

Differential brain response to one- or two-hand handling action: an fMRI study

Keiko Tagai¹
Hitomi Shimakura¹
Sadaki Takata¹
Masayoshi Nagai²
Katsumi Watanabe³
Kazuhisa Niki²
Sunao Iwaki²
Takatsune Kumada²

¹Shiseido Research Center, Kanagawa, Japan; ²National Institute of Advanced Industrial Science and Technology (AIST), Ibaraki, Japan; ³The University of Tokyo, Tokyo, Japan

Abstract: In interpersonal communication, body posture and actions serve as important channels for transmitting social signals, which often vary among cultures and possess functional and affective elements. In Asian cultures, it tends to be commonly considered that handing an object with two hands is more polite than using only one hand. Using functional magnetic resonance imaging (fMRI), we examined whether an individual handing an object with one versus two hands would produce differential brain activity in the receiver. Thirteen participants observed 10 second movie clips in which a model moved an object using either two hands or one hand and the perceived politeness of each action was evaluated. In the control condition, two static images of the first and last frames of a movie were presented. Results showed that ratings of politeness were significantly higher for actions involving two hands compared to one hand. Significant fMRI signal changes were found in the bilateral occipital lobe in both the two-handed and one-handed conditions relative to the control condition. Compared to the use of one hand, observing an action involving two hands was associated with a higher politeness rating and increased activation in the inferior frontal gyrus. These results suggest that activation in the bilateral occipital lobe is involved in the processing of hand actions and the inferior frontal gyrus is associated with interpersonal cognition.

Keywords: fMRI, social cognition, nonverbal behavior, handing action, politeness

Introduction

In interpersonal communication, body posture and action serve as important channels for transmitting social signals. This nonverbal behavior has the potential for forming communicative messages if another person interprets the behavior and attributes meaning to it.¹ In actions that are performed in interpersonal relationships, the agent and receiver of an action mutually communicate reciprocal intention and affect behind the action, which can be considered one of the basic aspects of social communication and behavior.

In this study, we attempt to shed light on specific body postures and actions that are intended to express consideration and thoughtfulness to others. In Asian cultures, such as Japanese, Chinese, and Korean, handing an object to another person with two hands serves more than a functional purpose. Rather, in such cultures, the use of two hands to pass an object when one hand could be used is a form of nonverbal information that conveys politeness. In Japan, a traditional manual on women's etiquette, *Onna Shorei Ayanishiki*, published in 1772, described how to use each finger of the two hands when handing objects to another person as an expression of politeness, consideration, thoughtfulness, and respect toward the receiver. Japanese culture, similar to a number of other cultures,

Correspondence: Keiko Tagai
2-2-1, Hayabuchi, Tsuzuki-ku,
Yokohama, Kanagawa
224-8558, Japan
Email keiko.tagai@to.shiseido.co.jp

places importance on the use of graceful hand and finger mannerisms. Such etiquette is exemplified in the traditional Japanese tea ceremony, in which a host expresses hospitality for visitors through the use of various ceremonious actions, including handing a teacup to another individual with two hands. This traditional form of expressing hospitality by hand actions is also popular in modern shops in Japan, where a retail assistant may pass a commodity to a customer using two hands rather than one hand. This kind of cultural response, which is referred to as “polite capitalism,” reportedly changed during the Edo period (1603–1868) in Japan.² Wealthy merchants began to emphasize business discipline and ethics, as well as manners and behaviors of dealing with customers.²

Thus, appropriate handing actions represent not only functional elements but also affective elements to the receiver of the action, even in modern Japanese culture. Although psychological mechanisms for affective aspects of action are unclear, especially for politeness, a recent behavioral study showed that slower actions were associated with stronger impressions of politeness.³ Therefore, the affective aspect of actions, such as impressions of politeness, beauty, and gracefulness, may be related to redundant, inefficient, and ceremonial aspects of action.

The neural basis for the affective impact of action remains equivocal. It is reasonable to consider that neural activities that occur while an individual observes an action performed by another individual are relevant. The exception was the finding of mirror neurons in the premotor cortex of the macaque monkey.⁴ A mirror neuron is a neuron that activates both when a monkey itself performs an action, as well as when it observes the same action being performed by another agent. On the assumption that there might be a comparable neural system in humans, the discovery of mirror neurons in monkeys prompted research in humans over the past two decades, focused on observing and imitating actions of the hand, figures, face, and feet.⁵ Baars and Gage⁶ reported that area F5 in the macaque and Brodmann’s area (BA) 44 in humans seem to code for handing actions, whereas both area F4 in the macaque and the ventral premotor cortex in humans respond to arm and wrist movement.⁷

A recent review⁸ examined 139 studies that used functional magnetic resonance imaging (fMRI) and positron emission tomography by combining activation likelihood estimation meta-analysis with probabilistic cytoarchitectonic maps of action observation and imitations of the human brain network. They concluded that the observation of object-related handing actions was consistently associated with activation in the inferior frontal gyrus (IFG), premotor

cortex, and inferior parietal lobule (IPL). These results may reflect the presence of a mirror neuron system in the human brain. Regarding the amount of motion, the IFG reportedly responds to other people’s leg movements or whole body and face movements more strongly than mouth and finger movements.⁸ For face movements, the IFG is known to be more sensitive to dynamic as opposed to static images.⁹ This indicates that the IFG tends to respond more to general movements that convey large amounts of information or meaning instead of specific movements.

It is also known that activities in the human mirror neuron system vary based upon how the receiver understands the intention of the others’ action. Shibata et al¹⁰ showed heightened activation of the right IFG during the observation of incongruent actions compared to the observation of congruent actions. Liew et al¹¹ suggested that unfamiliar gestures more strongly activated regions associated with the posterior component of the putative human mirror neuron system (pMNS) in the IPL, whereas familiar gestures more strongly activated a region associated with mentalizing (the dorsal medial prefrontal cortex) when asked to infer the intentions of intransitive gestures. The results suggest that perceptual and motor familiarity modulates both pMNS and mentalizing regions during action observations. Iacoboni et al¹² found differential brain activity, specifically in the right IFG, while participants observed an action of reaching out and picking up a cup versus other conditions involving the use of a cup. This finding suggests that the human mirror neuron system is involved in understanding an agent’s action intention in different contexts. Newman-Norlund et al¹³ reported that the right supramarginal gyrus (SMG) of the IPL was activated when responding to meaningful object-directed actions (ODAs), whereas the left SMG was more strongly activated when responding to meaningless ODAs. On the other hand, there was no difference in activation of the bilateral IFG in response to meaningful and meaningless ODAs. Based on these results, Tunik et al¹⁴ proposed that knowledge for how to use objects or the interaction between objects and effectors, such as the hand or foot was represented in the SMG.

This study aims to explore the neural basis involved in the processing of others’ affect aspects of actions, focusing on examining whether the frontal and parietal regions covering the frontoparietal mirror neuron system differentially responds to actions that are perceived to be polite versus impolite. To explore this question, fMRI was used to measure brain activity in individuals while they observed actions that involved handing objects with two hands versus one hand. We assumed that

handing objects with two hands was perceived to be relatively more polite than handing them with one hand. Although prior research has examined associations between the frontoparietal mirror neuron system and observations of various behaviors, no study to date has examined the nonfunctional aspect of actions associated with the perceived intentions of behaviors. If results showed differential responses between the use of two hands and one hand, this would indicate that the frontoparietal mirror neuron system is involved in perceived positive intentions and affect as well as functional aspects of handing an object to another person. Such a result may be interpreted as an indication that familiar nonverbal behavior reflects a neural process associated with positive affect in the receiver.

In order to emulate an everyday scenario, a face-to-face situation was simulated in which a salesperson at a cosmetics counter handed a product to a customer. Across different cultures, it is a common practice to act with politeness in service to customers in a variety of settings, including cosmetic counters. Typically, in such face-to-face cosmetics sales, the majority of the customers served are women. Thus, in the present research, only females were selected as participants in the study. Because females are more accustomed to face-to-face sales in purchasing cosmetics than males, females would be expected to respond psychologically and physiologically to stimuli in the study much as they would in a non-research context. Ikeda et al³ suggested that women tended to be more attracted to polite handing actions in the context of interpersonal cognition, whereas men were more sensitive to slickness and speed. Prior to the collection of fMRI data, we collected psychophysical data to determine whether hand and finger arrangements of an actor affected the subjective impressions of the receiver. Specifically, we examined the following three hypotheses. First, we explored whether handing an object with two hands results in a stronger impression of politeness in the receiver than using one hand. Second, we examined whether the shape of one's fingers affected perceptions of politeness. Third, we examined whether subjective impressions of politeness were correlated with favorable ratings of action and attractiveness of the products. The latter research question is particularly relevant to marketing, since politeness may be indirectly communicated by the actions of a salesperson, which can influence the perceived attractiveness of products.

Materials and methods

Participants

Nineteen healthy, right-handed Japanese females (mean age 33.5 years, standard deviation [SD] = 4.7) participated in

a stimulus evaluation test; thirteen different healthy right-handed Japanese females (mean age 29.7 years, SD = 7.0) participated in an fMRI study. Each participant provided their informed consent in accordance with the Internal Review Board of the National Institute of Advanced Industrial Science and Technology guidelines of the Neuroscience Research Institute of the National Institute of Advanced Industrial Science and Technology, Ibaraki, Japan.

Stimulus evaluation

A stimulus evaluation test was conducted on video recordings depicting different ways that an object can be handed to another individual. Participants rated the video clips in terms of perceived degree of politeness. The presentation order was counterbalanced across participants. We also investigated the relationship among impressions of politeness, likability of handing action, and the perceived attractiveness of products. A situation was staged in which a face-to-face sale occurred involving 20 cosmetic products, including nine different bottles of lotion, seven different jars of cream, and four different tubes of cream. In the video, different ways of handing the product to a customer were recorded. Each condition varied based on the number of hands used to transfer the object and finger alignment. The following five conditions were included in the video: (1) two hands with fingers aligned; (2) two hands with fingers not aligned; (3) one hand with fingers aligned; (4) one hand with fingers not aligned; and (5) one hand grabbing from above. In the video recording, a salesperson placed the 20 products at the center of the counter using one of the five different ways of transferring the product. To enhance the sense of receiving the product, the hands were shown in the video in such a way that made the participant feel as though she was the customer. The presentation of conditions was randomized and participants rated the level of politeness, likability, and degree of attractiveness of the product by clicking along a horizontal line ranging from 0 (I don't think so) to 100 (I think so).

fMRI task design

Based on the results of the stimulus evaluation test, two conditions were chosen: namely, the two-hand condition and the one-hand condition. In each video clip, salespersons acted as if they were handing a cosmetic container, such as a bottle, or a tube to the participant using either two hands, or just one hand. In the two-hand condition, both hands transferred the object with both fingers aligned. In the one-hand condition, one hand transferred the object and the fingers were not

aligned. In each video clip, the salesperson acted as if they were handing a cosmetic, either a bottle or a tube container, to the participant using either two hands or one hand. In the control condition, two static images of the first and last frames of the video were presented. All these video clips were edited so that they were exactly 10 seconds long.

Figure 1 provides an overview of the time course of stimulus presentation and politeness ratings. The fMRI experiment was conducted using a block design. The fMRI session consisted of 12 trials in the two-hand condition, 12 trials in the one-hand condition, and 12 trials in the control condition, which were presented in a pseudo-random order. In each block, after viewing a fixation point for 2 seconds as a rest period, participants observed the 10 second video clip, followed by viewing the fixation point for 16 seconds, which was followed by a 3 second response period, and finally viewing the fixation point again for 16 seconds. During the response period, participants pressed a key to evaluate the politeness of each action on a scale ranging from 1 (very impolite) to 4 (very polite). In the generalized linear model (GLM) analysis, the video presentation period (10 s) and the response period (3 s) were modeled separately as independent regressors. In total, it took 1692 seconds to complete the functional scanning session.

fMRI data acquisition

All scanning was performed on a 3.0 T MRI Scanner (GE 3T Signa; GE Healthcare Corp, Waukesha, WI, USA) equipped with echo-planar imaging capability. The blood oxygenation level-dependent (BOLD) signal was measured by using a T2*-weighted echo-planar imaging sequence (repetition time 2000 ms, echo time 30 ms, flip angle 70 degrees). Twenty-seven axial slices (slice thickness 4.1 mm, gap 0.2 mm,

matrix size 64×64 , field-of-view: 20×20 cm) were acquired to cover the entire brain. A high-resolution T1-weighted anatomical image ($1 \times 1 \times 1$ mm) was collected for each subject after the functional scans (T1 anatomical scan parameters: slice thickness 1.2 mm, gap 0 mm, matrix size 256×192 , field-of-view: 200 mm, repetition time 10.7 ms, echo time 3.54 ms, flip angle 30 degrees). To avoid head movement, participants wore a neck brace and were asked not to talk or move during the scanning procedure.

fMRI data analysis

Statistical Parametric Mapping software (University College London, London, UK)¹⁵ was used for both individual and group analyses of the functional imaging data. Images were realigned using a six-parameter rigid-body spatial transformation and normalized to standard anatomical space (the Montreal Neurological Institute T1 template). Functional data were then smoothed with an isotropic 8 mm full-width-half-maximum Gaussian kernel and temporally processed using a high-pass filter with a frequency cutoff of 128 seconds. Serial correlations were modeled as a first-order autoregressive process.

Functional activation maps for individual subjects were computed from local BOLD signals by applying a linear multiple regression with conditions modeled as boxcar functions convolved by the hemodynamic response function. GLM regression parameters were estimated at each voxel for each subject and were subject to a group analysis.

Contrast analysis

Individual results were entered to a random effect group analysis to test if there were significant differences in brain activity between the two handing conditions and the control condition. Statistical inferences are based on *t* statistics over

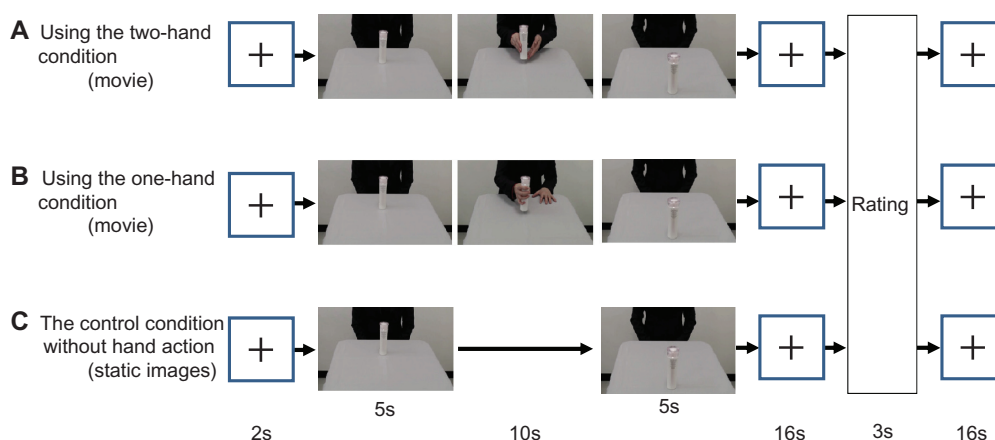


Figure 1 Time course of stimulus presentation and subjective rating of the politeness of each action (A–C).

Note: The time lapse between the rating of a video by the participants and the start of the next stimuli was 16 seconds.

the estimated regression parameters converted into normal distribution units. Significant increases in brain activity were found in the target conditions compared to the control condition, identified with a voxelwise significance threshold ($P < 0.005$, uncorrected). Significant increases in brain activity for the target conditions were identified relative to the control condition, based upon Lieberman and Cunningham¹⁶ as a voxelwise significance threshold of $P < 0.005$ (uncorrected) and a cluster extent threshold of 10 voxels.

Region of interest (ROI) analysis

A priori ROIs were selected that involved passive observation of handling actions following the previous meta-analysis results.⁸ Specifically, the following ROIs were analyzed: the left IFG/precentral gyrus (PrG), the left IPL, the left primary somatosensory cortex (SI)/intraparietal sulcus (IPS), the left lateral occipital (latOcc)/posterior middle temporal gyrus (pMTG), the left dorso-lateral premotor cortex/middle frontal gyrus (MFG), the right IFG/PrG, the right SI/IPS, the right superior parietal lobule (SPL), the right latOcc, and the right pMTG. The statistical parametric mapping toolbox MarsBar (CHU La Timone, Marseille Cedex, France)¹⁷ was used to test if there were significant changes in the regression parameter estimates (β weights), extracted from the spherical ROIs with 10 mm radius, between conditions. Significant changes in brain activity in each ROI were identified with a significance threshold $P < 0.01$ (false discovery rate < 0.05 , corrected).

Results

Stimulus evaluation

Means and standard deviations for subjective ratings of politeness, likability, and attractiveness of handling over the product were examined. Significant main effects were found for subjective ratings of politeness ($F(4,224) = 209.39$, $P < 0.01$), likability ($F(4,224) = 220.81$, $P < 0.01$) and attractiveness of the product ($F(4,224) = 120.64$, $P < 0.01$). Multiple comparisons (Bonferroni, $\alpha = 0.05$) revealed that, for all subjective ratings, the condition of two hands with fingers aligned was rated significantly higher than the other handling actions (see Table 1). For politeness ratings, the conditions of one hand with fingers not aligned and one hand grabbing from above received lower subjective ratings than the other handling actions. A similar tendency was also shown for the type of container. For likability rating, the condition of one hand grabbing from above received the lowest subjective ratings. In terms of the product's attractiveness, subjective ratings for two hands with fingers not aligned, one hand with

Table 1 Means and standard deviations for subjective ratings of politeness, likability, and how attractive the product was of 5 different ways of handling over the product

Subjective rating	Both hands with fingers aligned		Both hands with fingers not aligned		One hand with fingers aligned		One hand with fingers not aligned		One hand grabbing from above	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
1. Politeness	74.31	10.12	22.28	15.92	50.02	19.17	17.97	14.01	15.88	14.15
2. Likability	71.38	14.94	17.10	13.94	46.84	19.95	14.36	12.25	12.08	11.63
3. How attractive the product was	63.93	15.24	24.48	16.05	47.94	19.23	22.33	14.73	20.99	14.52

Note: $n = 19$.

Abbreviation: SD, standard deviation.

fingers not aligned, and one hand grabbing from above were lower than for the other handing actions. Subjective ratings of likability ($r = 0.90$, $P < 0.01$) and product attractiveness ($r = 0.96$, $P < 0.01$) were significantly correlated with ratings of politeness. Subjective ratings of likability and product attractiveness were also significantly correlated ($r = 0.91$, $P < 0.01$).

Behavioral ratings of politeness recorded during the fMRI task

Paired t tests revealed a significant difference in subjective ratings of politeness recorded during the fMRI task between the two-hand and one-hand conditions ($t(12) = 45.3$, $P < 0.0001$). Participants evaluated handing actions using two hands with aligned fingers as more polite than actions involving one hand with unaligned fingers (see Figure 2).

Contrast analysis of fMRI data

Effects of two-hand condition and one-hand condition relative to control condition

Table 2 and Figure 3 depict the brain regions where increased activities were observed in the two-hand and one-hand conditions, relative to the control condition. Activities in the bilateral IFG, the MFG, and the SPL were observed in both conditions ($P < 0.005$, uncorrected). The activities observed for the two-hand condition were much higher than for the one-hand condition, with the exception of the left IFG.

Results of the direct comparison between the two-hand condition and the one-hand condition are also shown in Table 3 and Figure 3. Increased activity in the two-hand condition was observed in the bilateral frontal lobe (PrG) and right IPL relative to the one-hand condition

($P < 0.005$, uncorrected). The main effect of the one-hand condition relative to the two-hand condition revealed significant differential activation in the left medial frontal gyrus ($P < 0.005$, uncorrected). Activities in the bilateral superior frontal gyrus were observed in both comparative conditions ($P < 0.005$, uncorrected).

Region of interest (ROI) analysis of fMRI data

Contrast analysis revealed that in comparison to the control condition, the two-hand condition produced large responses in the IFG, whereas the one-hand condition caused small responses. Furthermore, large responses in the bilateral IFG, the bilateral PrG, and the right IPL were observed in the two-hand condition compared to the one-hand condition.

Based upon a prior meta-analysis of object-related hand actions,⁸ further analyses were conducted using an ROI approach. Figure 4 shows GLM regression parameters for 10 ROIs averaged across participants. Activity in the bilateral latOcc/pMTG areas was significantly increased in both the two-hand condition and the one-hand condition relative to the control condition. In the right IFG/PrG, a significant increase in brain activity was observed in the two-hand condition but not in the one-hand condition. In the left IFG/PrG, greater activity in the two-hand condition was observed in no correction for multiple comparisons ($P = 0.0242$, uncorrected), but was not statistically significant after false discovery rate correction.

Correlations between subjective ratings of handing action during the fMRI task and local BOLD signals estimated by GLM parameters were calculated separately for the one-hand and the two-hand conditions (Table 4). In the one-hand condition, the signal showed a significant negative correlation with subjective ratings for handing action in the left IPL, and a marginally significant positive correlation in the left IFG/PrG and the right SPL. In the two-hand condition, there was a marginally significant positive correlation in the right SPL and a negative correlation in the right SI/IPL. Signals in other areas did not show significant correlations with subjective ratings of handing action.

Discussion

The present study suggests that differential brain activity occurs when Japanese individuals observe the action of two hands compared to that of one hand. This result was found even though the action had the same purpose. One possible interpretation of this finding is that there are differences in the perceived amount of motion, such that a larger amount of motion is required for a two-handed action in comparison

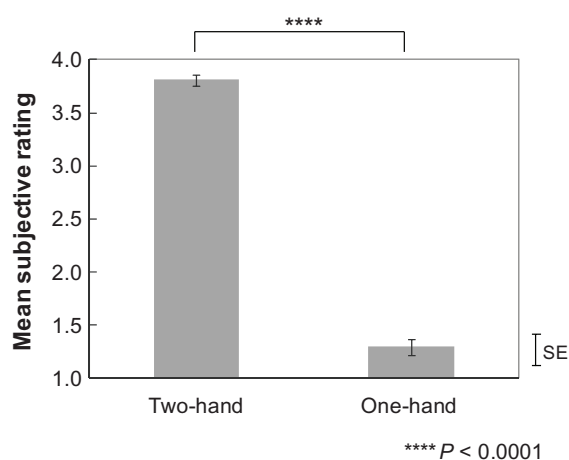


Figure 2 Mean behavioral ratings of politeness recorded during the fMRI task.

Note: Error bars refer to standard error of the mean.

Abbreviations: fMRI, functional magnetic resonance imaging; SE, standard error.

Table 2 Brain regions of significantly increased activation in comparison of the two-hand condition and the one-hand condition with the control condition

Anatomical region	Whole brain analysis						
	Hemisphere	BA	MNI coordinates			t value	Cluster size (voxels)
			x	y	z		
Two-hand minus control contrast							
Superior parietal lobule	R	7	30	−48	56	10.32	1653
Superior parietal lobule	L	7	−24	−68	58	9.78	931
Middle occipital gyrus	R	37	52	−64	−8	8.49	2652
Inferior temporal gyrus	L		−56	−68	2	6.64	832
Inferior frontal gyrus	R	45	50	26	0	5.6	66
Precentral gyrus	L	6	−36	−8	64	5.19	140
Middle frontal gyrus	R	6	36	−6	62	5.14	141
Inferior frontal gyrus	L	45	−52	28	4	5.07	84
Middle frontal gyrus	L	9	−54	14	30	4.8	191
Middle frontal gyrus	R	9	54	14	32	4.61	155
Inferior frontal gyrus	R	47	46	28	−12	4.43	28
Posterior lobe	L		−26	−88	−20	4.34	214
Postcentral gyrus	R	40	58	−30	54	3.78	32
Cuneus	R	19	−26	−84	24	3.6	30
Parahippocampal gyrus	R	27	18	−30	−4	3.43	15
Inferior frontal gyrus	R	46	46	38	10	3.43	18
One-hand minus control contrast							
Inferior temporal gyrus	R	37	52	−68	−2	10.44	1964
Inferior frontal gyrus	R	47	26	12	−20	8.33	55
Inferior occipital gyrus	L	19	−44	−78	−4	8.32	870
Inferior frontal gyrus	L	46	−50	38	12	5.57	33
Superior parietal lobule	R	7	24	−68	62	5.08	775
Inferior frontal gyrus	L	47	−30	32	−18	4.46	102
Middle frontal gyrus	L	10	−38	52	4	4.19	65
Middle frontal gyrus	R	11	28	34	−18	3.97	47
Inferior frontal gyrus	L	9	−46	12	28	3.94	60
Superior parietal lobule	L	7	−38	−54	64	3.75	44
Middle frontal gyrus	R	46	44	40	14	3.4	17

Notes: Brain regions were identified with a voxelwise significance threshold (Height: $P < 0.005$, uncorrected; extent-threshold > 10 voxels).

Abbreviations: MNI, Montreal Neurological Institute; BA, Brodmann's area; R, right; L, left.

to a one-handed action. Findings revealed that the superior lobule and occipital gyrus were activated for conditions involving two hands and one hand, whereas these regions were not activated during the control condition. ROI analysis also revealed that the bilateral latOcc (MT/V5) region and the pMTG, which are considered the centers for motion perception, were activated in the two-hand and one-hand conditions compared to the control condition.^{18,19} However, neither the contrast analysis, nor the a priori ROI analysis, indicated any significant differences between these areas when directly comparing the two-hand and one-hand conditions. Therefore it was considered that rather than reflecting differences in the number of moving hands, these responses reflected differences in the perception of hand motions in still and moving images. When static images

were compared to videos, MT/V5 and MTG demonstrated greater activity not only for hand movements but also for body and face movements. Furthermore, these regions have been found to respond more to movements of people rather than to objects, which signifies their role in visual human motion perception.⁹ In addition, V1 has been found to be the only motor region involved in perceptions of the amount of motion.²⁰ The differences in activity between the video and static image is likely due to difference in volumes of perceived information in visual perception of human motion across the two conditions. Our finding that there was no difference between actions involving two hands in comparison to one hand in the lateral occipital region and the MTG indicates that there was no difference associated between the two conditions in terms of human visual motion perception.

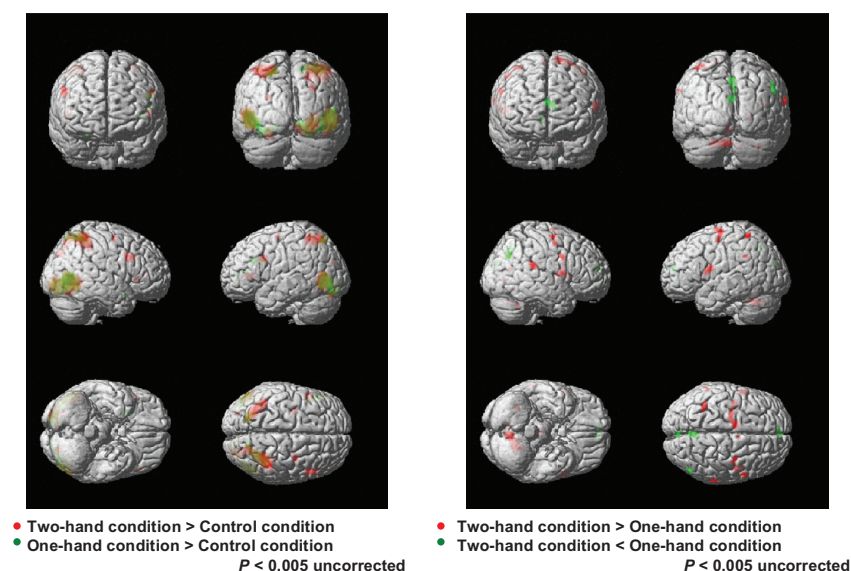


Figure 3 Statistical parametric map showing the group activations for the conjunction of the two-hand condition and the one-hand condition versus the control condition and the contrast between the two-hand condition and the one-hand condition.

Notes: Red color; Two-hand condition > Control condition. Green color; One-hand condition > Control condition. Brain regions of increased activation associated with handing action: conjunction between Two-hand condition, One-hand condition, and Control condition (Height: $P < 0.005$, uncorrected; extent-threshold > 10 voxels).

Table 3 Brain regions of significantly increased activation in comparison of the two-hand condition with the one-hand condition

Anatomical region	Whole brain analysis						Cluster size (voxels)
	Hemisphere	BA	MNI coordinates			t value	
			x	y	z		
Two-hands minus one-hand contrast							
Posterior lobe	L		-8	-68	-34	6.87	418
Inferior parietal lobule	R	40	66	-36	22	5.66	82
Precentral gyrus	L	44	-60	8	12	5.53	159
Posterior lobe	L		-2	-62	-12	4.94	110
Midbrain	L		-2	-26	-8	4.47	69
Precentral gyrus	R	44	56	10	6	4.45	185
Precentral gyrus	R	6	50	-4	52	4.04	56
Superior frontal gyrus	L	6	-16	-10	70	4	124
Lingual gyrus	R	19	24	-72	0	3.98	21
Cerebellar tonsil	R		34	-56	-34	3.97	30
Posterior lobe	R		10	-84	-22	3.89	10
Precentral gyrus	L	6	-44	-4	58	3.83	53
Postcentral gyrus	L	5	-40	-48	62	3.71	57
Precentral gyrus	R	6	58	6	34	3.65	33
Precentral gyrus	R	6	40	-10	62	3.59	22
Superior frontal gyrus	R	6	6	-2	68	3.51	11
Middle temporal gyrus	R	39	42	-66	16	3.48	15
One-hand minus two-hands contrast							
Cuneus	L	18	0	-86	24	5.56	81
Medial frontal gyrus	L	9	-4	52	16	4.77	107
Angular gyrus	R	39	52	-68	36	4.72	138
Superior frontal gyrus	R	10	10	58	-4	3.72	41
Precuneus	R	7	4	-60	46	3.71	104
Superior temporal gyrus	R	38	44	12	-34	3.65	13
Superior frontal gyrus	R	8	38	28	52	3.63	15
Anterior cingulate	L	32	-6	42	6	3.62	12
Superior frontal gyrus	L	8	-38	30	52	3.54	11

Notes: Brain regions were identified with a voxelwise significance threshold (Height: $P < 0.005$, uncorrected; extent-threshold > 10 voxels).

Abbreviations: MNI, Montreal Neurological Institute; BA, Brodmann's area; R, right; L, left.

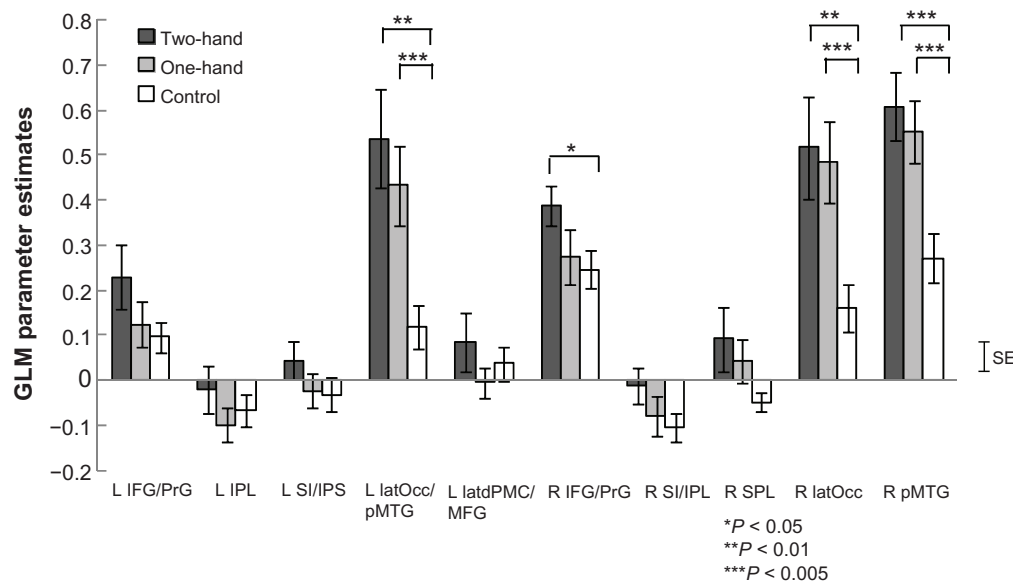


Figure 4 GLM parameter estimates for the two-hand condition and the one-hand condition relative to the control condition in ten regions of interest.

Note: Error bars refer to standard error of the mean.

Abbreviations: GLM, generalized linear model; IFG, inferior frontal gyrus; PrG, precentral gyrus; IPL, inferior parietal lobule; SI, primary somatosensory cortex; IPS, intraparietal sulcus; latOcc, lateral occipital; pMTG, posterior middle temporal gyrus; latdPMC, dorso-lateral premotor cortex; MFG, middle frontal gyrus; SPL, superior parietal lobule; R, right; L, left.

Differences in activation of the IFG between two hands and one hand may not be a simple by-product of different amounts of movement. Rather, such differences could reflect alterations in perceived context or interpretation of the action. Consistent with the work of Grosbras et al,⁹ in which IFG was activated by motions of large volumes or with special meaning, our findings suggest the possibility that activation of the IFG reflects a psychological process in which motion information is imbued with special meaning. This also supports the contention that subjective ratings of handing action reflected activation of the left IFG in the one-hand condition.

Findings regarding stimulus evaluation indicate that the position of fingers affects one's subjective evaluation of politeness. In contrast, in their study comparing brain responses to observed finger positions, Costantini et al²¹

reported that both the IFG and the PrG were activated in response to both anatomically possible and impossible motions. Thus, based upon the results of the present study, it can be inferred that the IFG is affected by whether the motion was made by two hands or one hand as opposed to by finger position.

Using two hands to hand over an object when the object can be transferred with one hand is an action that is unnecessary and incongruent in terms of its functionality. The use of two hands, rather than one, to pass an object can also be considered excessive since it unnecessarily involves a greater amount of movement. Thus, the present results may reflect the degree of extra movements that occurred above and beyond the necessary movements required to fulfill the functional role of passing an object to another individual. The psychological effect produced by excessive motion could

Table 4 Correlation (*r*) between subjective rating of handing action and BOLD signal change in each ROI, shown with the probability of significance (*P*)

	Left					Right				
	IFG/ PrG	IPL	SI/ IPS	latOcc/ pMTG	latdPMC/ MFG	IFG/ PrG	SI/IPL	SPL	latOcc	pMTG
Two-hands	-0.22	-0.08	0.01	-0.11	0.32	-0.29	-0.42 [†]	0.42 [†]	-0.14	-0.29
One-hand	0.44 [†]	-0.53*	0.18	-0.09	-0.04	-0.28	-0.23	0.47*	0.08	0.12

Notes: **P* < 0.05; [†]*P* < 0.1.

Abbreviations: BOLD, blood oxygenation level-dependent; ROI, region of interest; IFG, inferior frontal gyrus; PrG, precentral gyrus; IPL, inferior parietal lobule; SI, primary somatosensory cortex; IPS, intraparietal sulcus; latOcc, lateral occipital; pMTG, posterior middle temporal gyrus; latdPMC, dorso-lateral premotor cortex; MFG, middle frontal gyrus; SPL, superior parietal lobule.

lead to different interpretations of intent. In the subjective ratings of action, the condition using two hands was rated as more polite than the condition using one hand. Ratings of politeness of this action correlated strongly with likability of the action and the product's perceived attractiveness. These strong positive correlations were thought to be causally related to the format of rating items. Regardless, it was shown that politeness was expressed as a positive aspect of the action. Observing actions that are associated with positive affect tends to result in positive affect in the observer. As a result, the observer may become more attached to a product that was handled in a manner associated with positive affect compared to product handling that is less related to positive affect. Thus, results of the present study suggest that polite movements and the perceived attractiveness of products may be linked with future purchase behavior.

The present findings suggest that both two-hand and one-hand actions have the same function and outcome since there were no significant differences in activity of the IPL. Biagi et al²² reported that more activities were elicited in the anterior intraparietal sulcus (AIP) by complex hand movements (eg, grasping an item followed by placing it in a box) than by simple movements (eg, grasping an item). The mirror-like responses in the AIP in response to hand movements indicate that activity in this region varies according to the complexity of the hand movements. Biagi et al²² also suggest that complex movements have more functional and useful results compared to simple movements. Fogassi et al²³ suggest that grasping neurons of the IPL in monkeys are modulated by the final action outcome. In addition, both two-handed and one-handed actions have been hypothesized to include the same meaningful actions.¹³

Though there were no significant differences in parietal lobe activity between two-hand and one-hand actions, the correlation analyses of subjective ratings during the fMRI task and local BOLD signals estimated by GLM parameters in ROI suggested that the parietal mirror system was related to the process of affective value of politeness. In both the two-hand and the one-hand conditions, a positive correlation was seen in the right SPL, whereas, a negative correlation was seen in the right IPL in the two-hand condition. This finding was identical for the left IPL in the one-hand condition. Since there was a tendency for a similar correlation to be observed in the IPL and the SPL for two-hand and one-hand actions, respectively, this suggests that the IPL and the SPL perform functions related to the affective value of politeness during handling actions. However, since the correlation in the SPL was positive and that of IPL was negative, this suggests that

the IPL and SPL have different functions related to the affective value of politeness, which cannot be identified from the results of this study.

The BA44 region in humans, considered analogous to the F5 region in macaques, has been found to respond to imitation or observations of handing actions in the mirror neuron system.^{5,7,24} Prior research has shown that the BA45 region is involved in observing behavior, the caudodorsal part of BA44 is activated during observations of behavior and imitation, and the caudoventral portion of BA44 is activated during the imitation of behavior.⁸ During hand actions, the IFG is activated when the hand may respond to the agent's intention of the action in context.¹² In this study, a response was not observed in the medial prefrontal cortex, but was observed in the IFG during conditions involving two hands and one hand. Based upon this finding, it is possible that the receiver understands the intention of the other's action. Moreover, these areas, which are known as Broca's area, control language function. According to Gallese,²⁵ mirror neurons that comprise the neural network for understanding other people's actions are the origin of language. Based upon this theory, information processing involved in non-verbal communication, such as the observation of behavior or imitation and information processing for verbal actions, are involved in the language acquisition process. Since interpersonal communication utilizes nonverbal and verbal communication simultaneously, frontal mirror systems may be associated with neural expressions in which nonverbal behavior is converted to nonverbal messages.

The results of the present study suggest that the expression within the brain of the affective value of politeness, which involves the intention of behavior, is located in the frontoparietal mirror system. However, there were several limitations in the present study that need to be clarified in the future. Firstly, this study examined only one variation of politeness using two hands relative to one hand. In order to better understand the role of brain regions involved in coding politeness, it would be necessary to use different body actions. Secondly, the control condition used in the present study did not include hands when comparing between the control condition and one- or two-hand handing conditions. Therefore, the brain response may have reflected two variables, hands, and the motion of hands. The contrast analysis indicated that different parts of the brain were activated depending on the one- or two-handed condition, whereas in the ROI analysis, there were no significant differences in brain activity based on these two conditions. Future studies would need to examine the effects of hand movements on brain

activity by including an extra control condition consisting of a static image of hands without movements. Comparison with such a control condition would more clearly isolate the differences in brain activity between one- and two-hand motions. Thirdly, there is a need to conduct a comparison with a condition in which the stimuli consist of two-hand movements, but without the intention of handing over an object, such as random, meaningless, two-hand movements. The results of such a comparison would confirm that the IFG activity during handing an object with two hands involves meaning rather than the perceived degree of motion. Newman-Norlund et al¹³ suggested that there was no difference in activation of IFG in response to meaningful and meaningless ODAs. The IFG was activated in the observation of both types of actions, and during action imagery, when predicting the goals of two-hand actions.²⁶ During the observation of correct actions and error movements with two hands, activation was induced within the right ventrolateral premotor cortex (vPMC), whereas object-related violations with two-hand induced activations within the left vPMC.²⁷

Lastly, the results of this study regarding men and non-Japanese participants can be considered from another perspective. Participants in the present study were all Japanese females. Yavas et al²⁸ and Noble et al²⁹ suggested that female customers attach more importance to interpersonal relationships and communication, that is to say, to social interactions than male customers. Therefore, the gender of the participants could have been a factor moderating the effects of empathy and reliability related to the satisfaction with the service.³⁰ Comparisons between people of different cultures are necessary to investigate brain functions related to cultural variables. Findings regarding the function of the frontal lobes in non-Japanese participants, when responding to the same stimuli as in the present study, would further clarify our understanding of cultural differences in the perception of one- and two hand actions.

Future studies should also compare handing an object paired with negative connotations that lead to attention and warnings. Schubotz and von Cramon have indicated that brain responses for different objects differ, even when the same action is performed.³¹ Another area of future research could involve comparisons between humans and robots performing the same action. In prior studies, only small differences were found in the mirror neuron system's response to a functional action performed by humans compared to robots.³² In pain research, differential brain responses were observed when pain was directed toward a human rather than a robot or mannequin.³³ If a recipient's brain response

from handing an object using two hands contains similar affective elements, such as politeness and respect for others, regardless of whether the giver is a robot or human, this would support the use of robots for service. The results of the present study suggest that finding a movement of another person polite, which elicits positive affects, increases trust in the other person and potential attraction to the product, possibly resulting in motivation to purchase. Face-to-face sales methods between humans are of significant economic value in modern globalized society and regardless of the outcome, a study contrasting humans versus robotic devices could elucidate the relationship between interpersonal communication and brain function.

Conclusion

In conclusion, we investigated whether specific brain activity would differentiate handing objects with two hands as opposed to one hand. The results of the current fMRI study suggest that differential brain responses occurred in the IFG when an individual observed the action of handing an object with two hands as opposed to one hand. Subjective ratings of politeness differed significantly based upon whether the handing action involved two hands versus one hand. The present results imply that the IFG is involved in interpersonal cognition during situations involving hand-action observations.

Disclosure

The authors report no conflicts of interest in this work.

References

1. Richmond VP, McCroskey JC. *Nonverbal Behavior in Interpersonal Relations*, 5th ed. Boston: Allyn and Bacon; 1995.
2. Ikegami E. *Bonds of Civility: Aesthetic Networks and the Political Origins of Japanese Culture*. New York: Cambridge University Press; 2005.
3. Ikeda H, Fukui T, Tagai K, Takata S, Watanabe K. Politeness Perception in Action: Subjective Impression of Handing Actions by Professional Sales Persons. Proceedings of the International Conference on Kansei Engineering and Emotion Research; May 22–25, 2012; Penghu, Taiwan.
4. Rizzolatti G, Fadiga L, Gallese V, Fogassi L. Premotor cortex and the recognition of motor actions. *Brain Res Cogn Brain Res*. 1996;3(2): 131–141.
5. Rizzolatti G, Fogassi L, Gallese V. Neurophysiological mechanisms underlying the understanding and imitation of action. *Nat Rev Neurosci*. 2001;2(9):661–670.
6. Baars BJ, Gage NM. Social cognition: perceiving the mental states of others. *Cognition, Brain, and Consciousness: Introduction to Cognitive Neuroscience*, 2nd ed. Burlington: Elsevier; 2010:445–463.
7. Rizzolatti G, Fogassi L, Gallese V. Motor and cognitive functions of the ventral premotor cortex. *Curr Opin Neurobiol*. 2002;12(2):149–154.
8. Caspers S, Zilles K, Laird AR, Eickhoff SB. ALE meta-analysis of action observation and imitation in the human brain. *NeuroImage*. 2010;50(3): 1148–1167.

9. Grosbras MH, Beaton S, Eickhoff SB. Brain regions involved in human movement perception: a quantitative voxel-based meta-analysis. *Hum Brain Mapp*. 2012;33(2):431–454.
10. Shibata H, Inui T, Ogawa K. Understanding interpersonal action coordination: an fMRI study. *Exp Brain Res*. 2011;211(3–4):569–579.
11. Liew SL, Han S, Aziz-Zadeh L. Familiarity modulates mirror neuron and mentalizing regions during intention understanding. *Hum Brain Mapp*. 2011;32(11):1986–1997.
12. Iacoboni M, Molnar-Szakacs I, Gallese V, Buccino G, Mazziotta JC, Rizzolatti G. Grasping the intentions of others with one's own mirror neuron system. *PLoS Biol*. 2005;3(3):e79.
13. Newman-Norlund R, van Schie HT, van Hoek MEC, Cuijpers RH, Bekkering H. The role of inferior frontal and parietal areas in differentiating meaningful and meaningless object-directed actions. *Brain Res*. 2010;1315:63–74.
14. Tunik E, Lo OY, Adamovich SV. Transcranial magnetic stimulation to the frontal operculum and supramarginal gyrus disrupts planning of outcome-based hand-object interactions. *J Neurosci*. 2008;28(53):14422–14427.
15. SPM8, Methodology group [webpage on the Internet]. London: Wellcome Trust Centre for Neuroimaging. Available from: <http://www.fil.ion.ucl.ac.uk/spm/>. Accessed January 12, 2013.
16. Lieberman MD, Cunningham WA. Type I and Type II error concerns in fMRI research: re-balancing the scale. *Soc Cogn Affect Neurosci*. 2009;4(4):423–428.
17. Brett M, Anton JL, Valabregue R, Poline JB. Region of interest analysis using an SPM toolbox [abstract]. Proceedings of the 8th International Conference on Functional Mapping of the Human Brain; June 2–6, 2002; Sendai, Japan.
18. Peuskens H, Vanrie J, Verfaillie K, Orban GA. Specificity of regions processing biological motion. *Eur J Neurosci*. 2005;21(10):2864–2875.
19. Beauchamp MS, Martin A. Grounding object concepts in perception and action: Evidence from fMRI studies of tools. *Cortex*. 2007;43(3):461–468.
20. Sunaert S, Van Hecke P, Marchal G, Orban GA. Motion-responsive regions of the human brain. *Exp Brain Res*. 1999;127(4):355–370.
21. Costantini M, Galati G, Ferretti A, et al. Neural systems underlying observation of humanly impossible movements: An fMRI study. *Cereb Cortex*. 2005;15(11):1761–1767.
22. Biagi L, Cioni G, Fogassi L, Guzzetta A, Tosetti M. Anterior intraparietal cortex codes complexity of observed hand movements. *Brain Res Bull*. 2010;81(4–5):434–440.
23. Fogassi L, Ferrari PF, Gesierich B, Rozzi S, Chersi F, Rizzolatti G. Parietal lobe: from action organization to intention understanding. *Science*. 2005;308(5722):662–667.
24. Kilner JM, Neal A, Weiskopf N, Friston KJ, Frith CD. Evidence of mirror neurons in human inferior frontal gyrus. *J Neurosci*. 2009;29(32):10153–10159.
25. Gallese V. Mirror neurons and the social nature of language: The neural exploitation hypothesis. *Soc Neurosci*. 2008;3(3–4):317–333.
26. Schubotz RI, von Cramon DY. Sequences of abstract nonbiological stimuli share ventral premotor cortex with action observation and imagery. *J Neurosci*. 2004;24(24):5467–5474.
27. Manthey S, Schubotz RI, von Cramon DY. Premotor cortex in observing erroneous action: an fMRI study. *Brain Res Cogn Brain Res*. 2003;15(3):296–307.
28. Yavas U, Benkenstein M, Stuhldreier U. Relationships between service quality and behavioral outcomes: a study of private bank customers in Germany. *International Journal of Bank Marketing*. 2004;22(2):144–157.
29. Noble S, Griffith D, Adjei M. Drivers of local merchant loyalty: understanding the influence of gender and shopping motives. *Journal of Retailing*. 2006;82(3):177–188.
30. Karatepe OM. Service quality, customer satisfaction and loyalty: the moderating role of gender. *Journal of Business Economics and Management*. 2011;12(2):278–300.
31. Schubotz RI, von Cramon DY. The Case of Pretense: Observing Actions and Inferring Goals. *J Cogn Neurosci*. 2009;21(4):642–653.
32. Gazzola V, Rizzolatti G, Wicker B, Keysers C. The anthropomorphic brain: The mirror neuron system responds to human and robotic actions. *Neuroimage*. 2007;35(4):1674–1684.
33. Jackson PL, Brunet E, Meltzoff AN, Decety J. Empathy examined through the neural mechanisms involved in imagining how I feel versus how you feel pain. *Neuropsychologia*. 2006;44(5):752–761.

Neuroscience and Neuroeconomics

Publish your work in this journal

Neuroscience and Neuroeconomics is an international, peer-reviewed, open access journal focusing on the identification of brain structures and measurement of neural activity related to behavior, behavioral predictions, and decision making in health and disease. The manuscript management system is completely online and includes a very quick and

Submit your manuscript here: <http://www.dovepress.com/neuroscience-and-neuroeconomics-journal>

Dovepress

fair peer-review system. Visit <http://www.dovepress.com/testimonials>.
php to read real quotes from published authors.