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Human Superior Parietal Lobule Is Involved in Somatic Perception of Bimanual Interaction With an External Object

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Naito E, Scheperjans F, Eickhoff SB, Amunts K, Roland PE, Zilles K, Ehrsson HH. Human superior parietal lobule is involved in somatic perception of bimanual interaction with an external object. *J Neurophysiol* 99: 695–703, 2008. First published November 14, 2007; doi:10.1152/jn.00529.2007. The question of how the brain represents the spatial relationship between the own body and external objects is fundamental. Here we investigate the neural correlates of the somatic perception of bimanual interaction with an external object. A novel bodily illusion was used in conjunction with functional magnetic resonance imaging (fMRI). During fMRI scanning, seven blindfolded right-handed participants held a cylinder between the palms of the two hands while the tendon of the right wrist extensor muscle was vibrated. This elicited a kinesthetic illusion that the right hand was flexing and that the hand-held cylinder was shrinking from the right side. As controls, we vibrated the skin surface over the nearby bone beside the tendon or vibrated the tendon when the hands were not holding the object. Neither control condition elicited this illusion. The significance of the illusion was also confirmed in supplementary experiments outside the scanner on another 16 participants. The "bimanual shrinking-object illusion" activated anterior parts of the superior parietal lobule (SPL) bilaterally. This region has never been activated in previous studies on unimanual hand or hand-object illusion. The illusion also activated left-hemispheric brain structures including area 2 and inferior parietal lobule, an area related to illusory unimanual hand-object interaction between a vibrated hand and a touched object in our previous study. The anterior SPL seems to be involved in the somatic perception of bimanual interaction with an external object probably by computing the spatial relationship between the two hands and a hand-held object.

INTRODUCTION

Bimanual manipulation of external objects is a skillful motor behavior that requires coordination between the hands. Previous studies on the neural mechanisms of bimanual coordination and bimanual manipulation have mainly focused on these issues from a motor control perspective (e.g., Sadato et al. 1997; Stephan et al. 1999; Wenderoth et al. 2004). When we hold a bottle with two hands, we can open it even if we can't see it because we sense the size, length, and orientation of the bottle in relation to the positions of our hands. Thus sensing the spatial relationships between the two hands and the size and shape of the hand-held object is important in bimanual manipulation.

In non-human primates, neurons in the anterior part of the superior parietal lobule (SPL; Brodmann's area (BA) 5/area PE) receive kinesthetic/proprioceptive and tactile inputs from the two hands and forearms, and many neurons have bilateral receptive fields (Brodmann 1909; Mountcastle et al. 1975; Pandya and Seltzer 1982; Sakata et al. 1973; Taoka et al. 1998). The discharge pattern of some of these cells depends on the relative positions and movements of the forelimbs (Sakata et al. 1973; Taoka et al. 1998). In the human brain, quantitative receptor autoradiography recently revealed that human BA 5 in the anterior SPL comprises three sub-areas (5L, 5M, and 5Ci) with distinct transmitter receptor distribution patterns and cytoarchitecture (Scheperjans et al. 2005a). Furthermore, these areas show receptor distributions similar to those of the somatosensory cortex, suggesting functional interactions (Scheperjans et al. 2005b). If human BA 5 corresponded to monkey BA 5, this area should have the anatomical and functional properties that subserve the somatic perception of spatial relationships between the two hands and hand-held objects that is important for bimanual manipulation. The aim of the present study is to directly test this hypothesis by using functional magnetic resonance imaging (fMRI) while healthy individuals experience a novel perceptual illusion of bimanual interaction with a hand-held object.

To dissociate the perception of the moving hand and its interaction with an object from the motor control processes, we utilized a kinesthetic illusion that is elicited by vibrating the tendon of a limb muscle (Goodwin et al. 1972a,b). The vibration excites muscle spindle afferents that signal limb movements (Burke et al. 1976; Roll and Vedal 1982; Roll et al. 1989), and these signals are processed by cortical motor areas, the cerebellum and fronto-parietal areas (Naito and Ehrsson 2006; Naito et al. 2002, 2005, 2007). This illusion is not associated with any actual movements, intention to move, or sense of effort and is thus a genuine perceptual illusion of a passive limb movement. In the present study, we introduce a

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new version of this illusion. When the blindfolded participants hold an object (a cylinder) between two hands and the tendon of the wrist extensor muscle of either the right or left hand is vibrated (Fig. 1, *right*), they experience the vibrated hand to be flexing toward the nonvibrated hand and, simultaneously, the hand-held cylinder to be shrinking ("bimanual shrinking-object illusion"). Likewise when the tendon of the wrist flexor muscle is vibrated (Fig. 1, *left*), they experience the vibrated hand to be extending away from the nonvibrated one and the hand-held cylinder to be elongating ("bimanual elongating-object illusion"). These illusions are not experienced when we vibrate the skin surface beside the tendon.

Thus these bimanual hand-object illusions are probably elicited because the brain receives and integrates the kinesthetic information indicating hand movement, haptic information from the hands touching the object, and information about the physical properties of the object (Naito and Ehrsson 2006). Hence by using this illusion, in combination with appropriate control conditions (see METHODS), we are able to investigate how the brain integrates this type of sensory information to generate the sensation that the size of a bimanually held object is changing. On the basis of the neurophysiological and anatomical studies in humans and non-human primates described in the preceding text, we hypothesized that human BA 5 is involved in the bimanual hand-object illusion.

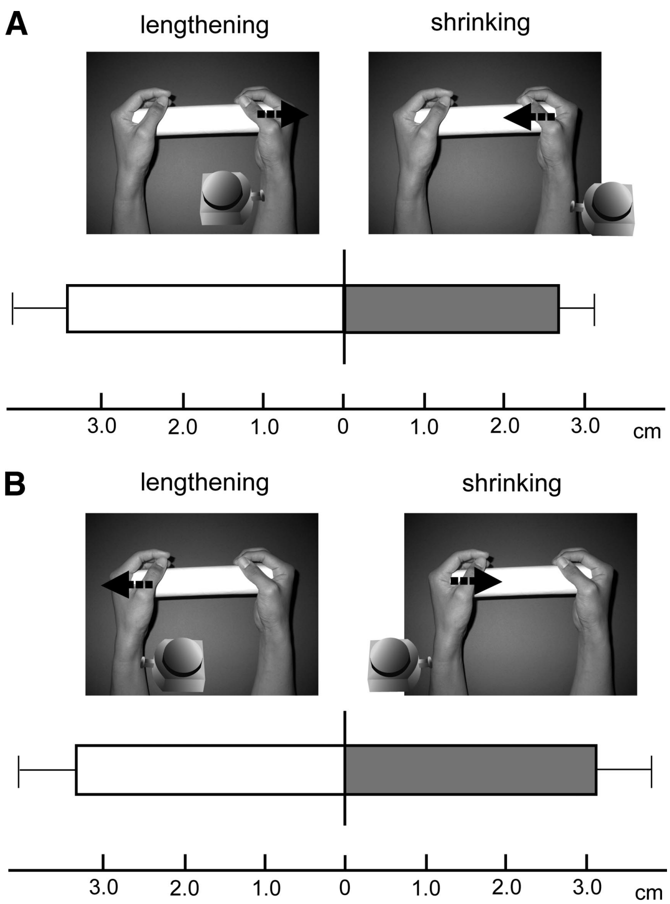

FIG. 1. Conditions and results in the behavioral experiment. We vibrated the tendon of the extensor carpi ulnaris (ECU, *right*) or flexor carpi ulnaris (FCU, *left*) muscle of the right (*A*) or left (*B*) hand while participants held the cylinder in both hands (contact tendon). →, direction of the illusion; ⊠, mean degree of object-shrinkage across the participants; □, mean degree of object-elongation. Error bars = SE, (n = 6).

METHODS

Participants

A total of 23 blindfolded right-handed male participants (aged 21–33 yr) with no history of neurological or psychiatric disease participated in the experiments. Their handedness was confirmed by verbally asking questions based on the inventory of Oldfield (1971). Six people participated in the behavioral investigation, 7 in the fMRI experiment, and 10 in the control investigation for surface electromyographic (EMG) activity during vibration. The Ethics Committee of the Karolinska Hospital approved the fMRI experiment, and all participants gave their informed consent. The fMRI experiment was carried out according to the principles and guidelines of the Declaration of Helsinki (1975).

Before we started each experiment, we performed a pretest. We asked a participant to relax the vibrated hand and first checked if he could experience an illusory hand movement when the hand was free. All participants reported that they indeed experienced illusion of free-hand within a couple of trials. Next, we asked the participants to passively hold a cylinder between the hands and tested if the tendon vibration elicited an illusion. After a trial, we asked the participant to describe what they were feeling. Again, within a couple of trials, all the participants (except one) reported that they experienced the bimanual hand-object illusion. After this procedure, the real experiments commenced. One candidate for fMRI experiment that denied feeling clear object-shrinkage was excluded from the study and not tested further.

Behavioral investigation

In a behavioral experiment, we investigated the bimanual hand-object illusion in six right-handed participants who held a cylinder (length: 21 cm; weight: 16 g; made of thick cardboard) in both hands (see Fig. 1). They were seated on a chair, and their elbows were placed on a table with their forearms comfortably supported by cushions proximal to the wrist. In four conditions, we vibrated the tendon of the wrist extensor muscle (extensor carpi ulnaris, ECU) or the wrist flexor muscle (flexor carpi ulnaris, FCU) of the right or the left hand for 30 s (Fig. 1). We used an electro-magnetic vibrator (80 Hz, amplitude ±2 mm, SL-0105sx No. A1B115, Asahi Seisakusho, Tokyo, Japan) that is controlled by an amplifier (APA-050FCA, No. B16111, Asahi Seisakusho), and the vibrated area was ~1 cm^2. An experienced experimenter (Naito) manually operated the vibrator, applying it to the skin with a light pressure. Three trials were assigned for each condition, and the order of conditions was pseudorandomized.

The participants were instructed to relax completely and to be aware of sensation from the hands. After each trial, to quantify the illusion, we asked the participants to replicate the amount of bimanual hand-object illusion by actually flexing or extending the vibrated hand. We measured the size of the illusory hand displacement with a scale. The mean of the illusory displacement was calculated per participant, and the grand mean across participants was calculated for each condition separately (Fig. 1). In this behavioral experiment, we also confirmed that the participants did not experience any quantifiable bimanual hand-object illusion when we applied identical stimuli to the skin surface over the nearby bone (the processus styloideus ulnae) beside the tendon. Indeed, from our previous studies we knew that bone vibration typically does not elicit kinesthetic illusions (Naito and Ehrsson 2006; Naito et al. 2002, 2005, 2007). Thus this condition was used as control (bone) condition in the fMRI and EMG experiments (see following text). The significance of bimanual hand-object illusion in each condition (df = 5) was evaluated by performing a one-sample t-test where we compared each illusory effect against 0, i.e., the value in the bone condition. Each P value was corrected based on the number of multiple comparisons (Bonferroni correction).

fMRI measurement and tasks

EXPERIMENTAL SETUP IN SCANNER. A 1.5 T General Electric scanner with a head-coil provided T1-weighted anatomical images (3D-SPGR) and functional T2*-weighted echoplanar images (64 × 64 matrix, 3.4 × 3.4 mm, TE = 60 ms). The functional image volume comprised 30 slices of 5-mm thickness (with 0.4-mm interslice gaps), which ensured that the whole brain was within the field of view.

The seven participants were blindfolded, and their ears were plugged. They rested comfortably in a supine position in the MR scanner. Their extended arms were oriented in a relaxed semi-prone position in front of them parallel to their trunks. To allow the participants to relax their arms, both arms were wrapped and supported proximal to the wrist. During fMRI scanning, the participants were instructed to relax completely, to make no movements, and to be aware of sensation from the hands.

The behavioral experiment revealed that the illusory hand displacement was consistently observed and its extent was nearly constant no matter when we vibrated the tendon of the right or left ECU or FCU muscle (Fig. 1). Thus in the fMRI experiment, we focused on the "bimanual shrinking-object illusion" when we vibrated the right ECU muscle and the participants experienced the hand-held cylinder to be shrinking from the right side. For sensory stimulation, we used a nonmagnetic vibrator that was driven by constant air pressure (Naito et al. 2002, 2005). The vibration frequency was ~80 Hz (amplitude: ±2 mm), and the area of vibration was ~1 cm^2. The experimenter (Naito) in the scanner room manually operated the vibrator, applying it to the skin with a light pressure.

To identify the activity related to the bimanual shrinking-object illusion, and to control for the effects related to the tendon vibration and to the tactile inputs from the hands touching the object, we used a two-by-two factorial design (4 experimental conditions; Fig. 2). One factor was skin contact with the cylinder (contact or free), and the other factor was the vibration site (tendon or bone). In the contact conditions, the cylinder was held in both hands (Fig. 2), and in the free conditions, the hands did not touch the cylinder. We carefully matched the angle of the wrist flexion in the contact and free conditions.

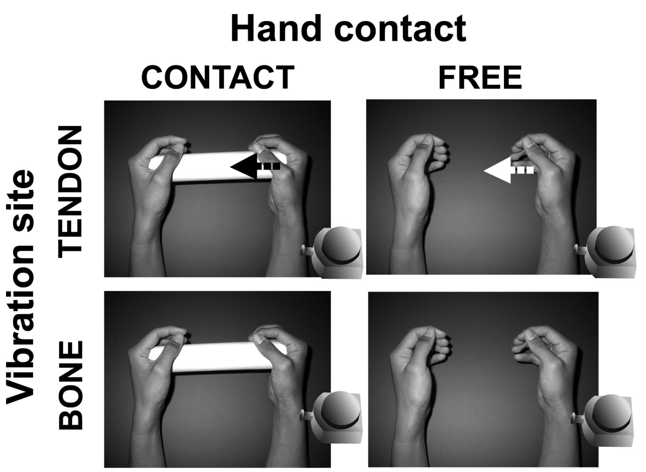

FIG. 2. Functional magnetic resonance imaging (fMRI) experimental conditions. To elicit the illusions (*top*), we vibrated the tendon of the right ECU muscle (tendon) when the participants held the cylinder between 2 hands (*left;* contact) or when they did not hold the object (*right;* free). Note that the angle of the wrist was matched in these 2 conditions. To control for the effect of skin vibration, we applied identical stimuli to the skin surface over the processus styloideus ulnae, which did not elicit any illusions (*bottom*; contact bone, free bone). Black and white arrows, directions of illusory object-shrinkage and flexion of free hand, respectively.

To elicit an illusory palmar flexion of the wrist, we vibrated the tendon of the right ECU (tendon). To control for the effect of skin vibration, we applied identical stimuli to the skin surface over the nearby bone beside the tendon (see preceding text), which did not elicit any illusions (bone). Thus the four experimental conditions were: contact tendon, contact bone, free tendon, and free bone. The participants experienced the bimanual shrinking-object illusion only in the contact-tendon condition, making it possible to identify the specific activity that generated this illusion by examining the interaction term in a factorial design [(contact tendon vs. contact bone) vs. (free tendon vs. free bone)]. We also included two rest conditions where the participants relaxed completely without receiving any vibration stimuli. In these rest conditions, the hands were either free (free) or held the cylinder (contact).

For each participant, we conducted three fMRI sessions and a total of 3 × 122 functional image volumes were collected. In each session, there were six conditions (4 experimental conditions and 2 rest conditions). Each condition lasted 32 s (8 functional images, TR = 4 s) and was repeated twice during each session. The order of conditions was randomized based on a balanced schedule. To change between the free and contact conditions, we included special periods that lasted 16 s, during which the scanner continued to collect images. The participants' hands were in contact with the object for ~4–8 s before the actual contact condition started. In the analysis, the data from these periods were modeled as conditions of no interest and thereby effectively not used.

In a training session before the fMRI experiment, we confirmed that all participants experienced vivid illusory palmar flexion of the vibrated hand when their hands were free and vivid bimanual shrinking-object illusion when their hands held the cylinder. We also confirmed that the illusions started 2–3 s after onset of vibration stimuli by asking the participants to say when the illusion started (see Naito and Ehrsson 2006) and therefore omitted the first 4 s for all conditions by defining these periods as conditions of no interest in the model.

After each of three fMRI sessions, we confirmed that the participants experienced the illusion by asking them to replicate the average amount of object-shrinkage experienced in a session by actually flexing the vibrated hand. We measured the size of the illusory hand displacement with a scale, and the mean of the illusory hand displacement was calculated per participant. The significance of the shrinking-object illusion across participants was also evaluated by performing one sample t-test against 0, i.e., the value in the contact-bone condition (see preceding text).

FMRI DATA ANALYSIS. The fMRI data were analyzed with Statistical Parametric Mapping software (SPM99; http://www.fil.ion.ucl.ac.uk/spm; Wellcome Department of Cognitive Neurology, London, UK). Details of the image processing were described elsewhere (Naito and Ehrsson 2006). The functional images were scaled to 100 to correct for global changes in the MR signal and were spatially smoothed with an 8-mm full width at half-maximum (FWHM) isotropic Gaussian kernel, and smoothed in time by a 4-s FWHM Gaussian kernel. We fitted a linear regression model (general linear model) to the pooled data from all participants to increase the sensitivity of the analysis (fixed-effects model). The validity of this approach, in terms of consistency of effects across all participants, was confirmed by conducting single-subject analyses (see following text). Because we had only seven participants, we did not use a random-effects model. Each condition was modeled with a boxcar function and convolved with the standard SPM99 hemodynamic response function.

BRAIN ACTIVATIONS RELATED TO THE BIMANUAL SHRINKING-OBJECT ILLUSION. To reveal activity that specifically reflects the bimanual shrinking-object illusion, we examined the interaction term between the factors of vibration site and hand contact with the object in the two-by-two factorial design [(contact tendon vs. contact bone) vs. (free tendon vs. free bone)] (Fig. 2). The rationale for this is that the interaction term reveals the illusion-specific activity, which cannot be attributed to the sum of the effects of the tendon vibration and skin contact with the cylinder. To make sure that only voxels that showed an increase in activity were included, we used the contrast of (contact tendon vs. contact bone) as an inclusive mask to exclude voxels that were not active at all during the bimanual shrinking-object illusions and also to exclude the possibility that brain activity detected by the interaction term was merely attributed to the deactivated effect during illusion of the free-hand, i.e., (free tendon vs. free bone). The threshold for the mask was set at a very liberal threshold of $P < 0.05$ uncorrected. To generate cluster images, we used a threshold of $P < 0.001$ ($T > 3.09$). For statistical inferences, we used a threshold of $P < 0.05$ after a correction for multiple comparisons in the whole brain based on a test of cluster size (Fig. 3).

We also examined the main effect of illusions, i.e., (contact tendon + free tendon vs. contact bone + free bone), to confirm that vibration of the tendon of the wrist muscle that elicits illusory hand movements implicated motor and fronto-parietal areas that have been repeatedly activated in the series of our studies (Naito et al. 1999, 2002, 2005, 2007).

SINGLE-SUBJECT ANALYSES. To make sure that the superior parietal activations detected in the fixed-effect analysis were representative for the seven participants and to refine the anatomical locations of individual activations in the standard anatomical space (*x, y, z*), we analyzed the data from individual participants (Naito and Ehrsson 2006). In this purely descriptive analysis, all image-processing steps were identical to those used in the group analysis. A linear regression model (general linear model) was fitted to the data of each participant in separate analyses. The same interaction, i.e., [(contact tendon vs. contact bone) vs. (free tendon vs. free bone)] was individually tested using the individual inclusive mask (contact tendon vs. contact bone; $P < 0.05$ uncorrected). We probed for increases of the BOLD signal ($T > 1.65$; $P < 0.05$ uncorrected) in a volume with a radius of 10 mm around each of the three voxels, corresponding to the peaks detected in the group analysis. The size of volume was selected by considering the final smoothness (FWHM = ~12 mm) of the functional images. Thus an individual activation within this volume could contribute to the activation obtained in the group analysis. We report the number of participants showing a BOLD signal increase and the locations of the parietal activations from the individual participants (Table 1).

ANATOMICAL DEFINITIONS. To topographically interpret the activations, we referred to probabilistic micro-anatomical maps in the MNI reference brain space. These maps are based on the observer-independent cytoarchitectonic analysis of ten human postmortem brains (Schleicher et al. 1999; Zilles et al. 2002). Guided by the locations of

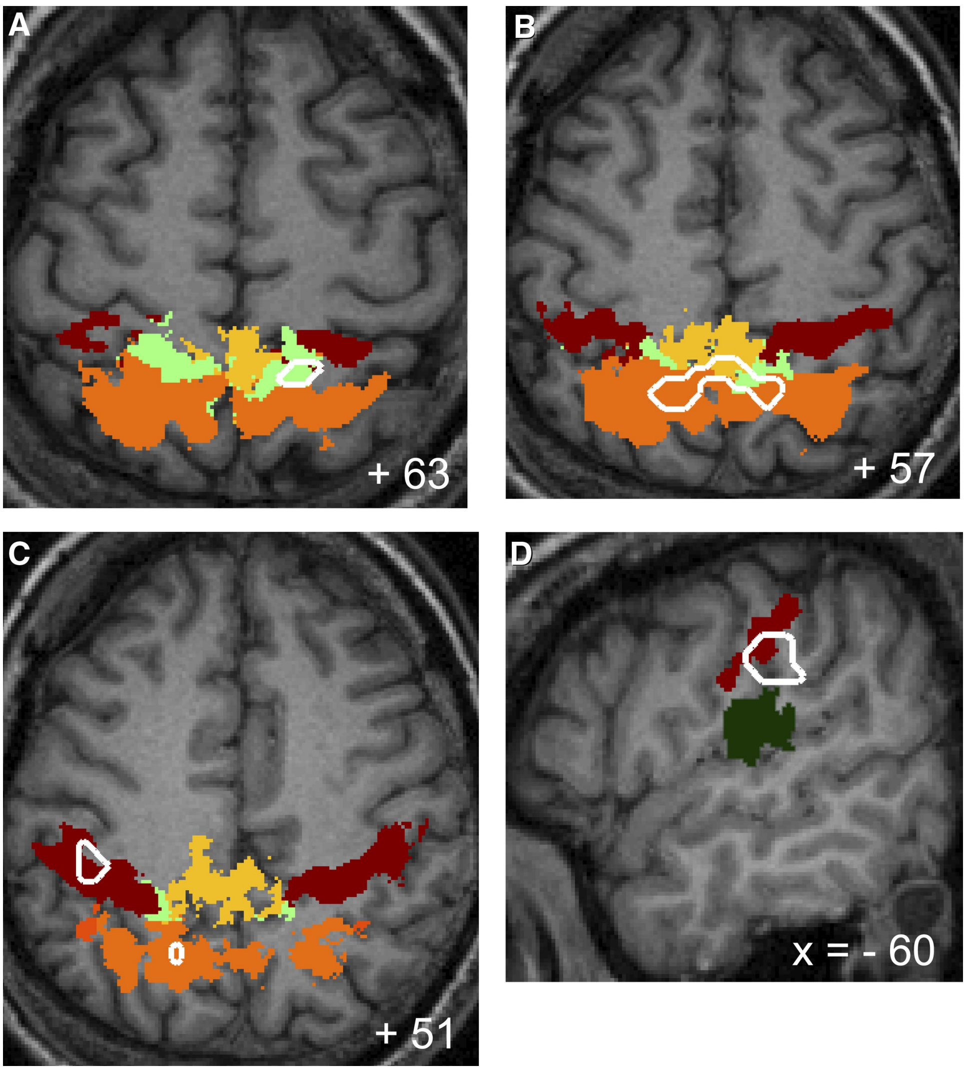

FIG. 3. fMRI results. Activations specifically related to the bimanual shrinking-object illusion that are superimposed on the maximum probability map for parietal cytoarchitectonic areas (yellow: area 5M; light green: area 5L; orange: area 7A; brown: area 2; dark green: area OP1). These are superimposed on the normalized anatomical image of a participant. Open-white sections (*A–D*) indicate active areas identified by the interaction term. Horizontal (*A*: $z = +63$; *B*: $z = +57$; *C*: $z = +51$) and sagittal (*D*: $x = -60$) sections are displayed.

TABLE 1. *Peak coordinates and their t values of individual SPL activations*

Subject	Area 7A (−15, −60, 57)				Area 5M (3, −54, 57)				Area 5L (15, −54, 63)			
	x	*y*	*z*	*t*	*x*	*y*	*z*	*t*	*x*	*y*	*z*	*t*
1	−21	−63	54	4.0	6	−51	60	3.4	6	−51	60	3.4
2					9	−51	63	2.4	9	−48	63	2.5
3	−15	−63	63	3.3	3	−60	54	2.5	6	−57	60	1.8
4	−6	−57	54	3.0	−3	−51	54	4.0	24	−51	60	3.4
5	−18	−63	51	2.9								
6					12	−54	60	2.4	18	−54	60	3.0
7	−21	−57	54	2.7	9	−60	60	2.0	12	−63	60	2.2
Mean	*−16*	*−61*	*55*	*3.2*	*6*	*−55*	*59*	*2.8*	*13*	*−54*	*61*	*2.7*

Interactions were (contact tendon vs. contact bone) vs. (free tendon vs. free bone). SPL, superior parietal lobe.

the detected parietal activations, we superimposed these activations with a maximum probability map containing the recently delineated areas 2 (postcentral sulcus), 5M, 5L, 7A (SPL), and OP1 (parietal operculum; Fig. 3) (Eickhoff et al. 2006a,b; Grefkes et al. 2001; Scheperjans et al. 2007). In this map, every voxel belongs to the area with highest probability if the individual probabilistic maps overlap in that voxel (Eickhoff et al. 2005). Area 5L is located on the lateral surface of the SPL in the postcentral region medial to BA 2. Area 5M is found on the posterior part of the paracentral lobule on the medial surface. Area 7A, i.e., the anterior part of BA 7, is located on the SPL caudally adjacent to these cytoarchitectonic areas. The anatomical location of the inferior parietal activation was visually evaluated based on a recently published cytoarchitectonic parcellation (Caspers et al. 2006). Our inferior parietal activation seemed to correspond to area PFt or PF. Area PFt is located in the rostral part of the inferior parietal lobule (IPL) and dorsally to the parietal opercular region. Area PF, which is the largest region of the IPL, lies caudal to area PFt.

Details of the cytoarchitectonic maps and the technique of combining functional imaging and cytoarchitectonic mapping of the human cerebral cortex were also described elsewhere (Eickhoff et al. 2006c; Naito and Ehrsson 2006; Zilles et al. 2002).

Control EMG experiment

During the fMRI scanning, we observed no overt hand movements in any of the conditions. To carefully check changes of muscle activity during the vibration stimulation, we conducted an additional behavioral control experiment outside the scanner. Ten right-handed blindfolded participants rested comfortably in a supine position on the bed like in the MR scanner. The posture of the arms and the ways of supporting their arms were identical to those in the fMRI experiment. The participants were instructed to relax their hands completely and to be aware of sensation from the hands.

We recorded electromyograms (EMGs) from the skin surface over the right flexor muscle (agonistic muscle for the shrinking-object illusion) while participants held the cylinder (contact) between the hands or when their hands were free (free). The same experimenter operated a very similar nonmagnetic vibrator (80 Hz, amplitude: ±2 mm) as used in the fMRI experiment (see preceding text). Great care was taken to handle the vibrator in the same way in the two experimental settings. Hereby the stimulation was kept as constant as possible between experiments.

In each condition, EMG was recorded for 30 s when we vibrated the tendon of the right ECU (tendon, illusion), when we vibrated the skin surface over the right nearby bone (bone, no illusion), or when the participants relaxed completely without receiving any vibration stimuli (rest). To monitor potential increases in muscular force between the hands and the object during the vibration stimulation, a small force plate (Type LP-200KSA19; Kyowa, Tokyo, Japan) was placed between the right hand and the object. Each of the six conditions was tested three times. The participants were instructed to relax their hand/arm muscles during the trials. Details of EMG recording have been described elsewhere (Kito et al. 2006).

After each trial in the contact-tendon and free-tendon conditions, the participants replicated the average amount of illusory hand displacement by actually flexing the vibrated hand. We measured the size of the displacement with a scale, and the mean of the illusory hand displacement in each condition was calculated per participant. The significance of the illusory object-shrinkage across participants was evaluated by performing one sample *t*-test (see preceding text), and the difference between the illusory object-shrinkage (contact tendon) and the illusory displacement of the free hand (free tendon) was evaluated by performing paired *t*-test.

For the EMG data analysis, we first rectified the EMG on a trial-by-trial basis and then calculated the mean integrated EMG across the three trials per condition for each participant separately. After that, we normalized the mean integrated EMG to the values obtained in the REST condition. This process was repeated for the tendon and bone conditions, respectively. For the statistical analysis, we performed a two-factorial [hand situation (contact or free) × vibration site (tendon or bone)] ANOVA (repeated measurement) for the normalized EMG. This factorial design corresponded to the one we used in the fMRI experiment (see preceding text).

RESULTS

Behavioral investigation

We observed no overt hand movements in any of the conditions. No matter whether we vibrated the right or left hand, all participants reported that they experienced the cylinder to be shrinking when we vibrated the tendon of the ECU muscle [right: 2.6 ± 1.0 (SD) cm, left: 3.1 ± 1.6 cm; Fig. 1, *right*]. They explained to us that they felt that the object was shrinking from the vibrated side as the vibrated hand was moving toward the nonvibrated hand. They reported no movement sensations from the nonvibrated hand. We also observed an analogous effect when the tendon of the FCU muscle was vibrated. This elicited an illusion of elongation of the cylinder (right: 3.4 ± 1.7, left: 3.3 ± 1.8 cm; Fig. 1, *left*). Each type of illusion was consistently reported by the participants across all trials in each condition. No participant reported any quantifiable bimanual hand-object illusions when we vibrated the skin surface over the nearby bone beside the tendon (see METHODS). The one-sample *t*-test revealed that each of the bimanual hand-object illusions was significant as compared with its control (bone) condition ($P < 0.05$ after the Bonferroni correction for the number of multiple comparisons).

Quantifying the illusion during fMRI scanning

As we found in the behavioral experiment, the participants reported that they experienced the cylinder to be shrinking by 3.2 cm on average (range: 2.0–4.8 cm) from the right side only when we vibrated the right ECU tendon (contact tendon). None of the participants reported any illusions when we vibrated the skin surface over the nearby bone (contact bone or free bone). Thus the experience of shrinking-object illusion was significant as compared with the contact-bone condition (df = 6, $t = 8.3$, $P < 0.001$). When we vibrated the tendon and the hands were not in contact with the object (free tendon), the participants told us that they merely experienced illusory flexion of the vibrated hand. When we asked the participants to compare the amplitude of the illusory hand movements when the hands were free (free tendon) and when they held the cylinder (contact tendon), all participants reported greater movement sensation when the hands were free (see following text). The experimenter, who was standing in the scanner room near the participant, observed no overt movements of the vibrated hands in any of the conditions. This was also confirmed in the control EMG experiment outside the scanner (see following text).

Brain activation

To identify brain activity that specifically reflected the bimanual shrinking-object illusion, we used the contrast [(contact tendon vs. contact bone) vs. (free tendon vs. free bone)]. In this contrast, the effects related to skin contact with the cylinder and the vibratory stimuli were matched (Fig. 2).

The bimanual shrinking-object illusion activated two parietal regions (Fig. 3). One cluster was located in the anterior SPL bilaterally. This cluster included parts of areas 5M, 5L, and 7A (Fig. 3, *A* and *B*: open white sections). In this cluster, we found three peaks of activation [left area 7A (−15, −60, 57) $T = 4.3$; right area 5M (3, −54, 57) $T = 3.7$; and right area 5L (15, −54, 63) $T = 3.6$]. These areas were not activated in the condition when the participants' hands didn't touch the object even when the participants experienced strong illusory hand flexion (free tendon vs. free bone). Nor were these areas active when the hands were in contact with the cylinder and the bone was vibrated producing no illusions (contact bone vs. free bone; $T < 1.65$, $P > 0.05$). The supplementary single-subject analyses revealed that all participants showed activity at least in one of the SPL regions during the bimanual shrinking-object illusion (Table 1). The second cluster identified when examining the interaction term was located at the junction of the left postcentral and intraparietal sulci [BA 2 (−45, −33, 51) $T = 4.2$; Fig. 3*C*] and in the left inferior parietal lobule [supramarginal gyrus: probably area PFt or PF (−60, −27, 36) $T = 4.3$; Fig. 3*D*].

Finally, we looked at the main effect of tendon vibration (illusion). This contrast activated the left motor areas (primary motor cortex: M1, dorsal premotor cortex: PMD, supplementary motor area: SMA) and additionally fronto-parietal areas that have been reported in several of our previous studies (see METHODS). Importantly, the SPL was not found active in this main effect contrast.

Control experiment

In the control EMG experiment outside the scanner, the participants experienced again the bimanual shrinking-object illusion only in the contact-tendon condition (2.8 ± 0.9 cm; 1-sample *t*-test: df = 9, $t = 8.8$, $P < 0.001$ as compared with the contact-bone condition). The illusory displacement (5.4 ± 1.9 cm) of free-hand (free-tendon) was significantly greater than the illusory object-shrinkage (paired *t*-test: df = 9, $t = 4.9$, $P = 0.001$) as the fMRI participants reported after the scanning. But the flexor activity was significantly greater when the participants held the object (contact) as compared with when the hands were free [free; main effect of hand situation; $F(1,9) = 5.1$, $P = 0.05$]. The activity level was nearly the same in the tendon and bone conditions (Fig. 4). Importantly, we found no specific increase of EMG activity that could be attributed to the shrinking-object illusion in the contact-tendon condition [no significant interaction for the EMG activity across the 4 conditions corresponding to those tested in the fMRI experiment; $F(1,9) = 1.0$, $P = 0.35$]. We observed no increase in force between the right vibrated hand and the object during the bimanual shrinking-object illusion.

DISCUSSION

The results of the behavioral experiment (Fig. 1) show that the bimanual hand-object illusion is a genuine perceptual illusion that follows a strict logic based on the direction of illusory hand movements. The imaging experiment showed that activity in the anterior SPL (most probably cytoarchitectonic areas 5M, 5L, and 7A) was associated with the illusion that an object held between the hands is shrinking. This region was never active in our previous studies when participants experience unimanual free-hand illusions (Naito et al. 2002,

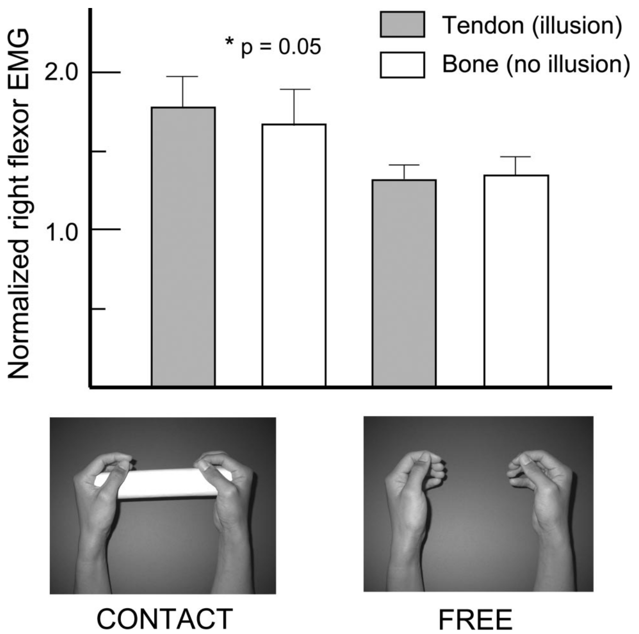

FIG. 4. Changes of electromyographic (EMG) activity in the right flexor muscle when either the tendon of the right extensor muscle (⊠, tendon) or the skin surface over the right nearby bone (□, bone) was vibrated while participants held the cylinder in both hands (contact: *left bars*) or the hands were free (free: *right bars*). Bars indicate the mean normalized EMG activity in the muscle across the participants. Error bars = SE, (n = 10).

2005, 2007), unimanual hand-object illusions when participants feel that the hand and a touched object are moving (Naito and Ehrsson 2006), or during illusory shrinkage of a body part caused by bilateral wrist tendon vibration (Ehrsson et al. 2005). Thus among the various types of kinesthetic illusions that can be induced by tendon vibration, the bimanual shrinking-object illusion appears to specifically engage the human anterior SPL.

Methodological considerations

The present SPL activation cannot be explained in terms of effects related to skin vibration, illusory wrist movement, skin contact with the object, or the different postures of hands because all these factors were controlled in our factorial design (Fig. 2). Likewise the activation is not due to the passive transduction of vibratory stimuli between the two hands because such effects should also be present in the control condition (contact bone).

As revealed by our control EMG experiment (Fig. 4), it is also unlikely that the SPL activation reflects changes in muscular activity or force that would be specifically related to the bimanual shrinking-object illusion. Increments of muscular activity and force are often associated with increases in activity in primary motor cortex and other sensorimotor areas (Cramer et al. 2002; Dai et al. 2001; Dettmers et al. 1995, 1996; Ehrsson et al. 2001; Thickbroom et al. 1998) but not in the anterior SPL. The increased flexor EMG activity in the contact condition as compared with when the hands were free (free) could be due to the effects of holding the cylinder even though they were instructed to do so without applying force. It is unlikely that this muscular activity was due to the effects of tendon vibration because the participants experienced stronger illusions when the hands were free (see RESULTS). Furthermore, this difference in muscular activity is not due to the application of the vibrator to the hand because there was no significant difference in the EMG activity level between the tendon and bone conditions.

Our results are based on a fixed-effects analysis of the pooled data from a relatively small number of participants ($n = 7$); however, the single-subject analyses demonstrated good reproducibility of the present SPL activations across participants when they experienced the bimanual shrinking-object illusion (Table 1). The combination of cytoarchitectonic maximum probability map and activation map only provides a probabilistic framework for the allocation of a particular activation to cytoarchitectonic areas and has moreover some limitations concerning the interpretation of fixed-effects results based on the intersubject variability (Eickhoff et al. 2005, 2007). But this approach still provides additional information about the most likely anatomical location of a particular activation that cannot be inferred from any other approaches. In the present study, the peaks of the SPL activation were located in anterior subregions of the SPL (most probably cytoarchitectonic areas 5M, 5L and 7A; Fig. 3, *A* and *B*), and the individual analyses revealed that at least five (~70%) of the participants had an activation in one of the anterior SPL regions (Table 1). Thus the present SPL activation, when the participants experienced the bimanual shrinking-object illusion, most likely corresponds to the anterior (not posterior) subregions of the SPL even though there is a possibility that an activation peak in a cytoarchitectonic area (ex. area 5M) in a participant might actually belong to adjacent area (ex. area 5L) in the individual brain. The main reasons for these potential deviations are the inter-individual variability of both brain structure and function and also in particular residual misalignments after spatial normalization.

Roles of parietal activations during the bimanual shrinking-object illusion

Recently it was demonstrated that the human anterior SPL (BA 5 and anterior part of BA 7) show receptor distributions similar to somatosensory areas, whereas the posterior part of this region (posterior part of BA 7) shows patterns that are more similar to those found in visual areas (Scheperjans et al. 2005b). This may be a structural correlate of a spatially heterogeneous predominance of the representations of the somatosensory (anterior) and visual (posterior) modalities in the human SPL (Scheperjans et al. 2005b). This view was supported by the present functional activations in the anterior SPL during the somatosensory illusion (Fig. 3) and by our recent finding that a more posterior part of the SPL is activated when visual information of the participants' vibrated (static) hand is available and attenuates the amount of illusory flexion (Hagura et al. 2007). A similar dissociation of superior parietal functions has recently been demonstrated also for goal-directed bimanual movements. Anterior activations were found if the movement was guided purely by somatosensory information, whereas more posterior regions were involved if visual information was additionally available (Wenderoth et al. 2006).

When participants perform such active bimanual tasks requiring complex spatial coordination between the right and left hand, activation is usually observed in the SPL together with frontal motor areas and other parietal areas (Wenderoth et al. 2004). In the present study, involving perception of bimanual hand-object interaction without any voluntary movements, we found no frontal motor activations but activity in the anterior SPL (Fig. 3, *A* and *B*). This suggests a sensory role of the anterior SPL during bimanual tasks that require updating of spatial relationships between the two hands. In non-human primates, the SPL has extensive anatomical connections with frontal motor areas (Darian-Smith et al. 1993; Jones et al. 1978; Leichnetz 1986; Matelli et al. 1998), and electrophysiological studies have shown that the discharge patterns of SPL neurons can encode the direction of limb movements (Kalaska et al. 1983, 1990; Lacquaniti et al. 1995). Thus the neuronal processing in the anterior SPL may reflect the computation of the spatial relationships between the two hands and the object. This could support bimanual motor behaviors when people have to coordinate the positions of two hands. This view would be consistent with a case study of a patient with bilateral atrophy of superior parietal regions (Rapcsak et al. 1995). This person, who expressed deficits in the position sense of the limbs bilaterally and impairments of joint-coordination of the forearms, was not able to correctly perceive the spatial relations between the body and external objects.

Different parietal areas are activated when people feel that an external object is shrinking compared with when they feel that a part of their own body is shrinking (Ehrsson et al. 2005). The present SPL activation was located ≥35 mm superior and medial to the activation found in the anterior intraparietal and postcentral region [peaks (−54, −30, 57) and (−45, −39, 60)] when people felt that their waist was shrinking in a similar illusion elicited by tendon vibration. The activation of the SPL in the present experiment (Fig. 3) could indicate a specialization of this region for the processing of spatial relationships between the limbs and objects in extrapersonal space (Connolly et al. 2003; Johnson et al. 1996; Lacquaniti et al. 1995; Roland et al. 1980).

In the human somatosensory system, BA 5 likely receives elementary somatosensory information from primary areas and processes it on a hierarchically higher level (Scheperjans et al. 2005a). Thus the activity in BA 5 associated with the bimanual shrinking-object illusion could be driven by kinesthetic inputs from frontal motor areas (see also Naito et al. 2002, 2005, 2007), and kinesthetic and haptic inputs from the BA 2 (Naito et al. 2005) (see Fig. 3*C*) and the IPL (Fig. 3*D*).

We have recently demonstrated that the left IPL is active when people feel a unimanual hand-object illusion (Naito and Ehrsson 2006). In this illusion, the participants touched a ball with one hand and experienced the hand and the object to be moving when we vibrated the wrist tendon. It was argued that the left IPL might be important for the integration of kinesthetic information about limb movement and haptic information about an external object (Naito and Ehrsson 2006; see also Nickel and Seitz 2005). Consistent with this view, we found that the present bimanual shrinking-object illusion was also associated with activity in a very similar region of the left IPL (Fig. 3*D*). A common denominator between the unimanual illusion and the present bimanual illusion is that both require the integration of movement information about the vibrated limb and haptic information about the touched-object. Thus the present left IPL activation (most likely area PFt or PF) (Caspers et al. 2006) is probably related to somatic integration of the representation of the right "moving" (vibrated) hand and the touched-object representation. This is probably different from the role of the SPL during the bimanual shrinking-object illusion, i.e., bimanual estimation about spatial relationship between the two hands and the hand-held object. As the IPL seems to be anatomically connected with both BAs 5 and 2 in non-human primates (Cavada and Goldman-Rakic 1989; Pandya and Seltzer 1982; Pearson and Powell 1978; Taoka et al. 1998), these regions, working in concert with each other, may represent the neuronal substrate of the somatic perception of bimanual hand-object interaction.

Finally in our previous studies, we have consistently found that kinesthetic illusory movement of the right vibrated hand when it free and not touching an object engages hand sections of multiple motor areas and other regions in fronto-parietal cortex (mainly right-sided) (Naito et al. 2002, 2005, 2007). In the present study, we observed the same pattern of activation in the main effect of illusion. But when the right vibrated hand interacts with an external object, this unimanual hand-object illusion requires additional activation in the left IPL (Naito and Ehrsson 2006) and during the bimanual hand-object illusion further additional activation in the SPL is seen. This indicates a hierarchical organization of neuronal correlates of somatic perception of limb movements and their interaction with external objects, probably reflecting the differing demands for interoceptive (within one's own body space) and exteroceptive (interaction with external objects) perception.

The present study supports the view that the parietal lobe plays a key role in the somatic perception of external objects (Roland 1987) and extends our understanding about how this brain region represents the relationship between our body and these objects. Our findings suggest that the anterior SPL integrates information about the relative configuration of the upper extremities and information about the shape and size of the hand-held object. It may therefore subserve the somatic perception of spatial relationships between the two hands during daily interactions with external objects.

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