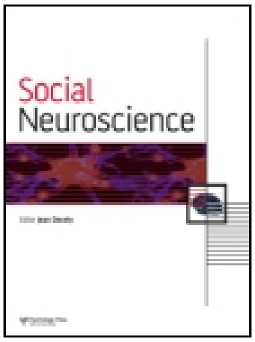

SOCIAL NEUROSCIENCE

ISSN: 1747-0919 (Print) 1747-0927 (Online) Journal homepage: https://www.tandfonline.com/loi/psns20

Effect of motion smoothness on brain activity while observing a dance: An fMRI study using a humanoid robot

Naoki Miura , Motoaki Sugiura , Makoto Takahashi , Yuko Sassa , Atsushi Miyamoto , Shigeru Sato , Kaoru Horie , Katsuki Nakamura & Ryuta Kawashima

To cite this article: Naoki Miura , Motoaki Sugiura , Makoto Takahashi , Yuko Sassa , Atsushi Miyamoto , Shigeru Sato , Kaoru Horie , Katsuki Nakamura & Ryuta Kawashima (2010) Effect of motion smoothness on brain activity while observing a dance: An fMRI study using a humanoid robot, SOCIAL NEUROSCIENCE, 5:1, 40-58, DOI: 10.1080/17470910903083256

To link to this article: https://doi.org/10.1080/17470910903083256

Published online: 07 Jul 2009.

SOCIAL NEUROSCIENCE, 2010, 5 (1), 40–58

Psychology Press
Taylor & Francis Group

Effect of motion smoothness on brain activity while observing a dance: An fMRI study using a humanoid robot

Naoki Miura

Kochi University of Technology, Kochi, and Tohoku University, Miyagi, and Japan Science and Technology Agency, Saitama, Japan

Motoaki Sugiura, Makoto Takahashi, and Yuko Sassa

Tohoku University, Miyagi, Japan

Atsushi Miyamoto

Sony Corporation, Tokyo, Japan

Shigeru Sato and Kaoru Horie

Tohoku University, Miyagi, Japan

Katsuki Nakamura

National Center of Neurology and Psychiatry, Tokyo, and Japan Science and Technology Agency, Saitama, Japan

Ryuta Kawashima

Tohoku University, Miyagi, Japan

Motion smoothness is critical in transmitting implicit information of body action, such as aesthetic qualities in dance performances. We expected that the perception of motion smoothness would be characterized by great intersubject variability deriving from differences in personal backgrounds and attitudes toward expressive body actions. We used functional magnetic resonance imaging and a humanoid robot to investigate the effects of the motion smoothness of expressive body actions and the intersubject variability due to personal attitudes on perceptions during dance observation. The effect of motion smoothness was analyzed by both conventional subtraction analysis and functional connectivity analyses that detect cortical networks reflecting intersubject variability. The results showed that the cortical networks of motion- and body-sensitive visual areas showed increases in activity in areas corresponding with motion smoothness, but the intersubject variability of personal attitudes toward art did not influence these active areas. In contrast, activation of cortical networks, including the parieto-frontal network, has large intersubject variability, and this variability is associated with personal attitudes

Correspondence should be addressed to: Naoki Miura, Department of Intelligent Mechanical Systems Engineering, Kochi University of Technology, 185 Miyanokuchi, Tosayamada-cho, Kami, Kochi, 782-8502 Japan. E-mail: miura.naoki@kochi-tech.ac.jp

This study was performed at Department of Functional Brain Imaging, IDAC, Tohoku University, Japan. We gratefully thank Yoshihiro Kuroki and Tomohisa Moridaira for their contribution to preparation of the experiment and helpful discussion. This research was supported by JST/RISTEX, R&D promotion scheme for regional proposals promoted by TAO, JST/CREST, and Research Center for Language, Brain and Cognition, Graduate School of International Cultural Studies, Tohoku University.

www.psypress.com/socialneuroscience DOI:10.1080/17470910903083256

about the consciousness of art. Thus, our results suggest that activity in the cortical network involved in understanding action is influenced by personal attitudes about the consciousness of art during observations of expressive body actions.

Keywords: Functional magnetic resonance imaging (fMRI); Motion smoothness; Intersubject variability; Dance; Parieto-frontal network.

INTRODUCTION

One important cognitive mechanism involves understanding the implicit information conveyed by the body actions of others, which operates the same as the process by which explicit intentions are understood. For example, the attractive expressions of professional dancers critically depend on their sophisticated, smooth body action. Ballet audiences experience the atmosphere created by the dancers and interpret the performances according to their own internal susceptibilities. If the observed action includes awkward movements, the observer interprets the motion as strange. Furthermore, if an audience cannot feel this atmosphere, the dance will be a boring exhibition. Several neuroimaging studies have investigated the cortical mechanism(s) involved in understanding the explicit intentions from body actions during nonverbal communication, such as gestures (Lotze et al., 2006), emotional facial expressions (Posamentier and Abdi, 2003; Sprengelmeyer, Rausch, Eysel, & Prezuntek, 1998), and body language (de Gelder, 2006). By contrast, little attention has been paid to the cortical mechanism(s) involved in interpreting the implicit information from body actions.

Information about body actions may be divided into verbal and nonverbal aspects. The former transmit verbal or symbolic information, as in a gesture or sign language; the latter can transmit nonverbal information that can provide implied meaning or convey information about the atmosphere, such as the beauty of a movement. Motion smoothness is one of the nonverbal aspects of body action, because it transmits implicit information about the atmosphere along with information about expressive body actions. In the case of perceiving a gesture or sign language, the information the performer wants to transmit is verbal information; thus, the receiver's interpretation is only modestly affected by differences in motion smoothness. In contrast, in the case of appreciating a dance, for example, an accomplished dance performance strongly demands motion smoothness, and the implicit atmosphere will not be conveyed only by the correct dance movements. Thus, motion smoothness provides important nonverbal information for expressing the emotional atmosphere. Previous studies have reported relationships between cortical activity during the observation of a dance and familiarity with the observed dance (Calvo-Merino, Jola, Glaser, & Haggard, 2005), the effects of training in relation to dancing (Cross, Hamilton, & Grafton, 2006), and the execution of dance-like foot movements (Brown, Martinez, & Parsons, 2005), but the effects of motion smoothness of expressive body actions have not been investigated.

Furthermore, it is expected that the interpretation of nonverbal aspects of body actions will include a large degree of intersubject variability. For example, differences in personal attitudes will affect interpretations of expressive activities, such as theatrical art. When different people observe the same dance performance, the subjective feeling of each person may be influenced by his/her background, emotional sensibility in relation to art, consciousness of body actions, or knowledge about the dance. Thus, the interpretation of the motion smoothness of expressive body actions will include intersubject variability, and it will affect personal attitudes associated with the consciousness of art. Recently, it was proposed that the posterior parietal and inferior frontal network, comprising the mirror neuron system, might work as a cognitive network of action understanding (see Iacoboni and Mazziotta, 2007; Rizzolatti, Fogassi, & Gallese, 2001; for reviews). Because it was expected that the mirror neuron system would be utilized for understanding dance, the activity of the mirror neuron system was expected to be affected by both the motion smoothness of observed dance action and the differences in personal attitudes associated with the consciousness of art during the observation of dance performance. This perspective is based on a subjectivist theory of aesthetics, and the interpretation of the relationship between the smoothness of body motion and its expressiveness depends on the personal attitudes of each observer. Previous neuroimaging studies using static art reported that the prefrontal area contributes to aesthetic judgments about what the subject likes or dislikes (Cela-Conde et al. 2004; Kawabata and Zeki, 2004). Research examining judgments about beauty with regard to motion enacted by the whole body have used functional magnetic resonance imaging (fMRI) to study the relationships between subjective evaluations of individual dance moves and brain activities from an aesthetic perspective (Calvo-Merino et al., 2008), and have suggested that the visual and sensorimotor brain areas contribute to an aesthetic evaluation of the dance motion. However, the intersubject variability in cognitive processing of the understanding of action and the relationships between any personal attitudes that underlie interpretations of nonverbal aspects of body action are poorly understood.

The purpose of this study was to investigate the effects of motion smoothness and its intersubject variability due to personal attitudes on the cortical mechanism(s) of understanding of body actions in the process of observing expressive body actions using fMRI. To directly address these effects, we used dance performances for the experimental stimulus to regulate the time series of body actions, because dance consists of a sequence of expressive body actions assigned by choreography and tied to music. The effect of motion smoothness on brain activity was evaluated by comparing the active areas of the brain during the observation of smooth dance performances with those active during awkward performances.

We used a small-biped humanoid robot named QRIO (Sony Corporation, Tokyo, Japan) as the dance performer or the experimental stimulus to regulate external appearance and precise body control. Unlike a robotic performer, when a human dancer performs a dance with awkward movements, the observer may interpret the movements as an intentional performance. It is also expected that differences in appearance may affect the cognitive process when more than one dancer performs the same series of movements. Thus, the effects of motion smoothness could not be readily distinguished using a human performer alone. QRIO was developed to interact socially with humans in a home environment (Kuroki, Ishida, Yamaguchi, & Nagasaka, 2002). It is capable of giving an attractive dance performance during which its body actions are precisely controlled. We prepared two dance performances by QRIO: an original smooth performance and a customized awkward performance. Because the differences between these two conditions were isolated to the differences in motion smoothness, we defined differential activation between these two conditions as smoothness-related responses, and the neural patterns of activation for such smoothness-related responses were analyzed.

To identify the cortical networks reflecting intersubject variability with regard to smoothness-related responses associated with personal attitudes, we performed a functional connectivity analysis using principal component analysis (PCA; Sugiura et al., 2007) and an attitude survey associated with expressive activity. Functional connectivity analysis is a method for finding the pattern of similar fluctuating regions of interest (ROIs) by analyzing the intersubject variability of the activation profile for each ROI using PCA, and then identifying a large-scale network showing the same fluctuation patterns of activation from a whole-brain functional connectivity analysis. We had predicted that some part of activation associated with smoothness-related responses would not reach statistical significance because of intersubject variability, even though these responses reflected specific differences between smooth and awkward dance conditions because the choreography of each dance was identical. It was claimed that the statistical sensitivity of the conventional subtraction analysis decreased when large intersubject variability was predicted for cortical activation (Holmes and Friston, 1998; Wei et al., 2004). Thus, we prepared movie clips of a professional dancer who performed the same dance in order to detect entire cortical networks acting as ROIs that are related to responses to motion smoothness by comparing the cortical activities evoked under this condition with those evoked under the awkward dance condition. Although the differences between the professional dance and the awkward dance conditions are not specific for smoothness-related responses because they involve any differences between humans and QRIO, such as appearance, this contrast is most sensitive with regard to the smoothness-related responses because the performance of a professional dancer is smoother and more sophisticated even in comparison with an advanced humanoid robot. By using differential activations of those ROIs in response to smooth and awkward dances performed by a robot, the functional connectivity analysis can summarize the specific pattern underlying the intersubject variability of smoothness-related responses. In addition, information from some ROIs that is related to certain differences between humans and QRIO, but is not associated with smoothness-related responses, would be eliminated in the results of PCA analysis.

We prepared 98 questions about the consciousness of art, sports, or handicrafts, and the tendency to communicate with others, animals, leafy plants, or machines for inclusion in the attitude survey examining the effect of personality on the intersubject variability of smoothness-related responses. We hypothesized that the consciousness of art would correlate with intersubject variability in the activation of the cortical network associated with understanding action, but it was also expected that other attitudes might be affected while the subject was observing the dance of a robotic performer. Thus, questions about other factors were also prepared to isolate those attitudes. From these questionnaires, a few principal components may have revealed personal attitudes associating expressive activities extracted by PCA, and a correlation analysis between these components and intersubject variability of smoothness-related responses was performed. It was expected that a correlation between the components and the intersubject variability of smoothness-related responses would be obtained when the intersubject variability of personal attitudes affected cortical activation.

MATERIALS AND METHODS

Subjects

Healthy, right-handed volunteers (38 males, 11 females; aged 19–29 years old) participated in the study. No subject had any sign or history of medical or neurological disease, and all were native Japanese speakers. We assessed their handedness by the Edinburgh Handedness Inventory (Oldfield, 1971). Written informed consent was obtained from each subject in accordance with the guidelines approved by the Strategic Research and Education Center for an Integrated Approach to Language, Brain and Cognition, Tohoku University, 21st Century Center of Excellence Program in Humanities, and the Helsinki Declaration of Human Rights, 1975.

Experimental task

Color video clips showing several dances by QRIO with dance-related music were used for the experimental stimuli. Two conditions were set for the motion smoothness of the dance performance: In one, QRIO danced according to its original, designated performance (Smooth; Figure 1a); in the other, QRIO danced with customized, awkward movements (Awkward; Figure 1b). This customized awkward movement sequence was designed to reflect a stiffer motion by decreasing the cooperative motion of each joint, the degrees of freedom of the joints, and changes in the acceleration of movement of each body part, as compared to its original performance. Eight video clips were prepared for each condition, in which a different set of dance movements and music was presented. The video clips were recorded with a digital video camera, and the length of each clip was 30 s. Eight video clips showing the same set of dances with music were also performed by a professional dancer (Human; Figure 1c) and were used as the reference condition (Human). In addition, video clips of moving mosaic pictures (Mosaic) were also prepared as a control condition, and the same sets of dance-related music were presented during each mosaic picture. In total, 32 kinds of video clips (8 clips $\times$ 4 conditions) were presented by a block design during the fMRI measurements. One video clip was presented in each task block, and the sequence of video clips was counterbalanced among the subjects. A resting condition, consisting of 15 s of a fixation cross, was inserted between each pair of stimuli, and a 21-s resting condition was inserted before the first video clip. Thus, the total time of the fMRI scan was 24 min and 21 s.

For fMRI measurements, the subject was placed in a supine position in the MRI scanner. A semilucent screen was positioned in front of the participant's face, and the visual stimuli were projected from outside the MRI room. A response pad was placed inside the chamber so that the participant could operate it comfortably with his/her right hand. The subjects were instructed to observe the video clips and to press the button with their right index finger when the video clip was finished, to confirm the arousal state of the subject. After fMRI scanning, subjects were asked to evaluate the motion smoothness of the performance in each clip by a rating scale with a range from 0 to 10.

Additionally, the subjects were asked to answer 98 questions relating to their consciousness about art, sports, and handicrafts and their tendency to communicate with animals, leafy plants, or machines and appliances. Table 1 presents examples

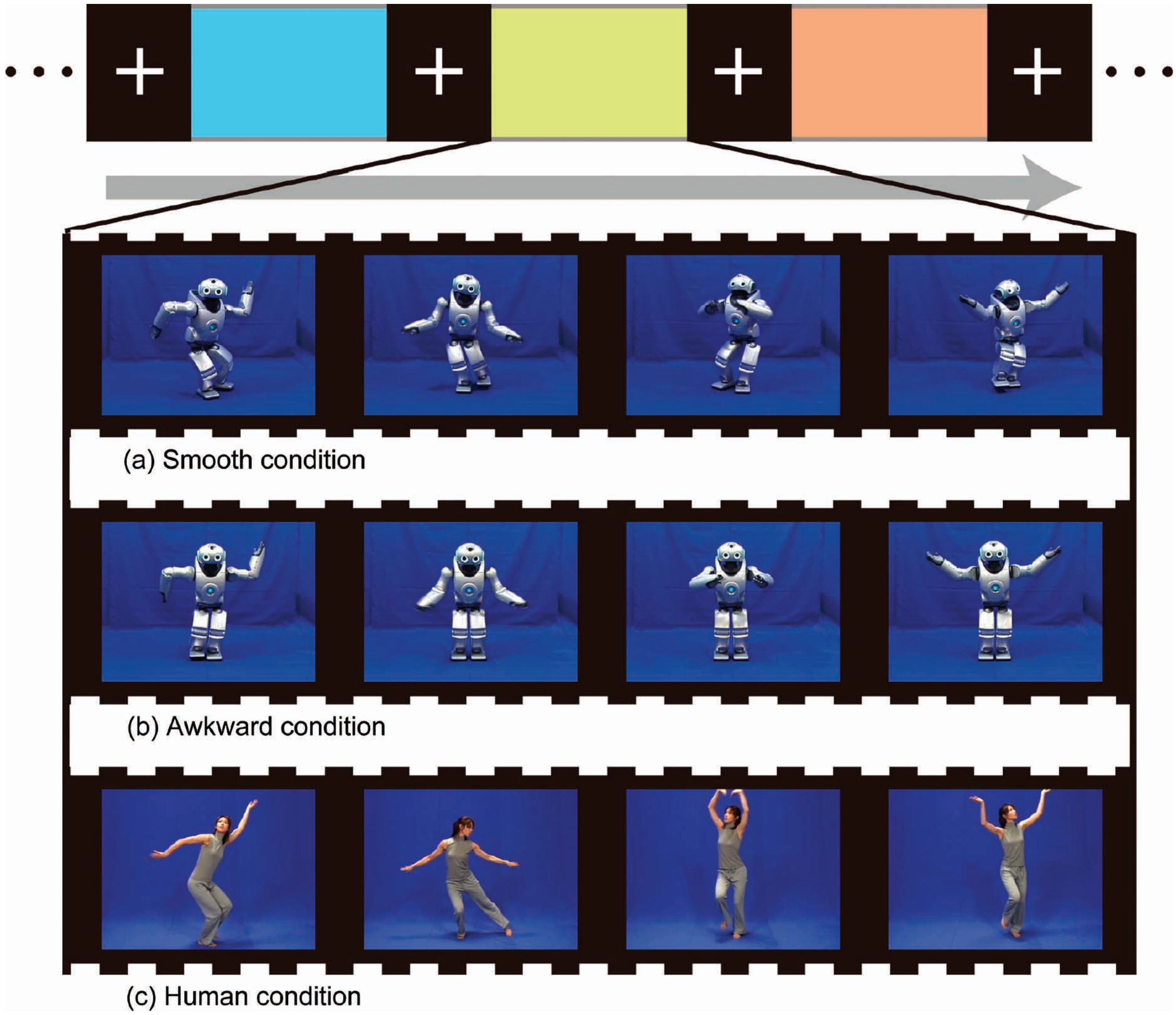

Figure 1. Examples of stimuli: (a) Smooth, (b) Awkward, and (c) Human conditions. The length of each video clip was 30 s, and resting condition consisting of 15 s of a fixation cross was inserted between each pair of clips.

of questions in each category, and information about all questions is presented in the appendix (Table A1). As it was expected that the smoothness-related responses during dance observation would be influenced by subjects' consciousness of arts and sports, we prepared 21- and 27-question surveys, respectively, about these issues. Moreover, given that a robot was used as the dance performer, we considered whether attitudes about a nonhuman presence might also have an impact. Thus, 15 questions about handcrafts and 35 questions about the tendency to communicate with machines, animals, and plants were also included. Subjects were instructed to answer each question on a scale of 0 to 10.

fMRI data acquisition

fMRI time series data covering the entire brain in 33 axial slices were acquired using gradient echo-echo planar imaging (GE-EPI) with a standard head coil (repetition time (TR) = 3000 ms; echo time (TE) = 50 ms; flip angle (FA) = 90°; field of view (FOV) = 192×192 mm; matrix size = 64×64; slice thickness = 3 mm; interslice gap = 1 mm; voxel size = $3 \times 3 \times 4$ mm) on a 1.5 T Siemens Magnetom Symphony scanner (Siemens, Munich, Germany). The initial two scans of each subject were dummy scans to equilibrate the state of magnetization and were discarded from the time series data; therefore, we collected 485 scans

TABLE 1
Examples of questions in each category in the attitude survey (English translations)

Questions about consciousness in relation to art	
Q1	You are impressed when you watch a difficult artistic performance.
Q4	You imagine performing works of art, even if you have no experience.
Q8	You are interested in the cultural background of art.
Questions about consciousness in relation to sport	
Q24	You are impressed when you watch a well–executed play in one of your favorite sports.
Q28	You imagine situations in which you play a particular sport, even if you have no experience of playing it.
Q45	You want to play your favorite sport well by practicing hard.
Questions about handicrafts	
Q49	When you craft an object, you are pleased when work progresses.
Q55	When you make an object, you want to make it close to your ideal image of that item.
Q62	When you make an object, you imagine showing another person your finished product.
Questions about tendencies to communicate with machines, animals, leafy plants	
Q64	Sometimes you think you are aware of the feelings of machines.
Q66	Sometimes you think you are aware of the feelings of animals.
Q69	Sometimes you think you are aware of the feelings of leafy plants.

Notes: Subjects were instructed to answer each question on a 0–10 scale. The order of the 98 questions was counterbalanced among the subjects.

during the measurement. In addition, T1-weighted anatomical MR images (TR = 1900 ms; TE = 3.22 ms; FA = 15°; FOV = 250 × 250 mm; matrix size = 256 × 256; 160 sagittal slices of 1.25 mm thickness) were also acquired.

fMRI data preprocessing

Data preprocessing and statistical analyses of fMRI data were carried out using the statistical parametric mapping 2 software (SPM2, Wellcome Department of Cognitive Neurology, London, UK). The effect of head motion across the scans was corrected by realigning all scans to the first one. The differences in acquisition timing among the 33 slices of each scan were adjusted to the sixteenth slice. Data were spatially normalized to the MNI-T1 template, which SPM2 provided, by a 12-parameter affine transformation and a nonlinear deformation (discrete cosine transformation with 7 × 9 × 7 basis functions) using the anatomical T1-weighted MRI image for each subject. Finally, each scan was smoothed with a Gaussian filter in a spatial domain (9-mm full-width at half maximum) to reduce noise and minimize the effects of normalization errors. Data from 12 subjects were excluded because of excessive head movement (more than 2 mm of movement, or 2° of rotation). Thus, we analyzed data from 37 subjects (28 males, 9 females).

Conventional subtraction analysis

The fMRI data were analyzed using a conventional two-stage approach in SPM2. First, the hemodynamic responses produced by the different experimental conditions were assessed at each voxel using a general linear model on an intrasubject basis. A hypothesis was made for each intrasubject model in which the hemodynamic response of the activation fields to each Smooth, Awkward, Human, and Mosaic block was assumed to be the canonical hemodynamic response function provided by SPM2, with a block length of a 30-s duration. Global changes were adjusted by proportional scaling, and low-frequency confounding effects were removed using a high-pass filter, with a 512-s cutoff. Multiple regression analyses were performed on each voxel to detect the regions where MR signal changes were correlated with the hypothesized model to obtain the partial regression coefficients of each voxel during each of the Smooth, Awkward, Human, and Mosaic conditions. We created subtraction images from the contrasts of Smooth > Awkward to identify cortical networks involved in smoothness-related responses, and from the contrasts of Human > Smooth to identify the cortical networks involved in the more general differences between observing dances performed by a human and a robot. The subtraction image of Human > Awkward was also created to determine ROIs for functional connectivity analysis of intersubject variability of smoothness-related responses. Although the contrast of Human > Awkward includes any differences between human and QRIO, such as appearance, it was expected that the contrast would be sufficiently sensitive to include the cortical regions relating to the smoothness-related responses. Thus, we can collect the ROIs from this contrast to find the pattern of intersubject variability in the smoothness-related responses. We also prepared subtraction images of Smooth and Human conditions compared with the Mosaic condition (Smooth > Mosaic and Human > Mosaic) to use as mask images in the second-level analyses.

Second, intersubject activation maps were created by performing a one-sample *t*-test on each voxel of each subtraction image of Smooth > Awkward, Human > Smooth, and Human > Awkward. To remove the voxels that did not reach the level of significance in the activation while observing dance compared to the Mosaic condition, the activation maps of Smooth > Mosaic (for Smooth > Awkward) and Human > Mosaic (for Human > Smooth and Human > Awkward) were used as mask images. The statistical threshold was set at $P < 0.05$ (corrected for family-wise error (FWE) by voxel level), and the statistical threshold for each mask image was set at uncorrected $p < 0.05$.

Principal component analysis for intersubject variability in smoothness-related responses

Intersubject variability on smoothness-related responses was analyzed using functional connectivity analysis by PCA (Sugiura et al., 2007). We used the peak locations for significant activation within Human > Awkward as ROIs for this analysis, and the parameter estimates of each ROI were collected from the subtraction image of Smooth > Awkward for each subject. Significant activations within Smooth > Awkward were not used for ROIs because we might not be able to specify entire regions as ROIs under this condition due to the decrease in the statistical sensitivity caused by intersubject variability. However, although the activation clusters from Human > Awkward include any differences between human and QRIO, the contrast is most sensitive to differences with regard to processing motion smoothness because a human dancer moves more smoothly and with greater sophistication. Because the smoothness-related responses reflect only a specific difference with regard to motion smoothness, the PCA approach for parameter estimates of Smooth > Awkward can summarize the pattern of intersubject variability of smoothness-related responses, and information from some ROIs, which is not related to smoothness-related responses, would be ignored in the PCA analysis. The PCA procedure was performed using a correlation coefficient matrix of parameter estimates collecting each ROI in each subject using the R software (version 2.2.1, The R Foundation for Statistical Computing). The number of principal components was determined by scree plot criteria.

To identify the cortical networks associated with each principal component (PC_{smooth}), voxel-by-voxel multiple regression analysis was performed between PC_{smooth} loadings, as explanatory variables, and parameter estimates of Smooth > Awkward on an intersubject basis. Because the PC_{smooth} represented intersubject variability of smoothness-related responses in the ROIs, other regions that were correlated with any PC_{smooth} loadings belonged to a cortical network in which activation fluctuated as a function of the intersubject variability of smoothness-related responses. Each partial regression coefficient representing a cortical network correlating positively or negatively with PC_{smooth} was tested by a one-sample *t*-test. The statistical threshold was set at $p < 0.05$ (corrected for FWE by voxel level).

Correlation analysis between intersubject variability and personal attitudes

To investigate the relationship between the subjects' personal attitudes associated with expressive activity and the cortical networks involved in intersubject variability of smoothness-related responses, we performed correlation analyses between the responses to the attitude survey and each cortical network correlating with PC_{smooth}. First, a PCA was performed based on the answer to each question of the attitude survey to summarize personal attitudes into several principal components ($PC_{questionnaire}$). The number of $PC_{questionnaire}$ was determined by scree plot criteria. Second, the correlation between each combination of $PC_{questionnaire}$ and PC_{smooth} loadings was tested to identify the causative factor of personal attitude that fluctuates with the activity of the cortical network. Because of our hypothesis that consciousness of art affects the activity of the cortical network involved in understanding action, the statistical threshold was set at $p < 0.05$ for the correlation analysis between $PC_{questionnaire}$ loading reflecting the consciousness of art and PC_{smooth} loading reflecting the intersubject variability of activation of the cortical network related to action understanding. With respect to the correlation of other combinations, the statistical threshold was set at $p < 0.05$ for multiple comparisons by the Bonferroni correction. The multiple comparisons were compensated for with the number of combinations of $PC_{questionnaire}$ and PC_{smooth} loadings.

RESULTS

Behavioral data

The average (*SD*) subjective ratings of the performer's motion smoothness in the Smooth, Awkward, and Human tasks were 6.7 (1.6), 2.9 (1.6), and 8.2 (1.3), respectively. The subjective rating of the Smooth condition was significantly higher ($p < 0.001$, paired t-test corrected for multiple comparisons with Bonferroni correction) than that of the Awkward condition. That is, the subjects felt that the original performance of QRIO was significantly smoother than its customized awkward performance. Furthermore, the subjective rating of the Human condition was significantly higher ($p < 0.001$, paired t-test corrected for multiple comparisons with Bonferroni correction) than that of the Smooth and Awkward conditions, respectively.

TABLE 2
Specific activation areas in Smooth > Awkward condition

Area	*L/R*	*MNI coordinates (mm)* *x*	*y*	*z*	*T-score*
Smooth–Awkward					
Cuneus	L	−4	−94	14	5.46
	L	−8	−92	30	4.99
	R	20	−92	18	5.48
	R	12	−86	40	5.38
	R	4	−96	12	5.26
Occipito-temporal junction	L	−44	−80	−6	5.06

Note: $p < 0.05$, corrected for FWE by voxel level.

Conventional subtraction analysis

Table 2 summarizes the MNI coordinates and the t-scores of peak activation in the contrast between Smooth > Awkward, Human > Smooth, and Human > Awkward. In Smooth > Awkward comparisons, small activation clusters were obtained in the bilateral cuneus and left occipito-temporal junction. The activated regions in Human > Smooth and Human > Awkward are listed in Table 3. Significant activations under the Human > Smooth and Human > Awkward conditions were typically observed bilaterally in the premotor area extending over the prefrontal area and intraparietal sulcus, the occipito-temporal junction extending over the fusiform gyrus and superior temporal gyrus, and several limbic regions such as the left amygdala and right midbrain/superior colliculus region. In addition, the right thalamus was significantly activated under the Human > Smooth condition, and the bilateral lateral occipital region, right parahippocampal gyrus, left thalamus, and left cerebellar posterior lobule were significantly activated under the Human > Awkward condition.

Functional connectivity analysis by PCA for intersubject variability in smoothness-related responses

The 22 regions showing significant activation in Human > Awkward (Table 3) were used as ROIs for the PCA. Five PC_{smooth} points were chosen by scree plot criteria (Figure 2a) to be used as the explanatory variable in the multiple regression analysis; the eigenvalues of each PC_{smooth} were 5.32, 2.66, 2.24, 1.78, and 1.61; and the proportions of variance were 24.2%, 12.1%, 10.2%, 8.1%, and 7.3%, respectively.

Table 4 summarizes the MNI coordinates and the T-scores of regions showing a significant correlation between each PC_{smooth} loading and parameter estimates of Smooth > Awkward. Figure 3 summarizes the regions showing a significant correlation between each PC_{smooth} loading. The $PC1_{smooth}$ loading was negatively correlated with the parieto-frontal network, composed of the bilateral premotor area and its adjacent region and supplementary motor area, the right superior and inferior parietal lobule, and the left intraparietal sulcus. Additionally, the left cuneus, fusiform gyrus, and inferior temporal

TABLE 3
Significant activation areas in Human > Smooth and Human > Awkward conditions

		MNI coordinate mm					*MNI coordinate (mm)*			
Area	*L/R*	*x*	*y*	*z*	*T-score*	*L/R*	*x*	*y*	*z*	*T-score*
	Human–Smooth					*Smooth–Awkward*				
Superior frontal sulcus						L	−36	−8	54	5.20
						R	26	−8	54	4.98
Middle frontal gyrus						R	46	−2	56	6.37
Inferior frontal gyrus	L	−54	0	40	5.05	R	46	6	30	5.59
Premotor area	L	−32	−10	54	6.54	L	−28	−8	70	5.45
	R	54	4	34	7.24	R	56	6	40	5.41
	R	46	−2	52	6.15					
Supplementary motor area						R	8	−8	74	5.87
Superior parietal lobule						R	26	−58	64	6.82
Intraparietal sulcus	L	−26	−60	−58	6.18	L	−28	−56	58	5.29
	R	36	−44	60	6.56					
	R	26	−58	56	5.37					
Lateral occipital						L	−16	−86	34	5.26
						R	16	−84	40	5.49
Fusiform gyrus	L	−44	−46	−22	6.31	L	−46	−46	−20	5.25
	R	48	−46	−20	8.97	R	50	−54	−20	7.12
Occipito-temporal junction	L	−52	−70	2	9.60	L	−52	−74	2	8.98
	R	56	−64	2	9.30	R	56	−66	4	9.02
Superior temporal gyrus	L	−54	−40	22	5.96	L	−54	−38	24	7.33
	L	−58	−26	12	5.07					
	R	60	−40	20	7.44	R	66	−38	20	7.44
Middle temporal gyrus	L	−58	−60	8	9.15					
Parahippocampal gyrus						R	30	6	−18	5.28
Amygdala	L	−20	−6	−14	5.20	L	−20	−4	−14	5.78
Thalamus	R	12	−12	12	5.23	L	−6	−20	8	5.02
Midbrain/Superior colliculus	R	4	−30	0	5.03	R	4	−32	−2	6.59
Cerebellar posterior lobule						L	−48	−60	−24	5.28

Note: $p < 0.05$, corrected for FWE by voxel level.

gyrus were also negatively correlated with $PC1_{smooth}$ loading. Several limbic regions, including the left amygdala and the bilateral hippocampus, positively correlated with $PC2_{smooth}$ loading. In contrast, the right superior parietal lobule negatively correlated with $PC2_{smooth}$ loading. The $PC3_{smooth}$ loading was negatively correlated with the left thalamus, pons, and cerebellar anterior lobule. The $PC4_{smooth}$ and $PC5_{smooth}$ loadings showed significant correlations with a small cluster of the paracentral lobule and the left superior temporal gyrus, respectively.

PCA for questionnaire and relationship between personal attitudes and smoothness-related responses

From the result of the PCA for questionnaires, four $PC_{questionnaire}$ were selected by scree plot criteria (Figure 2b); the eigenvalues for each $PC_{questionnaire}$ were 21.94, 13.28, 7.15, and 6.27; and the proportions of variance of each $PC_{questionnaire}$ were 22.2%, 13.4%, 7.2%, and 6.3%, respectively. As a principal component loading of each $PC_{questionnaire}$ of each question, the $PC1_{questionnaire}$ could be interpreted as indicating a tendency toward high scores on the entire questionnaire, $PC2_{questionnaire}$ indicated a tendency to personify a non-human presence, $PC3_{questionnaire}$ indicated a tendency toward higher consciousness of art, and $PC4_{questionnaire}$ indicated a tendency to communicate with others.

Table 5 summarizes the correlation coefficients between each PC_{smooth} and $PC_{questionnaire}$ loading. Because five PC_{smooth} and four $PC_{questionnaire}$ were obtained, the statistical test of each combination without an *a priori* hypothesis was corrected with the number of combinations ($5 \times 4 = 20$). In contrast, a correlation between $PC1_{smooth}$ and $PC3_{questionnaire}$ loading was tested without multiple comparisons, because $PC1_{smooth}$ and $PC3_{questionnaire}$ loading reflected an intersubject

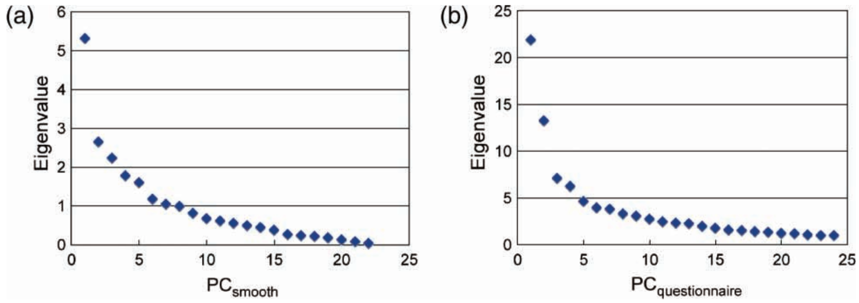

Figure 2. Scree plot showing each eigenvalue of (a) PC_{smooth} and (b) $PC_{questionnaire}$. On the plot of (b) $PC_{questionnaire}$, principal components with smaller eigenvalues (<1) were omitted.

variability concerning the activity on the parieto-frontal network and consciousness of art, and this combination conformed to our *a priori* hypothesis. The correlation between $PC1_{smooth}$ and $PC3_{questionnaire}$ loading ($r = -0.364$; $p = 0.027$) was a significantly negative correlation (Figure 4a). Thus, subjects who had lower $PC3_{questionnaire}$ scores tended to have more activity in the cortical network negatively correlating with $PC1_{smooth}$. Although a statistically significant correlation using the multiple comparison analysis could not have been obtained, there was a trend toward negative correlation between $PC3_{smooth}$ loading and $PC2_{questionnaire}$ loading ($r = -0.329$; $p = 0.047$, uncorrected; Figure 4b). Thus, subjects who had lower $PC2_{questionnaire}$ scores had a

TABLE 4
Cortical areas showing a correlation between PC_{smooth} loading and smoothness-related response

Area	*L/R*	*MNI coordinate [mm]* x	*Y*	*z*	*T-score*
Negative correlation with $PC1_{smooth}$					
Superior frontal sulcus	L	−30	−12	62	6.47
/Precentral sulcus	L	−28	−10	68	5.95
	R	26	−12	54	5.88
Precentral sulcus	L	−38	−10	32	6.19
Inferior frontal gyrus	R	56	6	26	6.68
Premotor area	L	−38	−8	52	7.37
	R	46	−4	52	7.54
Supplementary motor area	L/R	0	−10	68	6.78
Superior parietal lobule	R	32	−52	62	7.00
Inferior parietal lobule	R	50	−36	50	6.07
Intraparietal sulcus	L	−28	−68	52	8.34
Cuneus	L	−20	−86	32	6.33
Fusiform gyrus	L	−46	−48	−18	6.42
Inferior temporal gyrus	L	−50	−58	−12	6.02
Positive correlation with $PC2_{smooth}$					
Amygdala	L	−20	−4	−14	7.76
Hippocampus	L	−24	−20	−12	6.04
	R	26	−16	−14	6.31
Parahippocampal gyrus	R	8	−38	−8	7.37
Negative correlation with $PC2_{smooth}$					
Superior parietal lobule	R	24	−56	62	5.90
Negative correlation with $PC3_{smooth}$					
Thalamus	L	−4	−16	8	7.28
Cerebeller anterior lobule	L	−18	−32	−28	7.29
Pons	L	−2	−26	−44	6.40
Positive correlation with $PC4_{smooth}$					
Paracentral lobule	L	−8	−24	62	6.10
Negative correlation with $PC5_{smooth}$					
Superior temporal sulcus	R	66	−38	20	6.23

Note: $p < 0.05$, corrected for FWE by voxel level.

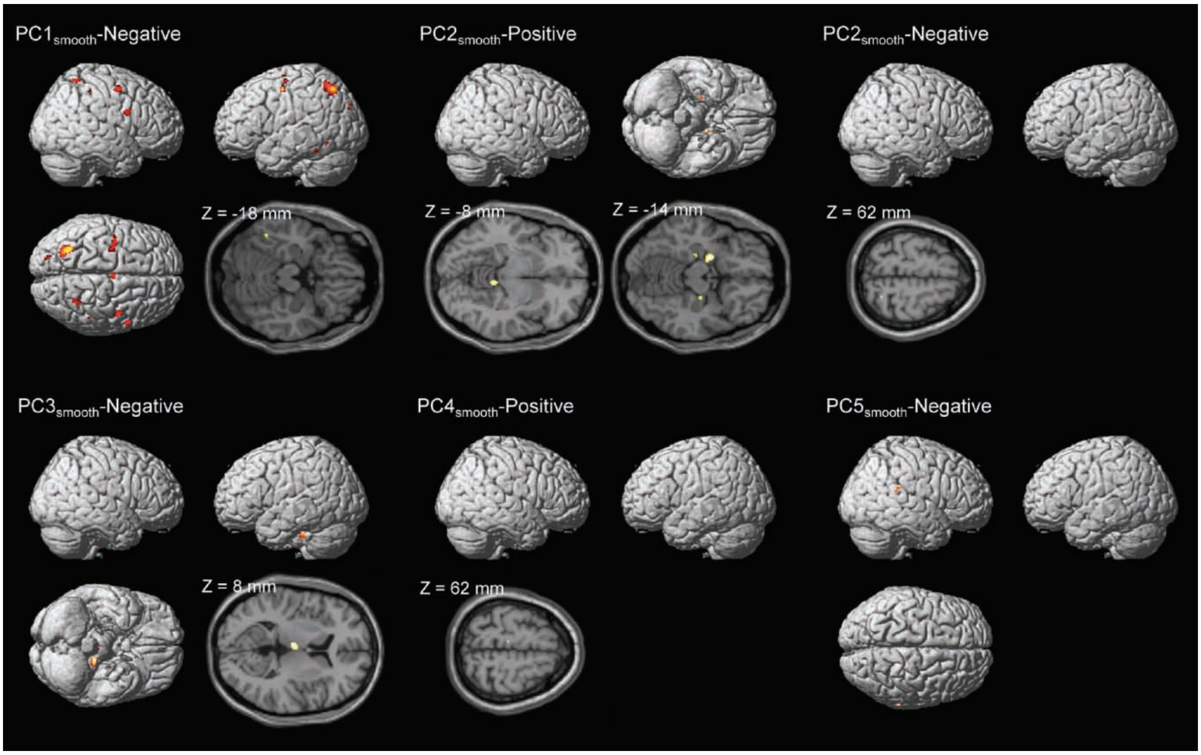

Figure 3. Functional networks showing positive or negative correlation with each PC_{smooth} loading ($p < 0.05$, corrected for FWE by voxel level).

tendency to increase the activity in the cortical network negatively correlating with $PC3_{smooth}$.

DISCUSSION

The purpose of this study was to investigate the effect of motion smoothness, as a nonverbal aspect of body action, on cognitive processes of persons observing a dance. Large intersubject variability was expected, so we performed two kinds of analysis: a conventional subtraction analysis to detect activated areas relating to perception of motion smoothness, and a functional connectivity analysis by PCA to clarify intersubject variability in smoothness-related responses.

From the conventional subtraction analysis of Smooth > Awkward, statistically significant activations were obtained in high-order visual processing areas, such as the left occipito-temporal junction and the bilateral cuneus. Furthermore, five cortical networks related to intersubject variability in smoothness-related responses were identified from the functional connectivity analysis. Therefore, smoothness-related responses during the observation of a dance had a large intersubject variability, which might result in a decreased statistical significance using a conventional subtraction analysis. In contrast, cortical areas related to body-sensitive and motion-sensitive visual processing areas did not show significant intersubject variability. Thus, the results suggest that the visual perceptual process of dance motions has little

TABLE 5
Correlation coefficients between each PC_{smooth} score and $PC_{questionnaire}$ score

	$PC1_{smooth}$	$PC2_{smooth}$	$PC3_{smooth}$	$PC4_{smooth}$	$PC5_{smooth}$
$PC1_{questionnaire}$	0.051	0.069	−0.177	0.004	0.167
$PC2_{questionnaire}$	0.093	−0.179	−0.329*	−0.013	0.109
$PC3_{questionnaire}$	−0.364*	0.192	0.294	−0.055	0.135
$PC4_{questionnaire}$	−0.211	0.054	−0.038	−0.154	0.070

Note: *Significant correlation ($p < 0.05$).

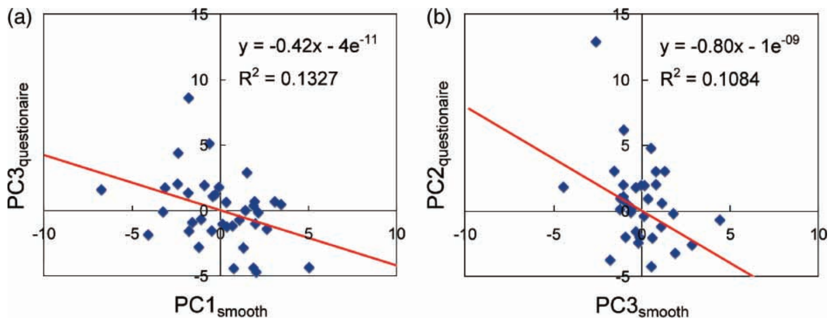

Figure 4. Scatter plot between (a) $PC1_{smooth}$ loading and $PC3_{questionnaire}$ loading, and (b) $PC3_{smooth}$ loading and $PC2_{questionnaire}$ loading. The red line shows the trend.

intersubject variability and that large intersubject variability appears to occur in the process of understanding the motion information and the extent of motion smoothness from the dance action.

Furthermore, we revealed a significant relationship between the personal attitude of consciousness of art and activity of a cortical network that included the parieto-frontal network, which is the main focus of the mirror neuron system (Iacoboni and Mazziotta, 2007; Rizzolatti et al., 2001). Thus, the results of this study support our hypothesis that the consciousness of art affects the activity of the cortical network of action understanding and suggest that the parieto-frontal network contributes cognitive mechanisms to interpreting the nonverbal aspects of body actions.

Cortical network that is not affected by intersubject variability

The activation peak in the left occipito-temporal junction was located close to the region that is associated with the perception of the human body (extrastriate body area (EBA); Downing, Jiang, Shuman, & Kanwisher, 2001; Downing, Wiggett, & Peelen, 2007; Spiridon, Fischl, & Kanwisher, 2006) and that responded during the observation of a goal-directed movement of body parts (Astafiev, Stanley, Shulman, & Corbetta, 2004). When the observed dance action included awkward movements, the subject interpreted it as strange action. In a subjective evaluation about the motion smoothness of dance action, there was a statistically significant difference between Smooth and Awkward conditions. Therefore, our results suggest that the left occipito-temporal junction involves the processing of expressive body actions, and the activity of this area is influenced by the extent of motion smoothness of body action.

In regard to the activation clusters in the bilateral cuneus, a previous study suggested that the superior part of the extrastriate visual area may also respond to visual motion (Tootell et al., 1997). In addition, Calvo-Merino et al. (2008) observed similar activations corresponding to differences with regard to essential kinematic aspects of observed dance movements, such as speed or movement direction. Because the choreography of each dance was identical for the Smooth and Awkward conditions, differences between each pair of conditions depended solely on the extent of motion smoothness and the differences of motion smoothness were represented by differences of motion for each body part on the movie clip. Thus, our results suggest that the perceived motion smoothness of body action reflects the activation of motion-sensitive visual processing areas, without intersubject variability.

Cortical network relating intersubject variability and relationship between personal attitudes

In the cortical network correlating with the $PC1_{smooth}$ loading, many activation peaks were observed in the bilateral premotor area and the neighboring regions, and the parietal regions, including the right inferior parietal lobule and bilateral intraparietal sulcus. Several neuroimaging studies have suggested that the dorsolateral parieto-frontal network has a role in understanding the actions of others, and that it works as a mirror neuron system during action observation and execution (Aziz-Zadah, Koski, Zaidel, Mazziotta,

& Iacoboni, 2006; Buccino et al., 2001; Iacoboni et al., 2001; Rizzolatti et al., 1996a) or imagery (Binkofski et al., 2000; Grafton, Arbib, Fadiga, & Rizzolatti, 1996). Furthermore, its activation is increased particularly in goal-directed actions (Buccino et al., 2001; Iacoboni et al., 2005). This network is also active during the observation of actions performed by non-conspecifics (Buccino et al., 2004b). In contrast, it was not involved when subjects observed point-light biological motions (Grossman et al., 2000) or certain actions performed by virtual agents (Perani et al., 2001). Although a representation of an awkward dance performance is semantically the same as a corresponding smooth performance, understanding the observed action may be obstructed because the viewer is distracted by its awkwardness. This is caused by a lack of nonverbal information, represented here by motion smoothness. Thus, our results suggest that the parieto-frontal network processes nonverbal aspects of body action in addition to verbal aspects, such as goal-directed action, in the process of understanding the observed action. There is considerable intersubject variability in individual sensitivity to motion smoothness.

Furthermore, $PC1_{smooth}$ loading was negatively correlated with $PC3_{questionnaire}$ loading. As a result of principal component loading of each $PC_{questionnaire}$ of each question, we interpreted the $PC3_{questionnaire}$ as indicating a tendency toward a higher consciousness relating to art. Thus, subjects who had a higher consciousness relating to art tended to show more activity in the parieto-frontal network. From the viewpoint of the "direct-matching hypothesis" (Rizzolatti et al., 2001), when the observer recognizes an action performed by others, the observer uses his/her internal representation of the actual execution of the observed action. A similar suggestion was reported by Cross et al. (2006), based on the relationship between cortical activity during the observation of a dance and familiarity with the observed dance. When people have higher consciousness relating to art, they may pay closer attention to the body action of the dancer and simultaneously become more sensitive to the atmosphere created by the dance. Furthermore, they will have a much clearer internal representation about the atmosphere created by expressive body action compared with people with a lower consciousness of art. Thus, our results suggest that the cognitive processing of the nonverbal aspects of body actions is influenced by personal attitudes about art. Previous neuroimaging studies about aesthetic experiences of dance performances (Calvo-Merino et al., 2008) or static art (Cela-Conde et al., 2004; Kawabata and Zeki, 2004) have reported that the activation of prefrontal cortices contributed to aesthetic evaluations of observed stimuli. Our results support these findings, and we expect that the investigation into the details of nonverbal aspects of body actions would lead to interpreting the cognitive mechanism of aesthetic representations. However, the nonverbal aspect of body actions is utilized not only in expressive performances such as dance, but also in everyday social communications to qualify verbal aspects with body actions in addition to the information from the verbal message. Our findings also indicate that the clarification of the cognitive mechanisms of perceiving nonverbal aspects of body actions would contribute to the progress in understanding the cognitive neuroscience of nonverbal communication.

$PC1_{smooth}$ loading also correlated with the activation in the left fusiform and inferior temporal gyri. These regions are part of the ventral visual pathway and are associated with the perception of multiple categorical objects (see Grill-Spector, 2003, for a review). In particular, several previous studies have reported that the mid-fusiform gyrus is a visual processing area specialized for human body parts such as the face (fusiform face area (FFA); Kanwisher, McDermott, & Chun, 1997; Puce, Allison, Asgari, Gore, & McCarthy, 1996) and body (fusiform body area (FBA); Peelen and Downing, 2005; Schwarzlose, Baker, & Kanwisher, 2005). Moreover, neuroimaging studies concerning biological motion have suggested that the FFA is a form-processing pathway involved in the perception of biological motion (Grossman and Blake, 2002; Michels, Lappe, & Vaina, 2005). There were some differences between the Smooth and Awkward conditions within the dance sequence (Figure 2). Even in the instantaneous pose, the Awkward condition was stiffer than the Smooth condition because of the limitations on joint motion. Thus, the smoothness of body action influenced the cognitive process depending on intersubject variability with respect to consciousness for art.

The left amygdala, bilateral hippocampus and neighboring areas, and the superior parietal lobule constitute a functional network that was significantly correlated with $PC2_{smooth}$. The functions of the amygdala and hippocampus largely concern the processing of emotions and memory

(LaBar and Cabeza, 2006). A previous study reported that interpretations of different types of body action are processed in different manners: Expressive body actions involve the activation of the amygdala and its neighboring regions, whereas hand actions involve the activation of the parietal region (Bonda, Petrides, Ostry, & Evans, 1996). Our results may be consistent with this hypothesis. When subjects observed a dance performance, different kinds of cognitive processing could occur. If a subject paid attention to the expressiveness of the body action, activation of the limbic network occurred, and the motion smoothness could affect the perception of expressiveness. In contrast, if the subject paid attention to another characteristic of body action, such as the sequence of motion by each body part, activity in the superior parietal lobule could increase, reflecting a subjective attention to this characteristic.

In the cortical network correlating with the $PC3_{smooth}$ loadings, the left thalamus, cerebellar anterior lobule, and pons were involved, and the $PC3_{smooth}$ network had a tendency to correlate with $PC2_{questionnaire}$ loading. Because $PC2_{questionnaire}$ could reveal a tendency to personify a non-human presence, subjects who had a higher tendency for this characteristic had slightly more activity in the $PC3_{smooth}$ network. Activation of the anterior cerebellar lobule reflects sensorimotor processing of foot movements (Brown et al., 2005), and Dhamala et al. (2003) reported that the activation of the thalamus reflected the complexity of rhythmic finger tapping. Because selective activation of the thalamus was also obtained in the subtraction analysis of Human > Awkward when there was a big difference in motion smoothness, this activation was commonly obtained, which exceeded the influence of intersubject variability. Thus, the activity of this network may reflect a subjective sensitivity for human likenesses in relation to the dance performance of the robot, because the differences in motion smoothness depended on the sophistication or human-like quality of the whole dance performance.

Left paracentral lobule activation correlated significantly with $PC4_{smooth}$. It is well known that the function of the paracentral lobule concerns the foot sensorimotor area, and Brown et al. (2005) reported that this region was activated during dance-like foot movements. Moreover, previous studies have reported that this region was activated when subjects imagined toe movements (Ehrsson, Geyer, & Naito, 2003) or whole-body movements of everyday life, compared with upper extremity movement (Szameitat, Shen, & Sterr, 2007). In the post-fMRI interview, subjects said that they focused on the movement of the hands and feet. Thus, our results may indicate that $PC4_{smooth}$ represents intersubject variability in the attention to motion smoothness of foot movements when observing a dance.

Activation in the right posterior superior temporal gyrus significantly correlated with $PC5_{smooth}$. Grossman and Blake (2002) and Michels et al. (2005) suggested that the posterior superior temporal sulcus was a motion-processing pathway underlying the perception of biological motions. Moreover, previous neuroimaging studies have reported that activity in the posterior superior temporal sulcus was involved in perceiving biological motions (Cross et al., 2006; Grossman et al., 2000; Peuskens, Vanrie, Verfaillie, & Orban, 2005; Thompson, Clarke, Stewart, & Puce, 2005). Thus, our results are consistent with previous suggestions that the cortical network related to $PC5_{smooth}$ is involved in the perception of biological motions and that intersubject variability exists in the magnitude of activation. In addition, the right posterior superior temporal sulcus responds to observations of goal-directed intentional actions (Castelli Happe, Frith, & Frith, 2000; Saxe, Xiao, Kovacs, Perrett, & Kanwisher, 2004; Zacks et al., 2001), imitated actions (Iacoboni et al., 2001), and expressive gestures (Lotze et al., 2006) and not just to biological motions. If the observed action were an awkward movement, it might be expected that the observer would interpret it as something odd, and it might be difficult for the observer to receive the performer's real intention. In the observation of an awkward dance performance, it is also difficult for the observer to receive the intentional information the performer wants to convey. Thus, our results may indicate that motion smoothness influences the cognitive process related to understanding the intention from body actions, and that this process depends on personal attitudes.

Differential activation during observations of whole-body motion by a human and a humanoid robot

Observation of the performance of the human professional dancer involved a large network of cortical activity compared with observation of the performance of the robot, especially in the parieto-frontal network and the temporal regions. Moreover, the subjects reported that the performance of the human dancer was significantly smoother than the smooth performance of the robot. Because the results of functional connectivity analysis suggested that the parieto-frontal network contributed the processing of nonverbal aspects of body action, just as it contributes to the processing of verbal aspects of body action, the subjects easily perceived the nonverbal aspects of body action on the basis of the sophisticated movements of the human dancer. Although the choreography of each dance was identical for the Human and Smooth conditions, the body movement of the robot was comparatively limited due to the smaller number of joints and the more restricted range of motion of each joint compared with those of the human dancer. Furthermore, the biggest visual difference between human and robot concerned external appearances. Therefore, it was expected that the activation of this contrast would derive from differences in motion smoothness and appearance as well as the interaction effect of these factors. A previous neuroimaging study using a biological motion classification task involving computer-animated characters indicated that a response bias towards the biological substrate separately affects the cortical networks involved in mentalizing and motor resonance (Chaminade, Hodgins, & Kawato, 2007). Our results partially support their finding, but further investigation will be necessary to clarify how each factor influences brain activity during the observation of body actions performed by a robotic agent. On the other hand, although it appeared only in the left hemisphere, the activation of the occipito-temporal junction was observed under the Smooth > Awkward condition. Because this area might be associated with perception of the human body (Downing et al., 2001, 2007; Spiridon et al., 2006) and motion (Astafiev et al., 2004), we considered the possibility that sophisticated dance movements by a human dancer caused increased activation in the occipito-temporal junction, although the influence of motion smoothness, appearance, and their interaction also contributed to this result.

CONCLUSIONS

During subjects' observation of a dance performance by the humanoid robot, motion smoothness, constituting a nonverbal aspect of body actions, influenced several cortical networks. Motion-sensitive and body-sensitive visual processing areas were commonly influenced by motion smoothness, and five cortical networks reflecting the intersubject variability of smoothness-related responses were identified. Thus, it is considered that these regions are associated with visual perception at the comparatively early phase of cognitive processing to understand the visually presented dance action. Activation of the parieto-frontal network and inferior temporal region was affected by personal attitudes about individual consciousness in relation to art. Thus, from the present results, we point to the cortical networks, including the parieto-frontal network, as involved in the processing of motion smoothness of expressive body action, and we also suggest that there is large intersubject variability in the sensitivity to motion smoothness due to personal attitudes of the consciousness of art.

Manuscript received 24 November 2008
Manuscript accepted 28 May 2009
First published online 7 July 2009

REFERENCES

Astafiev, S. V., Stanley, C. M., Shulman, G. L., & Corbetta, M. (2004). Extrastriate body area in human occipital cortex responds to the performance of motor actions. *Nature Neuroscience*, *7*(5), 542–548.

Aziz-Zadeh, L., Koski, L., Zaidel, E., Mazziotta, J., & Iacoboni, M. (2006). Lateralization of the human mirror neuron system. *Journal of Neuroscience*, *26*(11), 2964–2970.

Binkofski, F., Amunts, K., Stephan, K. M., Posse, S., Schormann, T., Freund, H-J., et al. (2000). Broca's region subserves imagery of motion: A combined cytoarchitectonic and fMRI study. *Human Brain Mapping*, *11*(4), 273–285.

Bonda, E., Petrides, M., Ostry, D., & Evans, A. (1996). Specific involvement of human parietal systems and the amygdala in the perception of biological motion. *Journal of Neuroscience*, *16*(11), 3737–3744.

Brown, S., Martinez, M. J., & Parsons, L. M. (2005). The neural basis of human dance. *Cerebral Cortex*, *16*, 1157–1167.

Buccino, G., Binkofski, F., Fink, G. R., Fadiga, L., Fogassi, L., Gallese, V., et al. (2001). Action observation activates premotor and parietal areas in a somatotopic manner: An fMRI study. *European Journal of Neuroscience*, *13*, 400–404.

Buccino, G., Binkofski, F., & Riggio, L. (2004a). The mirror neuron system and action recognition. *Brain and Language*, *89*, 370–376.

Buccino, G., Lui, F., Canessa, N., Patteri, I., Lagravinese, G., Benuzzi, F., et al. (2004b). Neural circuits involved in the recognition of actions performed by nonconspecifics: An fMRI study. *Journal of Cognitive Neuroscience*, *16*, 114–126.

Calvo-Merino, B., Glaser, D. E., Grezes, J., Passingham, R. E., & Haggerd, P. (2005). Action observation and acquired motor skills: An fMRI study with expert dancers. *Cerebral Cortex*, *15*(8), 1243–1249.

Calvo-Merino, B., Jola, C., Glaser, D. E., & Haggard, P. (2008). Towards a sensorimotor aesthetics of performing art. *Consciousness and Cognition*, *17*(3), 911–922.

Castelli, F., Happe, F., Frith, U., & Frith, C. (2000). Movement and mind: A functional imaging study of perception and interpretation of complex intentional movement patterns. *NeuroImage*, *12*(3), 314–325.

Cela-Conde, CJ., Marty, G., Maestú, F., Ortiz, T., Munar, E., Fernández, A., et al. (2004). Activation of the prefrontal cortex in the human visual aesthetic perception. *Proceedings of the National Academy of Sciences of the United States of America*, *101*(16), 6321–6325.

Chaminade, T., Hodgins, J., & Kawato, M. (2007). Anthropomorphism influences perception of computer-animated characters' actions. *Social Cognitive and Affective Neuroscience*, *2*(3), 206–216.

Cross, E. S., Hamilton, A. F., de, C., & Grafton, S. T. (2006). Building a motor simulation de novo: Observation of dance by dancers. *NeuroImage*, *31*, 1257–1267.

de Gelder, B. (2006). Towards the neurobiology of emotional body language. *Nature Reviews Neuroscience*, *7*, 242–249.

Dhamala, M., Pagnoni, G., Wiesenfeld, K., Zink, C. F., Martin, M., & Berns, G. S. (2003). Neural correlates of the complexity of rhythmic finger tapping. *NeuroImage*, *20*(2), 918–926.

di Pellegrino, G., Fadiga, L., Fogassi, L., Gallese, V., & Rizzolatti, G. (1992). Understanding motor events: A neurophysiological study. *Experimental Brain Research*, *91*, 176–180.

Downing, P. E., Jiang, Y., Shuman, M., & Kanwisher, N. (2001). A cortical area selective for visual processing of the human body. *Science*, *293*, 2470–2473.

Downing, P. E., Wiggett, A. J., & Peelen, M. V. (2007). Functional magnetic resonance imaging investigation of overlapping lateral occipitotemporal activations using multi-voxel pattern analysis. *Journal of Neuroscience*, *27*(1), 226–233.

Ehrsson, H. H., Geyer, S., & Naito, E. (2003). Imagery of voluntary movement of fingers, toes, and tongue activates corresponding body-part-specific motor representations. *Journal of Neurophysiology*, *90*, 3304–3316.

Grafton, S. T., Arbib, M. A., Fadiga, L., & Rizzolatti, G. (1996). Localization of grasp representations in humans by positron emission tomography. *Experimental Brain Research*, *112*(1), 103–111.

Grill-Spector, K. (2003). The neural basis of object perception. *Current Opinion in Neurobiology*, *13*, 1–8.

Grossman, E. D., & Blake, R. (2002). Brain areas active during visual perception of biological motion. *Neuron*, *35*, 1167.

Grossman, E. D., Donnelly, M., Price, R., Pickens, D., Morgan, V., Neighbor, G., et al. (2000). Brain areas involved in perception of human biological motion. *Journal of Cognitive Neuroscience*, *15*, 553–582.

Holmes, A. P., & Friston, K. J. (1998). Generalisability, random effects and population inference. *NeuroImage*, *7*, S754.

Iacoboni, M., Koski, L. M., Brass, M., Bekkering, H., Woods, R. P., Dubeau, M.-C., et al. (2001). Reafferent copies of imitated actions in the right superior temporal cortex. *Proceedings of the National Academy of Sciences of the United States of America*, *98*(24), 13995–13999.

Iacoboni, M., & Mazziotta, J. C. (2007). Mirror neuron system: Basic findings and clinical applications. *Annals of Neurology*, *62*(3), 213–218.

Iacoboni, M., Molnar-Szkacs, I., Gallese, V., Buccino, G., Mazziotta, J. C., & Rizzolatti, G. (2005). Grasping the intentions of others with one's own mirror neuron system. *PLoS Biology*, *3*(3), 529–535.

Kanwisher, N., McDermott, J., & Chun, M. M. (1997). The fusiform face area: A module in human extrastriate cortex specialized for face perception. *Journal of Neuroscience*, *17*(11), 4302–4311.

Kawabata, H., & Zeki, S. (2004). Neural correlates of beauty. *Journal of Neurophysiology*, *91*(4), 1699–1705.

Kuroki, Y., Ishida, T., Yamaguchi, J., & Nagasaka, K. (2002). Small biped walking entertainment robot SDR-4X with a highly integrated motion control. *Proceedings of the 20th Annual Conference of the RSJ*, 1C17, 2002.

LaBar, K. S., & Cabeza, R. (2006). Cognitive neuroscience of emotional memory. *Nature Reviews Neuroscience*, *7*, 54–63.

Lotze, M., Heymans, U., Birbaumer, N., Veit, R., Erb, M., Flor, H., et al. (2006). Differential cerebral activation during observation of expressive gesture and motor acts. *Neuropsychologia*, *44*, 1787–1795.

Michels, L., Lappe, M., & Vaina, L. M. (2005). Visual areas involved in the perception of human movement from dynamic form analysis. *NeuroReport*, *16*(10), 1037–1041.

Oldfield, R. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia*, *9*, 812–815.

Peelen, M. V., & Downing, P. E. (2005). Selectivity for the human body in the fusiform area. *Journal of Neurophysiology*, *93*, 603–608.

Perani, D., Fazio, F., Borghese, N. A., Tettamanti, M., Ferrari, S., Decety, J., et al. (2001). Deferent brain correlates for watching real and virtual hand actions. *NeuroImage*, *14*, 749–758.

Peuskens, H., Vanrie, J., Verfaillie, K., & Orban, G. A. (2005). Specificity of region processing biological motion. *European Journal of Neuroscience*, *21*, 2864–2875.

Posamentier, M. T., & Abdi, H. (2003). Processing faces and facial expressions. *Neuropsychology Review*, *13*(3), 113–143.

Puce, A., Allison, T., Asgari, M., Gore, G. C., & McCarthy, G. (1996). Differential sensitivity of human visual cortex to faces, letterstrings, and textures: A functional magnetic resonance imaging study. *Journal of Neuroscience*, *16*(16), 5205–5215.

Rizzolatti, G., Fadiga, L., Matelli, M., Bettinardi, V., Paulesu, E., Perani, D., et al. (1996a). Localization of grasp representations in humans by PET: 1. Observation versus execution. *Experimental Brain Research*, *111*(2), 246–252.

Rizzolatti, G., Fogassi, L., & Gallese, V. (1996b). Premotor cortex and the recognition of motor actions. *Cognitive Brain Research*, *3*(2), 131–141.

Rizzolatti, G., Fogassi, L., & Gallese, V. (2001). Neurophysiological mechanisms underlying the understanding and imitation of action. *Nature Reviews Neuroscience*, *2*, 661–669.

Saxe, R., Xiao, D.-K., Kovacs, G., Perrett, D. I., & Kanwisher, N. (2004). A region of right posterior superior temporal sulcus responds to observed intentional actions. *Neuropsychologia*, *42*, 1435–1446.

Schwarzlose, R. F., Baker, C. I., & Kanwisher, N. (2005). Separate face and body selectivity on the fusiform gyrus. *Journal of Neuroscience*, *25*(47), 11055–11059.

Spiridon, M., Fischl, B., & Kanwisher, N. (2006). Location and spatial profile of category-specific regions in human extrastriate cortex. *Human Brain Mapping*, *27*, 77–89.

Sprengelmeyer, R., Rausch, M., Eysel, U. T., & Prezuntek, H. (1998). Neural structures associated with recognition of facial expressions of basic emotions. *Proceedings of the Royal Society B: Biological Sciences*, *265*(1409), 1927–1931.

Sugiura, M., Friston, K. J., Willmes, K., Shah, N. J., Zilles, K., & Fink, G. R. (2007). Analysis of intersubject variability in activation: An application to the incidental episodic retrieval during recognition test. *Human Brain Mapping*, *28*(1), 49–58.

Szameitat, A. J., Shen, S., & Sterr, A. (2007). Motor imagery of complex everyday movements: An fMRI study. *NeuroImage*, *34*(2), 702–713.

Thompson, J. C., Clarke, M., Stewart, T., & Puce, A. (2005). Configural processing of biological motion in human superior temporal sulcus. *Journal of Neuroscience*, *25*(39), 9059–9066.

Tootell, R. B. H., Mendola, J. D., Hadjikhani, N. K., Ledden, P. J., Liu, A. K., Reppas, J. B., et al. (1997). Functional analysis of V3A and related areas in human visual cortex. *Journal of Neuroscience*, *17*(18), 7060–7078.

Wei, X., Yoo, S. S., Dickey, C. C., Zou, K. H., Guttmann, C. R., & Panych, L. P. (2004). Functional MRI of auditory verbal working memory: Long-term reproducibility analysis. *NeuroImage*, *21*, 1000–1008.

Zacks, J. M., Braver, T. S., Sheridan, A., Donaldson, D. I., Snyder, A. Z., & Ollinger, J. M. (2001). Human brain activity time-locked to perceptual event boundaries. *Nature Neuroscience*, *4*(6), 651–655.

APPENDIX

TABLE A1
English translation of the 98 questions of the attitude survey

Questions about consciousness in relation to art	
Q1	You are impressed when you watch a difficult artistic performance.
Q2	When you attend an artistic event, you make arrangements in advance.
Q3	You admire specific works of art.
Q4	You imagine performing works of art, even if you have no experience.
Q5	You think that it is cool to own works of art.
Q6	You would like to undertake works of art, even if you have no experience.
Q7	You think that friendship is improved by works of art.
Q8	You are interested in the cultural background of art.
Q9	You think that it is valuable to undertake works of art in the future.
Q10	You practice hard to give a good performance.
Q11	You feel good when undertaking/performing a work of art.
Q12	You like it when you can devote time to a work of art.
Q13	With respect to art, you prefer individual performances to group performances.
Q14	You want to perform your particular art form well by practicing hard.
Q15	You think that you would like to undertake a performance in accordance with your ideal image.
Q16	You want to make friends with various people by undertaking/performing works of art.
Q17	You appreciate the feeling of togetherness that ensues in working with other actors to express an idea in a work of art.
Q18	With respect to art, you prefer group performances to individual performances.
Q19	You would like a lot of people to watch your artistic performance.
Q20	You feel an attraction to creating something beautiful from something you have imagined.
Q21	You want to always perform your artistic performance better than the performer of the same role.
Questions about consciousness in relation to sport	
Q22	When you attend a sporting event, you make plans in advance.
Q23	Your feelings are influenced by the results of your favorite sports team.
Q24	You are impressed when you watch a well-executed play in one of your favorite sports.
Q25	You are impressed when you watch an expert performing in your favorite sport.
Q26	When you watch an exciting sporting activity, you want to take part in it immediately.
Q27	You are interested in the world of athletes.
Q28	You imagine situations in which you play a particular sport, even if you have no experience of playing it.
Q29	You are impressed when you watch a well-executed play in a sport, even if you have no experience in that sport.
Q30	You want to take part in a particular sport, even if you have no experience of it.
Q31	You have admiration for specific sports that you have not experienced.
Q32	You are interested in the cultural background of sports.
Q33	You think that it is valuable to play sports in the future.
Q34	You want to train your mental powers through sports.
Q35	You want to train your physical powers through sports.
Q36	You want to make friendships through sports.
Q37	You are attracted to team sports.
Q38	When you take part in a sport, your motivation is enhanced when someone arouses your admiration.
Q39	You want to make friends with various people through participating in sport.
Q40	You want a lot of people to watch you take part in a sport.
Q41	You are pleased when people cheer your execution in playing a sport.
Q42	You prefer team sports to individual sports.
Q43	You prefer individual sports to team sports.
Q44	You like it when you can devote time to your favorite sport.
Q45	You want to play your favorite sport well by practicing hard.
Q46	You feel good when playing sports.
Q47	When there is a competition, you want to achieve a good result by practicing hard.
Q48	When taking part in sports, you feel good when you play well, in accord with your self-image.
Questions about handcrafts	
Q49	When you craft an object, you are pleased when work progresses.
Q50	When you craft an object, you like working with your hands.
Q51	When you craft an object, you are excited when a procedure is difficult.

Q52	When you craft an object, you imagine the outcome from a working procedure.
Q53	When you make an object, you imagine specific procedures for making it before starting work.
Q54	In a crafting procedure, repetition of simple work is relaxing for you.
Q55	When you make an object, you want to make it close to your ideal-image of that item.
Q56	When you make an object, you choose size, form, and function as needed.
Q57	When you make an object, you clearly imagine the completed state before beginning work.
Q58	When you make an object, you want to complete it quickly and use it yourself.
Q59	When you make an object, you modify it to make it more useful.
Q60	When you make an object, you want to compare it with the same object made by your friend.
Q61	There is an object that you want to be able to make in the future.
Q62	When you make an object, you imagine showing another person your finished product.
Q63	When you make an object, you want another person to use it.
Questions about tendencies to communicate with machines, animals, leafy plants	
Q64	Sometimes you think you are aware of the feelings of machines.
Q65	Sometimes you think you understand the feelings of machines.
Q66	Sometimes you think you are aware of the feelings of animals.
Q67	Sometimes you think you understand the feelings of animals.
Q68	You name animals that are not your pet nor that of a friend.
Q69	Sometimes you think you are aware of the feelings of leafy plants.
Q70	Sometimes you think you understand the feelings of leafy plants.
Q71	You name the machines and the goods that you use.
Q72	You criticize in your mind an animal that does not listen to what you say.
Q73	When a machine breaks while you are operating it, you might think that the machine is unfriendly.
Q74	When you and another person are together, you verbally criticize an animal that does not listen to what you say.
Q75	When you and another person are together, you might say that a machine was unfriendly if it broke while you operated it.
Q76	When you and another person are together, you verbally criticize a machine that has some fault.
Q77	You criticize in your mind a machine that has some fault.
Q78	When you are alone, you verbally criticize an animal that does not listen to what you say.
Q79	When you are alone, you might say that a machine was unfriendly if it broke while you operated it.
Q80	When you are alone, you verbally criticize a machine that has some fault.
Q81	You say tender things to a pet, such as “grow big,” in your mind.
Q82	When you are alone, you speak to leafy plants.
Q83	When you give a plant water, you think of things to say like “grow well” in your mind.
Q84	When you and another person are together, you speak to your pets.
Q85	When you and another person are together, you speak positively to a machine.
Q86	You say in your mind things like “you look very fine” to a machine that is working well.
Q87	When are you alone, you say things to pets, such as “grow well”.
Q88	When you are alone, you speak positively to a machine.
Q89	When you and another person are together, you speak to leafy plants.
Q90	When you and another person are together, you apologize to goods that you broke by accident.
Q91	When you and another person are together, you speak of being worried about a machine that is in bad condition.
Q92	When you and another person are together, you speak encouragingly to a machine that is in bad condition.
Q93	You apologize to goods that you broke by accident in your mind.
Q94	You say things in your mind to encourage a machine that is in bad condition.
Q95	You worry about a machine that is in bad condition.
Q96	When you are alone, you verbally apologize to goods that you broke by accident.
Q97	When you are alone, you verbally worry about a machine that is in bad condition.
Q98	When you are alone, you verbally encourage a machine that is in bad condition.

Notes: Subjects were instructed to answer each question on a 0–10 scale. The order of the 98 questions was counterbalanced among the subjects.