Neurofunctional Modulation of Brain Regions by the Observation of Pointing and Grasping Actions

Andrea C. Pierno[1], Federico Tubaldi[1], Luca Turella[1], Paola Grossi[2], Luigi Barachino[3], Paolo Gallo[2] and Umberto Castiello[1,4]

[1]Department of General Psychology, University of Padova, Padova 35131, Italy, [2]Department of Neuroscience, University of Padova, Padova 35131, Italy, [3]Euganea Medica, Albignasego, Padova 35131, Italy and [4]Department of Psychology, Royal Holloway College, University of London, London WC1E 6BT, UK

Previous neuroimaging research on healthy humans has provided evidence for a neural system underlying the observation of another person's hand actions. However, whether the neural processes involved in this capacity are activated by the observation of other transitive hand actions such as pointing remains unknown. Therefore, using functional magnetic resonance imaging we investigated the neural mechanisms underlying the observation of static images representing the hand of a human model pointing to an object (pointing condition), grasping an object (grasping condition), or resting in proximity of an object (control condition). The results indicated that activity within portions of the lateral occipitotemporal and the somatosensory cortices modulates according to the type of observed transitive actions. Specifically, these regions were more activated for the grasping than for the pointing condition. In contrast, the premotor cortex, a neural marker of action observation, did not show any differential activity when contrasting the considered experimental conditions. Our findings may provide novel insights regarding a possible role of extrastriate and somatosensory brain areas for the perception of distinct types of human hand–object interactions.

Keywords: action observation, fMRI, occipitotemporal cortex, pointing, somatosensory cortex

Introduction

Amongst the variety of actions a complex apparatus such as the human hand can perform, grasping and pointing with the index finger have been the focus of extensive neuroimaging research (for review see Castiello 2005; Culham et al. 2006; Castiello and Begliomini 2008). Relating to pointing, a number of early positron emission tomography (PET) studies reported motor, premotor, and parietal activations contralateral to the hand used to perform the action (Decety et al. 1992; Grafton et al. 1996; Kawashima et al. 1996; Kertzman et al. 1997). More recently these previous observations have been refined by using functional magnetic resonance imaging (fMRI). In particular, activations related to the planning and execution of pointing movements have been revealed within specific sectors of the parietal cortex, namely the medial intraparietal sulcus (mIPS), the precuneus (Grefkes et al. 2004; Grefkes and Fink 2005) and the extrastriate body area (EBA; Astafiev et al. 2004). As regards to grasping, converging evidence from a variety of PET and fMRI studies has revealed activation of a grasp-specific region within the anterior intraparietal sulcus (AIP; Grafton et al. 1996; Faillenot et al. 1997; Binkofski et al. 1998; Culham et al. 2003; Frey et al. 2005; Begliomini, Caria, et al. 2007; Begliomini, Wall, et al. 2007) and both the ventral and the dorsal sectors of the premotor (PM) cortex (Ehrsson

et al. 2000; Grèzes et al. 2003; Begliomini, Wall, et al. 2007). A direct comparison between brain activation evoked by the execution of grasping relative to that evoked by the execution of reach-to-point movements revealed 2 significant sites of activation within the hemisphere contralateral to the performing hand (Grafton et al. 1996; Frey et al. 2005). The first area is located in the left parietal cortex at the approximate intersection of the IPS with the postcentral sulcus. The second activation is located in the left lateral sulcus extending into the parietal operculum (SII).

Recently the investigation into the neural control of hand actions has been extended to action observation. The main finding is that observing a hand action triggers activity within a network of areas commonly termed as the "action observation system" which broadly matches the neural system underlying hand action execution (Rizzolatti et al. 1996; Decety et al. 1997; Decety and Grezes 1999; Buccino et al. 2001; Keysers and Perrett 2004; Tai et al. 2004; Gazzola et al. 2007). Specifically, the "action observation system" includes the PM cortex, the inferior parietal lobule (IPL), the inferior frontal gyrus (IFG) and the superior temporal sulcus (STS).

Whereas it has been demonstrated that this system is activated by the sight of grasping actions, its involvement for the coding of observed pointing actions remains unexplored. This might be an important issue to consider because one of the notions stemming from the grasping observation studies is that the same action representation underpins both action execution and action understanding. In other words, observation of hand actions would automatically induce the observer to re-enact the observed actions. With pointing, things might be different given that pointing actions may offer the observer different types of "motor" understanding. As suggested by Tomasello et al. (2007) pointing is a prelinguistic communicative gesture that can convey an almost infinite variety of meanings and whose understanding may require some sort of mindreading. In action execution terms, there is still a debate on whether pointing gestures are used by young infants to influence the intentional/mental states of others (cause someone to know something) or whether they are simply used to achieve certain behavioral effects in others (cause someone to do something). The same debate may thus be extended to action observation. Pointing with the index finger toward an object may be interpreted by the viewer as a simple hand–object interaction (e.g., signaling the presence of an object) or, alternatively, as an indication to interact (e.g., grasp) with that object.

Therefore the aim of the present study was to determine whether the observation of pointing actions elicits significant activity within the neural network classically thought to

subserve the perception of grasping action or whether the observation of pointing actions recruits a different set of brain regions. To do so, we conducted a whole-brain fMRI experiment in which subjects were scanned while they observed 3 types of display depicting a human hand either pointing at an object (pointing condition), grasping an object (grasping condition), or resting alongside an object (control condition).

Two main predictions might be advanced. If the observation of a pointing action elicits a "motor" representation which differs from that elicited by the observation of grasping actions, then neural differences as those demonstrated when comparing the execution of pointing and grasping actions (Grafton et al. 1996; Frey et al. 2005) might be evident. Conversely, if the observation of a pointing action is interpreted as an indication to act upon the object (e.g., grasp or manipulate it), then no differences in neural activation between grasping and pointing should be found. This is because the observation of pointing may not trigger activations strictly related to this type of action, but activations related to the overarching communicative meaning that pointing to an object may convey (e.g., grasp the object). If this is the case, then activation of parietal and premotor areas classically involved during the observation of grasping actions should be observed. In this perspective studying the observation of pointing action may shed new light on the communicative functions that pointing actions may subserve.

Materials and Methods

Participants
Fifteen volunteers (8 males and 7 females, mean age 34) were recruited for the present study. All participants were right handed with no history of neurological problems. The study was approved by a local ethical committee. Informed consent was obtained from all of the participants before the testing session in accordance with the declaration of Helsinki.

Stimuli and Experimental Design
In the present study different types of black and white digital photographs (bitmap format, resolution 1024 × 768 pixels), which proved to be effective in eliciting activation within areas concerned with action observation (e.g., Johnson-Frey et al. 2003), were utilized as stimuli. During scanning participants were presented with static images depicting 1) a human right hand with the index finger pointing toward an object positioned on a dark surface (pointing condition; Fig. 1A), 2) a human right hand grasping an object positioned on a dark surface (grasping condition; Fig. 1B), or 3) a human right hand resting alongside an object with the palm adjacent to the dark surface (control condition; Fig. 1C). We chose to implement a control condition which entails the presence of both the hand and the object as this would allow to precisely ascribe the nature of the activations (if any) to the observed hand–object interactions (i.e., pointing or grasping) and not to the mere presence of a hand and an object. Note that for the control condition any sort of hand–object interaction was avoided. For all conditions the same set comprising eleven objects (e.g., a glass, a tin box, a candle, a can, a jar, a tennis ball, etc.) were utilized. All stimuli were presented by means of a laptop PC that ensured synchronization with the MR scanner using the software "E-prime" (Psychology Software Tools Inc, Pittsburgh, PA). An LCD computer-controlled projector was employed to present the stimuli on a screen positioned outside the bore of the magnet which was viewed by the participants through a mirror mounted on the head coil. To minimize head motion, cushions and pads specifically designed to restrain head translations and rotations within the head coil were utilized. In addition, participants were instructed to keep their head still during scanning.

Activation Paradigm
During the experiment participants laid supine in the scanner and were requested to carefully observe all the displayed pictures. All 3 experimental conditions were presented in a block design in which 3 different types of block (corresponding to the experimental conditions), each lasting 15 s, were implemented. Within each block eleven static images were displayed on the screen for 1100 ms and were separated by 290-ms intervals of blank screen. Consecutive blocks were separated by a 15-s rest period consisting of a blank screen with a white fixation cross. The experiment consisted of 4 functional runs. Within each run 12 periods of activation were alternated with thirteen periods of rest. The 3 experimental conditions (grasping, pointing, and control) were pseudorandomly presented 4 times per run resulting in a total of sixteen repetitions throughout the entire experiment.

MRI Data Acquisition and Analysis
Using a whole body 1.5T Philips Achieva scanner (Philips Medical System, Best, the Netherlands), functional images were obtained with a standard single shot echo-planar imaging (EPI) T_2^*-weighted sequence in order to measure blood oxygenation level–dependent (BOLD) contrast throughout the whole brain (32 contiguous axial slices, slice thickness 3.5 mm/0.5 mm gap, field of view [FOV] = 224 × 224 mm^2, matrix 64 × 64, in-plane resolution of 3.5 × 3.5 mm, flip angle = 90°, time repetition [TR] = 3000 ms, time echo [TE] = 50 ms). Five hundred and sixteen volumes were acquired in 4 scanning runs (129 volumes for each run). In addition, high-resolution images (anatomical scans) were also acquired for each participant with a T_1-weighted 3D Fast-field Echo sequence (120 axial slices, slice thickness 1.2 mm, FOV = 250 × 250 mm^2, matrix 256 × 256, in-plane resolution of 0.98 × 0.98 mm; flip angle = 30°, TR = 25 ms, TE = 4.6 ms). The initial 4 functional volumes of each run were discarded to eliminate magnetic saturation effects. Subsequent image volumes were preprocessed using SPM5: www.fil. ion.ucl.ac.uk/spm. First, EPI images from all sessions were spatially realigned to the first volume of the first session of scanning (Friston et al. 1995). Second, high quality T_1 images were coregistered to the mean EPI image. Lastly, the EPI images were normalized (Ashburner and Friston 1999) to the standard space defined by the Montreal Neurological Institute (MNI) template and spatially smoothed with an 8-mm full-width at half-maximum isotropic Gaussian kernel to ameliorate differences in intersubject localization. High-pass filtering with a cut off of 128 s was also applied to remove low-frequency drifts in signal. Data were

Figure 1. Sample stimuli utilized in the present study for the 3 experimental conditions. (A) "Pointing" condition; (B) "grasping" condition; (C) "control" condition. A set of 11 different objects was utilized to construct the stimuli.

subsequently analyzed by applying a General Linear Model separately for each individual using SPM5. Additional regressors of no interest were modeled to account for translation and rotation along the 3 possible dimensions as measured during the realignment stage of the pre-processing. All conditions were modeled using a box-car function convolved with the canonical hemodynamic response function (HRF) and contrasts were defined in order to pick out the main effects of each experimental condition. These contrasts were subsequently entered into a second level analysis in which participants served as a random effect in a within-subjects one-way ANOVA. The experimental hypotheses were then tested by specifying appropriately weighted linear contrasts. Unless specified, the voxel-level threshold for these second-level contrasts was set at $P < 0.0001$ (uncorrected); the extent threshold was of at least 15 contiguous voxels. The resulting SPM$\{t\}$ maps reflected areas in which variance related to the experimental manipulation was captured by the canonical HRF.

Localization

Anatomical details of significant signal changes were obtained by superimposing the SPM$\{t\}$ maps on the T_1 canonical MNI template image. Results were also checked against normalized structural images of each participant. We used 2 atlases as a general neuroanatomical reference (Duvernoi and Bourgouin 1999; Mai et al. 2004). Further, the SPM Anatomy Toolbox (Eickhoff et al. 2005) based on 3-dimensional probabilistic cytoarchitectonic maps was used to determine the cytoarchitectonic probability (when available) of the peak activity voxels.

Results

Conjunction Analysis between Pointing, Grasping, and Control Conditions

First, we used a strict conjunction analysis across all experimental conditions to assess common significant increases in BOLD signal ($P < 0.05$, FWE corrected) for the 3 hand/object interactions relative to baseline. A network of extrastriate, parietal and frontal brain areas was activated, including the fusiform, the inferior and the middle occipital gyri, the medial intraparietal cortex together with the precentral and the inferior frontal gyri. All clusters were bilateral except for the IFG activation which was confined to the right hemisphere (Table 1; Fig. 2). Although this right-lateralized pattern of activation within the IFG may suggest that (implicit) language processes are not involved in the observation of the adopted stimuli, it should be noted that exploring the conjunction contrast at a more liberal threshold revealed activation also in the left IFG.

Because the premotor cortices play a key-role in the coding of hand action observation (e.g., Buccino et al. 2001; Gazzola et al. 2007) it is of interest that here they do activate for all conditions. Specifically the percent signal change (PSC) for the bilateral precentral gyrus and the right IFG was not sensitive to the type of observed stimulus (Fig. 3).

Observation of Pointing Movements

We next tested the effects of viewing pictures showing transitive pointing movements by comparing the "pointing" with the "control" condition. As shown in Table 2 and Figure 4A the contrast pointing > control revealed significant differential activity within lateral occipitotemporal, middle temporal and parietal regions. All these activations were confined to the left hemisphere. The peak coordinates for the occipitotemporal region correspond to the lateral middle occipital gyrus and are similar to those previously reported for the EBA (Downing et al. 2001; Astafiev et al. 2004; Peelen and Downing 2005; Downing et al. 2006), a region which responds selectively to the visual analysis of human bodies and body parts (but not to faces). Activation within the parietal cortex reached its peak within the postcentral gyrus (somatosensory cortex) extending to a small portion of the IPS. Similar activations within the somatosensory cortex (cytoarchitectonic area 2) have been reported for hand action observation both in nonhuman (Raos et al. 2007) and human (Avikainen et al. 2002; Rossi et al. 2002; Oouchida et al. 2004) primates. Finally, the reported temporal cluster is located in the posterior sector of the left middle temporal gyrus in a region adjacent to the posterior STS previously identified for the perception of goal-directed hand actions (e.g., Bonda et al. 1996). The reverse contrast control > pointing did not lead to significant differential activity.

Observation of Grasping Actions

We investigated the effects of viewing pictures depicting grasping transitive actions by comparing the "grasping" with the "control" condition. As shown in Table 2 and Figure 4B, the grasping > control contrast revealed significant differential activity in 2 main regions: the lateral occipitotemporal cortex and the somatosensory cortex bilaterally. The peak activation for the occipitotemporal cortex largely corresponds to that previously reported for the pointing > control contrast and is located in the lateral middle occipital gyrus. The peak

Table 1

MNI stereotaxic coordinates of the peaks of BOLD signal change as revealed by the conjunction analysis

Region	Probabilistic cytoarchitecture	t	Z	Coordinates (x, y, z) (mm)		
Grasping ∩ pointing ∩ control						
Frontal cortex						
IFG (pars opercularis)	Area 44 (40%)	6.01	5.08	46	8	29
Precentral gyrus	Area 6 (40%)	5.67	4.86	46	−1	54
Precentral gyrus	Area 6 (100%)	6.15	5.17	−48	−2	50
Parietal cortex						
IPL		10.9	7.49	32	−56	50
IPL	hIP1 (20%)	6.73	5.52	−34	−56	50
Occipital cortex						
Fusiform gyrus		20	Inf.	34	−56	−14
Fusiform gyrus		19.7	Inf.	−34	−74	−12
Inferior occipital gyrus		16.4	Inf.	34	−76	−10
Inferior occipital gyrus		17.9	Inf.	−38	−86	−12
Middle occipital gyrus	Area 18 (10%)	16.2	Inf.	36	−92	12
Middle occipital gyrus	Area 18 (10%)	12.5	Inf.	−32	−94	6
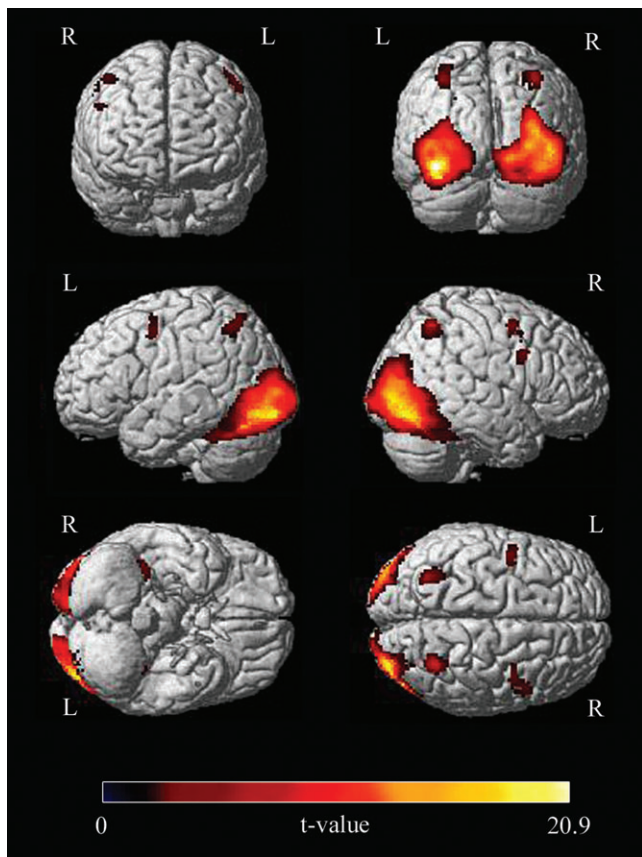
Figure 2. Three-dimensional rendering of the activation map for the conjunction analysis of all experimental conditions (pointing ∩ grasping ∩ control). Brain regions showing common significant increases in BOLD signal for all conditions were the fusiform, the inferior and the middle occipital gyri, the medial intraparietal cortex, the precentral and the inferior frontal gyri. All clusters were bilateral except for the IFG activation which was confined to the right hemisphere. (L) Left, (R) right. $P < 0.05$, FWE corrected.

coordinates for the somatosensory activation correspond to the postcentral gyrus. Further, this cluster also extends to the inferior sector of the parietal lobe including a small portion of the AIP sulcus. Differential activations were also found in the right lingual gyrus and the left fusiform gyrus. The reverse contrast control > grasping did not lead to significant differential activity.

For the peak activation voxels within the middle occipital (Fig. 5) and the postcentral gyri (Fig. 6), the average PSC elicited by the different experimental conditions was computed using the SPM Anatomy Toolbox (Eickhoff et al. 2005). One-way repeated measures analyses of variance (ANOVAs) with "condition" as within-subjects factor (grasping, pointing, control) were used to analyze the PSC data. Post hoc comparisons were conducted using t-test statistic. For the left lateral middle occipital gyrus the main effect of "condition" was significant ($F_{2, 28} = 35.3$, $P < 0.0001$). PSC for the grasping condition was significantly greater than PSC for the pointing ($t_{14} = 4.1$, $P < 0.001$; Fig. 5) and the control ($t_{14} = 8.6$, $P < 0.0001$; Fig. 5) conditions. In addition PSC for the pointing condition was higher than PSC for the control condition ($t_{14} = 4.2$, $P < 0.001$; Fig. 5). Similarly, the PSC data extracted from the right lateral middle occipital gyrus indicated a significant main effect of "condition" ($F_{2, 28} = 32.8$, $P < 0.0001$). PSC for the

grasping condition was significantly greater than PSC for the pointing ($t_{14} = 6.3$, $P < 0.001$; Fig. 5) and for the control ($t_{14} = 6$, $P < 0.0001$; Fig. 5) conditions. In addition PSC for the pointing condition was higher than PSC for the control condition ($t_{14} = 2.1$, $P = 0.05$; Fig. 5). For the left postcentral gyrus there was a significant main effect of "condition" ($F_{2, 28} = 20$, $P < 0.0001$). Specifically, PSC for the grasping condition was significantly greater than that for the pointing ($t_{14} = 2.7$, $P < 0.05$; Fig. 6) and for the control ($t_{14} = 5.3$, $P < 0.0001$; Fig. 6) conditions. PSC for the pointing condition was higher than PSC for the control condition ($t_{14} = 4.3$, $P < 0.001$; Fig. 6). Finally, the ANOVA conducted on the PSC data extracted from the right postcentral gyrus yielded a significant main effect of "condition" ($F_{2, 28} = 9.8$, $P < 0.001$). PSC for the grasping condition was significantly greater than PSC for the pointing ($t_{14} = 3.3$, $P < 0.005$; Fig. 6) and for the control ($t_{14} = 3.3$, $P < 0.005$; Fig. 6) conditions. In contrast, PSC for the pointing condition was not significantly different from that observed for the control condition ($t_{14} = 1$, $P > 0.05$).

Comparison between Pointing and Grasping Movements

The direct comparison between the observation of pictures representing grasping and pointing (grasping > pointing) led to significant differential activations within the lateral occipito-temporal cortex (lateral middle occipital gyrus) and the postcentral gyrus bilaterally (Table 2 and Fig. 4C). Peak coordinates for these activations matched those found for the grasping > control contrast (see Table 2). The reverse contrast pointing > grasping did not lead to significant differential activity at the applied statistical threshold.

Discussion

We set out to investigate the possible involvement of the "action observation system" for the perception of other's people pointing actions. To this end we asked subjects to view still photographs representing the hand of a human model pointing to an object, grasping an object, or resting in proximity of an object. On the basis of previous action observation studies (e.g., Buccino et al. 2001; Gazzola et al. 2007) it was expected a pattern of activation involving inferior parietal and frontal areas; at least when contrasting the grasping with the control condition. However, as indicated by the conjunction analysis the parietal region and both the dorsal and the ventral sectors of the PM cortex were significantly activated for all experimental conditions. Whereas activity within the parietal region appears to be moderately modulated by the type of observed stimuli, our data indicated that the premotor cortices activated in a similar fashion for all conditions as shown by the lack of differential premotor activity for the pointing > control and the grasping > control contrasts (Table 2; Figs 3, 4A and B). This seems to suggest that the viewing of our control condition in which both the hand and the object are present may be sufficient to activate the premotor cortices.

Rather, the results indicated that chiefly the lateral occipitotemporal and the somatosensory cortices were differentially activated depending on the type of observed hand/object interaction (Figs 5 and 6). We elaborate on the specific pattern of activity for these 2 areas and their possible role in action observation within the ensuing sections.
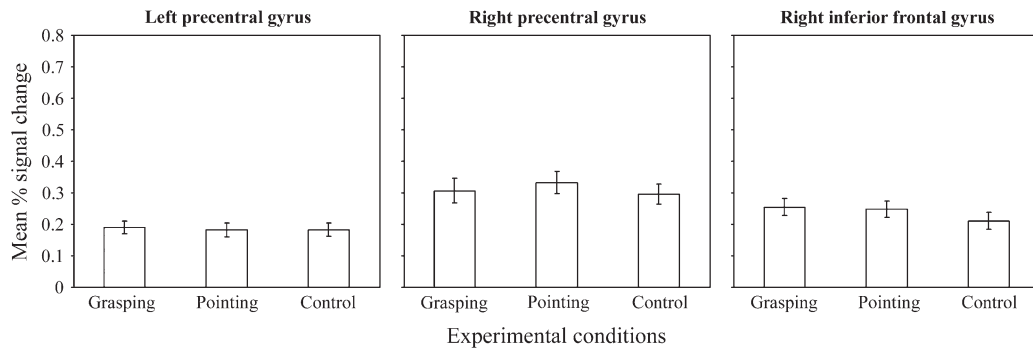
Figure 3. Averaged percent signal changes as a function of the 3 experimental conditions for the left precentral gyrus ($x = -48$; $y = -2$; $z = 50$), the right precentral gyrus ($x = 46$; $y = -1$; $z = 54$) and the right IFG ($x = 46$; $y = 8$; $z = 29$). These activation profiles refer to the premotor activations reported in Figure 2. All charts show a similar premotor BOLD response for all conditions. Bars represent standard errors.

Table 2
MNI stereotaxic coordinates of the peaks of BOLD signal change as revealed by the contrasts of interest

Region	Probabilistic cytoarchitecture	t	Z	Coordinates (x, y, z) (mm)		
Pointing > control						
Temporal cortex						
Middle temporal gyrus		5.33	4.63	−50	−50	−2
Parietal cortex						
Postcentral gyrus	Area 2 (70%); Area 1 (40%)	6.40	5.32	−52	−34	54
Supramarginal gyrus	hIP2 (10%)	4.62	4.13	−48	−44	30
Occipital cortex						
Lateral middle occipital gyrus (EBA)	hOC5 (50%)	4.42	3.98	−42	−68	4
Grasping > control						
Parietal cortex						
Postcentral gyrus	Area 2 (80%); Area 1 (40%); hIP2 (10%)	6.40	5.32	−50	−34	52
Postcentral gyrus	Area 2 (100%); Area 3b (30%); Area 1 (10%); hIP2 (10%)	3.85	4.24	38	−34	48
Postcentral gyrus	Area 2 (30%); Area 3b (20%); Area 3a (10%); Area 4p (10%)	5.77	4.92	48	−22	36
IPL	Area 2 (60%); hIP2 (20%); Area 3b (10%)	6.09	5.13	−50	−28	42
Occipital cortex						
Lateral middle occipital gyrus (EBA)	hOC5 (10%)	7.19	5.78	−48	−72	0
Lateral middle occipital gyrus (EBA)	hOC5 (20%)	6.91	5.62	48	−63	−3
Lingual gyrus	Area 18 (70%); Area 17 (10%)	6.34	5.28	26	−92	−8
Fusiform gyrus		4.75	4.22	−40	−46	−20
Grasping > pointing						
Parietal cortex						
Postcentral gyrus	Area 2 (50%); hIP2 (10%)	4.56	4.09	44	−28	40
IPL	Area 2 (50%); Area 1 (10%); Area 3b (10%); hIP2 (10%)	4.44	4.00	−54	−26	40
Occipital cortex						
Calcarine gyrus	Area 17 (100%)	6.49	5.37	18	−100	−2
Lateral middle occipital gyrus (EBA)	hOC5 (20%)	5.99	5.06	48	−62	−4
Lateral middle occipital gyrus (EBA)		4.55	4.08	−50	−74	−1

### The Involvement of the Lateral Occipitotemporal Cortex in Action Observation

The use of functional imaging in humans has revealed that a focal region of the lateral occipitotemporal cortex, better known as the EBA, responds strongly and selectively to the sight of static images of human bodies and body parts, but weakly to faces, objects and object parts (e.g., Downing et al. 2001). Recent findings suggest that this area also responds to self-produced movements of the limbs in the absence of visual feedback (Astafiev et al. 2004) and plays a role in action observation when the requirement is to discriminate between coherent and incoherent intransitive actions (Downing et al. 2006) or biomechanically possible and impossible biological actions (Costantini et al. 2005).

Therefore, our study confirms and significantly expands this literature by showing that a portion of the lateral occipitotemporal cortex, whose peak coordinates closely resembles those previously reported for the EBA, responds differentially to the observation of grasping actions with respect to the control condition. In other words, the lateral occipitotemporal cortex not only responds to the observation of the transitive actions considered in the present study, but it also responds differentially depending on the type of observed actions as the grasping > pointing contrast seems to suggest. Specifically this area is significantly more activated by the sight of grasping rather than pointing (Figs 3*C* and 5).

This may signify that the lateral occipitotemporal cortex modulates according to the type of observed transitive actions (i.e., grasping, pointing). Therefore, EBA not only seems to have a general role concerned with action observation, but also a role concerned with the discrimination of specific aspects characterizing the observed actions. Support for this view comes from previous evidence suggesting that the EBA is differentially activated when, for instance, there is a need to discriminate between coherent and incoherent actions (Downing et al. 2006).

However, before these conclusions can be fully accepted an issue needs to be discussed. Because body-selective voxels
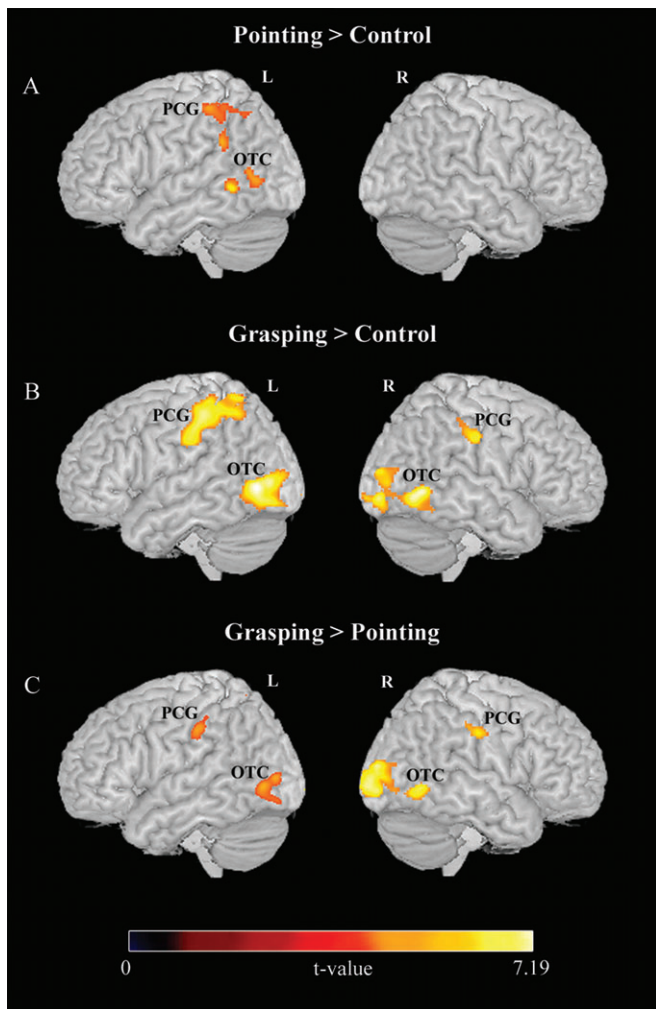
Figure 4. Regions of increased activation for the pointing versus the control condition (*A*), for the grasping versus the control condition (*B*), and for the grasping versus the pointing condition (*C*). The SPM{*t*} maps for the contrasts of interest are overlaid on the 3-dimensional surface of the MNI standard brain. Note that this projection renders onto the surface activity which may in fact be located in the sulci. PCG, postcentral gyrus; OTC, occipitotemporal cortex including the lateral middle occipital gyrus (EBA); L, left; R, right.
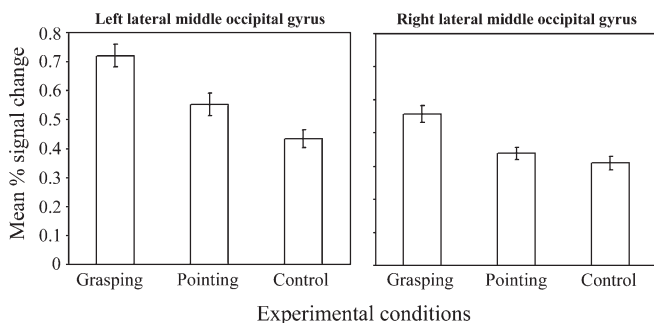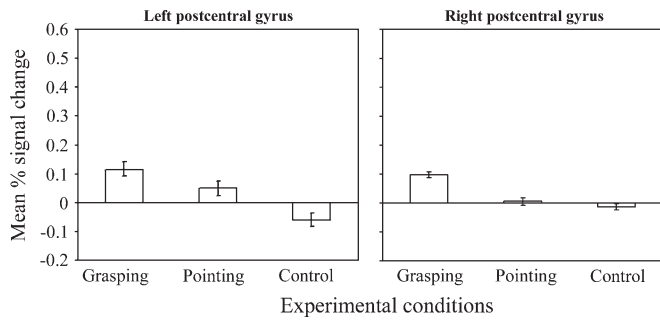

Figure 5. Averaged percent signal changes as a function of the 3 experimental conditions for both the left ($x = -48$; $y = -72$; $z = 0$) and the right ($x = 48$; $y = -63$; $z = -3$) lateral middle occipital gyrus (EBA). Both charts show a higher level of activation for the grasping than for the pointing and the control conditions. Bars represent standard errors.

overlap with the human motion selective area MT it is important to establish whether our activations can be genuinely ascribed to action perception and not motion or implied motion. With regard to motion, the strategy of having adopted static images should have avoided this possible confound. With regard to implied motion (e.g., Kourtzi 2004; see also Kourtzi and Kanwisher 2000), that is the sense of motion expressed by static stimuli depicting a specific phase of an ongoing action, a close inspection of our stimuli may help to rule out such alternative interpretation. For both the grasping and the pointing stimuli great care was taken as to select stimuli which did not convey the sense of an action in progress (Fig. 1). For the control stimuli, they did not entail any sort of interaction with the object and therefore they did not carry any dynamic information. Importantly, as shown in Figure 5 the PSC data indicate that the lateral occipitotemporal cortex also responded to the control condition. If activation within this region for the grasping and the pointing conditions were triggered by implied motion, then we should not have found any sign of BOLD signal change within this area for the control condition. This may signify that for this condition BOLD activity in the lateral occipitotemporal cortex is simply triggered by the visual perception of the hand, and that observing a grasping or pointing actions magnifies such activity.

The Involvement of the Somatosensory Cortex in Action Observation

Here we show that observing someone's hand grasping an object activates the bilateral somatosensory cortex, corresponding to cytoarchitectonic area 2, despite the observer's hands being relaxed and immobile. This finding may be interpreted as evidence that during observation of hand actions visual information reaches this high-order somatosensory area. A previous account of the possible involvement of area 2 in action observation has been provided by Oouchida et al. (2004). They found that this area was activated by observing intransitive flexion/extension hand movements. Although this result is certainly relevant for the definition of the neural network underlying the action observation system, the question of whether such an area is also involved in the observation of transitive actions is still unsolved. The present findings seem to provide some answers to this question revealing robust activity in area 2 for the observation of grasping as compared with the sight of a resting hand. Our view about this finding is that mechanisms different from direct sensory feedback may be capable of modulating activity in somatosensory cortex. In this perspective the perception of action does not solely rely on sensory processing, but potentially also on activation of sensory regions by means of top down modulation mediated by a network comprising brain structures involved in motor preparation and sensory motor integration.

Whereas for grasping activation within this area was somewhat expected given previous similar reports (Avikainen et al., 2002; Rossi et al. 2002; Oouchida et al. 2004), it is surprising that the contrast between pointing and control led to area 2 significant activation (although only left lateralized). However, as we predicted it might well be that the pointing action could be also understood in terms of a signal to act upon the indicated object. If the observer interpreted the pointing action in these terms, then she may have prepared a manipulative action toward that object. This may explain why

Figure 6. Averaged percent signal changes as a function of the 3 experimental conditions for both the left ($x = -50$; $y = -34$; $z = 52$) and the right ($x = 38$; $y = -34$; $z = 48$) postcentral gyrus (somatosensory cortex). Both charts show a higher level of activation for the grasping than for the pointing and the control conditions. Bars represent standard errors.

activation in this area survives the contrast of interest. An alternative account for the activation of somatosensory areas during the observation of pointing actions may be found in a study by Lamm et al. (2007) in which similar activations were reported in a reaching range prediction task. Results from this study indicated that predicting the reaching range of others activated the somatosensory cortex even if the observed stimuli (as for our pointing condition) did not feature any perceivable contact between the models and the targets. In line with the interpretation given by the authors, we suggest that the involvement of the somatosensory cortex may in some circumstances reflect the anticipation of touch (i.e., the contact of hand with the object). Such a proposal is supported by studies demonstrating that SI and SII are activated by anticipation of touch in the absence of any tactile stimulation (e.g., Carlsson et al. 2000).

Finally, when grasping and pointing are compared in execution tasks the somatosensory cortex shows a greater level of activity for grasping than for pointing (Grafton et al. 1996; Frey et al. 2005). Here we mirror this result showing that a similar gradient of activation also applies to action observation situations. As shown in Figure 6, area 2 shows a greater level of activity for the grasping than for the pointing and the control condition, respectively.

Conclusions

The goal of the present study was to extend current literature on the "action observation system" to pointing actions. To this end we compared hemodynamic activity triggered by the observation of pointing actions with hemodynamic activity triggered by the observation of grasping actions. We believe that our findings contribute to extend current literature on this topic in 3 important ways. First, in contrast to previous hand action observation studies, we have been unable to reveal differential activation within the premotor cortices (e.g., Buccino et al. 2001; Gazzola et al. 2007). We suspect that this might be due to the nature of our control condition. In contrast to the majority of previous action observation studies which compared the action conditions with control stimuli depicting scrambled figures, our control condition provides a very high baseline (as it includes in a noninteracting fashion both the biological effector and the object). This may suggest that merely viewing a hand and an object activates the premotor

cortices. Second, the present results indicate that a portion of the lateral occipitotemporal cortex (possibly corresponding to the EBA) is strongly implicated in action observation. Importantly, as witnessed by the modulation of activation depending on the experimental conditions, it seems that this area plays a specific role in detecting differential types of hand–object interactions. Finally, they not only confirm, in line with previous evidence the important role played by somatosensory cortex in action observation (e.g., Avikainen et al. 2002) but they also indicate that observing a pointing action may induce in the observer an intention to act upon the object as the area 2 activation seems to suggest.

Notes

Conflict of Interest: None declared.

Address correspondence to Umberto Castiello, PhD, DSc, Department of General Psychology, University of Padova, Via Venezia 8, 35131, Padova, Italy. Email: umberto.castiello@unipd.it.

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