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Abstract

Through training using distorted vision, the perception of the trained limb position is shifted based on visual information. We investigated whether and how such proprioceptive recalibration transfers to untrained limbs. The results of experiments using human-like virtual limbs confirmed that transfer to some limbs occurred. The manner in which the transfer occurred varied according to the participants' body posture and the type of trained limb. When the participants sat, the recalibration transferred from one arm to another arm symmetrically around the body midline. Conversely, in the case of a sitting leg and standing arm, it was directly copied to another leg or arm.

Keywords: proprioceptive recalibration, interlimb transfer, body representation, virtual limb

Introduction

Proprioceptive sensation allows humans to recognize the position and movement of their own body parts without visual information. However, proprioception can be recalibrated through training using a distorted vision. In this study, we investigated whether this recalibration transfers to untrained body parts and, if so, how this transfer occurs.

Proprioceptive Recalibration

The proprioceptive system receives stimulation mainly from muscles, tendons, and joints and relates to the perception of a body position and its movement (Sainburg, Ghilardi, Poizner, & Ghez, 1995; Sherrington, [1947] 1906). This sensation allows us to move our bodies without other sensations; for example, we can touch our nose even if we close our eyes. However, our body perception does not rely only on proprioception; rather, information from other systems. such as the visual and vestibular systems, is also integrated to construct body perception (Ernst & Banks, 2002; Fitzpatrick & McCloskey, 1994).

In particular, visual information is an important source of the information on the position and movements of body parts. When individuals perform actions using distorted vision, they adjust their body (limb) movement based on the distorted vision, which is termed visuomotor adaptation (Scheidt, Conditt, Secco, & Mussa-Ivaldi, 2005; Wei & Kording, 2009).In the series of studies reported by Henriques, Cressman, and their colleagues (Balitsky Thompson & Henriques, 2010; Cressman & Henriques, 2015; Mostafa, Salomonczyk, Cressman, & Henriques, 2014; Mostafa, Kamran-Disfani, Bahari-Kashani, Cressman, & Henriques, 2015), the participants carried out a reaching task by operating a cursor with their covered hand. When the participants were trained using a misaligned cursor, their hand movement was adapted to the visual feedback, and eventually, this distorted reaching action was observed without visual feedback.

Furthermore, in a hand position estimation task, after sufficient training, the participants became able to recognize their hand at the distorted position, which meant that proprioceptive recalibration occurred; i.e., they acquired new mapping between the visual input and proprioceptive output through training. Mostafa et al. (2015) demonstrated that the participants distortedly estimated the relative position of their hand to a marker or their body midline after the training session.

This type of proprioceptive recalibration was observed in experiments using avatars or robots (Kokkinara, Slater, & López-Moliner, 2015; Romano, Caffa, Hernandez-Arieta, Brugger, & Maravita, 2015). In those studies, consistent visuomotor information was provided, i.e., the avatars or robots moved in synchrony with the participants' body. The participants felt that the avatars or robots belonged to their body and perceived that part to be nearer to the avatars or robots' position than the actual position. This is called proprioceptive drift and is also observed by providing consistent visuotactile information, such as the rubber hand illusion (Botvinick & Cohen, 1998).

Transfer to Untrained Parts

Several researchers investigated whether visuomotor adaptation and proprioceptive recalibration transfer to untrained body parts. The visuomotor adaptation in the trained hand partially transferred to the opposite untrained hand and facilitated its visuomotor adaptation (Balitsky Thompson & Henriques, 2010; Berniker & Kording, 2008; Sainburg & Wang, 2002; Wang & Sainburg, 2006). Moreover, Wang and Sainburg (2004) reported a limitation of this transfer: the facilitation happened only from a non-dominant hand to a dominant hand if the visual distortion direction in successive training was identical. Conversely, there was no clear evidence that proprioceptive recalibration could be transferred from one hand to the other hand.

Based on the results of their experiment, Mostafa et al.

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(2014) concluded that proprioceptive recalibration did not transfer to the opposite untrained hand. Their study participants moved a cursor to a target circle using a handle while observing the monitor in which the cursor was displayed 4 cm rightward from their actual hand position. After training using their right or left hand, the participants took a test to estimate their opposite untrained hand position. The estimation of the untrained hand position was not significantly biased, which demonstrated that transfer of the proprioceptive recalibration did not occur.

In this study, we re-examined the possibility of the transfer of proprioceptive recalibration by modifying the experimental settings as shown in Figure 1. First, we used a virtual limb as visual feedback. The experiments using avatars and robots showed that proprioceptive drift tended to be observed when the participants felt a sense of ownership of the avatars and robots (Botvinick & Cohen, 1998; Romano et al., 2015). Therefore, using a virtual limb in a reaching task seemed to induce a firm proprioceptive recalibration, which could be easily transferred to the untrained parts.

Second, we shifted the trained limb position from its root to end (e.g., shift of a virtual arm from the shoulder to the fingertips) and hid other body parts. This procedure leads to the proprioceptive recalibration of the whole of the target limb, and other hidden body parts would be mapped based on the recalibrated limb, available sensory information, and the knowledge of body structure.The knowledge of body structure is crucial to recognize the own body in VR space. Kondo, Tani, Sugimoto, Inami, and Kitazaki (2020) showed that only when all hands and feet were placed consistent with the human body structure, the participants felt as if the hidden parts of their body were there.

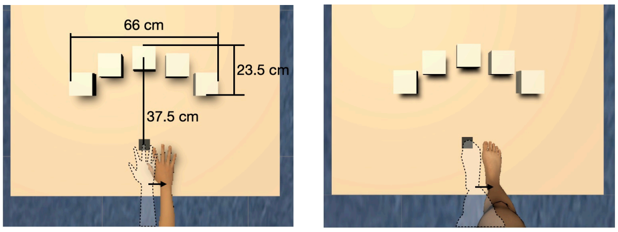
Finally, we added a leg to the body parts to be trained and tested. During the training, the limb was shifted horizontally; thus, the limbs on the same side as the trained limb would be affected more than those on the contralateral side. Therefore, we trained the right arm or leg and tested all four limbs (i.e., right arm and leg, left arm and leg).

Purpose and Hypotheses

We aimed to test whether transfer of the proprioceptive recalibration occurs in our modified experimental settings. Our hypotheses are summarized in Figure 2. First, at the trained limb, the proprioceptive recalibration would occur as shown in previous studies. Second, we predicted that it would be transferred to the limb on the same side. Third, we tested whether it transferred to the limb on the opposite side. If this occurs, two exclusive shift directions in the untrained limb are possible.

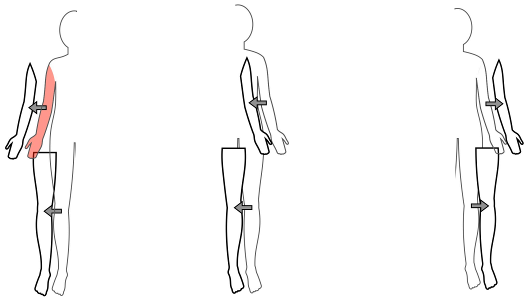
H1: ***Copy transfer.*** The proprioceptive recalibration of the trained limb is directly copied. The position of the untrained limb is perceived at the shifted position in the same direction as the trained limb.

H2: ***Body-structure-based transfer.*** The limbs are located at symmetric positions around the body midline. Based on this body structure knowledge, the distance of the trained limb from the midline and that of the untrained limb must be identical. Therefore, when the visual feedback is manipulated horizontally, the untrained limbs on the opposite body side would be perceived at the shifted position in the opposite direction as the trained limb.



(a) Arm training (b) Leg training

Figure 1: Examples of training scenes. The transparent arm and leg indicate the position of the real limbs. Each figure shows the training using the (a) arm and (b) leg.



(a) Trained side (b) Untrained side Copy (c) Untrained side Body-structure-based

Figure 2: Summary of the hypotheses. The trained limb is shown in red. (a) The predicted shift on the trained side limbs. The predicted shift on the untrained side limbs based on (b) the "*copy transfer*" hypothesis or (c) the "*body-structure-based*" hypothesis.

Previous work revealed a tendency to support the "*copy*" hypothesis. However, this result was not significant, and we modified the experimental setting to one in which the body structure knowledge is utilized more easily. To test the transfer and its direction, we conducted two experiments, i.e., sitting posture in Experiment 1 and standing posture in Experiment 2, using the following task and manipulation.

Task and Manipulation

Our experiment consisted of a training phase and a subsequent test phase.

Training

The participants performed a reaching task using a virtual limb (i.e., arm or leg) in a VR environment. At the start of the phase, the center mark and five white virtual cubes with sides of 10 cm were presented as shown in Figure 1. The center mark was placed in front of the participants' body midline. When the trained limb was the arm, the cubes and the mark were placed on a virtual desk aligned to the real desk; whereas when the trained limb was the leg, those items were placed on a virtual floor aligned to the real floor.

At 2 s from the time at which the participants placed their virtual hand on the center mark, one of the boxes turned red. They touched the target cube with their right hand or foot as accurately and fast as possible. As the touch was detected, the target cube turned white. The participants backed their hand or foot to the center mark and, after 2 s, the target cube was indicated again. The order of the target cube was randomized and each cube became a target 6 times. We instructed the participants to not touch the desk or floor while moving their limbs to the target.

Our experiment included two visual feedback conditions. In one condition (i.e., no-shift condition), the virtual limbs were displayed aligned to the participants' real limbs. In the other condition (i.e., shift condition), the virtual limbs' position was shifted 10 cm rightward. We had confirmed than those who performed the following two experiments that they could not find the shift within 10 cm.

Test

The participants moved their specified limb (hand or foot) in front of their body midline (belly button in the instructions). The movement pattern was completely different from the training, and no visual feedback was provided. When the tested limb was the arm, the participants placed both hands on the desk with sufficient distance between them. They rifted and stretched the specified arm outward from the body and moved it so that the tip of their middle finger reached in front of their body midline while keeping their arm straight. When they perceived that their hand had reached the midline, they placed their hand on the desk. The procedure was identical in the leg test, with the exception that we instructed the participants to move their foot so that their big toe reached in front of their midline.

The distance from the body midline to the tip of the middle finger of their hand or the big toe of their foot was measured. When their hands or feet were placed on the right side of their body midline, we defined the difference as positive; in contrast, when they were placed on the left side, we defined it as negative. All left hands and feet and right hands and feet were tested in the test phase. We assessed both sides in each hand or foot test successively.

In summary, we prepared the four training conditions by changing two factors: body part (arm and leg) and visual feedback (no-shift and shift). We measured proprioceptive recalibration in four limbs (body part: hand and foot, side: right and left) after all training conditions.

Experiment 1

Method

Participants Twenty-two undergraduate or graduate students participated in this experiment ($M = 22.591$, $SD = 1.875$; 19 men and three women). Seventeen participants were right-handed, three were left-handed, and two were ambidextrous. The right foot was dominant in 18 of the participants.

Apparatus We used a head-mounted display (HMD; HTC VIVE pro, HTC, New Taipei, Taiwan) to present the virtual space and its trackers (VIVE Tracker) to acquire the participants' body movements. The trackers were attached to the participant's right wrist, right foot, and waist. The virtual environment was constructed using the Unity game engine.

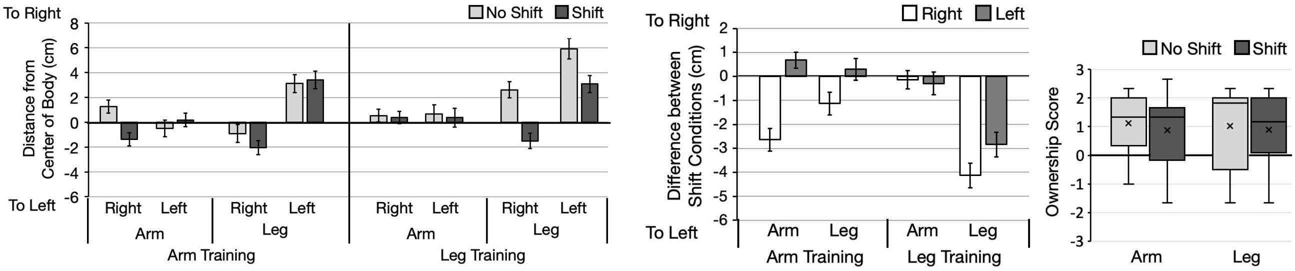
Procedure First, the participants read an explanation of the experiment and filled in a consent form. As a preparation, we adjusted the height of the desk and chair and attached the trackers to the participants. All participants were instructed on how to move their limb during the training and test phases and practiced until they understood it.

Before every training condition, we used a procedure to cancel the effects of the preceding condition. The participants touched the specified digit among pieces of paper on the desk using their specified-side hand, or floor using the specified-side foot, while observing their own body without the HMD. After the cancelling task, the participants wore the HMD and the training phase started. As soon as the 30 trials finished, the word "finish" was presented and then the HMD blacked out. The test phase followed, in which the participants performed the test task once for each of the four limbs while keeping their eyes closed. Finally, the HMD was removed to answer a question about the sense of body ownership: "I felt that the right arm (leg) observed in the training phase belonged to my body." The answer's score ranged from -3 (strongly disagree) to 3 (strongly agree). One session consisted of four training conditions and the participants completed three sessions, namely 12 sets of the training and test conditions. The order of the conditions in a session was random. The Ethics Review Committee for Research Involving Human Subjects of the Ritsumeikan University approved the study (BKC-LSMH-2022-062).

Index and Predictions

We compared the distance from the body midline to the tested hand or foot position between the no-shift and shift conditions. Regarding the trained limbs, in the shift condition, the proprioceptive information of those limbs was remapped to a position located more to the right than the actual limbs' position based on the manipulated visual feedback (Figure 2). Because of this remapping, when the participants moved their hand or foot to their body midline, they would perceive that it must be located more right than the midline. As a result, the participants would place their hand or foot more left than the midline or than the position adopted in the no-shift condition, i.e., smaller value.

Regarding the untrained limbs on the same side as the trained ones, they were recalibrated in the same direction as the trained ones. Therefore, similar results to those obtained for the trained limbs would be acquired at the limbs.For the



(a) Distance from the body midline

(b) Difference between the no-shift and shift conditions

(c) Ownership score

Figure 3: Results of Experiment 1.

untrained limbs on the opposite body side, different results are predicted from each hypothesis. If the *copy* hypothesis is supported, the recalibration would be copied directly by keeping the shift direction in the trained limbs. The participants would move their hand or foot more left than that in the no-shift condition, i.e., a smaller distance is predicted. Conversely, if the *body-structure-based* hypothesis is supported, the recalibration in the trained limbs would be transferred symmetrically around their body midline. In this case, the participants would move their hand or foot more right than that in the no-shift condition, i.e., a larger distance is predicted.

Results

We analyzed each trained limb (arm and leg) separately. In all conditions, the data showed a normal distribution, and outliers were detected using the Smirnov–Grubbs test. We removed one participant's data from the arm training condition and two participants' data from the leg training condition.

Figure 3a shows the average distance from the body midline in the test phase. To confirm the effect of the manipulation of visual information, we calculated the difference between the no-shift and shift conditions for each limb for each participant; the results are reported in Figure 3b. Zero means that there was no difference between the no-shift and shift conditions. The positive and negative values mean that the participants moved their hand or foot more right and left in the shift condition, respectively.

We compared the difference in each condition to zero. When the right hand was trained, the right hand and foot were significantly placed more left in the shift condition (right hand $t(20) = 5.562, p < .001, d = 1.214$; right foot $t(20) = 2.390, p = .027, d = 0.522$), and the left hand was placed more right (with marginal significance), but with a moderate effect size ($t(20) = 1.989, p = .0605, d = 0.434$). There was no significant difference from zero at the left foot ($t(20) = 0.640, p = .529, d = 0.140$). When the right foot was trained, both feet were significantly placed more left in the shift condition (right $t(19) = 7.997, p < .001, d = 1.788$; left $t(19) = 5.616, p < .001, d = 1.256$), whereas the position of the hands did not change ($ts(19) < 0.615, ps > .545, ds < 0.138$)[2].

In summary, when the right arm was trained, the proprioceptive recalibration seemed to transfer to all other limbs other than the left foot. The opposite shifts observed in the right and left hands support the *body-structure-based* hypothesis. When the leg was trained, both feet tended to be placed in the more left position, which supports the *copy* hypothesis.

Finally, the ownership score shown in Figure 3c did not differ significantly between the no-shift and shift conditions in both arm and leg training ($ps > 0.115$, $drs < .350$). The score in the shift condition of both the arm and leg training conditions was greater than zero in most of the participants.

We considered that the leg training did not transfer to the hands because the participants sat on the chair. Their bottoms were fixed; therefore, the upper and lower bodies were separated around their hips. We conducted Experiment 2 to investigate whether the leg training effect could transfer to the hands when the participants' bottoms were not fixed, i.e., training in the standing position.

Experiment 2

The participants completed almost identical tasks to those described in Experiment 1, with the exception that they remained standing throughout all tasks.

Method

Participants Twenty-three undergraduate or graduate students participated in this experiment ($M = 21.783$, $SD = 0.930$, 15 men and eight women). Twenty-two participants were right-handed and the others were left-handed. The dominant foot was right in 21 of the participants, left in one participant, and both in one participant.

Procedure The procedure was identical to that described in Experiment 1 with the exception that the participants performed all tasks in a standing position. We instructed them to stand with their feet shoulder-width apart. For their safety, during the task in which they used their foot, they lightly grabbed pillars on both sides with each hand. We asked them

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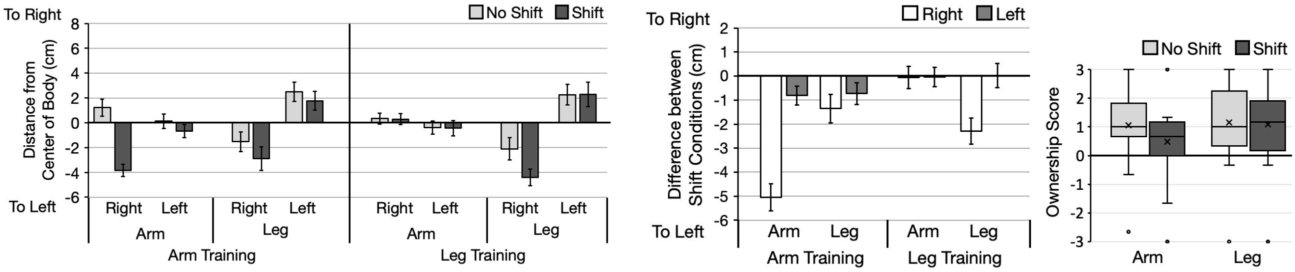
[2] We obtained identical results via a 2 (shift: no-shift and shift) × 2 (body part: hand and foot) × 2 (side: right and left) ANOVA on the data in Figure 3a.



(a) Distance from the body midline

(b) Difference between the no-shift and shift conditions

(c) Ownership score

Figure 4: Results of Experiment 2.

to grab the poles as lightly as possible, to avoid placing their weight on the poles.

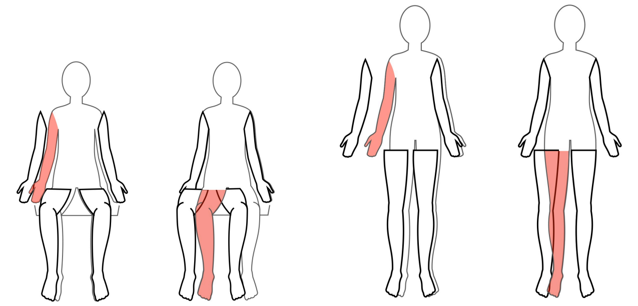
Results

Figure 4a shows the average differences from the body midline. We excluded two participants from the arm training data and three participants from the leg training data using the same procedure as that described in Experiment 1.

The differences between the no-shift and shift conditions indicated a positive value in all tested body parts with the right arm training, as shown in Figure 4b. Statistical comparisons to zero showed that the difference was significantly larger than zero in the trained right hand ($t(20) = 5.562, p < .001, d = 1.214$) and the untrained right foot ($t(20) = 2.269, p = .034, d = 0.495$). At the untrained left hand, the difference was marginal and had a moderate effect size ($t(20) = 2.041, p = .055, d = 0.445$). There was no significant difference in the left foot ($t(20) = 1.619, p = .121, d = 0.353$). After the right leg training, the difference was significantly larger than zero only in the trained right foot (right foot $t(19) = 4.194, p < .001, d = 0.938$; others $ts(19) < 0.128, ps > .900, ds < 0.030$)[3].

In summary, when the right arm was trained, the proprioceptive recalibration seemed to transfer to all other limbs other than the left foot. Those perceived positions shifted in the same direction as that of the trained arm, although the effect was smaller in the limbs on the opposite side. The overall results in Experiment 2, in contrast with Experiment 1, support the *copy* hypothesis when the arm was trained. Moreover, when the leg was trained, the recalibration did not transfer to any other body parts.

Figure 4c reports the ownership score in each condition. The ownership score in the shift condition was smaller than that in the no-shift condition for the arm training ($p = .005$, $r = .613$). There was no significant difference in the leg training condition ($p = .474$, $r = .160$). Most participants gave a score greater than zero in the shift condition in both the arm and leg training conditions.



(a) Sitting arm training

(b) Sitting leg training

(c) Standing arm training

(d) Standing leg training

Figure 5: Summary of the results. Changes in the perceived position of limbs with (a) arm and (b) leg training in the sitting position, and (c) arm and (d) leg training in the standing position. The trained limb is shown in red.

General Discussion

We investigated the proprioceptive recalibration and its transfer after training using distorted vision. After the training of the right arm or leg, we measured the accuracy of the perception of the position of the trained and the other untrained limbs. The results are summarized in Figure 5, which corresponds to the figure illustrating our hypotheses (Figure 2).

Trained Limb

After the training using distorted vision, the participants perceived their trained limb to have a more right location. As shown in previous studies (Cressman & Henriques, 2015; Mostafa et al., 2015), the visual feedback was associated with their real limb position, which led to proprioceptive recalibration. In our experiments, all training was conducted in the virtual space and there was no tactile or force feedback. The participants retained the modified mapping between the visual and proprioceptive information acquired in the virtual space even after the virtual space disappeared.

Transfer to Untrained Limb

Whether and in which direction the transfer occurred varied according to the trained limb and the participants' posture. Before conducting our experiments, we formulated the following hypotheses (see Figure 2): for the limb on the same

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[3] We obtained identical results via a 2 (shift: no-shift and shift) × 2 (body part: hand and foot) × 2 (side: right and left) ANOVA on the data presented in Figure 4a.

side as the trained one, its perceived position would shift in the same direction as the trained limb (i.e., right). On the opposite side of the trained limb, if transfer occurred, there were two possibilities: if the *copy* hypothesis was supported, a rightward shift (as the trained one) would be observed. If the *body-structure-based* hypothesis was supported, the shift would be opposite to that of the trained limb (i.e., left).

Same Side The expected transfer on the same side as the trained one was observed only when the arm was trained. We considered that the differences observed between the arm and foot training in Experiment 1 could be attributed to the posture. However, because of the limitation of the experimental setting (as described later) in Experiment 2, further experiments are necessary to test this possibility.

Furthermore, the localization ability and how easily it could be affected must differ between the hands and feet. Our results in the no-shift condition showed that by only completing leg training without visual distortion, the accuracy decreased in the foot test. Although we did not generate formal data, in the preparation phase of the experiment, we found that the localization performance was worse in the foot test than in the hand test. For this reason, transfer to the leg on the same side would have occurred only in the arm training condition.

Opposite Side For the right hand training in the sitting position, the left hand was placed on a more right position in the shift condition than in the no-shift condition, which supported the *body-structure-based* hypothesis. Conversely, the *copy* hypothesis was supported when the right leg was trained in the sitting position and the right hand was trained in the standing position. When the right leg was trained in the standing position, no transfer occurred.

Before discussing these results, the results of the leg training condition in the standing position would have been produced by the experimental procedure. In this condition, for the safety of the participants, they grabbed the pillars beside them using each hand during the training. Because of these procedures, the limbs other than the right leg were fixed at a specific position in the external environment, which helped maintain the original mapping between the visual and proprioceptive information; as a result, transfer from the trained limb was not observed.

The different results obtained in each condition could be explained by the effect of posture. Tajadura-Jiménez, Tsakiris, Marquardt, and Bianchi-Berthouze (2015) showed that, even after participants performed an identical task, they perceived their arm length differently depending on their posture.

In the arm training conditions, the sitting and standing positions yielded support for opposite hypotheses. In both posture trainings, the participants acquired the position of the (shifted) limb from the visual information, and their viewpoint position provided their head position. Furthermore, when they sat on the chair, the position of their bottoms in space was fixed. Therefore, they had a relatively firm representation of their right arm and body midline based on the visual and haptic feedback. In contrast, when they stood, their body midline was unstable because the feet were located far from the head and any part between them was not fixed at a specific position in the external environment. They estimated their body midline based on the positional information of their right arm, which was the most reliable. As a result, the participants placed their left hand in a more left position in the shift condition.

For the leg training, transfer occurred at least in the sitting position, in contrast with the sitting hand training condition. This may be because the upper and lower bodies can move separately around the hip. Furthermore, during the training, the participants had to keep their body balance using the upper body position. For these reasons, the positional relationship between the body midline (from head to belly) and the right leg, especially the right foot, became unstable compared with the arm training. As a result, the participants estimated their body midline based on the positional information of their right leg, similar to the standing arm training condition.

However, additional experiments are necessary to investigate the postural effect on leg training. We could not assess this effect because, as mentioned above, unexpected factors affected the performance in the standing leg training.

Recalibration and Transfer Process

We consider the transfer process of proprioceptive recalibration as follows. Visual feedback is reliable and has a large effect on the perception of the position of body parts, thus causing proprioceptive recalibration (Cressman & Henriques, 2015; Mostafa et al., 2015). Haptic feedback would be an important cue to decide whether and how its transfer occurs. Positional information on untrained body parts based on touch at a specific point in the environment represents superior information compared with the transfer effect, as shown in the leg training in Experiment 2.

Finally, if the representation of a body part can be constructed based on such reliable feedback mapping between proprioceptive information and its position in the untrained limbs would be completed by applying the representation to the body structure knowledge, (arm training in Experiment 1). However, if such representation is unstable or insufficient, the participants move the untrained limbs based on the trained limbs, the reliable positional information of which is provided from vision. Concretely, the participants move their untrained limbs to the position of the midline perceived by the trained limbs (the leg training in Experiment 1 and the arm training in Experiment 2).

The use of human-like virtual limbs would facilitate the transfer in our experiments. Such virtual limbs increase the sense of ownership, which leads to a large proprioceptive drift (Botvinick & Cohen, 1998; Romano et al., 2015). Similarly, the proprioceptive recalibration in the trained limbs would be facilitated. Finally, it would encourage the use of body structure knowledge.

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