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Hand Cooling Enhances the Proprioceptive Drift during Rubber Hand Illusion

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Abstract

Background: The neural representation of the body is easily altered by integrating multiple sensory signals in the brain. The "Rubber Hand Illusion" (RHI) is one of the most popular experimental paradigms to investigate this phenomenon. During this illusion, ownership of a rubber hand is temporarily induced. It was shown that external and continuous cooling of the palm enhanced the RHI, suggesting an association between altered the autonomic nervous system regulation and altered the sense of ownership of a specific limb. **Purpose:** To investigate whether artificially cooling the entire hand for a short period affects the magnitude of the illusion. **Methods:** Participants immersed their entire hand in cool, cold, or warm water for 1 min before the RHI procedure. **Results:** We found that cooling the entire hand enhanced the proprioceptive drift during the RHI but not the subjective feeling of ownership. In contrast, warming and intense cooling of the entire hand did not affect the RHI strength. **Conclusion:** Our results suggest that transient and moderate cooling of the entire hand was sufficient in enhancing the illusory disembodiment of one's own hand.

Keywords

Hand Temperature, Cooling, Rubber Hand Illusion, Ownership, Proprioceptive Drift

1. Introduction

Neural representation of the body in the brain can be briefly and easily altered by delivering multiple integrated sensory signals to the brain. One of the most popular experimental paradigms to investigate this phenomenon, the rubber hand illusion (RHI), was introduced by Botvinick and Cohen [1]. In the paradigm, watching a fake rubber hand being stroked by a paintbrush in synchrony and the same direction as one's own concealed hand creates the perception of owning the rubber hand, although the participant is aware of not having a rubber hand. Furthermore, the perceived position of the real hand drifts toward the rubber hand (proprioceptive drift) [1] [2]. Therefore, when visual and tactile signals conflict, the visual sense overrides the tactile one, and the brain incorporates a non-corporeal object into the body representation [2].

Moseley *et al.* [3] have reported that the RHI was accompanied by a decrease in the skin temperature of the real hand. The decrease was specific to the limb where the illusion occurred. Furthermore, the magnitude of the skin temperature decrease was positively correlated with the vividness of the illusion. Similar findings were obtained in other studies [4]-[6]. The decreases in hand skin temperature following modulation of body ownership have also been observed in the mirror-box illusion paradigm [7]. However, many other studies found no modulation of the real hand temperature during the RHI [8]-[11]. Factors that may cause differences in findings include the exact type of stroking or the pressure of tactile stimuli [12]. Since reports on the hand temperature change during the RHI seemed inconsistent, it is important to clarify whether a physiological change such as decreased hand temperature can be one of the suitable biomarkers for the illusion strength.

Kammers *et al.* [4] have demonstrated a link in the opposite direction; external manipulation of the body temperature influenced body ownership as measured by the RHI. They found that the RHI strength increased while they externally and continuously cooled the palm of the participants' hand, but not while the hand was warmed. They also proposed that cooling the limb may be useful when one desires to decrease the awareness of the limb, as during training to use a teleoperated prosthesis instead of one's limb, or when attention to and use of a healthy limb is discouraged as part of constraint-induced therapy for paresis. In their experimental paradigm, the participants' hand was placed on a thermoelectric metal plate while the plate temperature was continuously adjusted electronically. Although the above idea presents a new possibility for therapy that requires changes in bodily awareness, practically, it would be easier to cool the hand in a simple manner and for a short time, e.g., by immersing the entire hand in cold water. However, it is unclear whether transient cooling of the entire hand by water could replicate the findings reported by Kammers *et al.* [4]. This study addressed this issue in order to develop a treatment that is easily applied in the field. To this end, we investigated the effects of immersing the entire hand in cool (Experiment 1), cold (Experiment 2), or warm (Experiment 3) water for 1 min on the strength of the RHI.

2. Methods

2.1. Participants

This study recruited 41 university students, aged 20 to 23 years (17 women and

24 men). All participants had normal physical and neurological examination findings, in particular, they had no peripheral pathologies, such as Raynaud's syndrome. All participants were provided written informed consent. The Human Research Ethics Committee of the Faculty of Education, Kumamoto University, approved this study (receipt number: 28 - 9). The experiments were conducted following the Declaration of Helsinki.

2.2. Room Temperature

During the experiments, the room temperature and humidity were adjusted at 24.7˚C ± 0.8˚C and 58.2% ± 5.7%, respectively.

2.3. Experiment 1

Fourteen participants (six female, 21.8 ± 0.4 years) participated in Experiment 1, conducted in a dimly lit room. The participants sat on a chair throughout the experiment. The participants' left hand and the fake left hand (see below) wore identical light blue colored rubber gloves to eliminate differences in appearance between them [13].

The participants' hand skin temperature at rest (base temperature; **Figure 1**) was measured by a hand-held Auto Pro laser thermometer (Raytek Minitemp MT, Raytek Corp., Santa Cruz, CA, USA). Three skin temperature readings were taken from the skin over the first dorsal interosseous muscle. Subsequently, the participants placed their left hand and forearm inside a wooden frame, with the forearm in the prone position. A rubber left hand was placed in a prone position 19 cm medial to the participants' concealed left hand. The experimenter placed black clothes over the participants' left upper arm and the forearm of the fake hand. Consequently, the participants could only see the fake hand during the experiment.

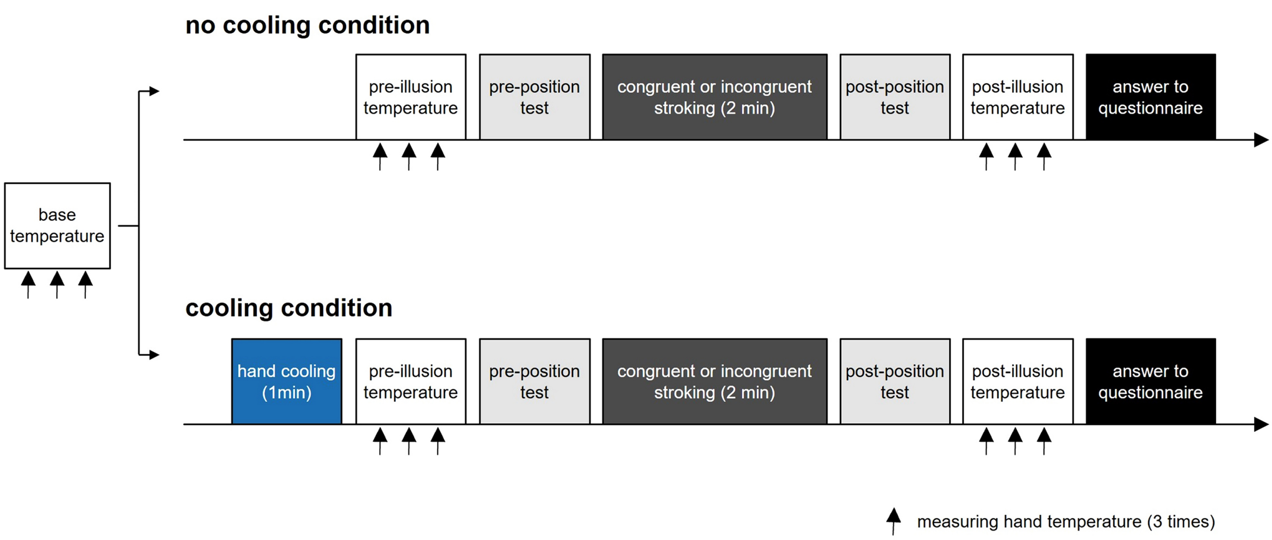

Figure 1. The design of Experiment 1. For the cooling condition, the participants' hand was immersed in water (25˚C ± 1˚C) for 1 min. Each condition was repeated three times.

The experiment included no cooling and cooling conditions (**Figure 1**). For the no cooling condition, the experimenter measured the pre-illusion skin temperature and the perceived position of the participants' left hand (pre-position test) before inducing the illusion. The participants were asked to close their eyes. The experimenter placed a large blackboard (21 cm × 91 cm) on a frame, hiding the rubber hand and the participant's hand from the participant's view. The board had a horizontal white line drawn across its surface with equally spaced marks, visible to the experimenter only, making it possible to measure distances in millimeters. After placing the blackboard, the experimenter asked the participants to open their eyes and then traced the white line with a stick starting from the participant's lateral to medial side. The participants were asked to verbally indicate when the stick was above the perceived position of their left index finger. The participants were allowed to correct the perceived position after their first verbal response, and the position on the scale was recorded.

After the pre-position test, the participants closed their eyes, the blackboard was removed, and the participants were asked to reopen their eyes and watch the fake hand. The experimenter delivered manual simultaneous stimulations to the real and rubber hands for 2 min using two identical paintbrushes. These were congruent (identical strokes to stroke locations) or incongruent (unmatched stroke timing and locations). The congruent and incongruent stroking events were repeated three times each in random order with 5 min rest between stroking events. After each stroking event, the perceived position of the left index finger (post-position test) and the left hand temperature (post-illusion temperature) were measured as described above.

Subsequently, the participants were asked to answer the RHI questionnaire, consisting of eight statements adopted based on Botvinick and Cohen's original report [1]. The statements were as follows: (S1) it seemed as if I were feeling the touch of the paintbrush in the location where I saw the rubber hand touched, (S2) it seemed as though the touch I felt was caused by the paintbrush touching the rubber hand, (S3) I felt as if the rubber hand were my hand, (S4) it felt as if my (real) hand were drifting towards the rubber hand, (S5) it seemed as if I might have more than one left hand or arm, (S6) it seemed as if the touch I was feeling came from somewhere between my hand and the rubber hand, (S7) it felt as if my (real) hand were turning "rubbery", (S8) it appeared (visually) as if the rubber hand was drifting towards my hand. These questions were used in many previous studies dealing with the RHI and were most appropriate for a subjective assessment of the illusion [1] [14]. The participants responded by choosing a value on a 10-point scale ranging from 1 (strongly disagree) to 10 (strongly agree).

For the cooling condition, the participants' left hand was first immersed in a basin of cold water (25˚C ± 1˚C) for 1 min. There were two reasons for adopting the duration of immersion. First, we wanted to decrease the participants' hand temperature by approximately 4˚C, almost the same as the previous study [4]. Second, we wanted to maintain the reduction of the hand temperature at least for 2 min which was the time for procedure of the RHI. As a result of a preliminary experiment, immersion of the entire hand for 1 min was sufficient to satisfy both of the above. The remainder of the procedure was identical to the no cooling condition (**Figure 1**). This procedure was repeated three times.

The no cooling and the cooling conditions were conducted in random order for each participant.

2.4. Experiment 2

Fourteen participants (seven female, 21.6 ± 0.6 years) participated in Experiment 2. The experimental procedure was the same as in Experiment 1, except that the water temperature was very cold (10˚C ± 1˚C).

2.5. Experiment 3

Thirteen participants (four female, 21.6 ± 0.7 years) participated in Experiment 3. The cooling conditions in Experiments 1 and 2 were replaced by a warming condition in which the participants immersed their left hand in a 38˚C ± 1˚C-water bath for 1 min. Otherwise, the experimental procedures were identical to Experiment 1.

2.6. Data Analysis and Statistics

For each stimulation (congruent or incongruent stroking), the shift in the perceived hand position toward the rubber hand (proprioceptive drift) was calculated based on the difference between the perceived hand positions in the pre-position and post-position tests. The proprioceptive drift was measured three times for each congruent and incongruent stroking and the obtained three values were averaged. We used the proprioceptive drift as an objective measure of the illusion strength, as previously done [1] [13] [15]. In addition, we subtracted the magnitudes of the proprioceptive drift in the incongruent stroking from those in congruent stroking. We defined these values as the "net" magnitude of the illusion [16].

The questionnaire statement ratings were obtained six times in each of the no cooling and the cooling conditions (three times for congruent stroking and three times for incongruent stroking). The statement ratings obtained for each stroking were averaged.

For the comparison between base temperature and pre- or post-illusion temperatures using the one-sample t-test, all temperatures were normalized by base temperature.

Data are expressed as mean ± standard deviation. The significance level was set at $p < 0.05$. IBM SPSS Statistics for Windows, Version 27 (IBM Corp., Armonk, NY, USA) was used for all statistical analyses. All the variables were tested for normal distribution using the Kolmogorov-Smirnov test (significance threshold $p < 0.05$), and nonparametric tests were used when one or more data sets were not normally distributed.

3. Results

3.1. Experiment 1

Figure 2(a) presents the hand temperature modulation during the experiment. Kolmogorov-Smirnov tests showed that the data for hand temperatures were normally distributed. The one-sample *t*-test demonstrated that under the no cooling condition, the respective pre- and post-illusion temperatures of the congruent ($p = 0.005$ and $p = 0.001$) and incongruent ($p < 0.001$ for both) stroke

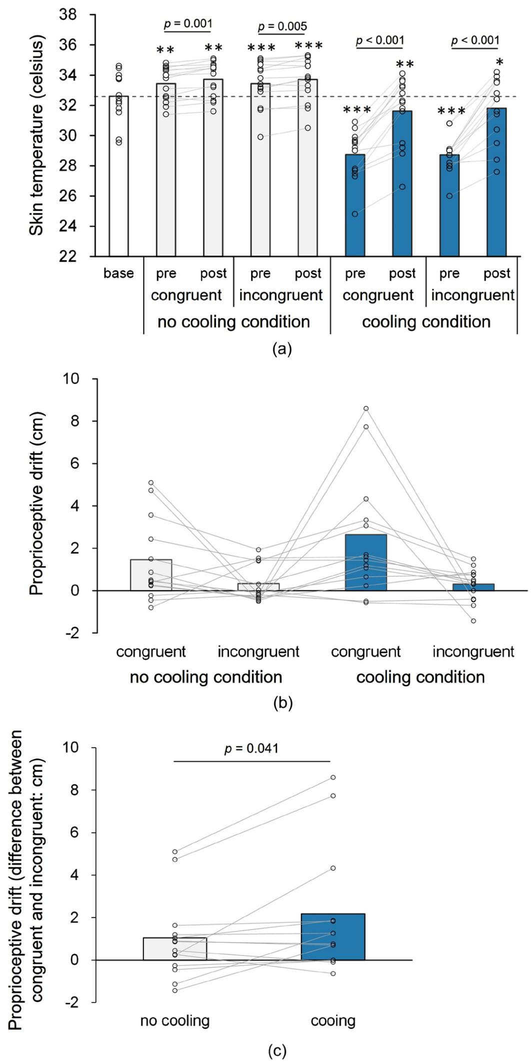

Figure 2. (a) Skin temperatures during Experiment 1. Asterisks indicate significant differences from the base temperature value. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. (b) The magnitude of the proprioceptive drift in Experiment 1. Proprioceptive drift was measured by calculating the difference between the perceived hand positions in the pre- and post-position tests. Values > 0 indicate drift toward the rubber hand. (c) The "net" magnitude of the proprioceptive drift in Experiment 1. The ordinate indicates the magnitude of the proprioceptive drift that was the difference between congruent and incongruent stroking. Positive and negative values indicate that the magnitudes of the proprioceptive drift in congruent stroking were larger and smaller than those in incongruent stroking, respectively.

types were significantly higher than the base temperature. Under the cooling condition, a group mean of the pre-illusion temperatures after 1-min cooling and before congruent and incongruent stroking, respectively, decreased by 3.8˚C ± 1.0˚C and 3.7˚C ± 1.0˚C ($p < 0.001$ for both). The hand temperatures remained lower than the base temperature at the post-illusion assessment (congruent stroking, $p = 0.003$; incongruent stroking, $p = 0.017$). Paired-samples *t*-test demonstrated that the post-illusion temperatures were significantly higher than the pre-illusion ones in all combinations (no cooling: congruent stroking, $p = 0.001$; incongruent stroking, $p = 0.005$; cooling: $p < 0.001$ for congruent and incongruent stroking).

Figure 2(b) shows the proprioceptive drift under all conditions. Kolmogorov-Smirnov tests showed that the data were not normally distributed. Friedman test demonstrated significant modulation of the proprioceptive drift across the four assessments (Chi-squared = 10.80, $p = 0.013$). However, the Bonferroni multiple comparisons did not show that the proprioceptive drift induced by congruent stroking under the cooling condition was significantly higher than under the no cooling condition ($p = 0.143$). To compare the value as the "net" magnitude of the proprioceptive drift, we subtracted the magnitudes of the proprioceptive drift in the incongruent stroking from those in congruent stroking. Wilcoxon signed-rank test showed that the net magnitude of the proprioceptive drift in cooling condition was significantly higher than that in no cooling condition ($p = 0.041$, Figure 2(c)).

The questionnaire statement ratings are shown in Table 1. Statement items 1, 2, and 3 in the congruent stroking tended to be higher than other statement items both in no cooling and cooling conditions. Wilcoxon signed-rank test showed that the ratings after congruent stroking under the cooling and no cooling conditions were not different for all eight statements (S1: $p = 0.546$; S2: $p = 0.603$; S3: $p = 0.589$; S4: $p = 1.00$; S5: $p = 0.436$; S6: $p = 0.577$; S7: $p = 0.157$; S8: $p = 0.705$).

Table 1. The questionnaire statement ratings.

	condition	stroke	S1	S2	S3	S4	S5	S6	S7	S8
Exp. 1	no cooling	congruent	7.9 ± 2.1	7.7 ± 2.2	7.1 ± 2.4	1.9 ± 0.9	2.0 ± 1.5	1.7 ± 1.1	1.5 ± 1.1	1.5 ± 0.8
		incongruent	2.0 ± 1.6	1.9 ± 1.9	1.6 ± 1.0	1.7 ± 1.2	1.8 ± 1.7	1.3 ± 1.1	1.1 ± 0.5	1.4 ± 0.8
	cooling	congruent	7.5 ± 2.4	7.6 ± 2.8	6.9 ± 2.7	1.9 ± 1.1	2.4 ± 1.3	1.6 ± 0.9	1.4 ± 0.8	1.4 ± 0.8
		incongruent	2.0 ± 1.7	2.6 ± 2.6	2.0 ± 1.8	1.7 ± 1.4	1.6 ± 1.6	1.3 ± 0.6	1.8 ± 1.5	1.2 ± 0.8
Exp. 2	no cooling	congruent	7.2 ± 2.5	5.8 ± 3.3	7.3 ± 2.7	2.9 ± 2.0	1.9 ± 0.9	1.9 ± 1.3	1.7 ± 1.0	1.8 ± 1.3
		incongruent	2.7 ± 2.5	2.6 ± 1.8	3.3 ± 2.8	3.2 ± 2.5	2.1 ± 1.9	2.3 ± 1.6	1.6 ± 1.2	1.4 ± 0.6
	cooling	congruent	6.4 ± 3.5	6.1 ± 3.5	6.9 ± 3.0	2.4 ± 1.7	1.9 ± 1.2	1.7 ± 0.8	1.8 ± 1.0	1.5 ± 0.9
		incongruent	3.4 ± 2.9	2.6 ± 2.1	3.6 ± 2.7	3.7 ± 2.5	1.9 ± 2.5	2.4 ± 1.7	1.4 ± 0.8	1.4 ± 0.9
Exp. 3	no warming	congruent	7.9 ± 1.9	8.2 ± 2.0	7.9 ± 2.2	2.0 ± 1.4	2.3 ± 1.4	2.2 ± 1.5	2.0 ± 1.3	1.5 ± 1.0
		incongruent	1.6 ± 0.7	1.5 ± 0.7	1.8 ± 0.7	1.5 ± 0.7	1.2 ± 0.6	1.3 ± 1.1	1.6 ± 0.8	1.2 ± 0.6
	warming	congruent	8.0 ± 2.2	7.8 ± 2.2	7.8 ± 2.5	1.8 ± 0.9	2.5 ± 1.3	1.6 ± 0.8	1.8 ± 1.0	1.8 ± 1.2
		incongruent	1.8 ± 0.7	1.7 ± 1.5	1.5 ± 0.9	1.4 ± 0.5	1.0 ± 0.0	1.2 ± 0.6	1.8 ± 1.0	1.2 ± 0.8

Figure 3 compared the cooling and no cooling conditions for the differences between the actual and perceived left index finger positions during the pre-position test. The paired-sample *t*-test demonstrated that no significant difference between them ($p = 0.444$).

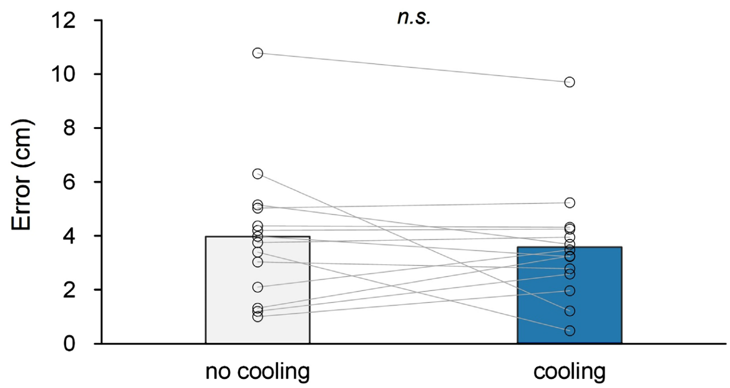

Figure 3. Differences in the actual and perceived left index finger positions during the pre-position test. Positive values indicate that the perceived hand position moved toward the rubber hand than the actual position.

3.2. Experiment 2

Figure 4(a) shows changes in the hand temperature during the experiment. Kolmogorov-Smirnov tests showed that the data for hand temperatures were normally distributed. The one-sample *t*-test demonstrated that under the no cooling condition, the pre- and post-illusion temperatures of both stroke types were significantly higher than the base temperature (congruent stroking: pre-illusion, $p = 0.009$; post-illusion. $p < 0.001$; incongruent stroking: pre-illusion, $p = 0.012$; post-illusion, $p = 0.003$). The hand temperature after cooling and before the congruent and incongruent stroking (pre-illusion temperatures) were 13.8˚C ± 1.9˚C and 13.3˚C ± 2.6˚C lower than the base temperature, respectively ($p < 0.001$ for both). The post-illusion temperatures following congruent and incongruent stroking remained lower than the base temperature ($p < 0.001$ for both). Paired-samples *t*-test demonstrated that the post-illusion temperatures were significantly higher than the pre-illusion ones under all situations (no cooling: congruent stroking, $p = 0.001$; incongruent stroking, $p = 0.02$; cooling: congruent and incongruent stroking, $p < 0.001$).

The magnitude of the proprioceptive drift under all conditions is shown in Figure 4(b). Kolmogorov-Smirnov tests showed that the data were not normally distributed. Friedman test demonstrated no significant modulation of the proprioceptive drift across the four assessments (Chi-squared = 7.40, $p = 0.060$). To compare the value as the "net" magnitude of the proprioceptive drift, we subtracted the magnitudes of the proprioceptive drift in the incongruent stroking from those in congruent stroking. Wilcoxon signed-rank test did not show that the net magnitude of the proprioceptive drift in cooling condition was significantly higher than that in no cooling condition ($p = 0.177$, Figure 4(c)).

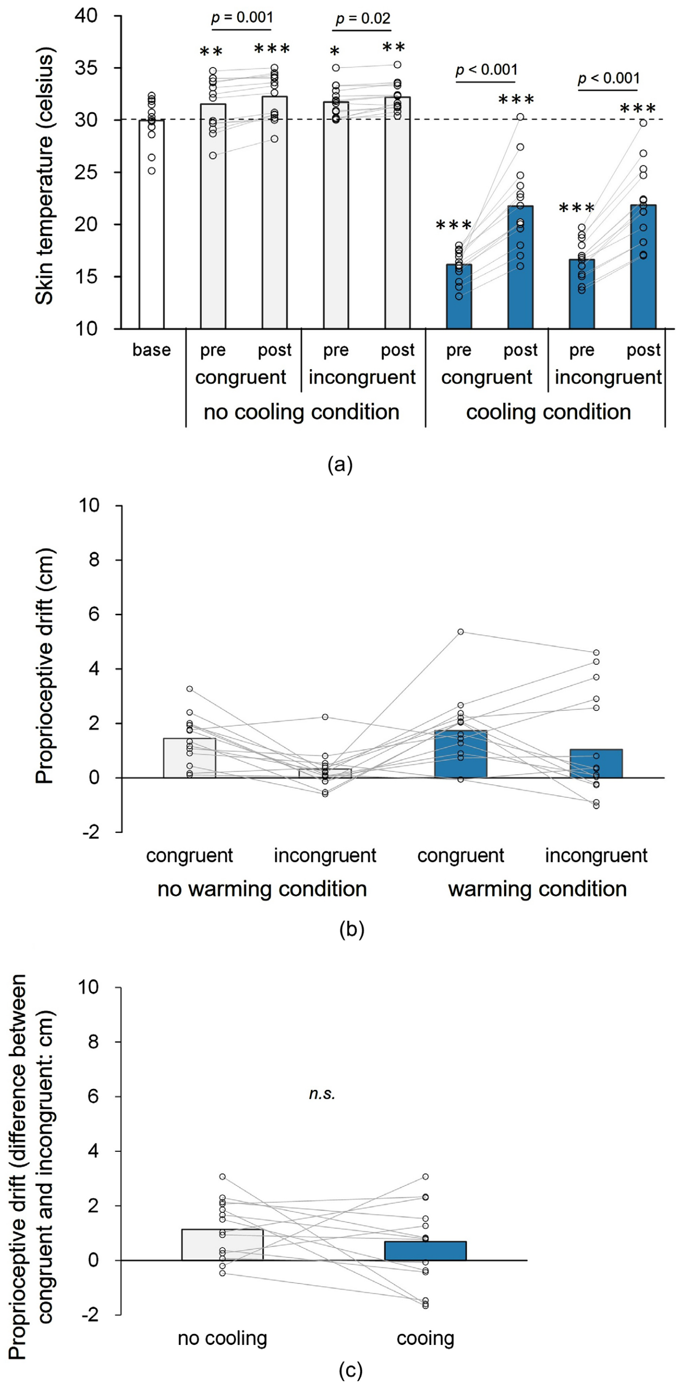

Figure 4. (a) Skin temperatures during Experiment 2. Asterisks indicate significant differences from the base temperature value. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. (b) The magnitude of the proprioceptive drift in Experiment 2. Proprioceptive drift was measured by calculating the difference between the perceived hand positions in the pre- and post-position tests. Values > 0 indicate drift toward the rubber hand. (c) The "net" magnitude of the proprioceptive drift in Experiment 2. The ordinate indicates the magnitude of the proprioceptive drift that was the difference between congruent and incongruent stroking. Positive and negative values indicate that the magnitudes of the proprioceptive drift in congruent stroking were larger and smaller than those in incongruent stroking, respectively.

The questionnaire statement ratings are shown in **Table 1**. Statement items 1, 2, and 3 in the congruent stroking tended to be higher than other statement items both in no cooling and cooling conditions. Wilcoxon signed-rank test showed that ratings after congruent stroking under the no cooling and cooling conditions did not significantly differ in all eight statements (S1: $p = 0.356$; S2: $p = 0.502$; S3: $p = 0.669$; S4: $p = 0.443$; S5: $p = 1.00$; S6: $p = 0.414$; S7: $p = 0.792$; S8: $p = 0.453$).

3.3. Experiment 3

Figure 5(a) shows changes in the hand temperature during the experiment. Kolmogorov-Smirnov tests showed that the data were not normally distributed. Wilcoxon signed-rank test demonstrated that under the no warming condition and congruent stroking, the pre-illusion and base temperatures were not different ($p = 0.156$). The post-illusion temperature with congruent stroking was significantly higher than the base temperature ($p = 0.020$) and the pre-illusion ($p = 0.041$). The pre- and post-illusion temperatures under the incongruent stroking condition were not different ($p = 0.090$). Under the warming condition, the pre-illusion temperatures before the congruent and incongruent stroking were, respectively, 3.7˚C ± 1.0˚C and 3.7˚C ± 0.9˚C higher than the base temperature ($p < 0.001$ for both). The higher hand temperatures were maintained through the post-illusion assessment (congruent stroking, $p = 0.003$; incongruent stroking, $p < 0.001$). The post-illusion temperatures following congruent and incongruent stroking were significantly lower than the pre-illusion temperatures ($p < 0.001$ for both).

Figure 5(b) presents changes in the proprioceptive drift. Kolmogorov-Smirnov tests showed that the data were not normally distributed. Friedman test demonstrated significant modulation of the proprioceptive drift across the four assessments (Chi-squared = 13.41, $p = 0.004$). However, the Bonferroni multiple comparisons did not show that the proprioceptive drift induced by congruent stroking under the warming condition was significantly higher than under the no warming condition ($p = 0.421$). To compare the value as the "net" magnitude of the proprioceptive drift, we subtracted the magnitudes of the proprioceptive drift in the incongruent stroking from those in congruent stroking. Wilcoxon signed-rank test did not show that the net magnitude of the proprioceptive drift in warming conditions was significantly higher than that in no warming conditions ($p = 0.875$, **Figure 5(c)**).

The questionnaire statement ratings are shown in **Table 1**. Statement items 1, 2, and 3 in the congruent stroking tended to be higher than other statement items both in no warming and warming conditions. Wilcoxon signed-rank test showed that the ratings after congruent stroking under the no warming and warming conditions were not different for all eight statements (S1: $p = 0.340$; S2: $p = 1.00$; S3: $p = 0.516$; S4: $p = 0.257$; S5: $p = 0.666$; S6: $p = 0.161$; S7: $p = 0.461$; S8: $p = 0.083$).

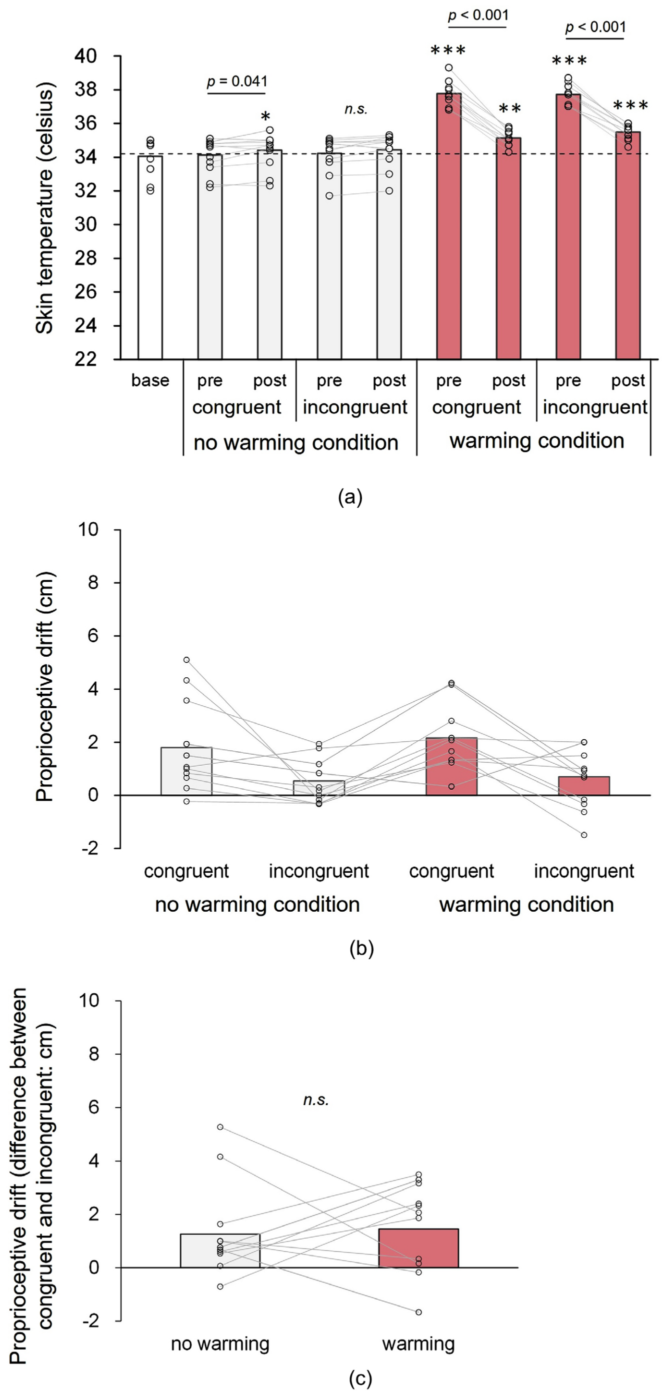

Figure 5. (a) Skin temperatures during Experiment 3. Asterisks indicate significant differences from the base temperature value. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. (b) The magnitude of the proprioceptive drift in Experiment 3. Proprioceptive drift was measured by calculating the difference between the perceived hand positions in the pre- and post-position tests. Values > 0 indicate drift toward the rubber hand. (c) The "net" magnitude of the proprioceptive drift in Experiment 3. The ordinate indicates the magnitude of the proprioceptive drift that was the difference between congruent and incongruent stroking. Positive and negative values indicate that the magnitudes of the proprioceptive drift in congruent stroking were larger and smaller than those in incongruent stroking, respectively.

4. Discussion

This study investigated the effects of external hand temperature manipulations by immersing the entire hand in cool, cold, or warm water on the RHI strength. Questionnaire statement items 1, 2, and 3 in the congruent stroking tended to be higher than other statement items in all conditions (**Table 1**) which suggests that the RHI was successfully induced properly in this study [1]. We found that cooling the hand enhanced the proprioceptive drift, while warming and intense cooling did not. These results are almost consistent with those reported by Kammers *et al.* [4]. Our results partially support the association between the RHI occurrence and the drop in the hand skin temperature.

In Experiment 1, we achieved a reduction of the participants' hand skin temperature by approximately 4˚C, almost the same as previously reported [4]. The pre- and post-illusion skin temperatures under the no cooling condition were slightly but significantly higher than in the base temperature, even though no external temperature manipulation was applied (**Figure 2**). This temperature increase was probably because of the heat buildup in the glove worn by the participants throughout the experiment. The warming effect wearing the glove had on the skin temperature also occurred under the cooling condition. Despite the skin warming effect of wearing gloves, the pre-illusion temperatures were significantly lower than the base temperature. These temperatures remained lower at the post-illusion assessment, although recovery of the temperature over time was noted. Therefore, the RHI could occur when the skin temperature was lowered under the cooling condition, although the temperature decrease was underestimated due to the warming effect of wearing the glove.

Cooling the hand did not affect the difference between the actual and perceived hand positions during the pre-position test (**Figure 3**). This indicated that a skin temperature drop did not merely modulate the perceived position of the hand but also enhanced the illusory disembodiment of one's own hand by integrating the visual and somatosensory information. Although this study could not clarify the neural mechanisms underlying the effect, we infer central and peripheral mechanisms were involved in enhancing the RHI. For the central mechanism, artificial cooling of the hand placed a strain on the participants' thermoregulatory mechanisms that may have contributed to the altered disembodiment of their hands. Previous studies have shown that disruption of the sense of body ownership is a characteristic of many pathological states, including schizophrenia [17], autism [18], epilepsy [19], and neuropathic pain [20]. Furthermore, many of these pathological conditions are also characterized by disruption of temperature regulation [21]-[23]. These findings suggest that body ownership and temperature regulation are partially shared by the same brain region.

As for the peripheral mechanism, the cooling stimulus might be modulating the transmission efficiency of afferent inputs. Cooling the hand decreases the conduction velocity and transmission efficiency of somatosensory afferent nerves [24]. In contrast, warming increases the conduction velocity and transmission efficiency of these nerves [25]. These suggest that the RHI is more likely to occur when the somatosensory signals are weakened. Makin *et al.* [26] mentioned that during the RHI, the integration of sensory information leans heavily in favor of vision, likely reducing the weight of the somatosensory inputs. This idea was partially supported by behavioral [27] [28] and neurophysiological [29] [30] studies. Therefore, weakening the somatosensory inputs by cooling the hand might augment the capturing of visual over somatosensory information, enhancing the proprioceptive drift during the RHI.

Cooling the hand did not affect the subjective feeling that the rubber hand was one's own (**Table 1**), as reported by Kammers *et al.* [4]. The hand proprioceptive drift and the subjective ratings for the questionnaire are typically used as an index for evaluating changes in the sense of body ownership [1]. Furthermore, the magnitude of the proprioceptive drift was shown to correlate with the strength of the ownership feeling reported in the questionnaire [1]. However, some studies have failed to detect such a correlation [31]-[34]. Rohde *et al.* [34] indicated that proprioceptive drift was a spatial update of the body in space according to the synchronous visuotactile stimulation; therefore, the process underlying proprioceptive drift was independent of that underlying the subjective feeling of limb ownership in the RHI. Considering these findings, the effect of cooling the hand in the RHI paradigm of this study was probably associated with the perceived hand position drift rather than the feeling of ownership of the rubber hand. Therefore, cooling the hand may be more effective when one wants to alter the perceived position of the hand toward an object located outside the body, for example, controlling a robotic arm by connecting brain activities to a computer [35] or using a rake to manipulate out-of-reach objects [36]. It is not necessary to create a sense of ownership of the objects in such cases.

The intense cooling (−10˚C) in Experiment 2 that decreased the skin temperature by around 13˚C did not modulate the RHI strength, supporting the results reported by Kammers *et al.* [4]. Cold stimulation below 17˚C activates the noxious cold sensation sensors [37] [38]. Therefore, many participants were likely to feel pain in their hands due to the intense cooling. Kammers *et al.* [4] stated that pain reminds us of our "real" body. During the RHI, pain neither abolishes nor enhances the relocation of one's hand or subjective feeling of ownership. We consider this the reason the RHI was not strengthened in Experiment 2.

Warming the hand in Experiment 3 did not affect the RHI strength, although the skin temperature modulation by warming was almost the same as that of the cooling stimulus in Experiment 1 (−3.7˚C). This finding differed from Kammers *et al.* [4], who showed that warming the hand attenuated the strength of the RHI. One reason for the difference between the studies might be the difference in the external temperature stimuli used; the entire hand was stimulated in this study, while only the palm was stimulated in the previous study. The finding that sensitivity to thermal stimuli on glabrous skin differed from that on hairy skin [39] partially supports this idea.

There were some limitations in this study. First, the participants wore the rubber glove to eliminate differences in appearance between the fake hand and the participants' hand, which may affect the results. Despite the skin temperature of the hand was kept lower compared with the base temperature in the cooling condition, the temperature increased during the procedure of the RHI. The alteration might attenuate the strength of the proprioceptive drift or prevent the generation of the feeling of ownership of the rubber hand. It is necessary to verify whether the same results can be obtained without the rubber glove. Second, we measured the participants' hand skin temperature at only one point. However, previous studies have recorded the skin temperature from multiple points on the same hand [3] or from both sides of the hand [7] [40]. To elucidate the relationship between body ownership and thermoregulation in detail, more accurate skin temperature measurements are needed. Finally, we did not collect quantitative data about pain sensation in Experiment 2. Therefore, it is difficult to distinguish whether the no modulation of the proprioceptive drift was due to substantial decrease in hand skin temperature or due to generation of the pain by the intense cooling of the hand. Further research is needed to resolve this point.

In conclusion, this study demonstrated that cooling the entire hand by immersing it in water for 1 min is sufficient for enhancing the illusory disembodiment of one's hand. In contrast, warming or intense cooling of the entire hand did not affect the RHI strength. These findings suggest that an externally induced decrease in body temperature may be useful for therapies or training that require changes in the perceived position of the limb. Further research is needed to clarify detailed conditions for practical application.

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Data Availability

Data will be made available on request.

Conflicts of Interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

References

[1] Botvinick, M. and Cohen, J. (1998) Rubber Hands 'Feel' Touch that Eyes See. *Na-*

ture, **391**, 756-756. https://doi.org/10.1038/35784

[2] Limanowski, J. (2022) Precision Control for a Flexible Body Representation. *Neuroscience & Biobehavioral Reviews*, **134**, Article ID: 104401. https://doi.org/10.1016/j.neubiorev.2021.10.023

[3] Moseley, G.L., Olthof, N., Venema, A., Don, S., Wijers, M., Gallace, A., *et al.* (2008) Psychologically Induced Cooling of a Specific Body Part Caused by the Illusory Ownership of an Artificial Counterpart. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 13169-13173. https://doi.org/10.1073/pnas.0803768105

[4] Kammers, M.P.M., Rose, K. and Haggard, P. (2011) Feeling Numb: Temperature, but Not Thermal Pain, Modulates Feeling of Body Ownership. *Neuropsychologia*, **49**, 1316-1321. https://doi.org/10.1016/j.neuropsychologia.2011.02.039

[5] Rohde, M., Wold, A., Karnath, H. and Ernst, M.O. (2013) The Human Touch: Skin Temperature during the Rubber Hand Illusion in Manual and Automated Stroking Procedures. *PLOS ONE*, **8**, e80688. https://doi.org/10.1371/journal.pone.0080688

[6] Tsakiris, M., Jiménez, A.T. and Costantini, M. (2011) Just a Heartbeat Away from One's Body: Interoceptive Sensitivity Predicts Malleability of Body-Representations. *Proceedings of the Royal Society B*: *Biological Sciences*, **278**, 2470-2476. https://doi.org/10.1098/rspb.2010.2547

[7] Crivelli, D., Polimeni, E., Crotti, D., Bottini, G. and Salvato, G. (2021) Bilateral Skin Temperature Drop and Warm Sensibility Decrease Following Modulation of Body Part Ownership through Mirror-Box Illusion. *Cortex*, **135**, 49-60. https://doi.org/10.1016/j.cortex.2020.11.015

[8] David, N., Fiori, F. and Aglioti, S.M. (2013) Susceptibility to the Rubber Hand Illusion Does Not Tell the Whole Body-Awareness Story. *Cognitive*, *Affective*, *& Behavioral Neuroscience*, **14**, 297-306. https://doi.org/10.3758/s13415-013-0190-6

[9] de Haan, A.M., Van Stralen, H.E., Smit, M., Keizer, A., Van der Stigchel, S. and Dijkerman, H.C. (2017) No Consistent Cooling of the Real Hand in the Rubber Hand Illusion. *Acta Psychologica*, **179**, 68-77. https://doi.org/10.1016/j.actpsy.2017.07.003

[10] Grynberg, D. and Pollatos, O. (2015) Alexithymia Modulates the Experience of the Rubber Hand Illusion. *Frontiers in Human Neuroscience*, **9**, Article 357. https://doi.org/10.3389/fnhum.2015.00357

[11] Lang, V.A., Zbinden, J., Wessberg, J. and Ortiz-Catalan, M. (2021) Hand Temperature Is Not Consistent with Illusory Strength during the Rubber Hand Illusion. 2021 43*rd Annual International Conference of the IEEE Engineering in Medicine & Biology Society* (*EMBC*), Mexico, 1-5 November 2021, 1416-1418. https://doi.org/10.1109/embc46164.2021.9630200

[12] Riemer, M., Trojan, J., Beauchamp, M. and Fuchs, X. (2019) The Rubber Hand Universe: On the Impact of Methodological Differences in the Rubber Hand Illusion. *Neuroscience & Biobehavioral Reviews*, **104**, 268-280. https://doi.org/10.1016/j.neubiorev.2019.07.008

[13] Tsakiris, M. and Haggard, P. (2005) The Rubber Hand Illusion Revisited: Visuotactile Integration and Self-Attribution. *Journal of Experimental Psychology*: *Human Perception and Performance*, **31**, 80-91. https://doi.org/10.1037/0096-1523.31.1.80

[14] Bertamini, M. and O'Sullivan, N. (2014) The Use of Realistic and Mechanical Hands in the Rubber Hand Illusion, and the Relationship to Hemispheric Differences. *Consciousness and Cognition*, **27**, 89-99. https://doi.org/10.1016/j.concog.2014.04.010

[15] Ismail, M.A.F.B. and Shimada, S. (2018) Inferior Parietal Lobe Activity in Visuo-Motor Integration during the Robot Hand Illusion. *Psychology*, **9**, 2996-3006. https://doi.org/10.4236/psych.2018.915174

[16] Sakamoto, M. and Ifuku, H. (2022) Experience-Dependent Modulation of Rubber Hand Illusion in Badminton Players. *Journal of Sport & Exercise Psychology*, **44**, 14-22. https://doi.org/10.1123/jsep.2020-0178

[17] Priebe, S. and Röhricht, F. (2001) Specific Body Image Pathology in Acute Schizophrenia. *Psychiatry Research*, **101**, 289-301. https://doi.org/10.1016/s0165-1781(01)00214-1

[18] Rogers, S.J. and Ozonoff, S. (2005) Annotation: What Do We Know about Sensory Dysfunction in Autism? A Critical Review of the Empirical Evidence. *Journal of Child Psychology and Psychiatry*, **46**, 1255-1268. https://doi.org/10.1111/j.1469-7610.2005.01431.x

[19] Boesebeck, F. and Ebner, A. (2004) Paroxysmal Alien Limb Phenomena Due to Epileptic Seizures and Electrical Cortical Stimulation. *Neurology*, **63**, 1725-1727. https://doi.org/10.1212/01.wnl.0000143064.81746.e9

[20] Moseley, G.L. (2005) Distorted Body Image in Complex Regional Pain Syndrome. *Neurology*, **65**, 773-773. https://doi.org/10.1212/01.wnl.0000174515.07205.11

[21] Holtkamp, M., Schmitt, F.C., Buchheim, K. and Meierkord, H. (2007) Temperature Regulation Is Compromised in Experimental Limbic Status Epilepticus. *Brain Research*, **1127**, 76-79. https://doi.org/10.1016/j.brainres.2006.10.034

[22] Jänig, W. and Baron, R. (2003) Complex Regional Pain Syndrome: Mystery Explained? *The Lancet Neurology*, **2**, 687-697. https://doi.org/10.1016/s1474-4422(03)00557-x

[23] Papežová, H., Yamamotová, A. and Uher, R. (2005) Elevated Pain Threshold in Eating Disorders: Physiological and Psychological Factors. *Journal of Psychiatric Research*, **39**, 431-438. https://doi.org/10.1016/j.jpsychires.2004.10.006

[24] Phillips, J. and Matthews, P. (1993) Texture Perception and Afferent Coding Distorted by Cooling the Human Ulnar Nerve. *The Journal of Neuroscience*, **13**, 2332-2341. https://doi.org/10.1523/jneurosci.13-06-02332.1993

[25] Russ, W., Sticher, J., Scheld, H. and Hempelmann, G. (1987) Effects of Hypothermia on Somatosensory Evoked Responses in Man. *British Journal of Anaesthesia*, **59**, 1484-1491. https://doi.org/10.1093/bja/59.12.1484

[26] Makin, T.R., Holmes, N.P. and Ehrsson, H.H. (2008) On the Other Hand: Dummy Hands and Peripersonal Space. *Behavioural Brain Research*, **191**, 1-10. https://doi.org/10.1016/j.bbr.2008.02.041

[27] Folegatti, A., de Vignemont, F., Pavani, F., Rossetti, Y. and Farnè, A. (2009) Losing One's Hand: Visual-Proprioceptive Conflict Affects Touch Perception. *PLOS ONE*, **4**, e6920. https://doi.org/10.1371/journal.pone.0006920

[28] Zopf, R., Harris, J.A. and Williams, M.A. (2011) The Influence of Body-Ownership Cues on Tactile Sensitivity. *Cognitive Neuroscience*, **2**, 147-154. https://doi.org/10.1080/17588928.2011.578208

[29] Isayama, R., Vesia, M., Jegatheeswaran, G., Elahi, B., Gunraj, C.A., Cardinali, L., *et al.* (2019) Rubber Hand Illusion Modulates the Influences of Somatosensory and Parietal Inputs to the Motor Cortex. *Journal of Neurophysiology*, **121**, 563-573. https://doi.org/10.1152/jn.00345.2018

[30] Sakamoto, M. and Ifuku, H. (2021) Attenuation of Sensory Processing in the Primary Somatosensory Cortex during Rubber Hand Illusion. *Scientific Reports*, **11**, Article No. 7329. https://doi.org/10.1038/s41598-021-86828-5

[31] Abdulkarim, Z. and Ehrsson, H.H. (2015) No Causal Link between Changes in Hand Position Sense and Feeling of Limb Ownership in the Rubber Hand Illusion. *Attention, Perception, & Psychophysics*, **78**, 707-720. https://doi.org/10.3758/s13414-015-1016-0

[32] Cowie, D., Makin, T.R. and Bremner, A.J. (2013) Children's Responses to the Rubber-Hand Illusion Reveal Dissociable Pathways in Body Representation. *Psychological Science*, **24**, 762-769. https://doi.org/10.1177/0956797612462902

[33] Holle, H., McLatchie, N., Maurer, S. and Ward, J. (2011) Proprioceptive Drift without Illusions of Ownership for Rotated Hands in the "Rubber Hand Illusion" Paradigm. *Cognitive Neuroscience*, **2**, 171-178. https://doi.org/10.1080/17588928.2011.603828

[34] Rohde, M., Di Luca, M. and Ernst, M.O. (2011) The Rubber Hand Illusion: Feeling of Ownership and Proprioceptive Drift Do Not Go Hand in Hand. *PLOS ONE*, **6**, e21659. https://doi.org/10.1371/journal.pone.0021659

[35] Hochberg, L.R., Bacher, D., Jarosiewicz, B., Masse, N.Y., Simeral, J.D., Vogel, J., *et al.* (2012) Reach and Grasp by People with Tetraplegia Using a Neurally Controlled Robotic Arm. *Nature*, **485**, 372-375. https://doi.org/10.1038/nature11076

[36] lriki, A., Tanaka, M. and Iwamura, Y. (1996) Coding of Modified Body Schema during Tool Use by Macaque Postcentral Neurones. *NeuroReport*, **7**, 2325-2330. https://doi.org/10.1097/00001756-199610020-00010

[37] Bandell, M., Story, G.M., Hwang, S.W., Viswanath, V., Eid, S.R., Petrus, M.J., *et al.* (2004) Noxious Cold Ion Channel TRPA1 Is Activated by Pungent Compounds and Bradykinin. *Neuron*, **41**, 849-857. https://doi.org/10.1016/s0896-6273(04)00150-3

[38] Kwan, K.Y., Allchorne, A.J., Vollrath, M.A., Christensen, A.P., Zhang, D., Woolf, C.J., *et al.* (2006) TRPA1 Contributes to Cold, Mechanical, and Chemical Nociception but Is Not Essential for Hair-Cell Transduction. *Neuron*, **50**, 277-289. https://doi.org/10.1016/j.neuron.2006.03.042

[39] Filingeri, D., Zhang, H. and Arens, E.A. (2018) Thermosensory Micromapping of Warm and Cold Sensitivity across Glabrous and Hairy Skin of Male and Female Hands and Feet. *Journal of Applied Physiology*, **125**, 723-736. https://doi.org/10.1152/japplphysiol.00158.2018

[40] Tieri, G., Gioia, A., Scandola, M., Pavone, E.F. and Aglioti, S.M. (2017) Visual Appearance of a Virtual Upper Limb Modulates the Temperature of the Real Hand: A Thermal Imaging Study in Immersive Virtual Reality. *European Journal of Neuroscience*, **45**, 1141-1151. https://doi.org/10.1111/ejn.13545