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Auditory Cues Influence the Rubber-Hand Illusion

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The perception of one's own body depends on the dynamic integration of signals from different sensory modalities. Earlier studies have shown that visual, tactile, and proprioceptive information contributes to this process. However, little is known about the role of auditory cues in the multisensory integration of bodily signals. To address this issue, we studied the effect of auditory feedback on the rubber-hand illusion and the somatic version of this illusion. In each experiment, we tested 30 healthy participants using four different conditions: synchronous touches without auditory cues (original illusion), asynchronous touches without auditory cues (original control), synchronous touches with synchronous auditory cues (illusion positively modulated by sound), and synchronous touches with asynchronous auditory cues (illusion negatively modulated by sound). For the classic rubber-hand illusion, we found that synchronous auditory cues made the illusion stronger compared with asynchronous auditory cues, as evidenced by both the results of the questionnaires and proprioceptive drift. In both versions of the illusion, proprioceptive drift indicated that the synchronous auditory cues enhanced the illusion compared with the condition without auditory feedback and that the asynchronous auditory cues reduced the illusion compared with the nonauditory condition. Taken together, these results demonstrate that auditory cues modulate the rubber-hand illusion, which suggests that auditory information is used in the formation of the coherent multisensory representation of one's own body.

Public Significance Statement

This study highlights the importance of sounds in the perception of our own bodies by demonstrating that auditory feedback modulates a classic perceptual illusion, the so-called "rubber-hand illusion." In the first experiment, we found that sounds of brushstrokes enhanced the illusion that a rubber hand was one's own when presented in synchrony with brushstrokes applied to the visible model hand and to the participant's real hand, which was hidden from view. Similarly, in the second experiment, we found that sounds of finger taps enhanced a nonvisual version of the illusion where the participants touched a right rubber hand with their own left finger while receiving corresponding touches on their real right hand. Taken together, these results are important because they reveal how sounds that the body makes contribute to the perception of what constitutes our own body.

Keywords: multisensory integration, body perception, body ownership, rubber-hand illusion, somatic rubber-hand illusion

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When we are awake and go about our daily activities, we always have a clear sense of our own body and how our body is distinct from the external environment. It has been shown that the perception of one's own body in space depends on the integration of bodily signals originating from different sensory modalities, particularly vision, touch, and proprioception (Botvinick & Cohen, 1998; Ehrsson, Spence, & Passingham, 2004; Gentile, Petkova, & Ehrsson, 2011; Lloyd, Shore, Spence, & Calvert, 2002; Makin, Holmes, & Ehrsson, 2008; Tsakiris & Haggard, 2005; for a review, see: Azañón et al., 2016). Vision is considered to play a leading role due to its ability to dominate other modalities under good viewing conditions (De Vignemont, Ehrsson, & Haggard, 2005; Hagura et al., 2007; Holmes, Snijders, & Spence, 2006; Longo, Cardozo, & Haggard, 2008; van Beers, Sittig, & Denier van der Gon, 1996; van der Hoort, Guterstam, & Ehrsson, 2011; but see also: van Beers, Wolpert, & Haggard, 2002), and it is the most reliable modality in terms of acquiring information about the position of the limbs (Marino, Stucchi, Nava, Haggard, & Maravita, 2010). Proprioception and touch obviously play critical roles in the sense of our own limbs in space (Edin, 2001; Lackner, 1988; Naito, Ehrsson, Geyer, Zilles, & Roland, 1999; Naito, Roland, & Ehrsson, 2002; Proske & Gandevia, 2012), especially

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when vision is not available (Lackner & Taublieb, 1984). Furthermore, body representation is also influenced by stored previous experiences regarding the body (Petkova & Ehrsson, 2008; Tsakiris, Carpenter, James, & Fotopoulou, 2010).

However, the possible influence of auditory cues on the integration of bodily signals has received far less attention than have visual, proprioceptive, and tactile cues. Although the role of auditory input on multisensory interactions has recently been explored and its influence on body representation has been demonstrated by changes in the peripersonal space (Ferri, Tajadura-Jiménez, Väljamäe, Vastano, & Costantini, 2015) and the perceptions of body size and length (Tajadura-Jiménez, Basia et al., 2015; Tajadura-Jiménez et al., 2014; Tajadura-Jiménez, Tsakiris et al., 2015; Tajadura-Jiménez et al., 2012, 2017), the role of audition in the perception of body parts as belonging to one's own body (sense of "body ownership"; see Ehrsson, 2012) still remains unclear. This is surprising because, whenever we move and interact with environmental objects, our body often produces sounds that can be used as feedback to identify and localize our limbs in space. For example, imagine you are walking through a dense rainforest in the dark: was that the sound of my hand moving against the leaves, or was that the sound of an insect that just landed on my arm?

In this paper, we examine the effect of ecologically relevant auditory feedback on body self-perception using a common paradigm in multisensory body representation and body ownership research: the rubber-hand illusion (Botvinick & Cohen, 1998). We studied both the "classic" version of this illusion with the rubber hand in full view in front of the participant (Botvinick & Cohen, 1998; see also: Ehrsson et al., 2004) and the somatic version with blindfolded participants touching the rubber hand (Ehrsson, Holmes, & Passingham, 2005). The classic rubber-hand illusion is elicited by stroking the rubber hand and the subject's hidden hand using two small paintbrushes, synchronizing the timing of the strokes as perfectly as possible. After about 10–20 s of such brushing, the majority of participants start to experience the rubber hand as their own (Ehrsson et al., 2004; Kalckert & Ehrsson, 2017; Lloyd, 2007). This is evident from their high affirmative ratings on the statement "I felt as if the rubber hand were my own hand" in a commonly used questionnaire (Botvinick & Cohen, 1998). Furthermore, participants also demonstrate the so-called "proprioceptive drift," a change of perceived hand location toward the rubber hand after the illusion, compared with before. This is a commonly used objective measure of the illusion that often correlates with subjective questionnaire ratings (Kammers, de Vignemont, Verhagen, & Dijkerman, 2009; Longo, Schüür, Kammers, Tsakiris, & Haggard, 2008; Lopez, Lenggenhager, & Blanke, 2010; Tsakiris & Haggard, 2005), but not always (Rohde, Di Luca, & Ernst, 2011), which has stimulated discussions about the exact relationship between the subjective experience of ownership and proprioceptive drift (Abdulkarim & Ehrsson, 2016; Rohde et al., 2011).

In the case of the somatic rubber-hand illusion, the feeling of ownership is elicited by repeatedly moving the blindfolded participant's left index finger so that it touches a right rubber hand, while synchronously touching the participant's real right hand at the corresponding site. After a short period of such stimulation, most participants experience an illusion of touching their own hand, which is captured by the statement "I felt as if I was touching my right hand with my left index finger" in the questionnaire (Ehrsson et al., 2005). This version of the rubber hand illusion can also be objectively quantified with proprioceptive drift (Ehrsson et al., 2005). In the present study, we included an experiment on the somatic rubber-hand illusion to investigate whether auditory information modulates the sense of limb ownership both when vision is available and when it is not.

To address whether auditory cues contribute to the classic and somatic rubber hand illusions, we created four conditions: synchronous touches without auditory cues (original illusion), asynchronous touches without auditory cues (original control), synchronous touches with synchronous auditory cues (illusion with positive sound modulation), and synchronous touches with asynchronous auditory cues (illusion with negative sound modulation). The two latter conditions are particularly important because they allowed us to directly test the effect of temporal congruency of auditory feedback on the hand ownership illusions. In light of previous research in the field of multisensory integration, which shows that combining information from many different senses requires between-modality synchrony (Senkowski, Talsma, Grigutsch, Herrmann, & Woldorff, 2007; Spence & Squire, 2003), we hypothesized that, compared with asynchronous auditory feedback, the synchronous auditory feedback in the rubber-hand illusion would increase both subjective and objective ratings of the illusory experience. Furthermore, based on the suggestion that task-irrelevant auditory cues modify proprioceptive drift in the rubber-hand illusion and the invisible hand illusion (Darnai et al., 2017; see also: Guterstam, Gentile, & Ehrsson, 2013), we hypothesized that ecologically relevant auditory cues should make the proprioceptive drift significantly more pronounced in the condition with the synchronous auditory feedback compared with the original rubber hand illusion conditions without auditory feedback. These predicted results would show that auditory information is used in the formation of the coherent multisensory representation of one's own body.

Method

Subjects

We tested a total of 60 healthy volunteers: 30 for Experiment 1 (mean age = 30.8, range = 20–60; 24 females, 6 males; 29 right-handed, 1 left-handed) and 30 for Experiment 2 (mean age = 26.5, range = 20–46; 23 females, 7 males; 25 right-handed, 4 left-handed, 1 ambidextrous). The sample size was based on previous experiments using the rubber hand illusion (e.g., Cowie, Makin, & Bremner, 2013; Marotta, Tinazzi, Cavedini, Zampini, & Fiorio, 2016). Group size was also confirmed by a power analysis for planned t tests with $\alpha = .05$, $\beta = .95$, and $d > .80$ (performed with G*Power 3.1; see Faul, Erdfelder, Lang, & Buchner, 2007). All participants were recruited through advertisements on the campus of the Karolinska Institute and on social media. Participants received a cinema voucher as compensation. All subjects had normal or corrected-to-normal vision.

The experiment was approved by the local ethical committee (Regional Ethical Review Board of Stockholm). A written consent form was obtained from each participant.

Apparatus and Stimuli

Auditory stimuli were prerecorded and processed with Audacity 2.1.2 (The Audacity Team, Pittsburgh, PA, USA). In Experiment

1, the stimulus lasted for 400 ms and was a sound of a smooth surface being stroked with a paintbrush. This stimulus resembled the sound of a hand being stroked with a paintbrush. In Experiment 2, the stimulus lasted for 300 ms. and was a sound of a tap on a smooth surface, similar to the sound of a hand being tapped by a digit. The stimuli were presented via binaural headphones (MEL 1600530 by Maxell, Tokyo, Japan). To transfer the information of when the brush (Experiment 1) or finger (Experiment 2) contacted the rubber hand to the computer with high temporal precision, a custom-made device was built. It consisted of a 3-m long fiber-optic cable (Omron, Osaka, Japan) with a light sensor (Avago Technologies, San Jose, CA, USA) that was activated each time it was close to the surface of the rubber hand. The light sensor was attached to the brush in Experiment 1 (Figure 1A) and the left index finger of the participant in Experiment 2 (Figure 2A; see further details below). The fiber-optic cable was connected to a computer, which triggered the sound either at the same moment as the movement (synchronous touches with synchronous auditory cues condition) or with a delay randomized between 500 and 1,000 ms (synchronous touches with asynchronous auditory cues condition).

Task and Procedure

Experiment 1: Classic rubber-hand illusion. During Experiment 1, participants placed their right hand in a relaxed position on a table in front of them, next to a gender-matched rubber hand (a cosmetic prosthetic glove filled with hard plastic). Both hands were placed with the palms facing down. The rubber hand and the right hand were separated from each other with a custom-made wooden partition, so that the participants were not able to see their real hand. The distance between the real and rubber hand was always 15 cm. During the experimental stimulation, participants were asked to place their left hand on their thigh and to fixate on the rubber hand. The tactile stimulation of the participant's hand consisted of single continuous strokes with a small paintbrush, from the knuckle of their index finger the top of the dorsal side of the hand (Figure 1B). The duration of each stroke was approximately 400 ms. One stroke was applied every second with the following rhythmic pattern: three strokes, one second without a stroke, two strokes, one second without a stroke, three strokes, one second without a stroke, and so on. We used this pattern instead of a strict, regular sequence because anecdotally it produced a stronger rubber hand illusion in the synchronous conditions. In the three conditions with synchronous visuotactile stimulation, the experimenter used an identical paintbrush to stroke the rubber hand in the same manner as the real hand while synchronizing the strokes as carefully as possible. In the asynchronous control condition, the stimulation was delayed for approximately 400 ms. The duration of each stroke was the same as in the synchronous conditions, but we brushed another finger on the real hand rather than on the rubber hand to further enhance the incongruency of the visuotactile stimulation to maximize the elimination of the illusion. Each period of repeated stimulation took approximately 60 s, such that one trial consisted of approximately 40 strokes.

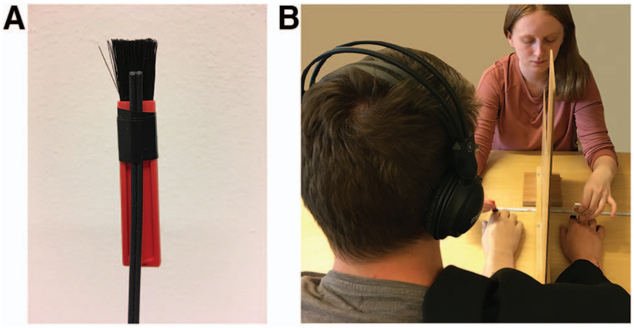

Figure 1. The setup used to induce the classic rubber hand illusion. (A) Position of light sensor attached to the brush. (B) The illusion induction. See the online article for the color version of this figure.

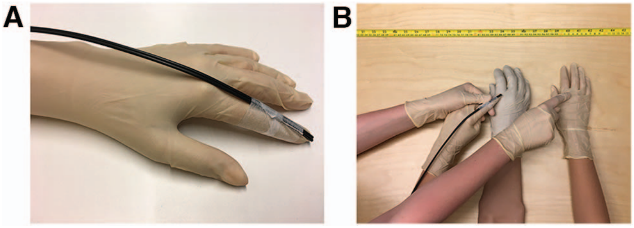

Figure 2. The setup used to induce the somatic rubber hand illusion. (A) Position of light sensor attached to the finger. (B) The illusion induction. See the online article for the color version of this figure.

Experiment 1 consisted of 16 semirandomized trials: first, 12 localization trials (three blocks of four trials) to measure proprioceptive drift and, second, four trials for the subjective measure (questionnaire). The conditions within the blocks were counterbalanced and randomized for each participant to minimize possible order effects. If the participant affirmed ownership of the rubber hand (his or her report was equal to or greater than 1 for the question "I felt as if the rubber hand were my own hand" in any of the three conditions of synchronous visuo-tactile stimulation), four additional trials were conducted to estimate the onset of the illusion (adapted from Kalckert & Ehrsson, 2017). During the proprioceptive drift trials, participants were asked to close their eyes, and the experimenter then positioned the participant's left index finger on a plastic ruler, which was placed on the table five centimeters over both the right hand and the rubber hand. The starting location was randomized between 40 and 60 cm to the left of the right hand. Then, the participant moved his or her left index finger toward the right until he or she perceived that it was directly above the right index finger. They were allowed to adjust the final position of their left finger. The procedure was repeated before and after each stimulation period. The proprioceptive drift score was calculated as the difference between the pretrial and posttrial finger localization measures (in line with previous studies; e.g., Abdulkarim & Ehrsson, 2016; Ehrsson et al., 2005; Tsakiris et al., 2005). After each of the subsequent four trials, participants were asked to complete a questionnaire regarding their experiences during the most recently experienced trial. The questionnaire consisted of eight statements from the study by Botvinick and Cohen (1998), in which there were three ownership statements (Q1: "It seemed as if I were feeling the touch of the paintbrush in the location where I saw the rubber hand touched," Q2: "It seemed as though the touch I felt was caused by the paintbrush touching the rubber hand," Q3:

"I felt as if the rubber hand were my hand"). The remaining five questions were meant to control for potential expectancy and task compliance effects (Q4: "It felt as if my (real) hand were drifting towards the left (towards the rubber hand)," Q5: "It seemed as if I might have more than one left hand or arm," Q6: "It seemed as if the touch I was feeling came from somewhere between my own hand and the rubber hand," Q7: "It appeared (visually) as if the rubber hand were drifting towards the right (towards my hand)," Q8: "The rubber hand began to resemble my own (real) hand, in terms of shape, skin tone, freckles or some other visual feature"). Participants rated each of the statements on a 7-point Likert scale from −3 to + 3, where −3 meant "I disagree very strongly," +3 meant "I agree very strongly," and 0 meant "I am uncertain."

During the trials measuring the onset of the illusion, participants were asked to verbally report the feeling of ownership by saying "now" as soon as they started to feel that the rubber hand was their own. Then, the stimulation continued for an additional 30 s. Afterward, the participants were asked to quantify the vividness and continuance of the illusion (adapted from Ehrsson et al., 2005) by choosing numbers between 0 and 9. In the case of the vividness rating, 9 meant that the feeling that the rubber hand was their own was very lifelike and realistic. In the case of continuance, the chosen number reflected the proportion of time during which the illusion was experienced, such that 9 meant that they felt the illusion for the entire time after illusion onset.

Experiment 2: Somatic rubber-hand illusion. During Experiment 2, the experimenter, the participant and the rubber hand all wore identical plastic surgical gloves to make the tactile surfaces of the hands as similar as possible. Participants placed both of their hands in a relaxed position on a table in front of them with the palms facing down, while a gender-matched rubber hand was placed between the participants' right and left hands. The distance between the participant's right index finger and the index finger of the left rubber hand was always 15 cm. The experimenter moved the participant's left index finger so that it touched the knuckle of the rubber hand's index finger (Figure 2B). At the same time, the experimenter touched the knuckle of the right index finger of the participant. Each tap lasted approximately 300 ms. The period between the taps was approximately one second. The taps were applied with the following pattern: three taps, 1-s break, two taps, 1-s break (the same pattern as used in the classic illusion, see above). In the asynchronous control condition, the duration of each tap was the same as that in the synchronous condition, but the taps were delayed by approximately 300 ms. Additionally, the taps were applied alternately to the knuckles of the index and middle fingers on the real hand to maximize the incongruency of the stimulation and thereby eliminate the illusion as effectively as possible. Each touching session lasted approximately 60 s, such that one trial consisted of approximately 46 taps. Participants were blindfolded with a disposable blindfold for the duration of experimental stimulation, except when they were filling out the questionnaire. Before the experiment, they were allowed to see and tactilely explore the surface of the rubber hand, so that, at the outset of experiment, participants knew they were touching the rubber hand just as they knew they were looking at a model hand in the classic version of the illusion.

Experiment 2 consisted of 16 semirandomized trials: first, 12 localization trials (three blocks of four trials) to measure proprioceptive drift and, second, four trials for the subjective measure (questionnaire). The conditions within the blocks were counterbalanced and randomized for each participant to avoid possible order effects. If the participant affirmed ownership of the rubber hand (his or her report was equal or greater than 1 for the question "It felt as if I was touching my right hand with my left index finger" in any condition except the control condition), four additional trials were conducted to estimate the onset of the illusion. During the proprioceptive drift trials, the experimenter placed the participant's left hand on a plastic ruler, which was placed on the table five centimeters over both the right hand and the rubber hand. The starting location was randomized between 40 and 60 cm from the location of the right hand. Participants slid their left index finger along the ruler toward the right until they perceived that it was directly above their right index finger. The procedure was repeated before and after each stimulation period (pretrial and posttrial measures as described in Ehrsson et al., 2005). The proprioceptive drift score was calculated as the difference between the pretrial and posttrial finger localization measures. Subsequently, after each of the next four trials (one for each condition), participants were asked to complete a questionnaire regarding their experiences during the most recent trial. The questionnaire consisted of five statements from the article by Ehrsson et al. (2005); there was the ownership statement (Q1: "It felt as if I was touching my right hand with my left index finger"), and the four remaining questions attempted to capture a possible expectancy effect: Q2: "It felt like I had more than one right hand," Q3: "It felt like my right hand was larger than normal," Q4: "It felt like my right hand was moving," Q5: "It seemed like I was not able to feel my own right hand." Participants rated each of the statements on a 7-point scale from −3 to + 3. During the final extra trials measuring the onset of the illusion, participants were asked to verbally report the feeling of ownership by saying "now" as soon as they started to feel like they were touching their right hand with their left index finger. Then, the stimulation continued for an additional 30 s. Afterward, participants were asked to quantify the vividness and continuance of illusion by choosing a number between 0 and 9, as described above in Experiment 1.

Data Analysis

For both Experiment 1 and Experiment 2, the proprioceptive drift data were normally distributed (Shapiro-Wilk test value always $>.05$). We analyzed these data by comparing the relevant conditions using planned comparisons with two-tailed *t* tests. Due to being on an ordinal scale, the questionnaire data were tested nonparametrically with the Friedman test and Wilcoxon signed-ranks test. Given that we used a small number of planned comparisons that were strongly based on our hypothesis, experimental design and previous studies, we did not correct for multiple comparisons. Correlations between the proprioceptive drift and the ownership statements were tested with the nonparametric Spearman's rank correlation.

Results

Experiment 1

Crucially, the proprioceptive drift toward the rubber hand was significantly greater in the synchronous touches with synchronous auditory cues condition than in the synchronous touches with asynchronous auditory cues condition (see Figure 3), $t(29) = 6.401$, $p < .001$, CI 95% = 1.421–2.756. This shows that the temporal congruency of the auditory cues with the visuo-tactile stimuli enhanced the illusion as measured by proprioceptive drift. Furthermore, the proprioceptive drift was significantly greater in the synchronous touches with synchronous auditory cues condition compared with the synchronous touches without auditory cues condition, $t(29) = 3.35$, $p = .002$, CI 95% = .379–1.566, which shows that additional auditory feedback made the proprioceptive drift toward the rubber hand greater. Additionally, the drift was significantly suppressed in the asynchronous auditory condition compared with the original illusion condition, $t(29) = 4.663$, $p < .001$, CI 95% = .627–1.606. As expected, we reproduced the classic illusion (Botvinick & Cohen, 1998) without any auditory feedback, as evidenced by the significantly greater drift in the synchronous condition without auditory cues compared with the asynchronous condition without auditory cues, $t(29) = 6.458$, $p < .001$, CI 95% = 1.249–2.407.

In the case of the questionnaire results, we found a significant difference between the synchronous touches with synchronous auditory cues condition and the synchronous touches with asynchronous auditory cues condition ($Z = -2.421$, $p = .015$). However, participants gave high affirmative ownership ratings for both the synchronous touches with synchronous auditory cues condition and the original illusion condition of synchronous touches without any auditory feedback (difference not significant: $Z = -1.075$, $p = .283$; see Figure 4). Crucially, the ratings for the synchronous touches with asynchronous auditory cues condition were significantly lower than those in the classic illusion condition ($Z = -2.275$, $p = .023$), which shows that asynchronous auditory feedback suppressed the subjective illusion. We also reproduced the classic illusion, finding a significant difference between the original illusion condition and the asynchronous control condition (without auditory feedback; $Z = -3.676$, $p < .001$). No significant differences were found between the conditions in terms of illusion onset or the vividness and continuance ratings of the subsequent illusion period (see Supplementary Figure 1).

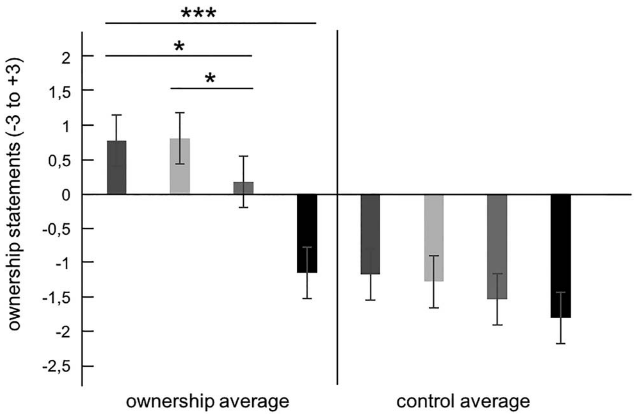

Figure 4. The results of Experiment 1. Questionnaire results for each condition (for full questionnaire results, see Supplementary Figure 2). Error bars represent standard errors of the mean. Asterisks indicate a significant difference between the conditions (*** $p < .001$, * $p < .05$).

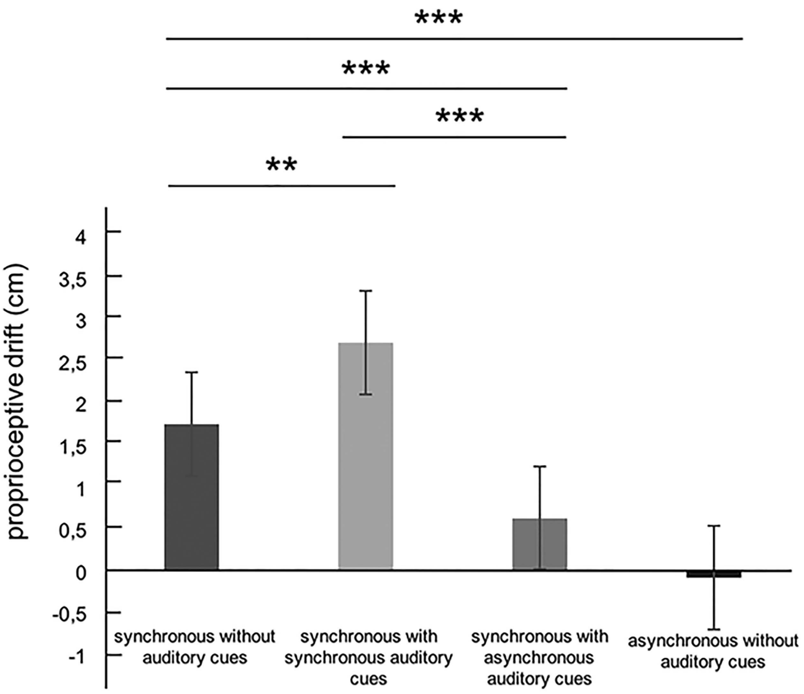

Figure 3. The results of Experiment 1. Average proprioceptive drift in each condition. Error bars represent standard errors of the mean. Asterisks indicate a significant difference between conditions (*** $p < .001$, ** $p < .01$).

Interestingly, in the synchronous touches with synchronous auditory cues condition, we found a significant correlation between proprioceptive drift and the average rating pooled across the three statements referring to the illusory experience (Q1–Q3, ownership of hand and referral of touch; ϱ = .495, *p* = .005; see Supplementary Figure 3), in line with previous research showing a link between these two measures (see Kalckert & Ehrsson, 2012; Tsakiris & Haggard, 2005). This relationship was not found among the other conditions, which were all nonsignificant.

Experiment 2

The results from the proprioceptive drift test in the somatic rubber hand illusion (see Figure 5) were very similar to the results observed in Experiment 1 with the classic version. The proprioceptive drift was significantly greater in the condition with synchronous touches and synchronous auditory cues compared with the synchronous touches with asynchronous auditory cues, $t(29) = 5.333$, $p < .001$, CI 95% = 1.445–3.244. This shows that temporal congruency of auditory cues enhanced the illusion as measured by proprioceptive drift. Furthermore, the proprioceptive drift toward the rubber hand was significantly greater in the condition with synchronous touches and synchronous auditory cues compared with the original illusion condition without auditory feedback, $t(29) = 2.908$, $p = .007$, CI 95% = .356–2.044, which shows that additional auditory feedback increased the proprioceptive drift. Additionally, the drift was significantly suppressed in the asynchronous auditory condition compared with the original illusion condition, $t(29) = 3.527$, $p = .001$, CI 95% = .481–1.808. The results reproduced the effect from the experiment by Ehrsson et al. (2005), because the synchronous condition without auditory feedback led to significantly greater proprioceptive drift compared with the asynchronous control condition (without auditory feedback), $t(29) = 4.621$, $p < .001$, CI 95% = .814–2.108.

In the case of the questionnaire results (Figure 6), participants gave high affirmative ownership ratings for the three conditions with synchronous movements of the left index finger taps on the right hand. There was no significant difference between these conditions ($\chi^2 = 1.286$, $p = .526$), and the planned comparison between the synchronous and asynchronous auditory feedback conditions revealed no significant differences (Z = −.77, *p* = .441). In the asynchronous control condition without auditory cues, participants strongly denied ownership, as evidenced by negative rating scores; we replicated the significant difference (Z = −3.719, $p < .001$) in ownership ratings between the synchronous and asynchronous conditions without auditory cues, which is in line with the findings of Ehrsson et al., 2005. No significant differences were found between the conditions in the illusion onset results or vividness and continuance ratings (see Supplementary Figure 4).

Discussion

In these experiments, we studied the effect of ecologically relevant auditory feedback on the classic and somatic rubber-hand illusions. For the classic version of the rubber hand illusion, we found that synchronous auditory cues enhanced the illusion compared with asynchronous cues. This effect was observed in both the questionnaire data and proprioceptive drift. In the somatic rubber-hand illusion, a significant effect of auditory synchrony (vs. asynchrony) was observed in the proprioceptive drift but not in the

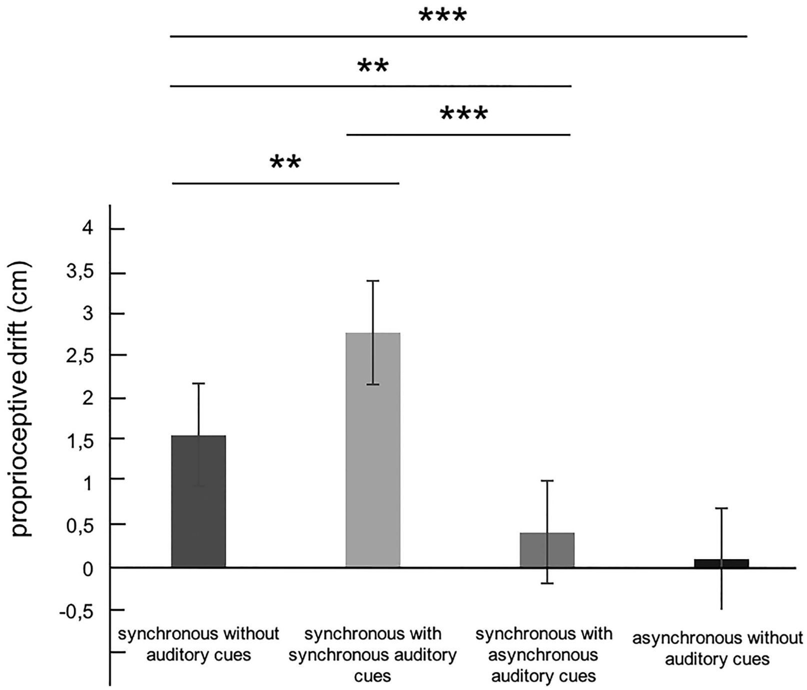

Figure 5. The results of Experiment 2. Average proprioceptive drift in each condition. Error bars represent standard errors of the mean. Asterisks indicate a significant difference between conditions (*** $p < .001$, ** $p < .01$).

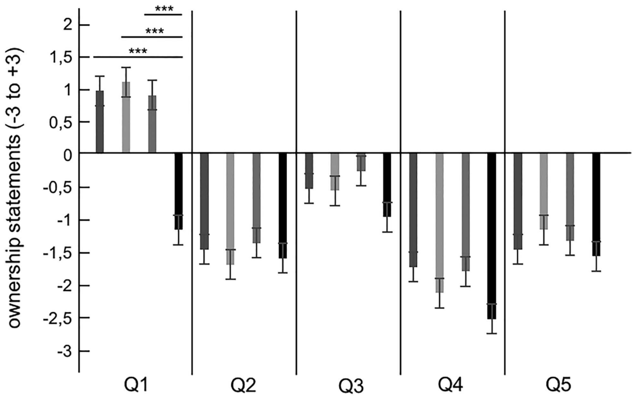

Figure 6. The results of Experiment 2. Questionnaire results for each condition. Error bars represent standard errors of the mean. Asterisks indicate a significant difference between conditions (*** $p < .001$).

questionnaire ratings. In both versions of the illusion, proprioceptive drift indicated that the synchronous auditory cues enhanced the illusion compared with the illusion condition without auditory feedback and that the asynchronous auditory cues reduced the illusion compared with the no-sound condition. Taken together, these results provide conclusive evidence that bodily related sounds modulate the rubber hand illusion and further suggest that temporally congruent auditory, tactile, and visual signals integrate in the process of feeling ownership of limbs. This is significant because it suggests an important role of audio-somatic integration in the updating of the central representation of one's own body in space.

Our results go substantially beyond the study by Darnai et al. (2017). In that study, the invisible hand illusion (Guterstam et al., 2013) was induced with or without the addition of a body-irrelevant metronome sound, and it was measured with a proprioceptive drift test. The visuo-tactile stimulation of the brush stroking was conducted in-phase with metronome beats and compared with a condition without any sounds. The results of by Darnai et al. (2017) showed that the participant's perceived hand position drifted more toward body-midline in the metronome condition compared with the no-sound condition. However, because no control condition involving sounds was used, it cannot be ruled out that this was an unspecific effect related to the additional sound stimuli. By contrast, in the present paradigm, we specifically examined the effect of the temporal congruency of auditory feedback by directly comparing sounds that occurred in synchrony versus out-of-synchrony with the brushstrokes (Experiment 1) and taps (Experiment 2) in otherwise equivalent experimental conditions. Moreover, in the present study, we used ecologically relevant body-related sounds created to resemble the stroke of a brush or the tap of a finger against skin, as opposed to metronome beats, which are unrelated to the human body. Finally, we observed consistent results from both the questionnaires and the proprioceptive drift in the case of the classic rubber hand illusion (Experiment 1), whereas Darnai and colleagues only reported changes in the proprioceptive drift, and such a finding from a single measure should be treated with caution. Thus, the present study is the first to demonstrate a specific effect of congruent auditory feedback on the rubber-hand illusion.

However, some questions remain. In both experiments, we observed significant differences in proprioceptive drift between the synchronous and asynchronous conditions, whereas, in the case of the questionnaire results, we found a significant difference between these conditions in the classic rubber-hand illusion but not in the somatic version. This inconsistency between the proprioceptive drift and questionnaire results in the second experiment could have several explanations. First, it could be that the 7-point Likert scale is less sensitive than proprioceptive drift, which is a continuous variable measured in centimeters. Although the questionnaires were sensitive enough to detect the sound-congruency effect in the classic rubber hand illusion, they were not sensitive enough to detect the enhancement and reduction of the illusion in the synchronous and asynchronous sound conditions, respectively, compared with the original illusion condition without sounds, as revealed by the proprioceptive drift data. Second, the difference in questionnaire results between the two illusions might be due to differences in the structure of the two questionnaires. The questionnaire used for the classic rubber-hand illusion included three statements that denoted ownership of the model hand and referral of touch. We used the average of these three statements as our index of illusion strength, which might produce a more reliable index of the subjective illusion than the single statement referring to ownership in the somatic rubber hand illusion questionnaire. Third, and more interestingly, it could be that the effect of congruent auditory feedback facilitates visuo-tactile-proprioceptive integration in the classic illusion more effectively than tactile-proprioceptive integration across the two hands in the somatic version. For example, one could speculate that there is a greater effect of audition on the visuo-tactile integration responsible for the referral of touch. This is also supported by the results of Sperdin, Cappe, and Murray (2010) and Noel and Wallace (2016), who demonstrated that judgments regarding the localization of touch are influenced by exteroceptive spatial information. However, the consistent proprioceptive drift data across the two versions of the illusion speak against this interpretation. Finally, we know that the subjective illusion and proprioceptive drift sometimes do not go hand in hand (Abdulkarim & Ehrsson, 2016; Holmes et al., 2006; Rohde et al., 2011). Thus, it may be that congruent auditory feedback influences proprioceptive drift more than it influences the subjective illusion. This would correspond to the idea that congruent sounds boost the spatial recalibration of vision and proprioception more than the multisensory integration leading to an explicit and coherent percept of the hand as one's own.

What could be the possible neural mechanism behind the present auditory effects on the rubber hand illusion? We know that auditory signals reach the ventral premotor cortex (Graziano, Reiss, & Gross, 1999) and that this region is active in both the classic (Ehrsson et al., 2004) and somatic versions of the rubber-hand illusion (Ehrsson et al., 2005; and in similar limb ownership illusions: Gentile, Guterstam, Brozzoli, & Ehrsson, 2013; Guterstam et al., 2013; Limanowski & Blankenburg, 2016). Interestingly, the ventral premotor cortex contains trimodal visual—tactile—auditory neurons that respond to both visual and auditory stimuli in space near a body part (within 30 cm) and touches applied to the same body part (Graziano et al., 1999). We thus speculate that such neuronal populations integrate auditory signals with the visual, tactile, and proprioceptive signals from the upper limb during the rubber-hand illusion with congruent sounds. Indeed, it has been suggested that multisensory neuronal populations in the premotor cortex (and intraparietal cortex) are involved in the critical multisensory integration mechanisms underlying the rubber-hand illusion phenomenon (Botvinick, 2004; Brozzoli, Gentile, & Ehrsson, 2012; Ehrsson et al., 2004; Graziano, Cooke, & Taylor, 2000; Makin et al., 2008).

While the majority of previous experiments on human body perception have been dedicated to vision, touch, and proprioception (see the Introduction), the present study focuses attention on the auditory contributions to body ownership. In doing so, we add to a small but recently growing literature that has investigated how sounds modulate body representation. One interesting previous study in this respect is the marble-hand illusion by Senna, Maravita, Bolognini, and Parise (2014). This study reported that replacing the natural auditory feedback of hitting the hand with a small hammer with the sound of a hammer hitting marble changed the participants' perceptions of the material quality of the body. Similarly, participants can develop a feeling of being made of metallic parts when they receive a combination of sounds and haptic feedback recorded from a robot actuation system when they move their arm (Kurihara, Hachisu, Kuchenbecker, & Kajimoto, 2013). Further studies have investigated the roles of the sounds generated during the body—environment interactions and found that key properties of the body representation, such as its length and size, are affected by action sounds (Tajadura-Jiménez et al., 2012, 2014, 2015, 2017). Our results, together with the results of these aforementioned studies, demonstrate that auditory information is used in the formation of the coherent multisensory representation of one's own body.

Our conclusions open several interesting avenues for future investigations. For example, it would be interesting to compare body-related sounds to sounds that do not resemble the contact with a body at all to test the "unity-assumption" principle of multisensory integration, which states that only meaningful combinations of cross-modal sensory stimuli are integrated (De Gelder and Bertelson, 2003; Vatakis & Spence, 2007). It would also be interesting to test the spatial principle of multisensory integration (Holmes & Spence, 2005; Stein & Stanford, 2008) by contrasting sounds that originate from the same place as the brush to sounds that originate from a different location or outside peripersonal space; the latter cases should produce weaker illusions (Brozzoli et al., 2012; Kalckert & Ehrsson, 2014b; Lloyd, 2007; Makin et al., 2008; Preston, 2013). Another opportunity for future experiments would be to use the present sound-enhanced somatic rubber-hand illusion to investigate body representation in blind individuals (Nava, Steiger, & Röder, 2015; Petkova, Zetterberg, & Ehrsson, 2012) to see whether such individuals rely more on auditory feedback than do sighted individuals. The present sound-enhanced rubber hand illusion could also be used as a novel approach to develop advanced prosthetic limbs that feel more like real limbs for amputees and paralyzed individuals (Collins et al., 2017; Ehrsson et al., 2008; Marasco, Kim, Colgate, Peshkin, & Kuiken, 2011). By providing the prosthesis with sound feedback from the fingertips, the ownership of the prosthesis could, in principle, be enhanced. Finally, a very interesting possibility would be to examine whether auditory feedback enhances the ownership of entire bodies, such as mannequins (Petkova & Ehrsson, 2008) or computer-simulated avatars in virtual reality (Kilteni, Bergstrom, & Slater, 2013; Maselli & Slater, 2013; Slater, Spanlang, Sanchez-Vives, & Blanke, 2010). This approach could be used to examine whether auditory cues also contribute to the sense of full-body ownership (Blanke, Slater, & Serino, 2015; Petkova et al., 2011).

In sum, the present results demonstrate that sounds modulate the rubber-hand illusion. This is important because it suggests that four-way interactions among vision, touch, proprioception, and sounds contribute to the sense of limb ownership. This conclusion not only advances our basic understanding of how coherent, multisensory representations of limbs in space are formed, but also opens new horizons for applied body representation research that accounts for sounds that the body produces.

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