Neuroscience 348 (2017) 288–301

SELF-FACE RECOGNITION SHARES BRAIN REGIONS ACTIVE DURING PROPRIOCEPTIVE ILLUSION IN THE RIGHT INFERIOR FRONTO-PARIETAL SUPERIOR LONGITUDINAL FASCICULUS III NETWORK

TOMOYO MORITA, [a,b*] **DAISUKE N. SAITO,** [c,d]
MIDORI BAN, [a,e] **KOJI SHIMADA,** [c,d] **YUKO OKAMOTO,** [c]
HIROTAKA KOSAKA, [c,d,f] **HIDEHIKO OKAZAWA,** [c,d]
MINORU ASADA [a] **AND EIICHI NAITO** [b,g]

[a] *Graduate School of Engineering, Osaka University, 2-1 Yamadaoka, Suita, Osaka 565-0871, Japan*

[b] *Center for Information and Neural Networks (CiNet), National Institute of Information and Communications Technology (NICT), 1-4 Yamadaoka, Suita, Osaka 565-0871, Japan*

[c] *Research Center for Child Mental Development, University of Fukui, 23-3 Matuokashimoaizuki, Eiheiji, Yoshida, Fukui 910-1193, Japan*

[d] *Biomedical Imaging Research Center, University of Fukui, 23-3 Matuokashimoaizuki, Eiheiji, Yoshida, Fukui 910-1193, Japan*

[e] *Faculty of Psychology, Doushisha University, 1-3 Tatara Miyakodani, Kyotanabe-shi, Kyoto 610-0394, Japan*

[f] *Department of Neuropsychiatry, Faculty of Medical Sciences, University of Fukui, 23-3 Matuokashimoaizuki, Eiheiji, Yoshida, Fukui 910-1193, Japan*

[g] *Graduate School of Frontier Biosciences and Medicine, Osaka University, 1-3 Yamadaoka, Suita, Osaka 565-0871, Japan*

Abstract—Proprioception is somatic sensation that allows us to sense and recognize position, posture, and their changes in our body parts. It pertains directly to oneself and may contribute to bodily awareness. Likewise, one's face is a symbol of oneself, so that visual self-face recognition directly contributes to the awareness of self as distinct from others. Recently, we showed that right-hemispheric dominant activity in the inferior fronto-parietal cortices, which are connected by the inferior branch of the superior longitudinal fasciculus (SLF III), is associated with proprioceptive illusion (awareness), in concert with sensorimotor activity. Herein, we tested the hypothesis that visual self-face recognition shares brain regions active during proprioceptive illusion in the right inferior fronto-parietal SLF III network. We scanned brain activity using functional magnetic resonance imaging while twenty-two right-handed healthy adults performed two tasks. One was a proprioceptive illusion task, where blindfolded participants experienced a proprioceptive illusion of right hand movement. The other was a visual self-face recognition task, where the participants judged whether an observed face was their own. We examined whether the self-face recognition and the proprioceptive illusion commonly activated the inferior fronto-parietal cortices connected by the SLF III in a right-hemispheric dominant manner. Despite the difference in sensory modality and in the body parts involved in the two tasks, both tasks activated the right inferior fronto-parietal cortices, which are likely connected by the SLF III, in a right-side dominant manner. Here we discuss possible roles for right inferior fronto-parietal activity in bodily awareness and self-awareness.

Key words: bodily awareness, proprioceptive illusion, right inferior fronto-parietal cortices, self-awareness, self-face recognition, superior longitudinal fasciculus.

INTRODUCTION

Proprioception is a somatic sensation that allows us to sense and recognize position, posture, and movements of our body parts, even when the eyes are closed. Thus, this sensation pertains directly to oneself, and cannot normally be shared with others, unlike vision and audition.

In our series of functional magnetic resonance imaging (fMRI) studies, we have consistently demonstrated that the cortical and subcortical sensorimotor cortices and the right inferior fronto-parietal cortices (in particular cytoarchitectonic areas 44 and 45, and area PF and its sub-regions) are recruited when blindfolded participants experience proprioceptive illusions of limb movement (changes in limb position or posture), even when the limbs are immobile (Naito et al., 2016). Compared to the sensorimotor cortices (Naito et al., 2016), the right inferior fronto-parietal cortices are less well understood.

The right inferior fronto-parietal cortices are usually more strongly activated when the participants

---

[*] Correspondence to: T. Morita, 2-1 Yamadaoka, Suita, Osaka, 565-0871, Japan. Fax: +81-6-6879-4843.
E-mail addresses: morita@ams.eng.osaka-u.ac.jp (T. Morita), sdaisuke@med.kanazawa-u.ac.jp (D. N. Saito), ekk1001@mail2.doshisha.ac.jp (M. Ban), kshimada@u-fukui.ac.jp (K. Shimada), yokamoto@u-fukui.ac.jp (Y. Okamoto), hirotaka@u-fukui.ac.jp (H. Kosaka), okazawa@u-fukui.ac.jp (H. Okazawa), asada@ams.eng.osaka-u.ac.jp (M. Asada), eiichi.naito@nict.go.jp (E. Naito).

Abbreviations: EPI, echo-planar imaging; fMRI, functional magnetic resonance imaging; FWE, family-wise error; FWHM, full-width-at-half-maximum; GLM, general linear model; MNI, Montreal Neurological Institute; pre-SMA, pre-supplementary motor area; ROI, region of interest; SLF, superior longitudinal fasciculus.

http://dx.doi.org/10.1016/j.neuroscience.2017.02.031

experience proprioceptive illusions than when they merely experience the cutaneous sensation that their limbs are vibrating (Naito et al., 2005, 2007; Amemiya and Naito, 2016). The right inferior fronto-parietal cortices are likely connected by the inferior branch of the superior longitudinal fasciculus tract (SLF III; Makris et al., 2005; Thiebaut de Schotten et al., 2011, 2012; Rojkova et al., 2015; Amemiya and Naito, 2016). In addition, the right inferior fronto-parietal regions that are active during the illusions are highly similar no matter whether the participants experience the illusions on their left or right hand or foot (Naito et al., 2007). Furthermore, activity in these regions usually had right-hemispheric dominance, even when the illusion is experienced at the right hand (Naito et al., 2005, 2007; Amemiya and Naito, 2016). Highly similar regions in the right inferior fronto-parietal cortices are also involved in visuo-proprioceptive multisensory processing, during which sighted participants recognize postural changes of the right hand by combining visual and proprioceptive information (Hagura et al., 2009). Most importantly, we have recently shown that the degree of right inferior fronto-parietal activity (cytoarchitectonic areas 44/45, and PF and its sub-regions) corresponds to subjective reports regarding the extent of the right hand illusion in blindfolded participants (Amemiya and Naito, 2016).

These lines of evidence indicate that the inferior fronto-parietal regions, which have blurred somatotopical representations and multisensory capability, appear to be involved in the proprioceptive awareness of ‘‘my limbs are moving” (changes in position or posture) in a right-hemispheric dominant manner. This view seems to be corroborated by other findings that robust right inferior fronto-parietal activity can only be observed in participants who experience reliable foot illusions (Cignetti et al., 2014), and that electrical stimulation to the human right inferior parietal cortex may elicit proprioceptive awareness of limb movements (Desmurget et al., 2009).

Another series of neuroimaging studies indicates that similar patterns of right inferior fronto-parietal activation have been reported when people visually recognize their own faces as distinct from others’, irrespective of their familiarity (Sugiura et al., 2005, 2006, 2008; Uddin et al., 2005; Platek et al., 2006; Kaplan et al., 2008; Morita et al., 2008). One’s face is a symbol of oneself (at least of the bodily self). Thus, visual self-face recognition directly contributes to recognition (awareness) of the bodily self, which is distinct from others. This may then lead to self-awareness (Gallup, 1982; Brooks-Gunn and Lewis, 1984).

On the other hand, as described above, proprioceptive signals are always derived from one’s own body, and they may elicit bodily awareness regarding one’s bodily posture and movements (proprioceptive awareness). We presume that this self-derived nature of proprioception may provide a basis that allows us to perceive ourselves as physically independent functional entities separate from other agents and the external world.

The right-side dominant activity of the inferior fronto-parietal cortices in the SLF III network during proprioceptive illusions (awareness) may provide the neuronal basis underlying bodily self-awareness, and hence, self-face recognition, which should be directly connected to bodily self-awareness, must also recruit these cortices connected by the SLF III tract in a right-side dominant manner. This may occur through the sharing of active brain regions in these cortices.

We scanned the brain activity of twenty-two healthy right-handed adult participants using fMRI while they performed both a proprioceptive illusion task and a self-face recognition task. In the former, we vibrated the tendon of the wrist extensor muscles of the relaxed right hand in blindfolded participants. In this case, the participants experienced a purely proprioceptive sensation of ‘‘my right wrist is flexing” based on the muscle spindle afferent inputs from the hand (Naito et al., 2016). In the latter, we presented visual images of the participant’s own face and those of others’ faces, and asked the participants to judge whether the face they saw was their own. Thus, this task required visual recognition of one’s own face as distinct from others’, which elicited visual awareness of ‘‘the face I see is my own”.

We tested the hypothesis that both self-face recognition and proprioceptive illusion commonly activate the right inferior fronto-parietal cortices in the SLF III network regardless of differences in sensory modality (proprioceptive vs. visual) or body parts (limb vs. face). We also examined the right-hemispheric dominance in the brain regions active during the proprioceptive illusion and in those active during the self-face recognition separately. For anatomical identification of the brain activation patterns, we referred to the tract probability map, which describes the cortices most likely connected by the SLF I, II, and III tracts, and cytoarchitectonic probability maps of the human brain.

EXPERIMENTAL PROCEDURES

Participants

Twenty-two healthy right-handed adults (12 men and 10 women; age range, 18–47 years) participated in the study. All had normal vision or corrected-to-normal vision. The participants’ right-handedness was confirmed using the Edinburgh Handedness Inventory (Oldfield, 1971). No participant had a history of neurological or psychiatric disorder. The protocol used for this study was approved by the ethics committees of the University of Fukui and the National Institute of Information and Communications Technology. We explained the details of the study to the participants before the start of the experiment. All participants provided written informed consent. The experiment was carried out following the principles and guidelines of the Declaration of Helsinki (1975).

Tasks

We used a proprioception illusion task and a self-face recognition task. The task order was randomized across participants. Before we started the fMRI experiment, we provided the participants with instructions. Every participant experienced both tasks outside the scanner so that they were familiarized with the tasks before they entered the MR room.

The participants lay in the fMRI scanner. At this time, their heads were immobilized using sponge cushions and their ears were plugged. We asked the participants to relax their entire body without producing unnecessary movements and to not think about anything that was not relevant to the tasks. We presented the visual stimuli on a projection screen. In the self-face recognition task, the participants viewed the stimuli through a mirror mounted on the head coil. In the proprioceptive illusion task, visual stimuli were used to provide instructions regarding the timing of the vibration stimuli to the experimenter, who provided the vibration stimuli in the scanner (see below).

Proprioceptive illusion task. In this task, the participants closed their eyes and relaxed their limbs. Both the left and right arms of the participants were naturally semi-pronated and extended in front of them. The participant's right hand was fixed onto a wooden apparatus using a hook and loop fastener (Fig. 1A), flexed at a 30-degree angle, and relaxed in this position (Fig. 1A).

The participants completed one experimental run for this task. One run was composed of six tendon-vibration epochs, each of which lasted for 15 s. During each epoch, we vibrated the tendon of the extensor carpi ulnaris muscle of the right wrist (Fig. 1A), which elicited an illusory flexion of the stationary right hand (Naito et al., 1999, 2002a,b, 2005, 2007, 2010, 2016). The illusion is elicited because the tendon vibration excites the muscle afferent fibers (Goodwin et al., 1972; Roll and Vedel, 1982; Roll et al., 1989) and the brain receives and processes the proprioceptive (kinesthetic) input.

There were 15-s baseline periods between the tendon-vibration epochs. During these periods, we vibrated the skin surface over a nearby bone (i.e. the processus styloideus ulnae of the hand). From our series of studies, we know that this bone-vibration mainly elicits vibration sensations without generating any reliable (vivid and strong) illusions. Thus, it can be used as the control for the tendon-vibration illusion, as it controls for attention to the vibration and the effect of the skin vibration around the wrist. Each run also included a 15-s period before the start of the first epoch and another 15-s period after the end of the last epoch. We performed the bone vibration during these periods so that the bone vibration was performed during all baseline periods. By examining the increase in brain activity during the tendon-vibration epochs as compared to the baseline periods, we were able to evaluate the effect directly associated with the proprioceptive illusion. This effect was not explained by the attentional effects, as the bone-vibration alone would have also drawn the participants' attention to the vibration.

We used a non-magnetic vibrator (110 Hz; Illusor, Umihira Ltd., Kyoto, Japan; Fig. 1A), driven by constant air pressure provided by an air compressor (Amemiya and Naito, 2016). We used vibration stimuli with amplitudes of approximately 3.5 mm. The contact surface on the skin was approximately 1 cm^2. One experimenter (EN) operated the vibrator by manually applying it to the skin using light pressure. Computer-generated visual cues were provided to the experimenter in order to instruct him regarding the timing of the tendon and bone vibrations. The blindfolded participants were unable to see these cues.

In this task, we asked the participants to be aware of movement sensations from the vibrated hand. Thus, this was a purely somatic perception (bodily awareness) task, wherein the blindfolded participants were aware of the change in hand posture. To verify that the participants really experienced the proprioceptive illusion during the tendon-vibration epochs, we asked them to remember the maximum illusory flexion angle experienced in each run and to show the maximum angle after the run. After the run was completed, we asked the participants whether they experienced the illusion. All participants reported that they experienced the illusion only during the tendon vibration. They also reported that they experienced the vibration sensation during the baseline (bone vibration) periods. We then asked the participants to indicate the maximum illusory flexion angle during the six tendon-vibration epochs. In the scanner, we showed the participants a protractor on which a hand-shape indicator was mounted. This indicator was first set at the 30-degree flexion (original) position, which corresponded to the actual position of the participants' relaxed hand. From this position, we began flexing the indicator. When the participants believed that the indicator had reached the maximum illusory angle that they experienced, they were asked to say "stop." We measured this angle as a change from the original position.

Self-face recognition task. In this task, we presented face photographs to the participants, who viewed them through a mirror placed in front of their eyes. The participants completed two experimental runs for this task. In each run, we presented 15 images of the participant's own face (SELF) and 15 images of unfamiliar faces (OTHERS) in a pseudorandom order, causing the participants to pay equal attention to each presented image. Each run also included 6 null-event trials, in which no stimulus was presented. We asked the participants to judge whether the face they saw was their own. This was thus a typical self-recognition task.

Each face stimulus was presented at the center of the screen for 2.5 s. Once the face stimulus had disappeared, a selection screen appeared for 2.5 s. On this screen, Japanese texts meaning "self" and "others" appeared side by side in light gray (Fig. 1B). The location of two words was counterbalanced across participants. The participants were instructed to judge whether the face stimulus was their own by pressing one of two buttons using their right index or middle fingers. The participants always pressed the left button with their index fingers and the right button with their middle fingers. The button to be pressed was also counterbalanced across participants. Half of the participants pressed the left

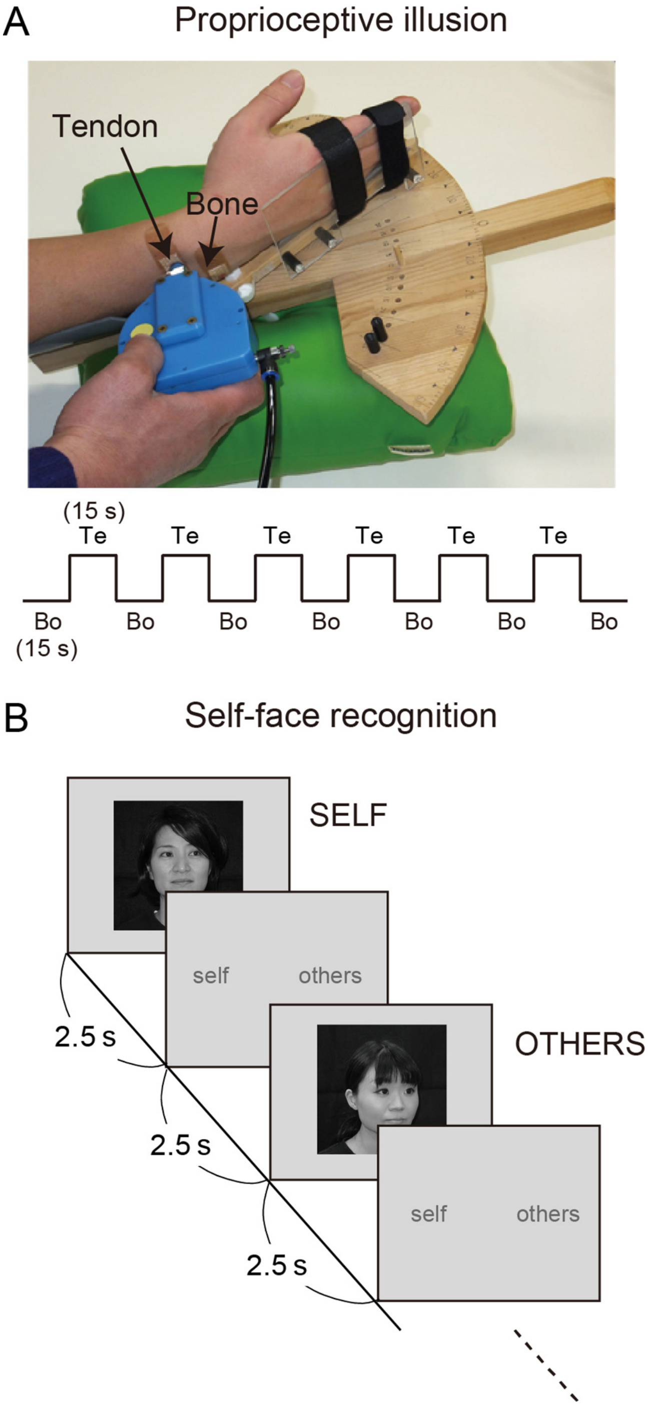

Fig. 1. (A) Experimental setup and procedure for the proprioceptive illusion task. Participants were subjected to either bone vibration (Bo) or tendon vibration (Te) alternately for 15 s per block. (B) Sequence of events in the self-face recognition task. In each trial, either a self-face or the face of an unfamiliar person was presented in a random order in the center of the screen for 2.5 s. Participants were required to judge whether the face they saw was their own and to press a button that corresponded to ‘‘self” or ‘‘others” using their right index or middle finger.

button, while the remaining half pressed the right button, when they selected ‘‘self” throughout the experimental runs. Fig. 1B shows an example of this task. When the face was the participant’s own, he or she pressed the left button using the right index finger, while when the face was another’s, the participant pressed the right button using the right middle finger. In order to indicate the selection (self or others), the color of the selected item changed to dark gray when the assigned button was pressed. The participants were instructed not to press any buttons at the time that the face stimulus appeared, but to press the button when the selection screen appeared. By doing so, we temporally dissociated the cognitive neuronal processes underlying self-face recognition from those associated with the motor component (button-press). We did this because the experimental design was based on a rapid event-related paradigm, wherein efficiency was highly dependent upon the temporal pattern of stimulus presentation (Dale, 1999; Friston et al., 1999). The detailed methods required to obtain a highly efficient experimental design are described elsewhere (Morita et al., 2008).

Before the fMRI experiment, we photographed each participant (without glasses) in front of a black background. Each participant wore the same black T-shirt. We took 15 different pictures of each participant’s face using a digital camera (FinePix F600EXR, Fujifilm Corporation). We presented these face images as those in the SELF condition. The 15 face images of the three sex-matched unfamiliar individuals (five images per person) were used as the stimuli for the OTHERS condition. These images were cropped to the same size and converted to gray scale.

fMRI data acquisition

Functional images were acquired using T2*-weighted, gradient echo, echo-planar imaging (EPI) sequences using a 3 T MR imager (Discovery MR750; GE Healthcare, Milwaukee, Wisconsin, USA) and a 32-channel array coil. For the proprioceptive illusion task, we collected a total of 82 volumes per run, while 80 volumes per run were collected for the self-face recognition task. Each volume consisted of 40 slices acquired in ascending order, with a thickness of 3.5 mm, and with 0.5-mm gaps. We thus covered the entire brain. The time interval between two successive acquisitions from the same slice (TR) was 2500 ms. We used an echo time (TE) of 30 ms and a flip angle (FA) of 83°. The field of view (FOV) was 192 × 192 mm, and the matrix size was 64 × 64. We thus had voxel dimensions of 3 × 3 mm.

Imaging data analysis

Pre-processing. The first four volumes of each fMRI run were discarded because of unsteady magnetization. Imaging data were analyzed using Statistical Parametric Mapping (SPM8; The Wellcome Department of Cognitive Neurology, London, UK) implemented in Matlab (Mathworks, Sherborn, MA, USA). Initially, EPI images were realigned to the first image and then to the mean image. We applied slice-timing corrections to adjust for differences in slice-acquisition times for the images from the self-face recognition task. We interpolated and re-sampled the data so that slices were acquired at the same time as the reference (middle) slice (Sladky et al., 2011). These realigned images were normalized to the Montreal Neurological Institute (MNI) space (Evans et al., 1994). Finally, the spatially normalized functional images were filtered using a Gaussian kernel with a full-width-at-half-maximum (FWHM) of 4 mm in the *x*-, *y*-, and *z*-axes.

Activation analyses for each task. After pre-processing, we evaluated task-related activations using a general linear model (GLM; Friston et al., 1995; Worsley and Friston, 1995) for each task. In the proprioceptive illusion task, the design matrix contained a boxcar function for the tendon-vibration (illusion) epoch, which was convolved with a canonical hemodynamic response function. To correct for residual motion-related variance after realignment, the six realignment parameters were also included in the design matrix as regressors of no interest. For each participant (single-subject analyses), we constructed an appropriate contrast image to examine brain regions showing illusion-related activity (tendon-vibration vs. bone-vibration [baseline]). To accommodate inter-participant variability, the contrast images from all participants were entered into a second-level random effects group analysis (Holmes and Friston, 1998). A one-sample *t*-test was performed.

In the single-subject analyses for the self-face recognition task, the design matrix contained two task-related regressors for the ‘‘SELF” and ‘‘OTHERS” conditions, as well as one regressor for button pressing. To correct for residual motion-related variance after the realignment, the six realignment parameters were also included in the design matrix as regressors of no interest. We constructed appropriate contrast images to examine brain areas showing self-face-related activity (SELF vs. OTHERS). In this contrast, the effect of motor preparation should be eliminated since the participants had to prepare the button press both in the SELF and in the OTHERS conditions. In the second-level analysis, a one-sample *t*-test was also performed for the contrast images, as described above.

In the second-level analyses, we used a voxel-wise threshold of $p < 0.001$ and evaluated significance of brain activations in terms of the spatial extent of the activations in the entire brain ($p < 0.05$, family-wise error-[FWE]-corrected for multiple comparisons). For the anatomical identification of the active brain regions, we referred to the cytoarchitectonic probability maps in the MNI standard brain of the SPM anatomy toolbox v1.8 (Eickhoff et al., 2005).

Conjunction analysis. We examined the brain regions commonly active during the proprioceptive illusion and the self-face recognition tasks by performing a conjunction analysis (Price and Friston, 1997). This type of analysis allows us to identify brain areas of common activation that may be associated with common neuronal processing components in the two tasks. Even though each task placed different demands on different sensory modalities, we conducted this analysis, as demands on different sensory modalities do not necessarily have to be matched in conjunction analyses (Price and Friston, 1997). Two contrast images (tendon-vibration vs. bone-vibration and SELF vs. OTHERS) obtained from each participant were used in the second-level group analyses. We adopted a voxel-wise threshold of $p < 0.001$ and evaluated the significance of brain activations in terms of the spatial extent of the activations in the entire brain ($p < 0.05$, FWE-corrected).

Region of interest (ROI) analysis. Next, we examined whether the right inferior fronto-parietal cortices active during both the proprioceptive illusion and the self-face recognition belong to the inferior fronto-parietal network, which is likely connected by the SLF III tract. If the commonly activated voxels form significant volumes of active clusters in the brain regions connected by the SLF III, we may conclude that these SLF III regions are substantially recruited during both the proprioceptive illusion and the self-face recognition.

In this analysis, we used a probability map to depict the tracts (SLF I, II, or III), which was originally obtained using elaborate methods (Thiebaut de Schotten et al., 2011, 2012; Rojkova et al., 2015). Each tract probability map describes a branch of the SLF (SLF I, II, or III) in each hemisphere. The maps were generated using diffusion imaging tractography and a spherical deconvolution technique from images obtained from 47 normal volunteers (ages ranging from 22 to 71 years) and normalized to the MNI standard brain. Thus, each map describes the stream of the tract and the cortical regions likely connected to each SLF tract in a probabilistic manner. We adopted a threshold of 0.5 as used in a previous study (Parlatini et al., 2016). This produced an image that described both the tract in the white matter and the connecting gray-matter cortical regions, considering the probability that a given tract existed in over 50% of the 47 individuals. We used the 50% map because the major cortical regions likely connected by the SLF III (Thiebaut de Schotten et al., 2012) are depicted when we use this map. We believe that these maps can be used as indicators allowing us to describe the most probable locations of brain activations in relation to cortical regions connected by the SLF tracts (in particular by the SLF III tract in the present study), even though these maps were not obtained from the participants in the present study. The validity of this approach (basically a simple overlay method) is discussed in our previous study (Amemiya and Naito, 2016).

We used a voxel-wise threshold of $p < 0.001$ and determined significant common brain activations in terms of spatial extent ($p < 0.05$, FWE corrected) using the probability map for SLF III in the right hemisphere as an inclusive mask. We also performed other two ROI analyses using the probability maps for the right SLF I or II in order to confirm whether the common activations only belong to the fronto-parietal regions connected by the SLF III.

Evaluation of hemispheric dominance. We examined hemispheric dominance in the illusion-related activity and in the self-face-related activity by adopting an approach employed by Shulman et al. (2010). In this analysis, first, the original EPI images for each participant were flipped across the midline to generate left–right reversed images (flipped EPI images). Then, these flipped images were realigned and normalized to the MNI space (Evans et al., 1994). Thus, the right (left) hemisphere was transformed in the best-fitting manner to the left (right) hemisphere. Finally, the normalized images were spatially smoothed using a 4-mm FWHM isotropic Gaussian kernel.

For each participant, in addition to the original GLM built for the analysis of the original EPI images (see above), we also constructed a second GLM for the flipped EPI images. For images obtained during the proprioceptive illusion, we generated two contrast images showing illusion-related activity (tendon vs. bone) obtained from the original GLM and from the second (flipped) GLM. In the second-level group analysis, we performed a paired t-test using the images obtained from all participants. This analysis allowed us to perform voxel-wise comparisons between the original and flipped images in the MNI space, which enabled us to perform a direct comparison between left and right hemisphere activation patterns.

We used a voxel-wise threshold of $p < 0.001$ and determined significant differences in terms of the spatial extent of active-voxel clusters ($p < 0.05$, FWE-corrected). Here, we used the image of illusion-related activity obtained from the original image (voxel-wise threshold of $p < 0.05$ uncorrected) as an inclusive mask. Using this mask image, we identified lateralized activation within brain regions where activity was increased during tendon vibration by eliminating the possibility that the lateralized activation was caused by deactivation in the corresponding brain region in the opposite hemisphere.

The same procedure was also performed to evaluate hemispheric dominance in the self-face-related activity (SELF vs. OTHERS).

RESULTS

Behavioral results

In the proprioceptive illusion task, all participants reported that they experienced vivid and strong sensations of right hand flexion when we vibrated the tendon of the wrist extensor muscle. They also reported that this sensation was substantially distinguishable from the merely cutaneous sensations experienced during bone vibration (baseline period). Since we confirmed that the hand was not actually moving during the tendon vibration, it is fair to say that all of the participants experienced substantial illusory flexion of the right stationary hand. Surprisingly, some of the participants reported that they experienced an illusory flexion angle beyond the natural endpoint of wrist flexion. This indicated that our body is represented as being flexible in our brain and that an illusory experience may sometimes evoke a physically impossible limb position. The mean maximum illusory flexion angle for all participants was 70.6° (standard deviation = 35.8°, range = 25–165°).

In the self-face recognition task, the participants easily recognized their own faces. The mean correct rate for all participants was 99.6% (standard deviation = 0.9).

Brain regions commonly activated during proprioceptive illusion and self-face recognition

Our main purpose was to determine whether self-face recognition and proprioceptive illusion commonly activate the right inferior fronto-parietal cortices, which are likely connected by the SLF III tract. Conjunction analysis showed that there are three areas of common brain activation in the inferior parietal lobule (activation peaks in cytoarchitectonic areas PFm, PF, hIP3, 7PC, and PFt), in the inferior frontal gyrus (area 44), and in the anterior insula of the right hemisphere (Table 1 and Fig. 2). These were the only regions in the entire brain that were commonly activated. Thus, common regions of activation were only observed in the inferior fronto-parietal cortices of the right hemisphere.

We set out to determine whether the commonly activated voxels form significant volumes of active clusters in brain regions that are connected by the SLF tracts (ROI analysis). We found two clusters of active voxels with significant volumes only in the right inferior fronto-parietal cortices, which are likely connected by the SLF III tract. One cluster was located in the inferior parietal lobule (peaks in areas PF, PFt, PFm, and hIP3) and the other was located in the inferior frontal gyrus (area 44). These regions corresponded well to the regions showing right-side dominant activity during the self-face recognition. The commonly activated regions in the right inferior parietal lobule also showed right-side dominant activity during the proprioceptive illusion (see below and Tables 2 and 3).

The results indicated that both self-face recognition and proprioceptive illusion use the right inferior fronto-parietal cortices, which are likely connected by the SLF III, in addition to the right anterior insula, which does not appear to be a region connected by the SLF III.

We could not find any significant active clusters in the brain regions likely connected by other SLF tracts, i.e., SLF I or II.

Brain areas active during proprioceptive illusion

The results of the proprioceptive illusion task are shown in Table A and Fig. 3A. In general, broader fronto-parietal regions were activated in the right cerebral cortex when compared to the left cerebral cortex, even when the participants experienced the illusion in the right hand. In the right cerebral cortex, we found significant illusion-related activation in the inferior frontal gyrus (cytoarchitectonic areas 44 and 45), anterior insula, inferior parietal lobule (areas PFm, PFt, hIP2, and PGa), superior frontal gyrus, middle orbital gyrus, middle frontal gyrus, and posterior parietal cortex (areas 7P and 7A). In the left cerebral cortex, we found significant anterior insular activation in addition to significant trend for the activation of the hand section of the primary

Table 1. Brain areas commonly activated during self-face recognition and proprioceptive illusion

Clusters	Size (voxels)	MNI coordinates			*T*-value	Anatomical identification (cytoarchitectonic area)
		x	*y*	*z*		
Whole brain						
Parietal cluster	496	46	−42	54	5.38	Area PFm
		52	−34	48	5.36	Area PF
		38	−50	48	4.37	Area hIP3
		42	−48	58	4.24	Area 7PC
		60	−24	36	3.85	Area PFt
Anterior insular cluster	209	40	8	−6	4.69	Anterior insula
Inferior frontal cluster	162	54	12	12	4.86	Area 44
SLF III						
Inferior parietal cluster	233	52	−34	48	5.36	Area PF
		50	−36	56	4.88	Area PFt
		46	−40	48	4.66	Area PFm
		38	−50	48	4.37	Area hIP3
Inferior frontal cluster	103	54	14	12	4.62	Area 44

Uncorrected height threshold, $p < 0.001$; extent threshold, $p < 0.05$, FWE-corrected.
For anatomical identification of peaks, we only considered cytoarchitectonic areas available in the anatomy toolbox that had a higher-than-30% probability. The cytoarchitectonic area with the highest probability was reported for each peak. When cytoarchitectonic areas with more than 30% probability were not available to determine a peak, we simply provided the anatomical location of the peak. In each cluster, we reported peaks that were more than 8 mm apart from each other in order of increasing *T*-values. To facilitate visualization, we avoided reporting a peak for each cluster when it was identified in the same cytoarchitectonic area or in the same anatomical structure already reported for a peak with a higher *T*-value.

motor cortex (M1: area 4a). In addition to these cerebral activations, bilateral activations were also observed in the medial-wall regions (area 6: pre-supplementary motor area; pre-SMA). Within subcortical structures, we found cerebellar activation in lobule VI and crus I of both hemispheres and in the bilateral vermis (lobules V and VI). These results in essence replicated our previous findings (Amemiya and Naito, 2016; Naito et al., 2016).

When we examined lateralized illusion-related activity in the whole brain by performing voxel-wise comparisons between the two hemispheres (Table 2), we found right-side dominant activity in the inferior parietal lobule (area PFt), the anterior parietal cortices (areas 2 and hIP2), the middle frontal gyrus, and the superior frontal gyrus. Right cerebellar activity in the right hand/wrist section of lobules V and VI also showed right-side dominance. In contrast, left-side dominant activity was only observed in the sensorimotor cortices (areas 4a, 3a, 6, and 3b). These results replicate those of a previous series of studies (Naito et al., 2016). In our previous study, we reported right-side dominant activity in area 44 (Amemiya and Naito, 2016). In the present study, we also observed right-side dominant increases in area 44 activity at the voxel-wise threshold of $p < 0.001$ ($T = 4.1$), though this increase did not reach significance when considering the spatial extent of the activation.

Brain areas active during self-face recognition

The results of the self-face recognition task are shown in Table B and Fig. 3B. As we observed for the illusion-related activity, broader fronto-parieto-temporal regions were activated in the right cerebral cortex when compared to the left cerebral cortex when the participants recognized their own faces as distinct from those of others. In the right cerebral hemisphere, we found significant self-face-related activation in the inferior parietal lobule (areas PFt, hIP3, and 2). This activation further extended posteriorly toward the occipital cortex (areas 7A, PGp, hOC3v, and 7P). We also observed activations in the inferior frontal gyrus (areas 44 and 45) including the anterior insula and in the inferior temporal gyrus. In the left cerebral hemisphere, we found activation in the inferior and middle occipital gyri, which extended dorsally toward the parietal cortices. We also found anterior insular activation in the left hemisphere. Within subcortical structures, we found activation in the left cerebellar hemisphere (lobules VIIb and crus II).

When we examined lateralized self-face-related activity in the whole brain (Table 3), we found right-side dominant activity in the inferior and superior parietal lobules (areas 2, hIPs, 7PC, and PFt), both posterior and anterior aspects of the inferior frontal gyrus (area 44), inferior temporal gyrus, and posterior parietal cortex (areas 7A and 7P). No regions showed left-side dominant self-face-related activity.

DISCUSSION

The present study demonstrated that self-face recognition shares brain regions activated during proprioceptive illusion in the right inferior fronto-parietal cortices (areas 44 and PF and its sub-regions), which are likely connected by the SLF III tract (Table 1 and Fig. 2). The present conjunction analysis allowed us to identify brain regions jointly activated by self-face recognition and proprioceptive illusion. Even though the common activations do not guarantee that both tasks employed

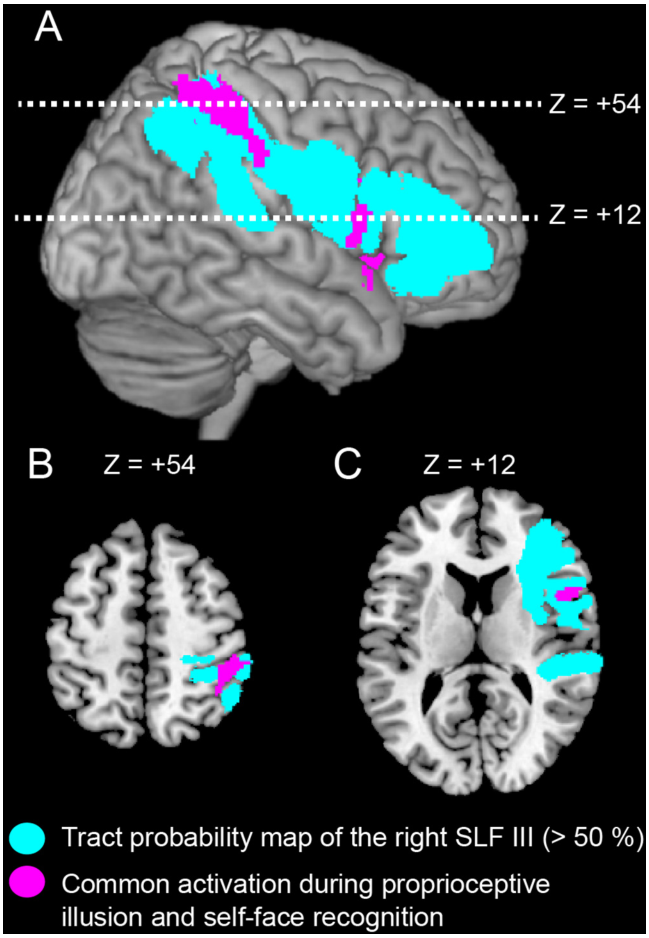

Fig. 2. Brain regions commonly active during proprioceptive illusion and self-face recognition (magenta sections). Cyan sections indicate the cortices that are likely connected by the SLF III. In panel A, commonly activated regions in the inferior parietal lobule, the inferior frontal gyrus (area 44), and the anterior insula are superimposed onto the right hemisphere. Commonly activated regions in the right inferior parietal lobule (B) and the inferior frontal gyrus (C) are also displayed in the transverse sections of the MNI brain.

identical sets of neuronal populations in the right inferior fronto-parietal cortices, the present results indicate that self-face recognition and proprioceptive illusion commonly require components of neuronal processing assigned to the right inferior fronto-parietal SLF III network in the brain.

Illusion-related activity

We observed similar patterns of illusion-related activity (Fig. 3A and Table A) to those reported in our series of previous studies (Naito et al., 2016). The patterns of right-dominant activity (Table 2) also essentially replicated our previous results (Naito et al., 2005, 2007; Amemiya and Naito, 2016). Since the proprioceptive illusion in our study is likely elicited when the brain processes the muscle spindle afferent inputs from the right hand (see *Introduction*), some of the illusion-related activity must reflect brain activities that involve this basic proprioceptive (kinesthetic) processing.

As we have carefully discussed in our series of studies, the sensorimotor network likely involves this processing (Naito, 2004; Naito et al., 2016). In the present study, we identified increase in activity in the hand section of the left M1 and the hand/wrist section of the right cerebellar lobule VI (Grodd et al., 2001), which is known to form a motor network with the left M1 in primates (Strick et al., 2009). In addition, we identified activity in cerebellar vermis lobules V and VI, which may also form motor networks with M1 (Coffman et al., 2011). Thus, these regions likely form motor networks and probably participate in basic proprioceptive (kinesthetic) processing (Naito, 2004; Naito et al., 2016).

Self-face-related activity

Self-face-related activity in the right inferior fronto-parietal cortices (Fig. 3B and Table B) was generally in line with previous findings of studies using the self-face recognition task (Uddin et al., 2005; Sugiura et al., 2005, 2006; Platek et al., 2006) and the self-face evaluation task (Morita et al., 2008). However, the present study is the first to statistically evaluate the right-hemispheric dominance of the inferior fronto-parietal activity for self-face recognition in addition to the posterior parietal and inferior temporal activity (Table 3), as suggested in a previous report (Devue and Brédart, 2011; Hu et al., 2016). The importance of the right inferior fronto-parietal cortices for self-face recognition seems to also be supported by the following findings: First, virtual lesions to the right inferior parietal lobule using repetitive transcranial magnetic stimulation may disrupt self-face recognition (Uddin et al., 2006). Second, patients with brain damage to the right cerebral hemisphere are unable to identify their own face when it is reflected in a mirror (Feinberg and Shapiro, 1982; Spangenberg et al., 1998; Feinberg, 2000; Breen et al., 2001). Finally, intracarotid injections of amytal to the right hemisphere lower the rate of self-attribution when individuals view self-other morphing faces (Keenan et al., 2001).

We also found self-face-related activities in the inferior and middle occipital cortices of both hemispheres and in the right inferior temporal cortex. These findings also generally agreed with previous findings (Sugiura et al., 2006, 2008; Platek et al., 2006; Morita et al., 2008, 2012). We may consider these regions as higher-order visual association areas. However, most of these regions are distinct from areas that generally involve visual processing of face stimuli, such as the fusiform face area, which is involved in the identification of individual faces (Kanwisher et al., 1997; Kanwisher and Yovel, 2006), and the occipital face area, which is involved in face part-based processing (Rotshtein et al., 2005; Pitcher et al., 2011). Thus, these regions seem to be specialized for the visual processing of one's own face (Sugiura et al., 2006, 2008).

Shared brain regions in the right inferior fronto-parietal cortices

As described in the introduction, the exact roles of the right inferior fronto-parietal cortices are not fully

Table 2. Lateralized illusion-related activity

Clusters	Size (voxels)	MNI coordinates			T-value	Anatomical identification (cytoarchitectonic area)
		x	*y*	*z*		
Right hemisphere dominance						
Inferior parietal cluster	211	60	−22	34	5.34	Area PFt
		62	−24	46	4.14	Supramarginal gyrus
Middle frontal cluster	121	40	46	28	5.04	Middle frontal gyrus
		42	38	12	3.87	Inferior frontal gyrus
Anterior parietal cluster	117	48	−40	62	4.41	Postcentral gyrus
		42	−38	52	4.21	Area 2
		40	−48	46	3.95	Area hIP2
Superior frontal cluster	114	28	8	62	4.55	Superior frontal gyrus
		36	12	62	4.01	Middle frontal gyrus
Cerebellar cluster	490	22	−48	−26	6.56	Lobule VI
		12	−50	−18	6.31	Lobule V
		4	−66	−22	4.46	Lobule VI (vermis)
Left hemisphere dominance						
Sensory-motor cluster	603	−34	−26	62	7.47	Area 4a
		−36	−24	48	5.37	Area 3a
		−30	−20	70	5.03	Area 6
		−28	−36	66	4.73	Area 3b

See footnote in Table 1.

Table 3. Lateralized self-face-related activity

Clusters	Size (voxels)	MNI coordinates			T-value	Anatomical identification (cytoarchitectonic area)
		x	*y*	*z*		
Right hemisphere dominance						
Inferior parietal cluster	687	54	−24	44	6.68	Area 2
		44	−38	52	5.64	Area hIP2
		42	−48	60	4.43	Area 7PC
		42	−24	40	3.95	Area PFt
Inferior frontal cluster (posterior aspect)	370	46	6	26	5.97	Area 44
		50	10	38	3.80	Precentral gyrus
Inferior frontal cluster (anterior aspect)	343	40	38	6	7.08	Inferior frontal gyrus
		46	46	4	5.02	Middle frontal gyrus
Inferior temporal cluster	195	50	−52	−14	5.92	Inferior temporal gyrus
Posterior parietal cluster	152	26	−68	54	4.10	Area 7A
		28	−56	46	4.00	Angular gyrus
		18	−74	56	3.86	Area 7P

See footnote in Table 1.

understood. However, cumulative evidence from previous studies and the present study allow us to speculate. First, it is shown that the parietal areas PF and PFm seem to have particularly stronger connections with the frontal area 44 in the human brain (Matsumoto et al., 2012). Thus, the right inferior fronto-parietal cortices might work together both during the self-face recognition and during the proprioceptive illusion by forming anatomical and functional networks in regions connected by the SLF III.

The proprioceptive illusion task used in our study required the somatic recognition of postural change (movement) of one's own hand. At the same time, the self-face recognition task used in our study required visual recognition of one's own face. Despite the clear differences in sensory modality and affected body parts, both tasks activated highly similar regions in the right inferior fronto-parietal cortices. We thus hypothesize that these cortices have blurred somatotopical representations. For example, it is reported that area 7b in monkeys (homologous area to human area PF) has neurons with variable receptive fields that may cover several different body parts including the face, arm, and hand (Hyvarinen, 1982). In humans, it is shown that highly similar regions in the right inferior fronto-parietal cortices are active whether the participants experience illusions of the left or right hand or foot (Naito et al., 2007) or view images not only of their own faces, but also of their own bodies (Sugiura et al.,

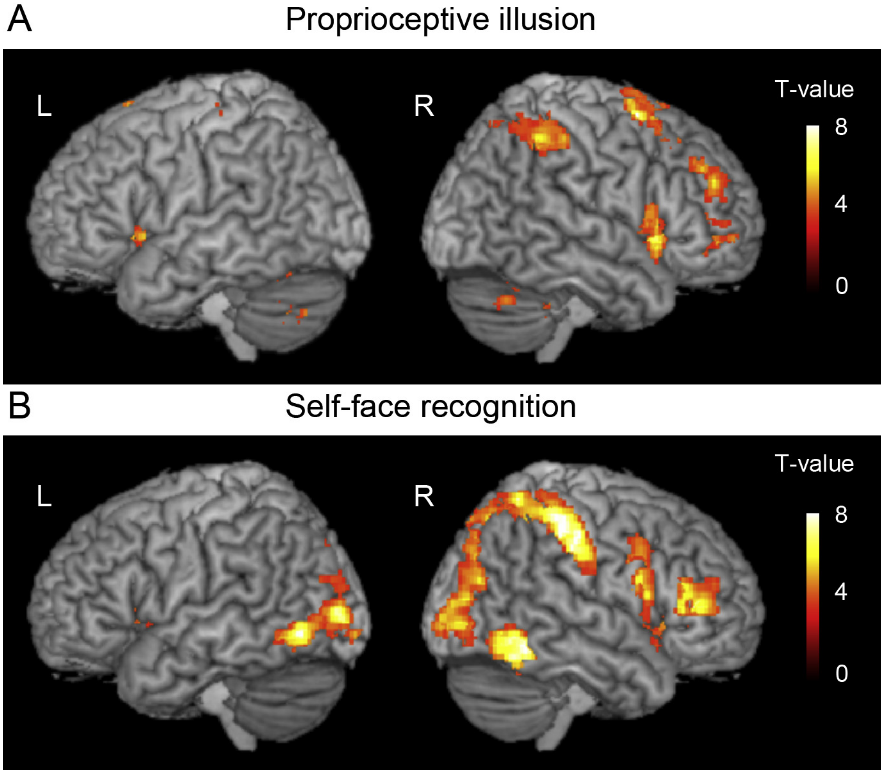

Fig. 3. Brain regions with illusion-related activity (A) and brain regions with self-face-related activity (B) are displayed. In each panel, brain activations are rendered onto the left and right hemispheres of the MNI brain.

2006). We may also consider these cortices to be higher order multisensory brain areas because it is known that cells in homologous areas in monkeys involve multisensory (visuo-somatic) processing pertaining to one's own body (face, arm, and hand; Hyvarinen, 1982; Graziano et al., 2004; Murata et al., 2016). In addition, these cortices in human brain are recruited during multisensory (visuo-somatic) processing for hand posture (Hagura et al., 2009) and self-face recognition (Apps et al., 2015; Bufalari et al., 2015). If the human brain contains regions capable of comprehensively representing the bodily self by integrating multisensory information pertaining to one's own body, the right inferior fronto-parietal cortices in the SLF III network could be strong candidates. This view does not contradict a recent view regarding bodily self-consciousness proposed by Blanke et al. (2015).

Notably, we show that these putative multisensory regions are substantially activated even during unimodal proprioceptive or visual processing. This indicates that even unimodal sensory information may somehow reach and activate the right inferior fronto-parietal cortices. When we carefully look at the brain regions connected by the right SLF III tract, we find that both area 2 (somatosensory association area) and area PGa (putative visual association area), which are adjacent to area PGp (hub area linking the occipital and parietal cortices; Caspers et al., 2013), seem to belong to regions connected by the SLF III tract (Naito et al., 2016). Thus, it is conceivable that both proprioceptive and visual inputs reach the SLF III network at least through these association areas. This may contribute to activity in the right inferior fronto-parietal cortices, probably in concert with right anterior insular activity (see below).

It is also very important to consider factors favorable for the activation of the right inferior fronto-parietal cortices. These cortices were strongly activated when the participants experienced the proprioceptive illusion (awareness) of "my hand is flexing" than when they merely experienced the cutaneous sensation (awareness) of "my hand is vibrating". This indicates that the proprioceptive processing that elicits bodily awareness regarding posture and movement (body image) is a favorable factor to activate the right inferior fronto-parietal cortices. Likewise, these cortices were strongly activated when the participants experienced the visual awareness of "the face I see is my own" than when they experienced the awareness of "the face I see is someone else's". Thus, self-face recognition, which is directly linked to bodily self-awareness, is also a favorable factor to activate the right inferior fronto-parietal cortices. Thus, the common factor seems to be information pertaining to the bodily self.

Since the common regions in the right inferior fronto-parietal cortices basically correspond to regions showing right-side dominant activity during both the self-face recognition (Table 3) and the proprioceptive illusion (Table 2), the right inferior fronto-parietal cortices appear to bear a preference for processing such information. The right SLF III is a useful brain tract with high-capacity information processing due to its significantly greater volume compared to the left SLF III (Thiebaut de Schotten et al., 2011; Hecht et al., 2015). Thus, this tract seems to be suitable for speedy processing of complex and massive information associated with the bodily self. This view seems to fit well with the clinical observations that brain damage to the right hemisphere often causes deficits in the recognition of one's own limbs (Halligan et al., 1993; Berlucchi and Aglioti, 1997; Berti et al., 2005) and one's own face (see above, e.g., Breen et al., 2001). These injuries thus affect normal bodily awareness and/or bodily self-awareness.

We may also point out the possibility that the shared right inferior fronto-parietal activations are somehow associated with modality-independent conscious process (Dehaene and Changeux, 2011). If the right inferior fronto-parietal activity contributes to the elicitation of bodily awareness and bodily self-awareness, we may speculate as follows. The co-activation of the sensorimotor network (e.g., hand

Table A. Illusion-related activations

Clusters	Size (voxels)	MNI coordinates			T-value	Anatomical identification (cytoarchitectonic area)
		x	y	z		
Cerebral cortex						
Right hemisphere						
Inferior frontal cluster	787	42	16	−2	6.91	Anterior insula
		48	14	6	6.40	Area 44
		44	22	4	4.11	Area 45
Inferior parietal cluster	657	46	−46	50	6.04	Area PFm
		50	−32	50	5.31	Area PFt
		46	−38	46	5.12	Area hIP2
		38	−50	46	5.10	Inferior parietal lobule
		32	−46	38	4.84	Angular gyrus
		46	−54	54	4.09	Area PGa
Superior frontal cluster	453	28	6	62	8.03	Superior frontal gyrus
		44	18	54	5.02	Middle frontal gyrus
Middle orbital cluster	163	36	48	−4	5.17	Middle orbital gyrus
		38	40	−10	4.54	Inferior frontal gyrus
		36	44	8	4.12	Middle frontal gyrus
Middle frontal cluster	141	40	46	28	6.00	Middle frontal gyrus
Posterior parietal cluster	87	16	−68	58	5.62	Area 7P
		26	−66	56	4.32	Area 7A
Left hemisphere						
Anterior insular cluster	199	−34	20	0	7.67	Anterior insula
M1 cluster*	75	−34	−26	60	6.44	Area 4a
Midline						
Pre-SMA/SMA cluster	398	2	12	52	5.98	Pre-SMA
		−8	14	52	5.61	Area 6
		2	28	36	4.65	Middle cingulate cortex
		4	24	50	3.91	Superior medial gyrus
Cerebellum						
Right cerebellar cluster	862	28	−42	−32	8.00	Lobule VI
		38	−60	−36	6.54	Crus I
		12	−48	−16	5.43	Lobule V
Left cerebellar cluster	374	−36	−62	−26	5.73	Lobule VI/Crus I
		−30	−56	−34	4.95	Lobule VI
Cerebellar vermis cluster	219	4	−72	−10	5.31	Vermis
		−6	−80	−14	5.03	Lobule VI
		6	−58	−8	4.77	Lobule V

See footnote in Table 1.

* Left M1 activity had a trend for significance (corrected $p = 0.06$).

sections of the left M1 and the right cerebellum) together with the right inferior fronto-parietal activity, allows us to experience proprioceptive bodily awareness as "my right hand is flexing". Likewise, the co-activation of the self-face preferential visual association areas and of the right inferior fronto-parietal cortices may enable us to experience visual bodily self-awareness as "the face I see is my own".

Shared brain activation in the right anterior insula

Unlike the right inferior fronto-parietal cortices, the right anterior insula does not seem to belong to the SLF III network (Fig. 2; Thiebaut de Schotten et al., 2012). In addition, the bilateral anterior insula were recruited during both the self-face recognition and the proprioceptive illusion, but had no right-dominant activity (Tables A and B). These findings agree with our previous findings (Naito et al., 2005, 2007; Amemiya and Naito, 2016, for proprioceptive illusion; Morita et al., 2008, 2012, for self-face recognition). Finally, in a previous study, we found that the extent of right inferior fronto-parietal activity, but not right insular activity, corresponds well to subjective reports regarding the extent of the right hand illusion in blindfolded participants (Amemiya and Naito, 2016). These lines of evidence indicate that the right anterior insula may have distinct roles than those of the right inferior fronto-parietal cortices.

Table B. Self-face-related activity

Clusters	Size (voxels)	MNI coordinates			*T*-value	Anatomical identification (cytoarchitectonic area)
		x	*y*	*z*		
Cerebral cortex						
Right hemisphere						
Parieto-occipital cluster	3692	50	−32	46	9.37	Area PFt
		24	−62	46	8.87	Area hIP3
		46	−36	54	8.04	Area 2
		38	−56	64	7.83	Area 7A
		34	−80	−2	6.51	Middle occipital gyrus
		38	−76	22	6.22	Area PGp
		26	−74	44	5.87	Superior occipital gyrus
		30	−96	2	5.59	Area hOC3v
		18	−80	54	4.89	Area 7P
Inferior frontal cluster	1643	42	36	8	9.67	Inferior frontal gyrus
		44	4	28	8.91	Area 44
		48	30	12	6.68	Area 45
		36	0	10	6.08	Anterior insula
		42	46	20	4.41	Middle frontal gyrus
Inferior temporal cluster	758	54	−52	−12	9.03	Inferior temporal gyrus
Left hemisphere						
Occipito-parietal cluster	1489	−52	−70	−6	8.68	Inferior occipital gyrus
		−30	−80	18	5.94	Middle occipital gyrus
		−38	−60	−12	5.93	Fusiform gyrus
		−18	−64	44	5.47	Superior parietal lobule
		−26	−98	−6	5.21	Area hOC3v
		−22	−78	30	4.57	Superior occipital gyrus
		−28	−48	48	3.72	Inferior parietal lobule
Anterior insular cluster	151	−28	18	8	5.07	Anterior insula
Cerebellum						
Cerebellar cluster	98	−18	−74	−50	6.66	Lobule VIIb
		−14	−82	−50	4.64	Crus II

See footnote in Table 1.

The anterior insula is considered an important constituent of the “salience network,” which detects salient stimuli (Menon and Uddin, 2010; Raichle, 2011). It is generally believed that a self-related stimulus has higher saliency. Thus, self-faces are thought to have higher saliency than others’ faces (Tong and Nakayama, 1999; Brédart et al., 2006). Likewise, saliency may be greater for proprioceptive stimulus than for merely cutaneous stimulus. Thus, the common activity in the right anterior insula might reflect higher arousal levels of participants when they receive salient stimuli pertaining to the bodily self in purely recognition tasks, such as those used in our study.

CONCLUSIONS

We showed that self-face recognition and proprioceptive illusion commonly activate the right inferior fronto-parietal cortices (areas 44 and PF and its sub-regions), which are likely connected by the SLF III, in a right-hemispheric dominant manner. As shown in a recent fMRI meta-analysis combined with SLF tractography (Parlatini et al., 2016), fronto-parietal SLF III activations have been reported in wide range of cognitive tasks. The present study added new knowledge that self-face recognition that may lead to self-awareness and proprioceptive illusion accompanied with bodily awareness also activate the fronto-parietal SLF III network, and further provided new evidence that both commonly recruit the inferior fronto-parietal cortices most likely connected by the right SLF III.

Acknowledgments—Funding: “This work was supported by a Grant-in-Aid for Specially Promoted Research (No. 24000012), by Scientific Research on Innovative Areas “Embodied-brain” (JSPS KAKENHI No. 26120003) to EN, and by a Grant-in-Aid for young scientists to TM (No. 15K21138)”. The authors thank T. Kochiyama for advice on the design of the fMRI experiments.

Author contributions: TM, HO, MA and EN planed the experiment. TM, DNS, MB, KS, YO, HK and EN conducted the experiment, TM and EN analyzed the data, and TM, DNS, HK, MA and EN wrote the article.

REFERENCES

Amemiya K, Naito E (2016) Importance of human right inferior frontoparietal network connected by inferior branch of superior longitudinal fasciculus tract in corporeal awareness of kinesthetic illusory movement. Cortex 78:15–30.

Apps MA, Tajadura-Jiménez A, Sereno M, Blanke O, Tsakiris M (2015) Plasticity in unimodal and multimodal brain areas reflects multisensory changes in self-face identification. Cereb Cortex 25 (1):46–55.

Berlucchi G, Aglioti S (1997) The body in the brain: neural bases of corporeal awareness. Trends Neurosci 20:560–564.

Berti A, Bottini G, Gandola M, Pia L, Smania N, Stracciari A, et al. (2005) Shared cortical anatomy for motor awareness and motor control. Science 309:488–491.

Blanke O, Slater M, Serino A (2015) Behavioral, neural, and computational principles of bodily self-consciousness. Neuron 88(1):145–166.

Brédart S, Delchambre M, Laureys S (2006) Short article one's own face is hard to ignore. Q J Exp Psychol 59(1):46–52.

Breen N, Caine D, Coltheart M (2001) Mirrored-self misidentification: two cases of focal onset dementia. Neurocase 7(3):239–254.

Brooks-Gunn J, Lewis M (1984) The development of early visual self-recognition. Dev Rev 4(3):215–239.

Bufalari I, Porciello G, Sperduti M, Minio-Paluello I (2015) Self-recognition with another person's face: the time relevant role of multimodal brain areas in the enfacement illusion. J Neurophysiol 113(7):1959–1962.

Caspers S, Schleicher A, Bacha-Trams M, Palomero-Gallagher N, Amunts K, Zilles K (2013) Organization of the human inferior parietal lobule based on receptor architectonics. Cereb Cortex 23 (3):615–628.

Cignetti F, Vaugoyeau M, Nazarian B, Roth M, Anton JL, Assaiante C (2014) Boosted activation of right inferior frontoparietal network: a basis for illusory movement awareness. Hum Brain Mapp 35 (10):5166–5178.

Coffman KA, Dum RP, Strick PL (2011) Cerebellar vermis is a target of projections from the motor areas in the cerebral cortex. Proc Natl Acad Sci U S A 108(38):16068–16073.

Dale AM (1999) Optimal experimental design for event-related fMRI. Hum Brain Mapp 8(2–3):109–114.

Dehaene S, Changeux JP (2011) Experimental and theoretical approaches to conscious processing. Neuron 70(2):200–227.

Desmurget M, Reilly KT, Richard N, Szathmari A, Mottolese C, Sirigu A (2009) Movement intention after parietal cortex stimulation in humans. Science 324(5928):811–813.

Devue C, Brédart S (2011) The neural correlates of visual self-recognition. Conscious Cogn 20(1):40–51.

Eickhoff SB, Stephan KE, Mohlberg H, Grefkes C, Fink GR, Amunts K, Zilles K (2005) A new SPM toolbox for combining probabilistic cytoarchitectonic maps and functional imaging data. NeuroImage 25(4):1325–1335.

Evans AC, Kamber M, Collins DL, MacDonald D (1994) An MRI-based probabilistic atlas of neuroanatomy. In: Shorvon SD, editor. Magnetic resonance scanning and epilepsy. New York: Plenum Press. p. 263–274.

Feinberg TE (2000) Altered egos: how the brain creates the self. New York: Oxford University Press.

Feinberg T, Shapiro R (1982) Misidentification-reduplication and the right hemisphere. Neuropsychiatr Neuropsychol Behav Neurol 2:39–48.

Friston KJ, Holmes AP, Poline JB, Grasby PJ, Williams SC, Frackowiak RS, Turner R (1995) Analysis of fMRI time-series revisited. NeuroImage 2(1):45–53.

Friston KJ, Zarahn E, Josephs O, Henson RN, Dale AM (1999) Stochastic designs in event-related fMRI. NeuroImage 10 (5):607–619.

Gallup Jr GG (1982) Self-awareness and the emergence of mind in primates. Am J Primatol 2:237–248.

Goodwin GM, McCloskey DI, Matthews PB (1972) Proprioceptive illusions induced by muscle vibration: contribution by muscle spindles to perception? Science 175(4028):1382–1384.

Graziano MSA, Gross CG, Taylor CSR, Moore T (2004) A system of multimodel areas in the primate brain. In: Spence C, Driver J, editors. Crossmodal space and crossmodal attention. Oxford: Oxford university Press. p. 51–67.

Grodd W, Hülsmann E, Lotze M, Wildgruber D, Erb M (2001) Sensorimotor mapping of the human cerebellum: fMRI evidence of somatotopic organization. Hum Brain Mapp 13(2):55–73.

Hagura N, Oouchida Y, Aramaki Y, Okada T, Matsumura M, Sadato N, Naito E (2009) Visuokinesthetic perception of hand movement is mediated by cerebro-cerebellar interaction between the left cerebellum and right parietal cortex. Cereb Cortex 19(1):176–186.

Halligan PW, Marshall JC, Wade DT (1993) Three arms: a case study of super-numerary phantom limb after right hemisphere stroke. J Neurol Neurosurg Psychiatry 56:159–166.

Hecht EE, Gutman DA, Bradley BA, Preuss TM, Stout D (2015) Virtual dissection and comparative connectivity of the superior longitudinal fasciculus in chimpanzees and humans. NeuroImage 108:124–137.

Holmes AP, Friston KJ (1998) Generalisability, random effects and population inference. NeuroImage 7:S754.

Hu C, Di X, Eickhoff SB, Zhang M, Peng K, Guo H, Sui J (2016) Distinct and common aspects of physical and psychological self-representation in the brain: A meta-analysis of self-bias in facial and self-referential judgements. Neurosci Biobehav Rev 61:197–207.

Hyvarinen J (1982) The parietal cortex of monkey and man. New York: Springer-Verlag.

Kanwisher N, Yovel G (2006) The fusiform face area: a cortical region specialized for the perception of faces. Philos Trans R Soc Lond B Biol Sci 361(1476):2109–2128.

Kanwisher N, McDermott J, Chun MM (1997) The fusiform face area: a module in human extrastriate cortex specialized for face perception. J Neurosci 17(11):4302–4311.

Kaplan JT, Aziz-Zadeh L, Uddin LQ, Iacoboni M (2008) The self across the senses: an fMRI study of self-face and self-voice recognition. Soc Cogn Affect Neurosci 3(3):218–223.

Keenan JP, Nelson A, O'Connor M, Pascual-Leone A (2001) Self-recognition and the right hemisphere. Nature 409(6818):305.

Makris N, Kennedy DN, McInerney S, Sorensen AG, Wang R, Caviness VS, Pandya DN (2005) Segmentation of subcomponents within the superior longitudinal fascicle in humans: a quantitative, in vivo, DT-MRI study. Cereb Cortex 15 (6):854–869.

Matsumoto R, Nair DR, Ikeda A, Fumuro T, Lapresto E, Mikuni N, et al. (2012) Parieto-frontal network in humans studied by cortico-cortical evoked potential. Hum Brain Mapp 33(12):2856–2872.

Menon V, Uddin LQ (2010) Saliency, switching, attention and control: a network model of insula function. Brain Struct Funct 214(5–6):655–667.

Morita T, Itakura S, Saito DN, Nakashita S, Harada T, Kochiyama T, Sadato N (2008) The role of the right prefrontal cortex in self-evaluation of the face: a functional magnetic resonance imaging study. J Cogn Neurosci 20(2):342–355.

Morita T, Kosaka H, Saito DN, Ishitobi M, Munesue T, Itakura S, Omori M, Okazawa H, Wada Y, Sadato N (2012) Emotional responses associated with self-face processing in individuals with autism spectrum disorders: an fMRI study. Soc Neurosci 7 (3):223–239.

Murata A, Wen W, Asama H (2016) The body and objects represented in the ventral stream of the parieto-premotor network. Neurosci Res 104:4–15.

Naito E (2004) Sensing limb movements in the motor cortex: how humans sense limb movement. Neuroscientist 10(1):73–82.

Naito E, Ehrsson HH, Geyer S, Zilles K, Roland PE (1999) Illusory arm movements activate cortical motor areas: a positron emission tomography study. J Neurosci 19(14):6134–6144.

Naito E, Kochiyama T, Kitada R, Nakamura S, Matsumura M, Yonekura Y, Sadato N (2002a) Internally simulated movement sensations during motor imagery activate cortical motor areas and the cerebellum. J Neurosci 22(9):3683–3691.

Naito E, Roland PE, Ehrsson HH (2002b) I feel my hand moving: a new role of the primary motor cortex in somatic perception of limb movement. Neuron 36:979–988.

Naito E, Roland PE, Grefkes C, Choi HJ, Eickhoff S, Geyer S, et al. (2005) Dominance of the right hemisphere and role of area 2 in human kinesthesia. J Neurophysiol 93(2):1020–1034.

Naito E, Nakashima T, Kito T, Aramaki Y, Okada T, Sadato N (2007) Human limb-specific and non-limb-specific brain representations during kinesthetic illusory movements of the upper and lower extremities. Eur J Neurosci 25(11):3476–3487.

Naito E, Matsumoto R, Hagura N, Oouchida Y, Tomimoto H, Hanakawa T (2010) Importance of precentral motor regions in human kinesthesia: a single case study. Neurocase 17 (2):133–147.

Naito E, Morita T, Amemiya K (2016) Body representations in the human brain revealed by kinesthetic illusions and their essential contributions to motor control and corporeal awareness. Neurosci Res 104:16–30.

Oldfield RC (1971) The assessment and analysis of handedness: the Edinburgh Inventory. Neuropsychologia 9(1):97–113.

Parlatini V, Radua J, Dell'Acqua F, Leslie A, Simmons A, Murphy DG, et al. (2016) Functional segregation and integration within fronto-parietal networks. NeuroImage 146:367–375.

Pitcher D, Walsh V, Duchaine B (2011) The role of the occipital face area in the cortical face perception network. Exp Brain Res 209 (4):481–493.

Platek SM, Loughead JW, Gur RC, Busch S, Ruparel K, Phend N, et al. (2006) Neural substrates for functionally discriminating self-face from personally familiar faces. Hum Brain Mapp 27(2):91–98.

Price CJ, Friston KJ (1997) Cognitive conjunction: a new approach to brain activation experiments. NeuroImage 5(4 Pt 1):261–270.

Raichle ME (2011) The restless brain. Brain Connect 1(1):3–12.

Rojkova K, Volle E, Urbanski M, Humbert F, Dell'Acqua F, Thiebaut de Schotten M (2015) Atlasing the frontal lobe connections and their variability due to age and education: a spherical deconvolution tractography study. Brain Struct Funct 221 (3):1751–1766.

Roll JP, Vedel JP (1982) Kinaesthetic role of muscle afferents in man, studied by tendon vibration and microneurography. Exp Brain Res 47(2):177–190.

Roll JP, Vedel JP, Ribot E (1989) Alteration of proprioceptive messages induced by tendon vibration in man: a microneurographic study. Exp Brain Res 76(1):213–222.

Rotshtein P, Henson RN, Treves A, Driver J, Dolan RJ (2005) Morphing Marilyn into Maggie dissociates physical and identity face representations in the brain. Nat Neurosci 8(1):107–113.

Shulman GL, Pope DL, Astafiev SV, McAvoy MP, Snyder AZ, Corbetta M (2010) Right hemisphere dominace during spatial selective attention and target detection occurs outside the dorsal fronto-parietal network. J Neurosci 30(10):3640–3651.

Sladky R, Friston KJ, Tröstl J, Cunnington R, Moser E, Windischberger C (2011) Slice-timing effects and their correction in functional MRI. NeuroImage 58(2):588–594.

Spangenberg K, Wagner M, Bachman D (1998) Neuropsychological analysis of a case of abrupt onset following a hypotensive crisis in a patient with vascular dementia. Neurocase 4:149–154.

Strick PL, Dum RP, Fiez JA (2009) Cerebellum and nonmotor function. Annu Rev Neurosci 32:413–434.

Sugiura M, Watanabe J, Maeda Y, Matsue Y, Fukuda H, Kawashima R (2005) Cortical mechanisms of visual self-recognition. NeuroImage 24(1):143–149.

Sugiura M, Sassa Y, Jeong H, Miura N, Akitsuki Y, Horie K, Sato S, Kawashima R (2006) Multiple brain networks for visual self-recognition with different sensitivity for motion and body part. NeuroImage 32(4):1905–1917.

Sugiura M, Sassa Y, Jeong H, Horie K, Sato S, Kawashima R (2008) Face-specific and domain-general characteristics of cortical responses during self-recognition. NeuroImage 42(1):414–422.

Thiebaut de Schotten M, Dell'Acqua F, Forkel SJ, Simmons A, Vergani F, Murphy DG, Catani M (2011) A lateralized brain network for visuospatial attention. Nat Neurosci 14 (10):1245–1246.

Thiebaut de Schotten M, Dell'Acqua F, Valabregue R, Catani M (2012) Monkey to human comparative anatomy of the frontal lobe association tracts. Cortex 48(1):82–96.

Tong F, Nakayama K (1999) Robust representations for faces: evidence from visual search. J Exp Psychol Hum Percept Perform 25(4):1016–1035.

Uddin LQ, Kaplan JT, Molnar-Szakacs I, Zaidel E, Iacoboni M (2005) Self-face recognition activates a frontoparietal ''msirror'' network in the right hemisphere: an event-related fMRI study. NeuroImage 25(3):926–935.

Uddin LQ, Molnar-Szakacs I, Zaidel E, Iacoboni M (2006) RTMS to the right inferior parietal lobule disrupts self-other discrimination. Soc Cogn Affect Neurosci 1(1):65–71.

Worsley KJ, Friston KJ (1995) Analysis of fMRI time-series revisited–again. NeuroImage 2(3):173–181.

APPENDIX A.

(Received 29 November 2016, Accepted 15 February 2017)
(Available online 24 February 2017)