When Gaze Turns into Grasp

**Andrea C. Pierno[1], Cristina Becchio[2], Matthew B. Wall[3],
Andrew T. Smith[3], Luca Turella[1], and Umberto Castiello[1,3]**

Abstract

■ Previous research has provided evidence for a neural system underlying the observation of another person's hand actions. Is the neural system involved in this capacity also important in inferring another person's motor intentions toward an object from their eye gaze? In real-life situations, humans use eye movements to catch and direct the attention of others, often without any accompanying hand movements or speech. In an event-related functional magnetic resonance imaging study, subjects observed videos showing a human model either grasping a target object (grasping condition) or simply gazing (gaze condition) at the same object. These two conditions were contrasted with each other and against a control condition in which the human model was standing behind the object without performing any gazing or grasping action. The results revealed activations within the dorsal premotor cortex, the inferior frontal gyrus, the inferior parietal lobule, and the superior temporal sulcus in both "grasping" and "gaze" conditions. These findings suggest that signaling the presence of an object through gaze elicits in an observer a similar neural response to that elicited by the observation of a reach-to-grasp action performed on the same object. ■

INTRODUCTION

Neuroimaging evidence suggests that in humans, the observation of a human model reaching to grasp an object evokes activity in a network of areas named the "action observation system" that includes the premotor (PM) cortex, the inferior parietal lobule (IPL), the inferior frontal gyrus (IFG), and the superior temporal sulcus (STS) (Keysers & Perrett, 2004; Tai, Scherfler, Brooks, Sawamoto, & Castiello, 2004; Buccino et al., 2001; Decety & Grezes, 1999; Decety et al., 1997; Rizzolatti et al., 1996). Contemporary thought suggests that this system, or at least part of it, might be not only sensitive to the observation of an overt action, but also plays a role in coding the intention behind another person's actions (Iacoboni et al., 2005; see also Pelphrey, Morris, & McCarthy, 2004). For instance, intentions associated with grasping actions have been investigated by Iacoboni et al. (2005). In their study, participants observed grasping actions performed in the presence or the absence of contextual information. Examples of contextual actions were grasping for drinking or grasping for cleaning. Their findings indicated significant blood oxygenation level dependent (BOLD) signal increases in the right IFG and the adjacent sector of the ventral PM cortex for contextual actions as compared to the observation of the same action without contextual

information. Thus, two components of the action observation system previously thought to be involved only in action recognition were also involved in understanding the intentions of others.

Here we further investigate this possibility by attempting to induce activation in the action observation system on the basis of gaze coding without showing overt hand actions. Gaze is an important source of information of others' intentions and actions. In real-life situations, humans use eye movements to catch and direct the attention of others, often without any accompanying hand movements or speech. Furthermore, we are also able to understand the intention of others and to act upon objects accordingly on the basis of observed eye movements alone (e.g., Pierno, Mari, Glover, Georgiou, & Castiello, 2005; Castiello, 2003). This suggests that under certain conditions, gaze may be an important cue from which motor intentions of others can be inferred.

Are there any reasons to suppose that a system sensitive to the observation of overt action is also sensitive to gaze direction? We propose at least three reasons why this might be the case. The first reason is concerned with the difficulty in inferring intentions from body movements. As Perrett et al. (1985) stated, "In many cases, the direction in which another person's head is pointing is not a good index of where his or her attention lies. Gaze direction is a much better guide to the focus of another's attention." Although normally strongly coupled, when head direction and gaze direction disagree, gaze direction serves as a better index of

[1]Università di Padova, Italy, [2]Università di Torino, Italy, [3]Royal Holloway, University of London, UK

intention. The second reason stems from neuroimaging evidence suggesting that the STS is involved in gaze processing (Pelphrey, Morris, et al., 2004; Wheaton, Thompson, Syngeniotis, Abbott, & Puce, 2004; Pelphrey, Singerman, Allison, & McCarthy, 2003; Allison, Puce, & McCarty, 2000; Hoffman & Haxby, 2000; Puce, Bentin, Gore & McCarthy, 1998). Given that the STS is a component of the action observation system, it might be reasonable to assume sensitivity of this system to gaze. The third reason is provided by studies on autistic children showing that although they are able to code gaze direction, they are unable to attribute intentions to other people's gaze (Baron-Cohen, Campbell, Karmiloff-Smith, Grant, & Walker, 1995). Along these lines, it has also recently been demonstrated how autistics' lack of ability to read intention from gaze may relate to action (Pierno et al., 2005). In this study, two participants, a human model and an observer, were seated facing each other at a table. In three experimental blocks, the model was required to grasp a stimulus, to gaze toward the same stimulus, or to gaze away from the stimulus without performing any action. The task for the observer was always to grasp the stimulus after having watched the model perform his or her task. It was found that normal children showed facilitation effects in terms of movement speed following the observation of the model grasping or simply gazing at the object. In contrast, autistic children did not show any evidence of facilitation in these conditions. Neither normal nor autistic children showed evidence of facilitation when the model's gaze was not directed toward the stimulus. These findings demonstrate that children with autism fail to use information from the model's action or gaze to plan their subsequent actions.

Crucially, in autistic people, structural abnormalities at the level of the STS and the prefrontal cortex have been reported (Waiter, Williams, Murray, Gilchrist, Perrett, & Whiten, 2005a, 2005b; Boddaert et al., 2004). In addition, a recent functional magnetic resonance imaging (fMRI) study conducted on subjects with autism indicated functional abnormalities in brain regions involved in gaze processing, including the STS, the right precentral gyrus, and the IPLs bilaterally (Pelphrey, Morris, & McCarthy, 2005, see also Dapretto et al., 2006). Because these areas are part of the action observation system, it seems reasonable to hypothesize an involvement of this system in both action and gaze processing, as the aforementioned behavioral study suggests (Pierno et al., 2005).

To test whether the action observation system is triggered not only by the observation of an overt action, but also by the intention to act signaled by gaze, we designed an event-related fMRI study in which healthy subjects observed a human model either grasping an object or simply observing an object. These two conditions were contrasted against each other and against a control condition in which the human model was standing behind the object performing neither a grasping nor a gazing action.

Our core finding is that brain areas involved in action observation are not only activated by the sight of overt reach-to-grasp actions, but also by the observation of the model's gaze, signaling the presence of an object as well as the intention to act upon the observed object.

METHODS

Subjects

Subjects were 14 normal, healthy, and right-handed volunteers (mean age, 28 years; range, 20–36 years). All subjects had normal or corrected-to-normal vision and gave informed consent to participate in the study; the study was approved by a local ethics committee.

Stimuli

While being scanned, subjects viewed three different types of movies (4 sec duration; AVI format, 25 frames per second) representing a human model seated at a table (100 × 100 cm) on top of which one spherical plastic object (diameter, 6 cm) was positioned. The object was located at a distance of 30 cm from the hand. Prior to each trial, the model put his right wrist on the starting position (diameter, 0.5 cm) positioned 25 cm in front of his midline. The target object remained visible throughout the duration of the trial. In the first condition, the human model initially gazed away from the observer, then he reached, gazed toward, and grasped the target object (grasping condition; see Figure 1A). In the second condition, the human model initially gazed away from the observer then directed his gaze toward the target object without performing any grasping action (gaze condition; see Figure 1B). In the third condition, the human model remained still and maintained the eyes away from the target object (control condition; see Figure 1C). In this condition, the target object was still present, but the eyes never gazed at it. For each condition, four different video clips representing different trials performed by the same model were presented. All movies were enclosed in a rectangular frame in a 720 × 540-pixel array. A computer-controlled projector was used to present the movies in color.

Design and Procedure

The stimuli were shown in random order and counter-balanced across participants. An event-related design (Rosen, Buckner, & Dale, 1998) was used to sample the functional imaging data. Stimuli were presented on a variable schedule, the interstimulus interval (ISI) being determined by a ''long exponential'' probability distribution (Hagberg, Zito, Patria, & Sanes, 2001), with a mean ISI of 6 sec and a range of 2–10 sec. Throughout the experiment, subjects performed the same explicit task, which was to carefully observe the stimuli backprojected
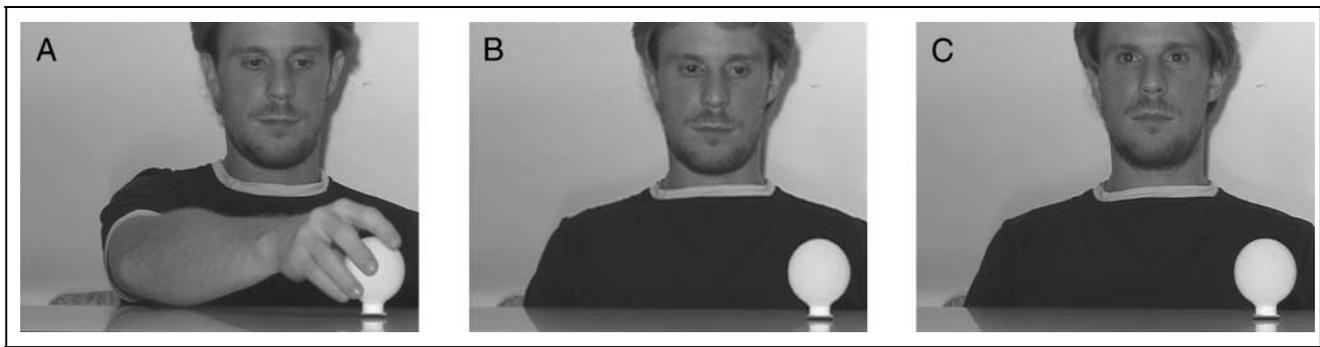
Figure 1. An example of representative frames extracted from the utilized experimental videos. Shown are frames from the grasping condition (A), the gaze condition (B), and the control condition (C).

onto a screen visible in a mirror mounted on the MRI head coil (visual angle, approx. 15° × 20°).

Functional Imaging and Data Analysis

Whole-brain fMRI data were acquired on a 3T scanner (Siemens Magnetom Trio, Erlangen, Germany) equipped with an eight-channel head array radio frequency coil. The generalized autocalibrating partially parallel acquisitions (GRAPPA) (Griswold et al., 2002) algorithm for integrated parallel acquisition technique (IPAT) was used with an acceleration factor of 2. Functional images were obtained with a gradient-echo-planar (EPI) T2*-weighted sequence in order to measure blood oxygenation level-dependent (BOLD) contrast throughout the whole brain (42 contiguous axial slices, 3 mm isotropic voxel size, in-plane resolution of 64 × 64 voxels, FOV = 192 × 192 mm, flip angle = 90°, echo time (TE) = 30 msec, bandwidth = 752 Hz/px). Volumes were acquired continuously with a repetition time (TR) of 3 sec. A total of 684 scans was acquired for each participant in six scanning runs (5:42 min each). In addition, high-resolution T1-weighted images (anatomical scans) were also acquired for each participant (MP-RAGE, 176 axial slices, in-plane resolution 256 × 256, 1 mm isotropic voxels, TR = 1830 msec, TE = 4.43 msec, flip angle = 11°, bandwidth = 130 Hz/px).

Functional MRI data were analyzed by using Statistical Parametric Mapping software (SPM2, Wellcome Department of Cognitive Neurology, London, UK). Individual scans were realigned to the first functional volume of each series to correct for any head movement occurring within the run. The images were then spatially normalized (Friston, Holmes, et al., 1995) using a template originally supplied by the Montreal Neurological Institute (the MNI152 template) and distributed with SPM2. Finally, the data were spatially smoothed using a 6-mm full width at half maximum (FWHM) Gaussian kernel. A high-pass temporal filter (cutoff 120 sec) was also applied to the time series. Analysis was carried out by the application of the general linear model (GLM) for analysis of fMRI time series (Friston, Ashburner, et al.,

1995) as implemented in SPM2. Regressors were defined based on the timing of presentation of each of the three conditions, and these functions were convolved with a canonical, synthetic hemodynamic response function (HRF) to produce the model. Individual models were generated for each subject and contrasts were defined in order to pick out the main effects of each experimental condition. These contrasts were then entered into several second-order random-effects analyses (paired *t* tests) that contrasted the various conditions against each other to produce contrasts of interest in line with the hypotheses of the experiment. The alpha level for these second-level analyses was set at $p < .001$ (uncorrected).

Localization

Anatomical localization and visualization of significant signal changes were obtained by superimposing the SPM{t} maps on the T1 canonical MNI template image, using the visualization software suite Mri3dX (version 5.50, www.jiscmail.ac.uk/archives/mri3dx.html). Mri3dX incorporates the Talairach Daemon Database (TCDB; Lancaster et al., 2000). However, our primary neuroanatomical reference for the PM cortex, the IFG, and the parietal operculum was the SPM anatomy toolbox developed by Eickhoff et al. (2005). The designations of Brodmann areas (1909) were also used as a rough guide to the location of cytoarchitectonic areas of the cortex.

RESULTS

We tested whether brain activity during video observation would modulate according to the type of behavior performed by the human model on the target object.

Effects of Observing a Reach-to-grasp Action

To individuate brain areas that activate during the observation of grasping actions, we subtracted the activation measured in the condition in which the human model

simply stands behind the target object without gazing at it (control condition) from the activation measured in the condition in which the human model grasped the designated target object (grasping condition). This comparison revealed significant differences in activation for a number of cortical regions with a z score above 3 and $p < .001$ (uncorrected). Peak activity, stereotaxic coordinates, and laterality indices for these activations are listed in Table 1. As illustrated in Figure 2A, activity was localized in the dorsal premotor (PMd, Brodmann's area [BA] 6) cortex bilaterally, the IFG bilaterally (pars triangularis, BA 45), and the bilateral inferior portion of the parietal lobe (BA 40). The location of the PMd, IFG, and IPL is consistent with similar areas identified by Grezes, Armony, Rowe, and Passingham (2003), Johnson-Frey et al. (2003), and Ehrsson et al. (2000), respectively, for the observation and execution of grasping actions. Furthermore, the posterior portion of the right STS that corresponds to BA 22 was significantly activated. The location of the right STS activity observed in this study (Figure 2A) and peak coordinates (see Table 1) are consistent with those identified by Pelphrey et al. (2004) and Wheaton et al. (2004). Finally, the middle temporal (MT) gyrus observed activation (see Table 1) is consistent with what has been previously reported in other studies (McCarthy, Spicer, Adrignolo, Luby, Gore, & Allison, 1995; Tootell et al., 1995; Watson et al., 1993; Zeki, Watson, Lueck, Friston, Kennard, & Frackowiak, 1991) for the more general and functionally defined motion-sensitive region MT/V5. Moreover, these activations are in line with those obtained in the majority of action observation studies comparing static versus moving effectors (e.g., Pelphrey, Morris, Michelich, Allison, & McCarthy, 2005).

Table 1. Local Maxima of the Foci Showing Grasping-related Activation Expressed in Talairach Coordinates

Anatomical Description	BA	Hemisphere	Talairach Coordinates			Peak z Score
			x	y	z	
PMd cortex	6	R	51	0	48	4.13
PMd cortex	6	L	−48	−5	48	4.31
IFG	45	R	55	28	24	3.15
IFG	45	L	−50	35	6	3.1
STS	22	R	53	−31	9	3.86
IPL	40	R	55	−30	25	4.37
IPL	40	L	−48	−36	24	4.71
MT gyrus/V5	19	R	50	−73	13	5.55
MT gyrus/V5	19	L	−50	−63	11	4.40

PMd = dorsal premotor; IFG = inferior frontal gyrus; STS = superior temporal sulcus; IPL = inferior parietal lobe; MT = middle temporal.
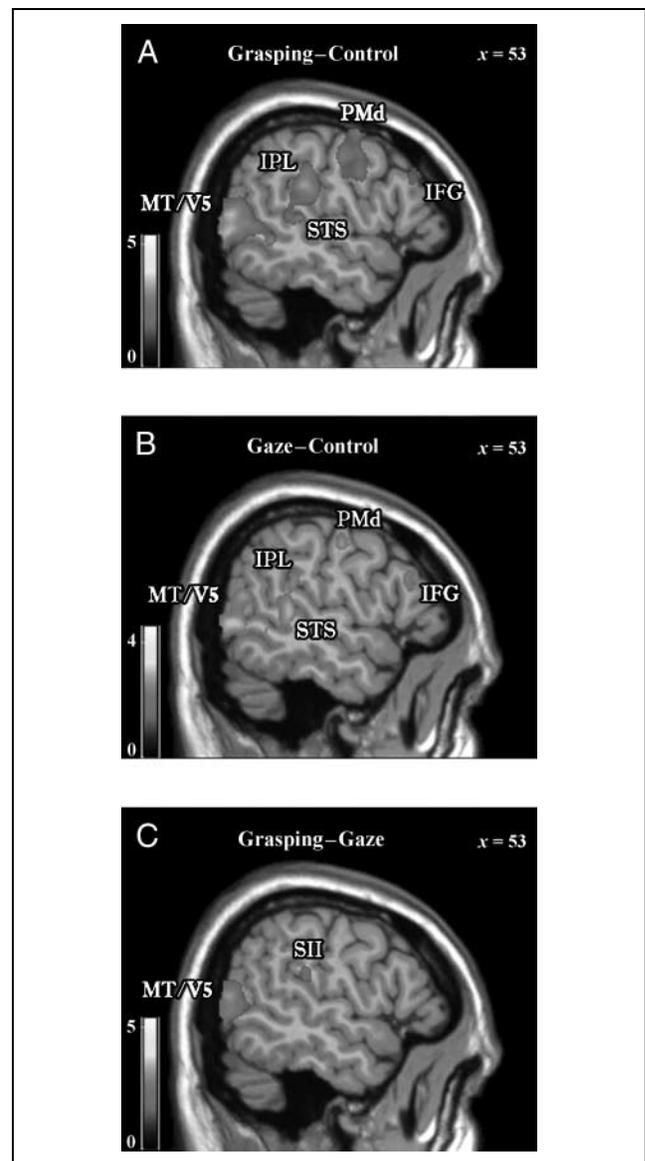

Figure 2. Areas of increased signal for the grasping versus the control condition (A), for the gaze versus the control condition (B), and for the grasping versus the gaze condition (C). The SPM{t} maps are overlaid on the canonical T1 image from the MNI series (for all panels the right side of the brain is represented).

Effects of Observing the Model's Gazing Action

The critical question for this study was whether observing another person gazing toward an object recruits the same network of areas as that activated by the observation of an overt action. The subtraction of the activation measured for the control condition from the activation measured for the condition in which the human model observed but did not grasp the target object revealed differential activation in areas that largely overlap those found active in the grasping condition (see Figure 2A). In particular, significant activation ($p < .001$, uncorrected) was found within the following areas: PMd, IFG, STS, and the IPL (see Figure 2B). Peak activity, stereotaxic

coordinates, and laterality indices for these activations are listed in Table 2. The observed bilateral PMd activation is consistent with that found by Grezes et al. (2003). In contrast to the bilateral IFG activation found for the grasping condition, here the IFG activation was confined to the right hemisphere. Furthermore, the same visual areas as those for the grasping condition were activated. In particular, bilateral activation was found for area MT/V5 (Table 2).

Comparing Grasping versus Gaze

Here we contrasted the gaze with the grasping conditions. Figure 2C and Table 3 show that the grasping condition yielded significant ($p < .001$, uncorrected) signal increases, compared with the gaze condition, in visual areas (MT/V5) and within the right parietal operculum (SII).

No significant differences in activation were found for the areas classically thought to be activated by action observation, namely, IFG, IPL, PMd cortex, and STS. As shown in Figure 3, for these areas the percentage of signal change is similar for the grasping and the gaze conditions. The reverse contrast did not show activation for the areas involved in action observation.

DISCUSSION

We investigated whether the BOLD signal within a specific set of brain areas known to be modulated during the observation of object-oriented grasping actions would additionally be modulated during the observation of object-oriented gazing. In line with previous work, we found activation of the action observation system in

Table 2. Local Maxima of the Foci Showing Gaze-related Activation Expressed in Talairach Coordinates

| Anatomical Description | BA | Hemisphere | Talairach Coordinates | | | Peak z Score |
			x	y	z	
PMd cortex	6	R	48	0	46	3.68
PMd cortex	6	L	−26	−14	60	3.3
IFG	45	R	59	24	15	3.29
STS	22	R	59	−35	9	3.93
STS	22	L	−57	−38	18	3.46
IPL	40	R	50	−34	20	3.73
IPL	40	L	−53	−34	26	3.39
MT gyrus/V5	19	R	55	−68	3	4.02
MT gyrus/V5	19	L	−46	−63	12	4.05

Abbreviations as in Table 1.

Table 3. Local Maxima of the Foci for the Grasping–Gaze Contrast-related Activation Expressed in Talairach Coordinates

| Anatomical Description | BA | Hemisphere | Talairach Coordinates | | | Peak z Score |
			x	y	z	
MT gyrus/V5	19	R	46	−70	9	4.47
Parietal operculum (SII)	43	R	50	−32	23	3.27

response to the observation of grasping actions. More importantly, we demonstrate that the same network of areas is recruited by the observation of gaze toward an object. This result for the "gaze-only" condition signifies that, for the action observation system to be activated, it is not necessary to observe an overt action. Observing another individual gazing toward an object might be sufficient.

The idea that the role of the action observation system may extend beyond the response to overt actions has already been advanced in previous studies. For instance, Pelphrey, Morris, et al. (2004) demonstrated differential STS activity for observed correct and incorrect action sequences. These findings were interpreted as evidence that the posterior STS is sensitive to the intentionality and appropriateness of an action embedded in a given context. Along the same lines, Iacoboni et al. (2005), found that understanding the intentions behind actions embedded in specific contexts elicits a significant BOLD signal increase in the right IFG and the adjacent sector of the ventral PM cortex. Clearly, if these areas were only involved in action recognition, then their response should have been independent of context.

The present results complement and extend previous research by demonstrating that the action observation system is activated even in the absence of overtly executed actions. As we demonstrate, this system is activated even in the absence of any overtly executed action, that is, by the mere observation of gaze. Such a result strongly suggests that the entire action observation system actively participates in the process of understanding the motor intention behind an observed gaze pattern. Gaze not only acts as an indicator of where another person is looking, but it also implies that the person may have some intentions or goals. In other words, the understanding of others' motor intention from gaze triggers in the observer's brain a similar pattern of activation to that elicited by the observation of an intended and executed overt action.

However, before this conclusion can be accepted, some issues must be addressed. First, could it be that the reported effects are merely due to observing the direction of gaze with no implications in terms of intentions? A strong argument against this possible
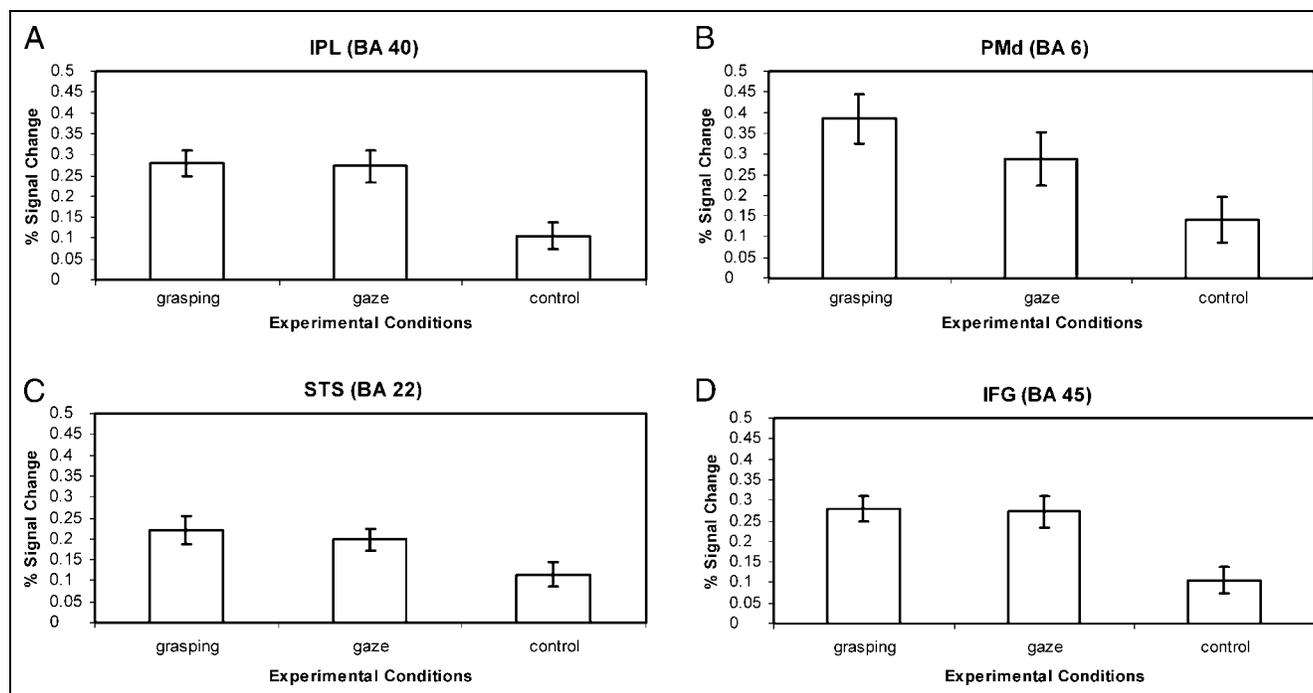
Figure 3. Mean percent change in BOLD signal as a function of the three experimental conditions for IPL (A), PMd (B), STS (C), and IFG (D). All panels show a similar BOLD response for the grasping and gaze condition. These activation profiles refer to the activations reported in Figure 2A and B.

alternative interpretation is that the reported activations would not have been present when contrasting the gaze condition against the control condition. If the reported activation simply reflects a gaze detector, there should be no difference in activation for directing gaze toward an object (gaze condition) and directing gaze toward an empty space (our control condition). Because the comparison between these conditions reveals significant differences in activation, an argument for an intentional relationship between gaze and object might be advanced.

Second, a surprising aspect of our results is that in contrast to previous studies (Iacoboni et al., 2005; Pelphrey et al., 2004) we found the involvement of all components of the so-called action observation system in the coding of motor intentions. We suspect that the reasons behind the difference between the present and previous studies may lie in the nature of the presented stimuli. For example, in the Iacoboni et al. (2005) study, the stimuli consisted of moving arm and hand ensembles, detached from the model's body. Thus, arm/hand information could not be linked with other types of information such as gaze. Because STS is chiefly involved in gaze coding, the absence of gaze information can probably explain why the intention condition yielded significant signal increases in the IFG and PM cortex, but not in the STS. In the Pelphrey et al. (2004) study, subjects viewed a virtual animated male figure performing the reach-to-grasp movements. Whereas some action observation studies in which virtual agents were used reported acti-

vation in frontoparietal and premotor regions (Mosconi, Mack, McCarthy, & Pelphrey, 2005; Pelphrey, Morris, Michelich, et al., 2005), other neuroimaging evidence argued that action reproduced in three-dimensional virtual reality only induces activation in areas that are exclusively concerned with visuospatial processing and not in areas classically involved in action observation such as the inferior parietal cortex and premotor areas (Perani et al., 2001). Thus, with a certain degree of caution, it might be possible to suggest that the lack of activation in the entire action observation network in the Pelphrey et al. (2004) study might be ascribed to the virtual nature of the agent.

Third, differences related to the type of stimuli may also account for the apparent contrast with previous reports (Pelphrey, Morris, Michelich, et al., 2005) suggesting that biological motion perception in the posterior STS is somatotopically organized. Here we report that the patterns of activation for the observation of reaching and gazing pattern in the STS largely overlap. A possible explanation is that, in the present study, the represented stimuli were object-directed actions, whereas the stimuli used by Pelphrey, Morris, Michelich, et al. (2005) represented non-object-directed actions. It might well be that in the absence of an object, participants' attention was chiefly oriented toward the effector rather than toward the action goal.

A further issue is concerned with differences in activation between grasping and gaze. The bilateral activations of STS, PMd, and IPL together with activation

within the right IFG reported for the gaze condition seem to indicate that these areas are all important to the functional representation of motor intention. Of course, the activation of similar areas for both the grasping and the gaze condition does not imply that there are no differences in brain response between observing a grasping action and observing a gaze toward an object. For example, in contrast to the bilateral IFG activation found for the ''grasping'' condition, IFG activation for the ''gaze'' condition was confined to the right hemisphere. A lateralized pattern of activation for IFG has already been found by Iacoboni et al. (2005), who reported increased right IFG activity in response to the observation of actions embedded in a context compared to the observations of actions without a context. The authors interpret this result as evidence that the right IFG is particularly important for understanding the intentions of others. The fact that we found right IFG for both grasping and gaze observation may thus reflect the presence of an intentional component.

Conclusions

By definition, understanding a perceived action requires representation of the agent's motor intentions. Previous evidence suggests that the action observation system allows the observer to represent the agent's motor intentions by matching executed and perceived actions. This matching mechanism has been proposed not only for observed actions (Buccino et al., 2001), but also for the coding of others' motor intentions (Iacoboni et al., 2005; Pelphrey, Morris, et al., 2004). Our results critically extend this evidence, revealing that the observation of object-directed gaze recruits similar brain areas to the observation of object-directed grasping actions. This suggests that under certain conditions, gaze may be equivalent to overt hand actions. In this respect, the present results might be linked to the work showing evidence of a general functional network shared by pointing actions independent of effector (i.e., hand vs. eye). In one such experiment, fMRI was used to monitor BOLD signal while subjects made either saccades or manual pointing movements in response to visual target cues (Connolly, Goodale, Desouza, Menon, & Vilis, 2000). Although the recruitment of certain brain areas was dependent on the effector (eyes vs. hands), a core pointing system included three separate foci within the inferior parietal cortex. These three sites were shown to be involved in pointing to visual stimuli, as well as inhibition of this dominant response (both types of responses may be important for joint action situations). Another experiment examined both execution and preparation of hand-based pointing movements and eye-based pointing (via saccades) movements (Astafiev, Schulman, Stanley, Snyder, Van Essen, & Corbetta, 2003). Data indicated that similar left-hemisphere intra-

parietal areas (aIPS and pIPS) were recruited during movement preparation for both eye- and hand-based-cued pointing movements, although this activation was slightly greater for hands as compared to eyes.

REFERENCES

Allison, T., Puce, A., & McCarthy, G. (2000). Social perception from visual cues: Role of the STS region. *Trends in Cognitive Science, 4,* 267–278.

Astafiev, S. V., Shulman, G. L., Stanley, C. M., Snyder, A. Z., Van Essen, D. C., & Corbetta, M. (2003). Functional organization of human intraparietal and frontal cortex for attending, looking, and pointing. *Journal of Neuroscience, 23,* 4689–4699.

Baron-Cohen, S., Campbell, R., Karmiloff-Smith, A., Grant, J., & Walker, J. (1995). Are children with autism blind to the mentalistic significance of the eyes? *British Journal of Developmental Psychology, 13,* 379–398.

Boddaert, N., Chabane, N., Gervais, H., Good, C. D., Bourgeois, M., Plumet, M. H., et al. (2004). Superior temporal sulcus anatomical abnormalities in childhood autism: A voxel-based morphometry MRI study. *Neuroimage, 23,* 364–369.

Brodmann, K. (1909). *Vergleichende Lokalisationslehre der Grosshirnrinde in ihren Prinzipien dargestellt auf Grund des Zellenbaues.* Leipzig: Barth.

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.

Castiello, U. (2003). Understanding other people's actions: Intention and attention. *Journal of Experimental Psychology: Human Perception & Performance, 29,* 416–430.

Connolly, J. D., Goodale, M. A., Desouza, J. F., Menon, R. S., & Vilis, T. (2000). A comparison of frontoparietal fMRI activation during anti-saccades and anti-pointing. *Journal of Neurophysiology, 84,* 1645–1655.

Dapretto, M., Davies, M. S., Pfeifer, J. H., Scott, A. A., Sigman, M., Bookheimer, S. Y., et al. (2006). Understanding emotions in others: Mirror neuron dysfunction in children with autism spectrum disorders. *Nature Neuroscience, 9,* 28–30.

Decety, J., & Grezes, J. (1999). Neural mechanisms subserving perception of human actions. *Trends in Cognitive Science, 3,* 172–178.

Decety, J., Grezes, J., Costes, N., Perani, D., Jeannerod, M., Procyk, E., et al. (1997). Brain activity during observation of actions. Influence of action content and subject's strategy. *Brain, 120,* 1763–1777.

Ehrsson, H. H., Fagergren, A., Jonsson, T., Westling, G., Johansson, R. S., & Forssberg, H. (2000). Cortical activity in precision versus power-grip tasks: An fMRI study. *Journal of Neurophysiology, 83,* 528–536.

Eickhoff, S. B., Stephan, K. E., Mohlberg, H., Grefkes, C., Fink, G. R., Amunts, K., et al. (2005). A new SPM toolbox for combining probabilistic cytoarchitectonic maps and functional imaging data. *Neuroimage, 25,* 1325–1335.

Friston, K. J., Ashburner, J., Frith, C. D., Poline, J. B., Heather, J. D., & Frackowiak, R. S. J. (1995). Spatial registration and normalization of images. *Human Brain Mapping, 3,* 165–189.

Friston, K. J., Holmes, A. P., Poline, J. B., Grasby, P. J., Williams, S. C. R., Frackowiak, R. S. J., et al. (1995). Analysis of fMRI time-series revisited. *Neuroimage, 2,* 45–53.

Grezes, J., Armony, J. L., Rowe, J., & Passingham, R. E. (2003). Activations related to ''mirror'' and ''canonical'' neurons in the human brain. *Neuroimage, 18,* 928–937.

Griswold, M. A., Jakob, P. M., Heidemann, R. M., Nittka, M., Jellus, V., Wang, J., et al. (2002). Generalized autocalibrating partially parallel acquisitions (GRAPPA). *Magnetic Resonance in Medicine, 47,* 1202–1210.

Hagberg, G. E., Zito, G., Patria, F., & Sanes, J. N. (2001). Improved detection of event-related functional MRI signals using probability functions. *Neuroimage, 14,* 1193–1205.

Hoffman, E. A., & Haxby, J. V. (2000). Distinct representation of eye gaze and identity in the distributed human neural system for face perception. *Nature Neuroscience, 3,* 80–84.

Iacoboni, M., Molnar-Szakacs, I., Gallese, M., Buccino, G., Mazziotta, J. C., & Rizzolatti, G. (2005). Grasping the intentions of others with one's own mirror neuron system. *PloS Biology, 79,* 529–535.

Johnson-Frey, S. H., Moloof, F. R., Newman-Norlund, R., Farrer, C., Inati, S., & Grafton, S. T. (2003). Action or hand–object interactions? Human inferior frontal cortex and action observation. *Neuron, 39,* 1053–1058.

Keysers, C., & Perrett, D. I. (2004). Demystifying social cognition: A Hebbian perspective. *Trends in Cognitive Science, 8,* 501–507.

Lancaster, J. L., Woldorff, M. G., Parsons, L. M., Liotti, M., Freitas, C. S., Rainey, L., et al. (2000). Automated Talairach atlas labels for functional brain mapping. *Human Brain Mapping, 10,* 120–131.

McCarthy, G., Spicer, M., Adrignolo, A., Luby, M., Gore, J., & Allison, T. (1995). Brain activation associated with visual motion studied by functional magnetic resonance imaging in humans. *Human Brain Mapping, 2,* 234–243.

Mosconi, M. W., Mack, P. B., McCarthy, G., & Pelphrey, K. A. (2005). Taking an ''internal stance'' on eye-gaze shifts: A functional neuroimaging study of social perception in children. *Neuroimage, 27,* 247–252.

Pelphrey, K. A., Morris, J. P., & McCarthy, G. (2004). Grasping the intentions of others: The perceived intentionality of an action influences activity in the superior temporal sulcus during social perception. *Journal of Cognitive Neuroscience, 16,* 1706–1716.

Pelphrey, K. A., Morris, J. P., & McCarthy, G. (2005). Neural basis of eye gaze processing deficits in autism. *Brain, 128,* 1038–1048.

Pelphrey, K. A., Morris, J. P., Michelich., C. R., Allison, T., & McCarthy, G. (2005). Functional anatomy of biological motion perception in posterior temporal cortex: An fMRI study of eye, mouth and hand movements. *Cerebral Cortex, 15,* 1866–1876.

Pelphrey, K. A., Singerman, J. D., Allison, T., & McCarthy, G. (2003). Brain activation evoked by the perception of gaze shifts: The influence of context. *Neuropsychology, 41,* 156–170.

Perrett, D. I., Smith, P. A., Potter, D. D., Mistlin, A. J., Head, A. S., Milner, A. D., et al. (1985). Visual cells in the temporal cortex sensitive to face view and gaze direction. *Proceedings of the Royal Society of London, Series B, 223,* 293–317.

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

Pierno, A. C., Mari, M., Glover, S., Georgiou, I., & Castiello, U. (2005). Failure to read motor intentions from gaze in children with autism. *Neuropsychologia.* E-pub ahead of print.

Puce, A., Allison, T., Bettin, S., Gore, J. C., & McCarthy, G. (1998). Temporal cortex activation in humans viewing eye and mouth movements. *Journal of Neuroscience, 18,* 2188–2199.

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

Rosen, B. R., Buckner, R. L., & Dale, A. L. (1998). Event-related functional MRI: Past, present, and future. *Proceedings of the National Academy of Science, U.S.A., 95,* 773–780.

Tai, Y. F., Scherfler, C., Brooks, D. J., Sawamoto, N., & Castiello, U. (2004). The human premotor cortex is mirror only for biological actions. *Current Biology, 14,* 117–120.

Tootell, R. B., Reppas, J. B., Dale, A. M., Look, R. B., Sereno, M. I., Brady, T. J., et al. (1995). Visual motion aftereffect in human cortical area MT revealed by functional magnetic resonance imaging. *Nature, 375,* 139–141.

Waiter, G. D., Williams, J. H. G., Murray, A. D., Gilchrist, A., Perrett, D. I., & Whiten, A. (2005a). Structural white matter deficits in high-functioning individuals with autistic spectrum disorder: A voxel-based investigation. *Neuroimage, 24,* 455–461.

Waiter, G. D., Williams, J. H. G., Murray, A. D., Gilchrist, A., Perrett, D. I., & Whiten, A. (2005b). A voxel-based investigation of brain structure in male adolescents with autistic spectrum disorder. *Neuroimage, 22,* 619–625.

Watson, J. D., Myers, R., Frackowiak, R. S., Hajnal, J. V., Woods, R. P., Mazziotta, J. C., et al. (1993). Area V5 of the human brain: Evidence from a combined study using positron emission tomography and magnetic resonance imaging. *Cerebral Cortex, 3,* 79–94.

Wheaton, K. J., Thompson, J. C., Syngeniotis, A., Abbott, D. F., & Puce, A. (2004). Viewing the motion of human body parts activates different regions of premotor, temporal, and parietal cortex. *Neuroimage, 22,* 277–288.

Zeki, S., Watson, J. D. G., Lueck, C. J., Friston, K. J., Kennard, C., & Frackowiak, R. S. J. (1991). A direct discrimination of functional specialization in human visual cortex. *Journal of Neuroscience, 11,* 641–649.