $p < .01$. *** $p < .001$.

tion. The purpose of Experiment 2 was to therefore compare the congruent visuo-vestibular condition to a visuo-vestibular control condition that included identical visual stimulation and a stimulation of the vestibular nerve, but without inducing any vestibular motion sensation in the participant. Thus, we introduced a noise GVS control condition (see below for details). The advantage of a noise stimulation is that it stimulates the vestibular nerve without inducing a perceptual sensation of motion and that participants experience the "tickling" sensation of the electrodes during the experiment (as in the congruent condition). Hence, the noise stimulation served as a good placebo condition in order to control for unspecific cognitive effects of GVS. Similar to Experiment 1, we expected higher illusory ownership in the congruent visuo-vestibular condition compared to the visuo-vestibular noise condition.

Method

Participants. In total, 25 volunteers participated in the second experiment (mean age = 24.6 years, *SD* = 5.25, 11 female). All participants had normal or corrected to normal vision and gave written informed consent. They received one cinema ticket as

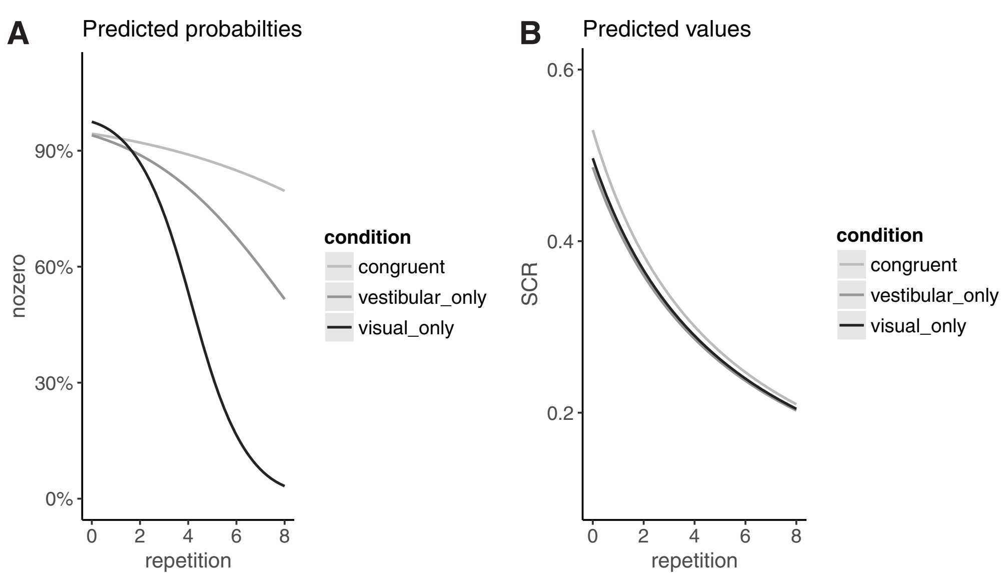

Figure 3. Predicted probabilities of (A) the logistic mixed models and (B) the gamma mixed model in Experiment 1. Figure A illustrates the significant interaction between condition and repetition (centered around the first trial), showing that the decrease of the positive skin conductance response (SCR) is stronger in the visual only condition than in the congruent visuo-vestibular condition. Figure B shows the gamma mixed model with both main effects (condition and repetition) in order to illustrate that there was no difference between the conditions concerning SCR amplitude.

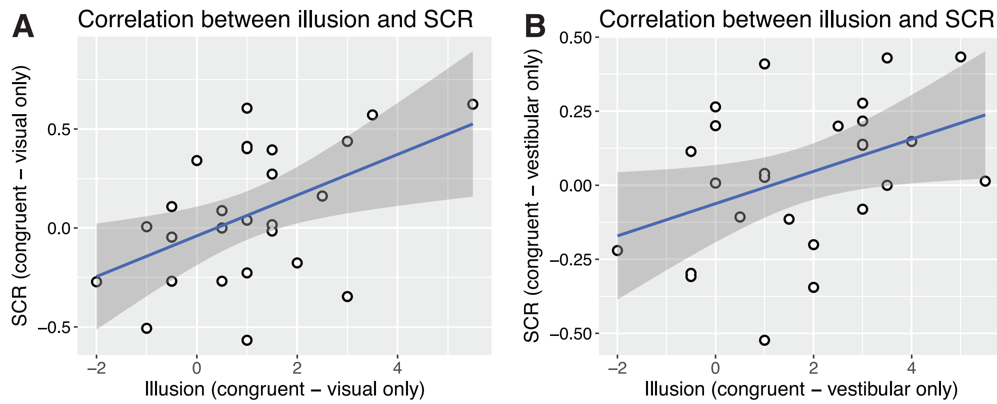

Figure 4. Relationship between the different scores of the illusion ratings (S1, S2) and the skin conductance responses (SCR): The *x*-axis reflects the difference between the congruent and control conditions (A, visual only; B, vestibular only) in the illusion statements. The *y*-axis reflects the difference between the congruent and control conditions (A, visual only; B, vestibular only) in terms of the SCR magnitude. Linear regressions between the questionnaire's illusion ratings and the SCR magnitude revealed a significant relationship for both comparisons. See the online article for the color version of this figure.

compensation for their participation. The experimental procedure was approved by the Regional Ethics Review Board of Stockholm.

Galvanic vestibular stimulation. The GVS procedure was similar to that used in Experiment 1. In addition to a current with a sinusoidal waveform (peak to peak 1.4 mA, offset 0 mA, frequency 0.5 Hz) that elicited a "swinging" vestibular sensation (same as in the congruent condition in Experiment 1), participants were exposed to noise stimulation. In the noise condition, a random current level was generated (normally distributed over time), and a high-pass filter was used to dampen frequencies below 100 Hz. The aim was to stimulate the vestibular nerve without inducing a conscious sensation of motion. Participants also underwent a threshold measurement similar to Experiment 1 (median = 1.7 mA)

Stimuli and apparatus. The stimulus material was identical to that used in Experiment 1.

Procedure. In contrast to Experiment 1, participants were exposed to only two different conditions in a randomized and counterbalanced order: (a) congruent visuo-vestibular stimulation and (b) a visuo-vestibular noise condition. The visual input of a moving body was identical in both conditions (see Figure 1). Each block lasted for 3 min. Illusory ownership of the mannequin's body was again measured using a questionnaire (subjective measurement) and SCR induced by threatening the mannequin's body with a knife (objective measurement). We only had a total of two blocks in this experiment; therefore, the knife threat was applied four times during each block (after 1 min, 1:50 min, 2:40 min, and 3:30 min). Hence, a total of eight responses were recorded.

Analysis. Data were analyzed in an identical manner as in Experiment 1. Five participants did not show any SCR, including the initial breathing response, and were therefore not included in the SCR data analysis (remaining total of 20 participants).

Results

The results of the questionnaire ratings are illustrated in Figure 5. Illusion statements were rated significantly more positively than control statements ($W = 276$, $p < .001$, BF >100). In line with our hypothesis and the results from the first experiment, the overall illusion score was significantly higher in the congruent visuo-vestibular condition compared with the noise control condition ($W = 206$, $p < .01$, BF = 14.98). The illusion rating score S2 was rated significantly higher in the congruent visuo-vestibular condition compared with the visuo-vestibular noise condition ($W = 151$, $p = .002$, BF = 34.5); however, there was no significant effect for S1 ($W = 114$, $p = .07$), only a statistical trend, and the BF of 1.23 only revealed anecdotal evidence of a difference between the congruent and noise conditions. Further results are summarized in Table 3. Dizziness ratings (S5) were relatively weak and differed between the congruent and noise conditions ($W = 121$, $p = .006$, BF = 11.7). There were no significant differences between the conditions for control questions S3 and S4. The data support the null hypothesis for S4 (BF = 0.21).

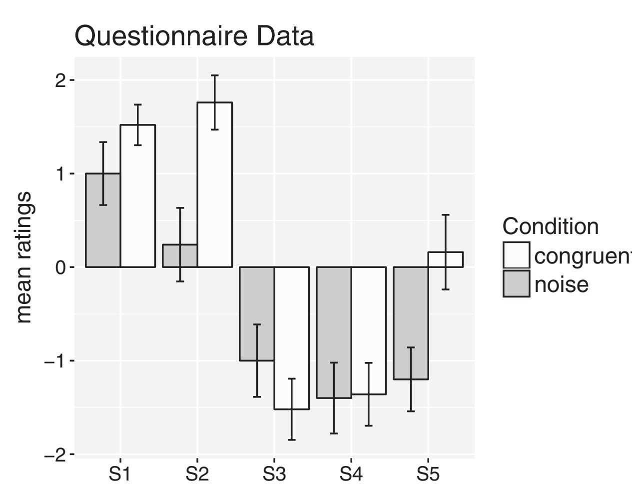

Figure 5. A. Results of the questionnaire data in Experiment 2. Means ratings (from −3 to +3) and standard error of the mean are depicted.

Table 3
Results of the Wilcoxon Signed-Rank Test in Experiment 2 for Each Statement With Bayes Factors Reported

Statement	Type	Condition	*W*	*p*	BF
S1	Illusion	Congruent vs. noise	144	.07	1.23
S2	Illusion		151	.002**	34.5
S3	Illusion control		41	.285	.43
S4	Illusion control		48.5	.858	.21
S5	Dizziness control		121	.006**	11.7

** $p < .01$.

Analysis of the SCR frequency using a logistic mixed model revealed a significant improvement of the model when adding the predictors repetition ($\chi^2 = 8.47$, $df = 1$, $p = .004$) and condition ($\chi^2 = 38.21$, $df = 1$, $p < .001$; Figure 6A). Including the interaction term did not significantly improve the model fit ($\chi^2 = 1.24$, $df = 1$, $p = .27$; Figure 6A). Analysis of the SCR amplitude revealed a significant effect of repetition on model performance ($\chi^2 = 8.7$, $df = 1$, $p = .003$; Figure 6B). Importantly, adding condition as a predictor significantly improved the model fit, which shows that the SCR amplitudes were greater in the congruent visuo-vestibular condition compared to the visuo-vestibular noise control condition ($\chi^2 = 8.61$, $df = 1$, $p = .003$). Including the interaction did not significantly improve the performance of the model ($\chi^2 = 3.02$, $df = 1$, $p = .08$; Figure 6B). This means that condition had a significant influence on SCR amplitude and that the decreasing effect of repetition was similar in both conditions. There was no significant difference in terms of SCR magnitude (combining frequency and amplitude) between the congruent visuo-vestibular condition and the visuo-vestibular noise condition ($W = 145$, $p = .07$, BF = 1). Interestingly, the linear regression between the different scores of the questionnaire's illusion ratings (the average of S1 and S2), subtracting the noise condition from the congruent condition and the SCR magnitude difference between these two conditions, revealed a highly significant relationship between the subjective and objective illusion indexes ($\beta = 0.19$, $t = 2.79$, $p = .005$, BF = 9; see Figure 7). This relationship was also significant when analyzing the ratings from ownership statement S1 separately ($\beta = 0.19$, $t = 2.84$, $p = .01$, BF = 7). These findings indicate that participants who felt a stronger increase in illusion in the congruent compared with the noise condition also had a greater increase in threat-evoked SCR magnitude when comparing these two conditions.

Summary

The purpose of Experiment 2 was to show that congruent visuo-vestibular stimulation results in stronger illusory body ownership compared to a visuo-vestibular noise condition. When averaging S1 and S2, participants reported a stronger illusion perception during the congruent condition compared with the noise condition. However, there was no difference between the congruent and noise conditions when analyzing only the ownership statement S1. After controlling for the effect of repetition, there were still significant relationships between condition and SCR frequency and between condition and SCR amplitude. That is, the probability of eliciting a detectable SCR after the knife threat and the amplitude of these SCRs were higher in the congruent condition compared with the noise condition throughout the trials. Importantly, there was a significant linear relationship between

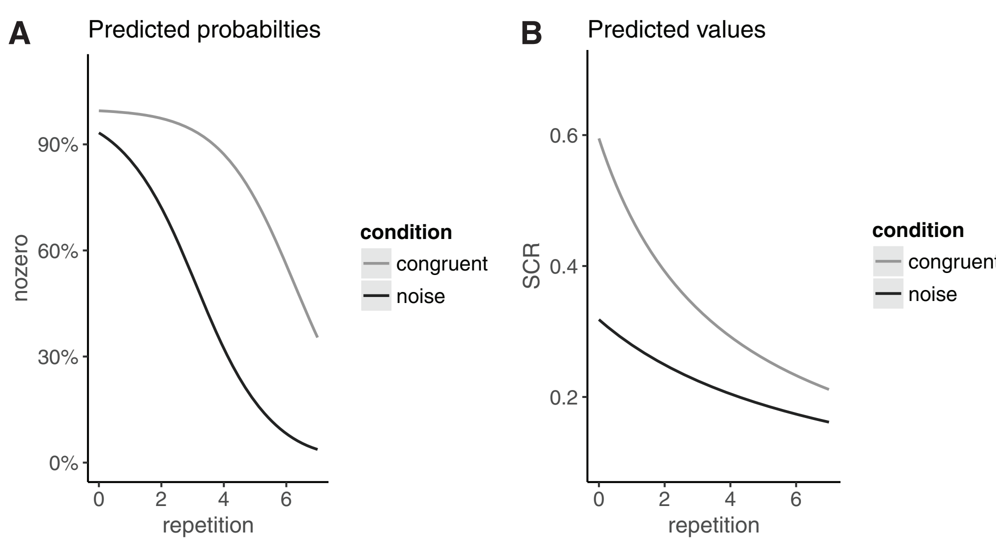

Figure 6. Predicted probabilities of (A) the logistic mixed models and (B) the gamma mixed model in Experiment 2. Figure A illustrates the main effects of repetition (centered around the first trial) and condition. The probability of having a positive skin conductance response (SCR) was higher in the congruent condition than in the noise stimulation condition. Furthermore, the probability decreased with increasing number of trials similarly in both conditions. Figure B illustrates the gamma mixed model with both main effects (condition and repetition) showing a significant effect of both repetition and condition. The SCR amplitude was higher in the congruent condition compared with the noise stimulation condition, and the SCR amplitude decreased with increasing number of trials similarly in both conditions.

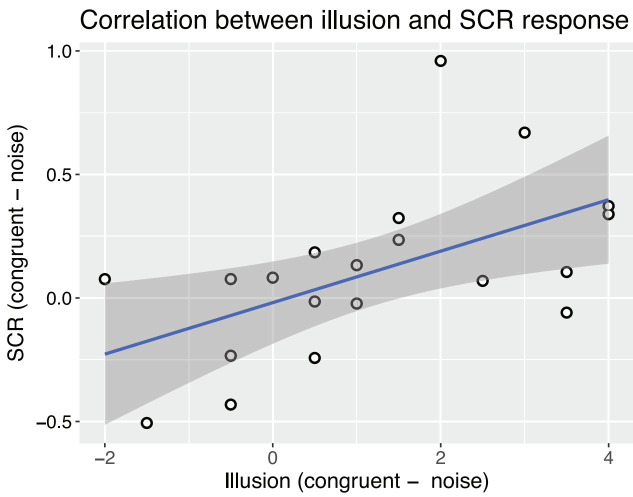

Figure 7. The relationship between the different scores of the illusion ratings (S1 and S2) and skin conductance responses (SCR): The *x*-axis reflects the difference between the congruent and noise conditions in the illusion statements. The *y*-axis reflects the difference between the congruent and noise conditions in terms of SCR magnitude. There was a positive relationship between the illusion ratings and SCR when comparing the congruent to the noise condition ($\beta = 0.19$, $t = 2.79$, $p = .005$). See the online article for the color version of this figure.

illusion ratings and SCR magnitude. Participants who perceived a stronger illusion also had a greater SCR magnitude, whereas participants with a weaker or no illusion had a lower SCR magnitude.

Experiment 3

We were able to show that congruent bimodal visuo-vestibular stimulation induced a stronger full-body ownership illusion than unimodal visual or vestibular motion stimulation in Experiment 1 and that congruent visuo-vestibular stimulation induced a stronger illusion than a visuo-vestibular noise control condition in Experiment 2. Although Experiment 2 allowed us to control for the unspecific effects of vestibular stimulation, participants did not feel any vestibular motion sensation in the noise control condition. This difference in motion perception might be a possible confound. We therefore designed Experiment 3 to directly compare congruent and incongruent visuo-vestibular stimulation in otherwise equivalent conditions. In the congruent condition, the participants were exposed to congruent visual and vestibular self-motion stimuli, whereas in the incongruent condition, there was a 3-s time delay between these stimuli. Thus, the design of Experiment 3 allowed us to test if the visuo-vestibular-induced full-body ownership illusion obeys the temporal congruency principle of multisensory integration (Holmes & Spence, 2005; Stein & Stanford, 2008) in a similar manner as full-body ownership illusions induced by congruent visuo-tactile stimulation (Blanke et al., 2015; Ehrsson, 2012; Petkova & Ehrsson, 2008).

Method

Participants. A total of 29 volunteers participated in the third experiment (mean age = 25.44 years, *SD* = 3.36, 14 female). All participants had normal or corrected to normal vision and gave written informed consent. The experimental procedure was approved by the Regional Ethics Review Board of Stockholm.

Galvanic vestibular stimulation. To optimize the comparison of temporally congruent and incongruent visuo-vestibular conditions in Experiment 3, we made some small modifications to the GVS stimulation protocol with respect to Experiments 1 and 2. In Experiment 3, we applied a single sinusoidal current pulse (1 mA, frequency 1 Hz), which elicited a brief 1-s "swinging-like" vestibular sensation of self-rotation to the left side. Thus, the GVS simulation lasted for 1 s instead of 2 s as in the preceding experiments, and the movement only occurred in one direction (left) instead of back and forth between right and left. Participants underwent a threshold measurement similar to that carried out in Experiment 1 (median = 1.25 mA), and they were instructed to report their perceived direction of rotation. Moreover, as in the preceding experiments, the participants were further instructed that the vestibular stimulation should not be uncomfortable or painful and that they should perceive a clear sensation of motion.

Stimuli and apparatus. The stimulus material was produced in a similar manner as in Experiments 1 and 2. In contrast to the previous experiments, however, the background was rotated 3°/s in a counterclockwise direction in order to induce a brief "swinging-like" self-rotation sensation to the left to carefully match the sensation triggered by the GVS stimulation (described above). This visual motion stimulus was presented for one second (same duration as the vestibular stimulation). A demonstration of the video material is included as online supplementary material.

Procedure. Participants underwent two different conditions in a randomized and counterbalanced order: (a) congruent visuo-vestibular stimulation and (b) incongruent visuo-vestibular stimulation. One motion trial lasted for 6 s and consisted of one visual motion stimuli and one vestibular motion pulse (applied by means of GVS), each lasting 1 s. In the congruent condition, the visual stimulus and vestibular motion pulse were applied simultaneously every 6 s (see Figure 8). In the incongruent condition, there was a delay of 3 s between the visual stimulus and the vestibular motion pulse. The trial and delay durations were carefully determined in pilot experiments to ensure that participants had a clear perception of when a vestibular motion started and ended and that the participants could clearly perceive the asynchrony between the visual and vestibular sensations in the incongruent condition. Each block lasted for 3:34 min. Similar to Experiments 1 and 2, illusory ownership of the mannequin's body was measured using a questionnaire (subjective measurement) and SCR induced by threatening the mannequin's body with a knife (objective measurement). Knife threats were applied a total of four times during each block (after 57 min, 1:45 min, 2:33 min, and 3:21 min), always at the 5-s mark of the trial so as not to occur at the same time as the visual and vestibular stimulation. A total of eight responses were recorded.

Analysis. Data were analyzed in an identical manner as in Experiments 1 and 2. Five participants did not show any SCR, including the initial breathing response, and were therefore not included in the SCR data analysis. One further participant was excluded due to a weak breathing response and no responses to any of the knife threats (remaining total of 23 participants).

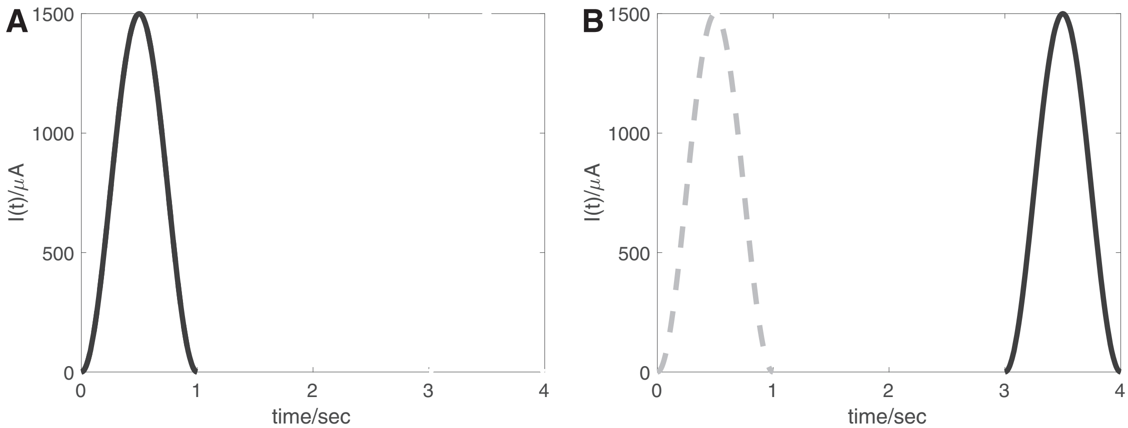

Figure 8. Illustration of the vestibular current pulse during congruent (A) and incongruent (B) visuo-vestibular stimulation. A stimulation of 1,500 μA is used in this example: i describes the current profile i = (current/2 × sin(2 × pi × t/T-pi/2)) + current/2 true for T = (1/frequency) and t = 0:0.01:T (for further information, see DC Stimulator User Manual, neuroCon GmbH, Illmenau, Germany). (A) The visual motion and vestibular motion pulse were applied in a temporally congruent manner in the congruent condition. (B) There was a 3-s temporal delay between the visual motion and vestibular motion pulse in the incongruent condition.

Results

The results of the questionnaire ratings are illustrated in Figure 9. Illusion statements were rated significantly more positively than control statements (W = 404.5, p < .001, BF >100). Overall illusion ratings were significantly higher in the congruent visuo-vestibular condition than in the incongruent condition (W = 372.5, p < .001, BF >100). Examining the illusion rating scores S1 and S2 separately revealed that both scores were rated significantly higher in the congruent visuo-vestibular condition compared to the incongruent condition (S1: W = 182, p = .003, BF = 32.6; S2: W = 351, p < .001, BF >100). The participants rejected the control statements, although we noted that this degree of rejection differed significantly for control question S3 (W = 44.5, p = .01, BF = 4.5), for which we have no good explanation. There were no significant differences between the conditions for control questions S4–S5. Data for both questions support the null hypothesis. Further results are summarized in Table 4.

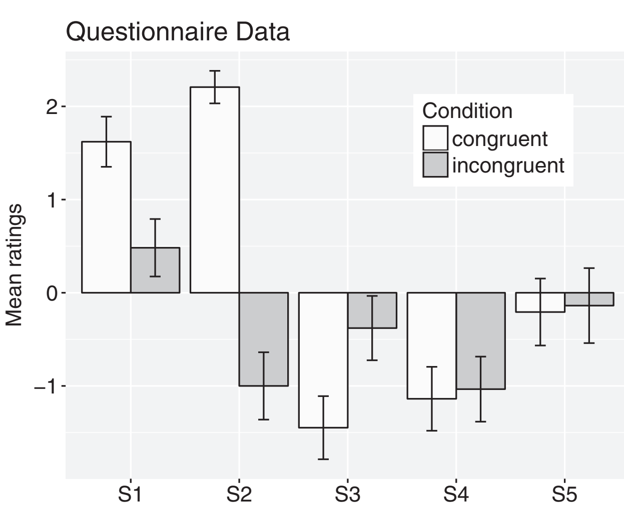

Figure 9. Results of the questionnaire data in Experiment 3.

Analysis of the SCR frequency using a logistic mixed model revealed a significant improvement of the model when adding the predictors repetition (χ^2 = 38.79, df = 1, p < .001) and the interaction between repetition and condition (χ^2 = 6.635, df = 1, p = .01; Figure 10A). Including the predictor condition did not significantly improve the model fit (χ^2 = 2.05, df = 1, p = .15). Analysis of the SCR amplitude revealed a significant effect of repetition on model performance (χ^2 = 25.74, df = 1, p < .001; Figure 10B). Neither adding condition (χ^2 = 0.02, df = 1, p = .88) nor adding the interaction between condition and repetition improved the performance of the model (χ^2 = 0.18, df = 1, p = .67; Figure 10B). There was no difference between the congruent and incongruent visuo-vestibular conditions when comparing the SCR magnitude (combining frequency and amplitude; W = 174, p = .06, BF = 0.5). Although the Wilcoxon's test revealed a tendency, the BF showed anecdotal evidence supporting the null hypothesis.

Importantly, the linear regression between the different scores of the questionnaire's illusion ratings and the different scores of the SCR magnitudes revealed a significantly positive relationship between the subjective and objective illusion measurements (β = 0.13, t = 2.35, p = .02, BF = 4; see Figure 11). This finding indicates that participants who subjectively reported a stronger illusion also had a stronger change of SCR in response to the knife threat. In line with this, analyzing ownership statement S1 separately revealed a tendency for a relationship between subjective ratings and threat-evoked SCR magnitude (β = 0.1, t = 1.55, p = .07, BF = 1.2).

Summary

In Experiment 3, we were able to show that temporally congruent visuo-vestibular stimulation leads to stronger illusory body ownership compared to a temporally incongruent stimulation condition. Ownership ratings were higher in the congru-

Table 4
Results of the Wilcoxon Signed-Rank Test in Experiment 3 for Each Statement With Bayes Factors Reported

Statement	Type	Condition	*W*	*p*	BF
S1	Illusion	Congruent vs. incongruent	182	.002	32.2
S2	Illusion		351	<.001**	>100
S3	Illusion control		44.5	.01	4.5
S4	Illusion control		40	.72	.21
S5	Dizziness control		44	.59	.02

** $p < .01$.

ent stimulation condition compared to the incongruent control condition. Although SCR showed only a statistical tendency toward a greater threat response in the congruent condition, the linear regression revealed a significant relationship between the increase in illusion ratings and the increase in SCR magnitude between the two conditions. Similar to the results of Experiments 1 and 2, participants perceiving a stronger illusion also showed stronger threat-related SCR, whereas participants with weaker or no illusion showed a weaker SCR. These results show that the full-body ownership illusion induced by visuo-vestibular stimulation obeys the temporal congruency principle of multisensory integration.

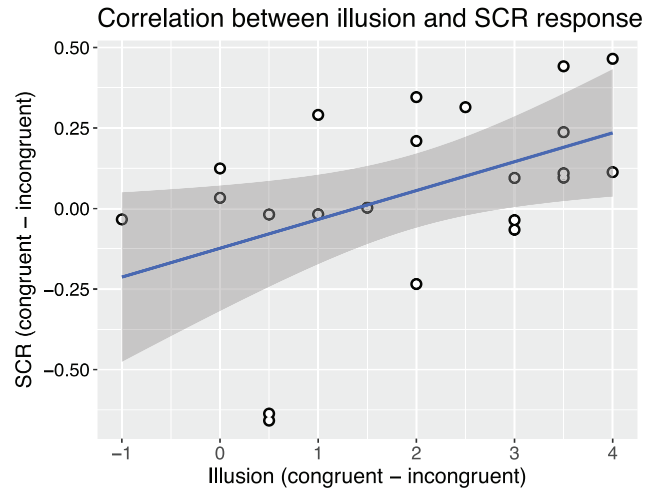

Figure 11. The relationship between the difference scores of the illusion ratings (S1, S2) and skin conductance responses (SCRs): The *x*-axis reflects the difference between the congruent and incongruent conditions in the illusion statements. The *y*-axis reflects the difference between the congruent and incongruent conditions in terms of SCR magnitude. There was a positive relationship between illusion ratings and SCR when comparing the congruent with the incongruent condition ($\beta = 0.13$, $t = 2.35$, $p = .02$). See the online article for the color version of this figure.

Discussion

We used a full-body ownership illusion and GVS in order to investigate vestibular contributions to body ownership. Congruent visuo-vestibular motion information in the same direction resulted in a stronger body ownership illusion than conditions with only visual or only vestibular information (Experiment 1). Moreover, the illusion was rated higher during the congruent visuo-vestibular stimulation compared with the incongruent visuo-vestibular stimulation condition (Experiment 3). The findings were further supported by threat-evoked SCR, serving as a physiological proxy of ownership, which showed a positive linear relation between the illusion ratings and magnitude of the SCR in all three experiments.

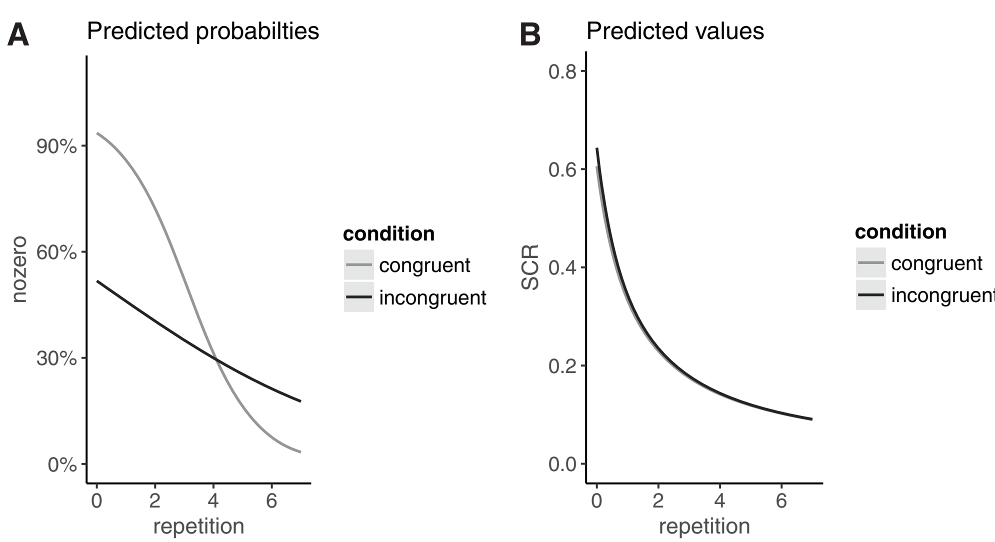

Figure 10. Predicted probabilities of (A) the logistic mixed models and (B) the gamma mixed model in Experiment 3. Figure A illustrates the main effects of repetition (centered around the first trial), condition, and their interaction. The probability of having a positive skin conductance response (SCR) was higher in the congruent condition than in the incongruent stimulation condition in the first trials. Figure B illustrates the gamma mixed model with both main effects (condition and repetition) showing that SCR decreased with increasing number of trials, but there was no difference between the two conditions.

That is, the more participants felt the illusion (average rating from Illusion Statements S1 and S2), the greater the threat-evoked SCR was. In summary, the present results provide evidence that congruent visuo-vestibular information increases the illusion of ownership over a mannequin's body.

In Experiment 2, the participants *did* report a significantly stronger illusion during the congruent condition compared with the noise condition when averaging illusion statements S1 and S2. However, when examining the statements separately, we only found a statistical trend (p = .07) for the effect of congruent visuo-vestibular stimulation on the S1 statement that directly assesses explicit body ownership. The Bayes factor was close to 1, indicating neither evidence for an effect nor evidence for the absence of an effect and showing that the noise condition was not an optimal control condition. A possible explanation is that the noise stimulation, which should not lead to any motion perception, was not perceived as incongruent in a similar manner as the "vestibular only" condition in Experiment 1 or the "incongruent" condition in Experiment 3. The mean rating of the ownership statement in the "noise" condition was relatively high compared with the means in the other control conditions. This might be explained by the fact that, during "noise" GVS, participants felt electrical stimulation behind their ears. This might have confused some participants into thinking that they perceived the same vestibular stimulation as during the threshold measurement. The relatively higher ownership ratings in the noise condition compared with the unimodal and incongruent conditions used in Experiments 1 and 3 are therefore most likely due to expectation effects.

In the present study, we analyzed SCR evoked by visually presented physical threats toward the mannequin's body, in line with earlier studies (Guterstam, Abdulkarim, & Ehrsson, 2015; Petkova & Ehrsson, 2008). SCR provides a peripheral measurement of activity in brain areas related to anxiety and pain anticipation and therefore serves as an objective measurement of illusory body ownership (Armel & Ramachandran, 2003; Ehrsson, Wiech, Weiskopf, Dolan, & Passingham, 2007). A threat to a rubber hand has been shown to elicit similar responses in anxiety- and pain-related brain areas as when a person's real body is threatened (Ehrsson et al., 2007). However, unlike the earlier full-body ownership illusion studies that only analyzed the absolute magnitude of the SCR averaged across trials, we conducted a more detailed analysis of the frequency, amplitude and magnitude of the responses relative to each participant's "maximal" response elicited by asking the participants to take a deep breath and hold the air for a few seconds. The issue with SCR magnitude alone is that it creates the impression that the strength of the response is changing, although it might be the frequency that changes (Dawson et al., 2007; Prokasy & Kumpfer, 1973). The present results mainly revealed an effect of condition on SCR frequency and, only in Experiment 2, on SCR amplitude. This means that our conditions primarily affected the occurrence of a positive SCR but not the strength of the response. As described in an article by Dawson, Schell, and Filion (2007), magnitude, amplitude, and frequency are all legitimate measurements for SCR, each with advantages and disadvantages. Using mixed models allowed us to handle variance in the data related to unspecific order effects. We were also able to reveal a positive linear relationship between the strength of the subjective full-body ownership illusion and the magnitude of the threat-evoked SCRs, a systematic relationship that earlier studies failed to detect. This finding both provides support for the main conclusion of our study and corroborates the threat-evoked SCR as an objective measure of body ownership.

Previous studies on full-body ownership mainly focused on visuo-tactile multisensory integration (Guterstam, Abdulkarim, et al., 2015; Petkova & Ehrsson, 2008; Petkova, Khoshnevis, et al., 2011; Preston & Ehrsson, 2014) and more complex integration of multisensory and motor signals that occur when moving limbs and heads of avatars in virtual reality experiments that use head-tracking technologies (Kilteni, Normand, Sanchez-Vives, & Slater, 2012; Maselli & Slater, 2013; Slater et al., 2010). In the former case, vestibular cues are held constant across conditions and are thus not directly investigated. In the latter case, however, it is not possible to disambiguate the contributions of vestibular inputs from proprioceptive, motoric and other kinds of signals when moving the head and looking around in the virtual environment. To the best of our knowledge, only one other study so far has examined the effect of visuo-vestibular integration on body ownership perception using passive motion stimuli (Macauda et al., 2015). Participants were exposed to passive body motion along the earth's horizontal axis using a motion platform while congruent or incongruent visual feedback was provided through an HMD. In the congruent condition, the seen and felt motion feedback was matched, and in the incongruent condition, the participants saw the movement after a 1-s delay and in the opposite direction. However, the illusion was surprisingly weak in the congruent condition, and no significant differences in ownership ratings between the congruent and incongruent conditions were observed. Even more intriguingly, the participants in this experiment did not experience the incongruent condition as more out-of-sync than the congruent condition. In contrast, we carefully fine-tuned our stimulation parameters in pilot experiments to ensure that the participants could clearly perceive the difference in synchrony between the congruent and incongruent conditions. We therefore opted for a longer delay (3 s) in the incongruent condition so that the participants could clearly perceive this discrepancy. This strategy was evidently successful, as we observed a significantly weaker illusion in this condition compared to the congruent condition. Hence, the present study provides conclusive evidence that congruent visuo-vestibular input is sufficient to create a subjective illusion of ownership of an entire body. This is an important observation because it shows that vestibular signals play an important role in the dynamic multisensory integration that leads to the formation of a coherent representation of one's own body in space. Thus, vestibular signals not only modulate the integration or processing of visuo-tactile signals, as demonstrated in previous studies, but also make a distinct contribution to the perceptual binding of multisensory cues that contribute to the subjective experience of owning a body.

The aims of the present study were to prove that the integration of congruent visual and vestibular signals is sufficient to elicit an illusion of full-body ownership of a mannequin's body and to show that such ownership sensations triggered by visuo-vestibular congruency are stronger than ownership experienced during incongruent or unimodal stimulation conditions. To this end, we used electrical stimulation of the vestibular nerve that allowed for a more direct investigation of the vestibular contribution to body ownership. GVS also has the advantages of being readily delivered and controlled in experimental studies without the need for a movement platform and of being compatible with fMRI. The latter advantage is important for future neuroimaging experiments that we are planning to conduct. However, a limitation of GVS is that the visuo-vestibular stimulation was probably never perfectly synchronized in the congruent conditions, as the electrodes affect the whole vestibular nerve, and therefore, precise onset of the vestibular sensations is difficult to control. Nevertheless, as indicated by the questionnaire results, participants perceived the GVS stimulation to be congruent with the visual motion information, and we did successfully elicit a significant full-body ownership illusion, which suggests that our visuo-vestibular congruency manipulation was effective.

Although the present and abovementioned studies provide evidence for an involvement of the vestibular system in body ownership perception, the underlying neural mechanisms are still unclear. The *parieto-insular vestibular cortex* (PIVC; Grüsser, Pause, & Schreiter, 1990; Guldin & Grüsser, 1998) is considered the core cortical "vestibular" area, which receives input from the vestibular nuclei in the brainstem and is highly connected to other areas involved in the processing of vestibular signals, such as the cortices lining the intraparietal sulcus, the inferior posterior parietal cortex, and the ventral premotor cortex (Eickhoff, Weiss, Amunts, Fink, & Zilles, 2006; Lopez, Blanke, & Mast, 2012; zu Eulenburg, Caspers, Roski, & Eickhoff, 2012). Interestingly, lesions or damages in vestibular areas, such as the temporal-parietal junction (TPJ), can result in impairments in multisensory integration and out-of-body experiences (OBE; Blanke & Arzy, 2005; Blanke, Landis, Spinelli, & Seeck, 2004; Blanke, Ortigue, Landis, & Seeck, 2002). Experimental studies in healthy participants using visuo-tactile stimulation reported that whole body ownership is associated with activation of the multisensory premotor-intraparietal cortex (Guterstam, Björnsdotter, et al., 2015; Petkova, Björnsdotter, et al., 2011; Preston & Ehrsson, 2016). The contribution of vestibular information to the cortical representation of body ownership is not completely understood; however, possible neural mechanisms might involve vestibular projections to the TPJ, ventral premotor cortex, and intraparietal sulcus. The paradigm we developed in the present study can be used in future functional MRI experiments to investigate visuo-vestibular multisensory integration in the human brain.

In the present study, we developed a new paradigm combining electrical vestibular stimulation, virtual reality technology and a full-body ownership illusion paradigm to investigate the contribution of visuo-vestibular integration to the sense of ownership of an entire body. We were able to show that congruent visuo-vestibular information can elicit a sensation of ownership of a mannequin's body—more strongly than incongruent and unimodal stimulation conditions—while effectively controlling for possible somatosensory influences by using GVS stimulation. Future studies should elucidate how the brain creates a unified experience of the bodily self by means of multisensory integration mechanisms, including vestibular signals.

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