

# Predicting others' actions via grasp and gaze: evidence for distinct brain networks

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**Abstract** During social interactions, how do we predict what other people are going to do next? One view is that we use our own motor experience to simulate and predict other people's actions. For example, when we see Sally look at a coffee cup or grasp a hammer, our own motor system provides a signal that anticipates her next action. Previous research has typically examined such gaze and grasp-based simulation processes separately, and it is not known whether similar cognitive and brain systems underpin the perception of object-directed gaze and grasp. Here we use functional magnetic resonance imaging to examine to what extent gaze- and grasp-perception rely on common or distinct brain networks. Using a 'peeping window' protocol, we controlled what an observed actor could see and grasp. The actor could peep through one window to see if an object was present and reach through a different window to grasp

the object. However, the actor could not peep and grasp at the same time. We compared gaze and grasp conditions where an object was present with matched conditions where the object was absent. When participants observed another person gaze at an object, left anterior inferior parietal lobule (aIPL) and parietal operculum showed a greater response than when the object was absent. In contrast, when participants observed the actor grasp an object, premotor, posterior parietal, fusiform and middle occipital brain regions showed a greater response than when the object was absent. These results point towards a division in the neural substrates for different types of motor simulation. We suggest that left aIPL and parietal operculum are involved in a predictive process that signals a future hand interaction with an object based on another person's eye gaze, whereas a broader set of brain areas, including parts of the action observation network, are engaged during observation of an ongoing object-directed hand action.

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## Introduction

Making sense of others' actions and predicting their future behaviour is a key process in social cognition (Wilson & Knoblich, 2005). In addition to helping us function effectively in a social world, our ability to link another agents' attention and actions with objects in the environment is critical for survival (Adolphs, 2009; Emery, 2000). However, the cognitive and brain systems involved in understanding and predicting other people's actions are not yet well understood.

The challenge of predicting and comprehending actions can be simplified if the human brain is able to take into account the typical structure of actions. For example, in the vast majority of cases, an individual will look at an object

before grasping that object (Johansson, Westling, Backstrom, & Flanagan, 2001; Land, Mennie, & Rusted, 1999). Thus, gaze toward an object may provide a useful cue predicting future grasp toward the object (Frischen, Bayliss, & Tipper, 2007; Wilson & Knoblich, 2005). In contrast, grasp of an object does not necessarily make any specific predictions about future gaze.

Past research on observation of other people's grasps and gaze has identified two distinct brain networks: an action observation network (AON) responding to observed grasps (Grèzes & Decety, 2001; Caspers, Zilles, Laird, & Eickhoff, 2010), and an attentional network responding to observed gaze-shifts (Grosbras, Laird, & Paus, 2005; Nummenmaa & Calder, 2009). The AON comprises the inferior frontal gyrus (IFG), premotor cortex, supplementary motor area (SMA), inferior parietal lobule (IPL) and occipitotemporal regions (Grèzes & Decety, 2001; Gazzola & Keysers, 2009; Caspers et al., 2010). Several of these regions are also engaged when participants perform or imitate actions (Iacoboni et al., 1999; Caspers et al., 2010), which has led to the suggestion that performed and observed actions share a common neural code (Prinz, 1997; Tipper, 2010; Blake-more & Frith, 2005; Jeannerod, 2001). It has further been suggested that a key function of the AON is to predict other people's actions (Grush, 2004; Kilner, Vargas, Duval, Blakemore, & Sirigu, 2004; Prinz, 1997, 2006; Wilson & Knoblich, 2005). In support of such an action prediction account, the motor system has been shown to be active *prior* to observing someone else's action (Kilner et al., 2004), in addition to when observing another's current actions (Alaerts, de Beukelaar, Swinnen & Wenderoth, 2011; Grèzes & Decety, 2001; Caspers et al., 2010). Furthermore, the gaze of an observer watching a hand action moves ahead of the observed hand in a predictive fashion (Flanagan & Johansson, 2003). However, it is not yet clear if information about the actor's eye gaze is taken into account when predicting the actor's future hand action.

Many studies have examined the cognitive and brain systems involved in perceiving eye gaze (Emery, 2000; Frischen et al., 2007). Seminal behavioural research has demonstrated that humans have an automatic tendency to reorient their own gaze and attention in the same direction as a perceived person's gaze-shift (Driver et al., 1999; Friesen & Kingstone, 1998; Langton & Bruce, 1999). As such, other people's gaze can be deictic, as it can "point out" the location of relevant objects or agents in the environment (Shepherd, 2010). Complementing these findings, neurophysiology and brain imaging studies have shown that the perception of gaze-shifts engages a broad network of brain regions, including the superior temporal sulcus (STS) and the intraparietal sulcus (IPS) (Grosbras et al., 2005; Nummenmaa and Calder, 2009; Ramsey, Cross, & Hamilton, 2011; Shepherd, 2010). More specifically, STS has

been associated with processing gaze direction (Allison, Puce, & McCarthy, 2000; Calder et al., 2007; Perrett et al., 1985), whereas IPS has been shown to respond more specifically to the attention-reorienting aspect of perceiving gaze-shifts (Hietanen, Nummenmaa, Nyman, Parkkola, & Hämäläinen, 2006; Materna, Dicke, & Thier, 2008; Shepherd, Klein, Deaner, & Platt, 2009). This proposal is compatible with suggestions that IPS is part of a dorsal frontoparietal attention-reorienting network that coordinates stimulus–response selection (Corbetta, Patel, & Shulman, 2008; Corbetta and Shulman, 2002).

Despite the wealth of studies investigating the perception of gaze and the perception of grasp, few have examined both in the same paradigm in order to consider how they interact. Thus, neuroimaging paradigms on grasp tend to show only an acting hand without gaze information (Grèzes and Decety, 2001; Caspers et al., 2010), while most studies of gaze perception have focused solely on eye movements (Grosbras et al., 2005). Instead, studies of gaze perception have mainly used simple 2D shapes as target objects in order to study reorienting of spatial attention and perception of communicative intent (Redcay et al., 2010; Schilbach et al., 2010; Materna et al., 2008; Bristow, Rees, & Frith, 2007; Williams, Waiter, Perra, Perrett, & Whiten, 2005).

A few studies have taken this a step further to examine gaze-shifts to graspable 3D objects (Pierno et al., 2006; Pierno, Becchio, Tubaldi, Turella, & Castiello, 2008). During functional magnetic resonance imaging (fMRI), Pierno et al., (2006) showed participants videos of another person gazing at an object or grasping the same object. These videos were compared to a control condition that comprised a still image of the person looking forward. Therefore, in all conditions the object was present, but what differed was the presence of object-directed gaze or grasp. The results showed that both gaze and grasp (compared to control) led to broad activation of the AON, including IFG adjacent to ventral premotor cortex (PMv), dorsal premotor cortex (PMd), IPL and STS. These findings suggest that observing someone gaze at a graspable object produces a representation of grasp in the observer (Becchio, Bertone, & Castiello, 2008; Pierno et al., 2006). Furthermore, the authors argue that this representation of grasp following gaze perception may contribute to predicting another person's subsequent actions (Becchio et al., 2008; Pierno et al., 2006). This suggestion is consistent with the idea that the motor system is involved in a predictive process that signals how a series of related actions will unfold over time, such as gazing at an object before grasping it (Wilson & Knoblich, 2005).

In the current study, we aim to examine this proposal further. Our study goes beyond previous work involving gaze-shifts to graspable objects (Pierno et al., 2006, 2008) where the control condition did not involve a gaze-shift;

instead, the agent looked straight ahead whilst the object was present. As such, previous work did not examine the influence that the presence of object has on simulation and prediction processes following gaze-shifts. Therefore, it is unclear which parts of the AON are sensitive to gaze-shifts directed toward a graspable object compared to gaze-shifts directed toward the same location in space without an object present. Furthermore, it is not known how the perception of gaze, which is directed toward an object, compares with the perception of grasping an object.

Here we test to what extent these processes—gaze and grasp perception—rely on common or distinct brain systems. Using fMRI we compare gaze toward an object or an empty space and grasp toward an object or an empty space. Separate predictions can be made for grasp and gaze perception. For grasping, we aim to replicate previous comparisons of object-directed to non-object-directed hand actions, which activate IFG/PMv, PMd, IPL, MTG and SPL regions of the AON (for a meta-analysis, see Caspers et al., 2010). For gaze, we can distinguish between two predictions. First, if the perception of another individual gazing at an object engages mainly motor simulation and prediction processes, which include a representation of grasp in the observer, we predict that parts of the AON should respond (Becchio et al., 2008; Pierno et al., 2006, 2008). The specific regions of the AON that respond should highlight which aspects of this network are particularly sensitive to the presence of a target object in motor simulation and prediction. Moreover, if the sensations felt by the agent when touching an object are predicted then this may engage the secondary somatosensory cortex (SII), located at the parietal operculum (Eickhoff, Schleicher, Zilles, & Amunts, 2006), which has previously been shown to respond to the perception of other's being touched (Keyers et al., 2004; Keyers, Kaas, & Gazzola, 2010). Alternatively, if perceiving another person direct her gaze toward an object is associated mainly with reorienting attention to specific target objects, we predict a dorsal frontoparietal network to respond, which has previously been associated with gaze perception and attention reorientation in monkeys (Shepherd et al., 2009) and humans (Grosbras et al., 2005; Hoffman and Haxby, 2000; Nummenmaa and Calder, 2009).

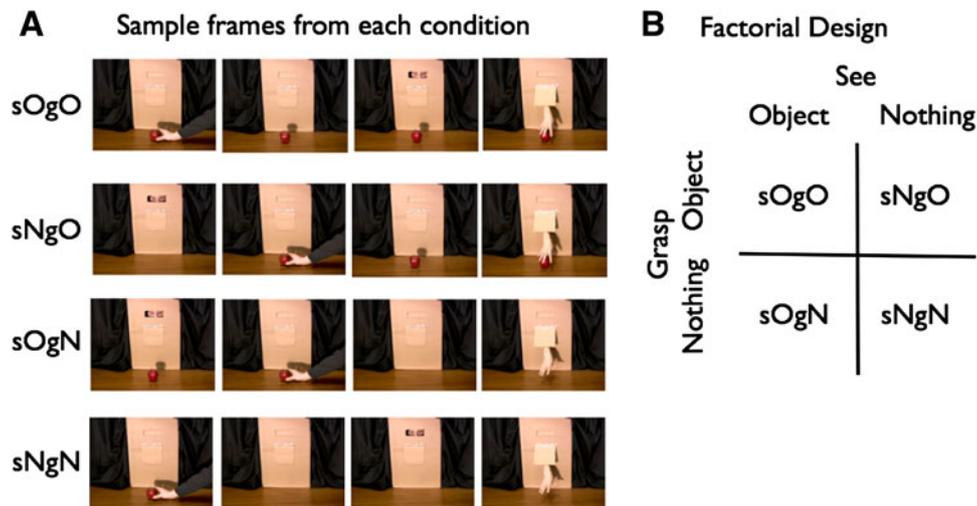
## Method

Twenty-three participants gave informed consent to take part in the study. One participant was removed from further analysis due to excessive head movement. The final sample of 22 comprised 12 females (mean age = 21.9). During fMRI scanning, participants observed short videos separated by a blank screen. Videos showed a cardboard box

with two doors, behind which a female actor was positioned. The top door was slid open, whereas the bottom door was pushed open. Sliding back the top door allowed the actor to see the table in front of her, whereas pushing her hand through the lower door allowed the actor to reach and grasp any objects on the table. The actor could not look through the top door and reach through the lower door at the same time. Thus, the actor could 'gaze' or 'grasp' at any one time (Fig. 1a). An experimenter was also filmed placing or removing an object from the scene in each video, but only his arm was visible. Participants were told that the two people in the videos were friends and liked to play games with each other. As such, one of the friends (the experimenter) could manipulate whether the actor gazed at an object (see-object) or at an empty table (see-nothing), and whether the actor grasped an object (grasp-object) or grasped towards an empty table (grasp-nothing).

Each trial involved two phases: gaze and grasp. First, the actor gazed through the top door and either observed an object or an empty table. Second, the actor reached through the bottom door to grasp an object or grasp towards an empty table (Fig. 1a). In two experimental conditions, the gaze and grasp phases were consistent (i.e., 'see-object, grasp-object' and 'see-nothing, grasp-nothing'). In the remaining two experimental conditions, the gaze and grasp phases were inconsistent (i.e., 'see-object, grasp-nothing' and 'see-nothing, grasp-object'). Therefore, in the inconsistent conditions the actor could expect an object and grasp nothing or expect nothing and grasp an object. The actor could not predict whether the object would be present or absent in the grasp phase so she always grasped with her hand (even if she had not seen an object in the gaze phase). In every trial, the experimenter's hand either placed or removed the object in the scene (Fig. 1a), but the hand was present for the same amount of time on every trial and could not impact our analyses of interest.

Six objects were used that afforded a whole-hand grasp, half of which were food items (e.g., apple) and half were non-food items (e.g., cricket ball). Baseline videos, which were devoid of human gaze or grasp, showed one coloured shape move between two other coloured shapes on a blue background (Marsh and Hamilton 2011). These baseline videos were included to provide a low-level control for shape and motion. In our final analysis, we did not need to use these control videos in any of our contrasts, so we do not discuss them further. Each of six baseline videos were shown twice (12 baseline trials). The task for participants during scanning was to make a button press when any video froze, which represented 'catch' trials. Three experimental videos and one baseline video were used as catch trial videos and each was shown twice (8 catch trials). All movies were 640 pixels wide by 480 pixels high, and between 6.5 and 7.5 s in duration (except for catch trials,



**Fig. 1** Stimuli and experimental design. **a** Key frames from video material presented during each condition. Each video showed a cardboard box with two doors, behind which a female actor was positioned. Sliding back the top door allowed the actor to see the table in front of her, whereas pushing her hand through the lower door allowed the actor to reach and grasp any objects on the table. In each video an experimenter was also filmed placing or removing an object from the scene, but only his arm was visible. Participants were told that the two people in the videos were friends and liked to play games with each other. One of the friends (the experimenter) could manipulate whether the actor gazed at an object or at an empty

table, and whether the actor grasped an object or grasped towards an empty table. As such, each trial involved two phases. First, the actor gazed through the top door and either observed an object or an empty table. Second, the actor reached through the bottom door to grasp an object or grasp towards an empty table. **b**  $2 \times 2$  factorial design. Videos evenly filled a  $2$  (see: object and nothing)  $\times 2$  (grasp: object and nothing) factorial design. Our primary analyses involved evaluating two main effects within the factorial design: see object > see nothing and grasp object > grasp nothing. *s* see, *g* grasp, *N* nothing, *O* object

which were 10 s). All stimuli were presented with Cogent running under Matlab 6.5.

Each participant completed one functional run of 68 trials, which were presented in a pseudorandom order. Scanning was performed in a 3T Phillips Achieva scanner using an 8 channel-phased array head coil with 38 slices per TR (3 mm thickness); TR, 2,500 ms; TE, 40 ms; flip angle, 80°; FOV, 24 cm; matrix, 80  $\times$  80. 210 brain images were collected and stored. Data were realigned, unwarped, corrected for slice timing, normalised to the MNI template with a resolution of 3  $\times$  3  $\times$  3 mm and spatially smoothed (8 mm) using SPM8 software. A design matrix was fitted for each participant with regressors for each movie type (sOgO, sNgO, sOgN, sNgN, baseline and catch; *s* = see, *o* = object, *g* = grasp, *n* = nothing). Each trial was modelled as a boxcar with the duration of that movie convolved with the standard hemodynamic response function. Baseline and catch trials were not analysed further.

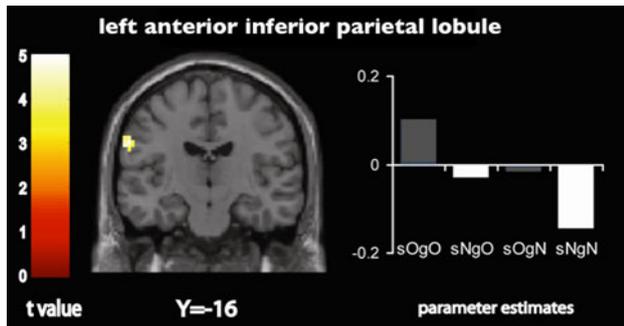
After removing baseline and catch trials, videos evenly filled a  $2$  (see: object and nothing)  $\times 2$  (grasp: object and nothing) factorial design (Fig. 1b). Our primary analyses involved evaluating two main effects within the factorial design: see object > see nothing and grasp object > grasp nothing. Statistical interactions between the main effects of See and Grasp were also calculated to determine whether the presence or absence of an object interacts with gaze and

grasp. The first interaction tested for brain regions showing a stronger response when an object was present in both See and Grasp conditions or absent in both: [(sOgO > sNgO) > (sOgN > sNgN)]. The second interaction tested for brain regions showing a stronger response when the presence of the object was inconsistent between See and Grasp conditions: [(sNgO > sOgO) > (sNgN > sOgN)]. Contrast images for all participants were taken to the second level for random effects analysis. Correction for multiple comparisons was performed at the cluster level (Friston et al. 1994), using a voxel-level threshold of  $p < 0.001$  and 10 voxels and a FWE cluster-level correction of  $p < 0.05$ . For each contrast, brain regions surviving the voxel-level threshold ( $p < 0.001$  and 10 voxels) are reported in tables with regions surviving the FWE cluster-correction highlighted in bold font. Brain regions were localised using a human brain atlas (Duvernoy, 1999) in combination with an online search tool (<http://sumsdb.wustl.edu/sums/>) and the SPM Anatomy toolbox (Eickhoff et al., 2005).

## Results

An anterior portion of the left IPL (aIPL) showed a main effect of See object > See nothing (Fig. 2; Table 1). This cluster was localised at the border of the IPL and the parietal operculum adjacent to the postcentral gyrus.

Furthermore, the cluster-peak is less than 12 mm from a brain region identified by prior work that examined the perception of another person being touched (Keyers et al., 2004, 2010). The activation identified by Keyers et al. (2004) covered aIPL and the functionally defined secondary somatosensory cortex (SII), located at the parietal operculum. In Fig. 2 the parameter estimates illustrate a greater response in aIPL when an actor looked at an object compared to when an actor looked in the same location but the object was absent. To further explore responses within the AON, we lowered the voxel-wise threshold ( $p < 0.005$ ,



**Fig. 2** Left anterior inferior parietal lobule showed a significantly greater response when the actor gazed at an object (grey bars) compared to when the actor gazed towards the same location but the object was absent (white bars). Cluster-average parameter estimates (SPM betas) are plotted. *s* see, *g* grasp, *N* nothing, *O* object

$K = 10$ ) and found two further regions that showed a similar pattern of response within the AON: left IFG adjacent PMv and a region of right IPL, which was localised to the supramarginal gyrus (Supplementary Table S1). There were no brain regions that showed the inverse pattern of response (See nothing > See object).

Bilateral posterior IPS/SPL, PMd, fusiform gyrus and middle occipital gyrus showed a main effect of Grasp object > Grasp nothing (Fig. 3; Table 1). In addition, left IFG adjacent to PMv and a region localised around the right parieto-occipital junction showed a similar pattern of response (Table 1). The left pIPS/SPL cluster extends ventrally into middle occipital gyrus and fusiform gyrus, as well as anteriorly into middle and anterior parts of the IPS. At the initial voxel-wise threshold ( $p < 0.001$ ,  $K = 10$ ), this cluster does not overlap with the aIPL cluster from the gaze contrast (See object > See nothing). However, at a lower voxel-wise threshold ( $p < 0.005$ ,  $K = 10$ ), these contrasts do overlap in aIPL. In Fig. 3 the parameter estimates illustrate a greater response in these brain regions when an actor grasped an object compared to when an actor grasped in the same location but the object was absent. There were no brain regions that showed the inverse pattern of response (Grasp nothing > Grasp object).

Statistical interactions between the main effects of see object and grasp object were also calculated. The first interaction [(sOgO > sNgO) > (sOgN > sNgN)] showed

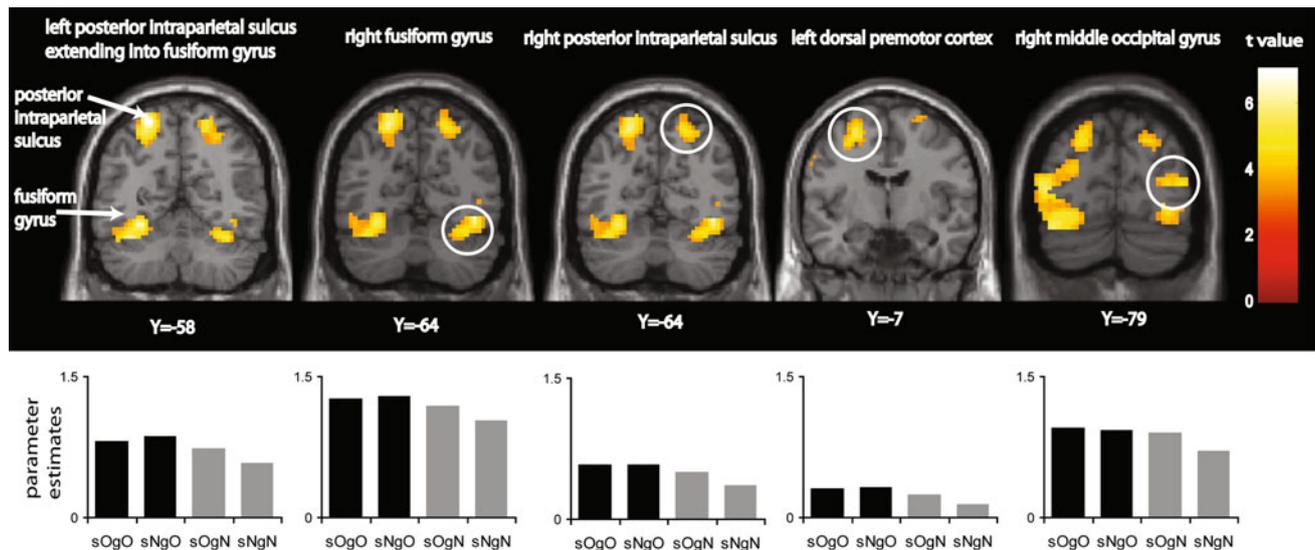
**Table 1** Brain regions showing the main effect of see object and grasp object

Region	Number of voxels	<i>T</i>	Montreal Neurological Institute coordinates		
			<i>x</i>	<i>y</i>	<i>z</i>
<i>See object &gt; see nothing</i>					
Left aIPL extending into parietal operculum	21	5.08	-60	-16	31
<i>Grasp object &gt; grasp nothing</i>					
<b>Left pIPS/SPL extending into IPS, aIPS, MOG and fusiform gyrus</b>	<b>1,602</b>	<b>7.43</b>	<b>-24</b>	<b>-58</b>	<b>67</b>
			<b>-36</b>	<b>-52</b>	<b>-26</b>
			<b>-30</b>	<b>-58</b>	<b>-14</b>
<b>Right fusiform gyrus</b>	<b>385</b>	<b>6.59</b>	<b>42</b>	<b>-64</b>	<b>-11</b>
			<b>36</b>	<b>-73</b>	<b>-8</b>
			<b>33</b>	<b>-55</b>	<b>-23</b>
<b>Right pIPS extending into SPL</b>	<b>141</b>	<b>6.48</b>	<b>21</b>	<b>-52</b>	<b>64</b>
			<b>21</b>	<b>-64</b>	<b>55</b>
			<b>33</b>	<b>-40</b>	<b>70</b>
<b>Left dorsal premotor cortex</b>	<b>108</b>	<b>5.67</b>	<b>-24</b>	<b>-7</b>	<b>58</b>
<b>Right middle occipitotemporal cortex</b>	<b>71</b>	<b>4.97</b>	<b>45</b>	<b>-79</b>	<b>10</b>
			<b>33</b>	<b>-85</b>	<b>13</b>
			<b>45</b>	<b>-67</b>	<b>4</b>
Right parieto-occipital junction	58	4.64	21	-79	40
Left inferior frontal gyrus	17	4.29	-57	-1	37
Right dorsal premotor cortex	17	3.93	27	-7	70
			33	-10	58

Only regions surviving a voxel-level threshold of  $p < 0.001$  and 10 voxels are reported.

Subpeaks more than 8 mm from the main peak in each cluster are listed. Bold indicates regions that survive the whole-brain cluster-corrected threshold at  $p < 0.05$

*IPL* inferior parietal lobule, *SPL* superior parietal lobule, *a* anterior, *m* middle, *p* = posterior, *IPS* intraparietal sulcus, *MOG* middle occipital gyrus



**Fig. 3** Brain regions showing grasp object > grasp nothing. Significantly greater activity was observed for grasping trials when the object was present (*black bars*) compared to grasping when the object was absent (*grey bars*) in bilateral posterior intraparietal sulcus (pIPS)/superior parietal lobule (SPL), fusiform gyrus, middle

occipital gyrus and left dorsal premotor cortex. The left pIPS/SPL cluster extends ventrally into middle occipital and fusiform gyri, as well as anteriorly into middle and anterior parts of the intraparietal sulcus. Cluster-average parameter estimates (SPM betas) are plotted for each cluster. *s* see, *g* grasp, *N* nothing, *O* object

activity in left medial occipitotemporal cortex/parahippocampal gyrus. The second interaction [(sNgO > sOgO) > (sNgN > sOgN)] showed activity in medial inferior occipital gyrus/lingual gyrus and left fusiform gyrus. The results of these interaction analyses are reported in Supplementary Table S2.

## Discussion

In the present study, we aimed to determine whether the observation of grasp and gaze engages common or distinct neural structures, and in particular, whether observing an actor gaze towards an object leads to predictions of grasp within the observer's AON. Our results demonstrate a division in the neural substrates underpinning the perception of deictic gaze and grasp. More specifically, we find engagement of left aIPL and parietal operculum when perceiving a person gaze towards an object, while a broader pattern of activation spanning much of the AON was found during observation of an ongoing object-directed hand action. In the following, we consider what these results contribute to our understanding of the AON's role in social cognition, specifically focusing on action simulation and prediction processes.

### Perceiving others' grasp and gaze

As found by many previous studies, observation of a person grasping an object compared to grasping an empty

space engaged the AON, specifically IPS/SPL, IFG/PMv, PMd and MO. This result is consistent with previous suggestions that sensorimotor brain systems are involved in the perception of action (Grèzes and Decety, 2001; Gazzola & Keysers, 2009; Caspers et al., 2010), and that subcomponents of this network, such as premotor, parietal and occipitotemporal, show specific sensitivity to actions directed to target objects (Caspers et al., 2010; Morin and Grèzes, 2008).

More critical to our hypothesis is the contrast of observed gaze to an object compared to observed gaze to an empty space. Here we found engagement of left aIPL and parietal operculum but no engagement of a dorsal frontoparietal attention network or STS. At a more lenient threshold we also found engagement of left IFG adjacent to PMv. As left aIPL and PMv are part of the AON, this result is consistent with our hypothesis that observation of gaze in the context of hand actions leads the observer to predict that the actor will grasp the object and engages the AON (Becchio et al., 2008). Moreover, the engagement of parietal operculum, which has been shown to be the anatomical correlate of SII (Eickhoff et al., 2006) as well as to respond to the observation of others being touched (Keysers et al., 2004, 2010), is consistent with the notion that one of the action features predicted is the sensation that the actor will feel when she touches the object.

These findings support the suggestion that observing another person's gaze forms a representation of grasp in the observer (Becchio et al., 2008; Pierno et al., 2006, 2008). It is also consistent with the claim that the motor system is

involved in predicting other people's actions (Prinz, 2006; Wilson & Knoblich 2005), because sensitivity in aIPL was observed prior to the observation of grasping (Kilner et al., 2004). This result extends previous research (Pierno et al., 2006, 2008), which showed widespread responses in frontal, parietal and temporal parts of the AON, but did not include a gaze-shift in the control condition. By including an identical gaze-shift in the control condition and only varying the presence of the target object, we show that aIPL is particularly sensitive to gaze–object relations rather than processing gaze-shifts alone. These data indicate a more specific process for aIPL; namely, one that involves linking gaze-shifts with objects that will subsequently be grasped.

Before expanding on the interpretation of these data and placing them within a broader theoretical context, we first outline two strengths of the design, which can rule out alternative interpretations. First, gaze-shifts and grasps were performed to the identical location in space when an object was present or absent, which means reorienting of spatial attention was balanced between object and non-object conditions. Therefore, a location-cueing or spatial attention explanation cannot account for our results. Second, object-directed and non-object-directed trials had the same visual motion, including motion of eyes and hand, which means motion differences also cannot account for our results. In sum, only the presence of the target object was manipulated between conditions of interest. In the following section we outline in more detail our primary interpretation of these data and how they relate to processes in social cognition.

#### Predicting grasp via gaze

Motor system involvement in action perception has been argued to be a predictive process by numerous researchers (Grush, 2004; Prinz, 2006; Kilner et al., 2004; Verfaillie & Daems, 2002; Wilson & Knoblich, 2005). Wilson and Knoblich (2005) argue that, based on prior experience with our own and others' actions, the motor system simulates and predicts a timeline of how a given social interaction between people or between people and objects is likely to unfold. Consistent with this view, we suggest that left aIPL plays a role in predicting future hand–object interactions based on the perception of someone else's gaze. This predictive signal enables the perceiver to anticipate the agent's future behaviour and program an appropriate motor response in advance of seeing the action performed to completion. Reliably anticipating others' future actions has benefits for many cooperative and competitive situations, from cooking a meal together to playing tennis (Prinz, 2006; Tomasello, Carpenter, Call, Behne, & Moll, 2005).

Previously, it has been suggested that the same brain systems engaged while performing eye movements are also used to perceive another person's eye movements (Frischen

et al., 2007). For example, neurons in monkey ventral intraparietal area respond to performed and observed eye movements (Shepherd et al., 2009), and human fMRI studies show a similar pattern of results in middle and posterior IPS as well as the frontal eye fields (Grosbras et al., 2005). As such, it has been suggested that a 'simulation' or 'mirror' system exists for eye gaze, similar to that which has previously been demonstrated for hand actions (Grosbras et al., 2005; Rizzolatti & Sinigaglia, 2010). Pertinent to the current findings, such eye gaze responses are typically found in middle or posterior segments of parietal cortex (Ramsey, Cross, & Hamilton, 2011; Shepherd et al., 2009; Silver, 2009).

Our results point to a different, although complementary, view to that put forward in prior gaze perception research. The response in the current study is in an anterior portion of parietal cortex, which has been more frequently associated with the control and perception of grasping actions (Culham, Cavina-Pratesi, & Singhal, 2006) as well as with predicting others' grasping actions (Kilner et al., 2004). When observing someone gaze at a graspable object, instead of simulating movement of the person's eyes using brain systems that control eye movements, we suggest that what is simulated in aIPL is the *future* grasping action of the hand. In this sense, eye gaze is cueing a motoric representation of an action that is likely to occur in the near future. As such, the response in aIPL is a *predictive* signal for a subsequent hand grasp rather than a strict simulation or mirror of the other person's current eye movements.

While a striking aspect of the results is the distinct location of response for gaze and grasp, overlap between both processes was observed in aIPL (following reduction of the voxel-wise threshold for grasp). However, overlap was observed in aIPL for gaze and grasp (at least when the voxel-wise threshold is reduced for grasp). This overlap could reflect a common process, such as predicting subsequent hand–object interactions. However, the overlap could also reflect two different cognitive processes, which are both implemented in a common brain area. Since inferior parietal cortex has many cytoarchitectonic divisions, it is likely to perform many processes (Caspers et al., 2006). For example, the gaze contrast could reflect the prediction of a subsequent hand–object interaction, whereas the grasp response could reflect the processing of a future action outcome. Possible action outcomes include what the person might do with the object, such as eat it or place it (Fogassi et al., 2005; Hamilton & Grafton, 2008). The current design cannot determine whether common or distinct processes are performed in aIPL during the perception of gaze and grasp, but we suggest further research may address the issue.

In the current study, we focused on the predictive processes performed in aIPL during deictic gaze perception, but we do not suggest that this is the only brain region

involved in motor prediction. At a lower statistical threshold we also found responses in IFG adjacent to PMv, which could reflect a similar predictive signal to aIPL or the response of canonical neurons that respond to the presentation of an object (Rizzolatti & Luppino, 2001). Moreover, the motor system in general has been frequently associated with predictive mechanisms when controlling one's own actions, by building forward models and acting as an anticipation device for one's own body (Desmurget & Grafton, 2000; Wolpert & Kawato, 1998; Wolpert & Flanagan, 2001). In action observation, it has been suggested that the motor system's capacity for prediction is extended to others' actions (Prinz, 2006). For example, other types of human and non-human prediction processes rely on lateral and medial premotor cortex (Cross, Stadler, Parkinson, Schutz-Boabach, & Prinz, 2011; Schubotz, 2007; Stadler et al., 2011). One possible avenue for future work is to examine how predictive processes performed by distinct components of the AON are bound together into a coherent prediction of other people's actions.

## Conclusion

We show divisions in the neural substrates underlying action simulation and prediction processes based on the perception of eye-gaze and hand actions. The findings suggest that when perceiving a person gaze towards an object, left aIPL and parietal operculum are involved in a predictive process that signals a future interaction with an object (i.e., a grasp). In contrast, a broader set of brain areas including parts of the AON is engaged during observation of an ongoing object-directed hand action, possibly reflecting the prediction of more temporally extended actions, such as moving or placing the object, rather than the initial grasp. Together these results fractionate processes of action simulation and prediction in the AON following gaze and grasp and suggest different but complementary roles in providing predictive signals, which anticipate what an observed agent will do next. A challenge for future research is to explore how these simulation and prediction processes from different cues are bound together to produce an accurate prediction of another person's future actions and the intentions those actions serve.

## References

- Adolphs, R. (2009). The social brain: Neural basis of social knowledge. *Annual Review of Psychology*, 60(1), 693–716.
- Alaerts, K., de Beukelaar, T. T., Swinnen, S. P., & Wenderoth, N. (2011). Observing how others lift light or heavy objects: Time-dependent encoding of grip force in the primary motor cortex. *Psychological Research*. doi:10.1007/s00426-011-0380-1 (this issue)
- Allison, T., Puce, A., & McCarthy, G. (2000). Social perception from visual cues: Role of the STS region. *Trends in Cognitive Sciences*, 4(7), 267–278.
- Becchio, C., Bertone, C., & Castiello, U. (2008). How the gaze of others influences object processing. *Trends in Cognitive Sciences*, 12(7), 254–258.
- Blakemore, S.-J., & Frith, C. (2005). The role of motor contagion in the prediction of action. *Neuropsychologia*, 43(2), 260–267.
- Bristow, D., Rees, G., & Frith, C. D. (2007). Social interaction modifies neural response to gaze shifts. *Social Cognitive and Affective Neuroscience*, 2(1), 52–61.
- Calder, A. J., Beaver, J. D., Winston, J. S., Dolan, R. J., Jenkins, R., Eger, E., et al. (2007). Separate coding of different gaze directions in the superior temporal sulcus and inferior parietal lobule. *Current Biology*, 17(1), 20–25.
- Caspers, S., Geyer, S., Schleicher, A., Mohlberg, H., Amunts, K., & Zilles, K. (2006). The human inferior parietal cortex: Cytoarchitectonic parcellation and interindividual variability. *NeuroImage*, 33(2), 430–448.
- Caspers, S., Zilles, K., Laird, A. R., & Eickhoff, S. B. (2010). ALE meta-analysis of action observation and imitation in the human brain. *NeuroImage*, 50(3), 1148–1167.
- Corbetta, M., Patel, G., & Shulman, G. L. (2008). The reorienting system of the human brain: From environment to theory of mind. *Neuron*, 58(3), 306–324.
- Corbetta, M., & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews Neuroscience*, 3(3), 201–215.
- Cross, E. S., Stadler, W., Parkinson, J., Schutz-Boabach, S., & Prinz, W. (2011). The influence of visual training on predicting complex action sequences. *Human Brain Mapping*. doi:10.1002/hbm.21450.
- Culham, J. C., Cavina-Pratesi, C., & Singhal, A. (2006). The role of parietal cortex in visuomotor control: What have we learned from neuroimaging? *Neuropsychologia*, 44(13), 2668–2684.
- Desmurget, M., & Grafton, S. (2000). Forward modeling allows feedback control for fast reaching movements. *Trends in Cognitive Sciences*, 4(11), 423–431.
- Driver, J., Davis, G., Ricciardelli, P., Kidd, P., Maxwell, E., & Baron-Cohen, S. (1999). Gaze perception triggers reflexive visuospatial orienting. *Visual Cognition*, 6(5), 509–540.
- Duvernoy, H. M. (1999). *The human brain: surface, blood supply, and three-dimensional sectional anatomy*. New York: Springer.
- Eickhoff, S. B., Schleicher, A., Zilles, K., & Amunts, K. (2006). The human parietal operculum. I. Cytoarchitectonic mapping of subdivisions. *Cerebral Cortex*, 16(2), 254–267.
- Eickhoff, S., Stephan, K. E., Mohlberg, H., Grefkes, C., Fink, G. R., Amunts, K., Zilles, K. (2005). A new SPM toolbox for combining probabilistic cytoarchitectonic maps and functional imaging data. *NeuroImage* 25(4), 1325–1335.
- Emery, N. J. (2000). The eyes have it: The neuroethology, function and evolution of social gaze. *Neuroscience and Biobehavioral Reviews*, 24(6), 581–604.
- Flanagan, J. R., & Johansson, R. S. (2003). Action plans used in action observation. *Nature*, 424(6950), 769–771.
- Fogassi, L., Ferrari, P. F., Gesierich, B., Rozzi, S., Chersi, F., & Rizzolatti, G. (2005). Parietal lobe: from action organization to intention understanding. *Science*, 308, 662–667.
- Friesen, C., K., & Kingstone, A. (1998). The eyes have it! Reflexive orienting is triggered by nonpredictive gaze. *Psychonomic Bulletin & Review*, 5, 490–495.
- Frischen, A., Bayliss, A. P., & Tipper, S. P. (2007). Gaze cueing of attention: Visual attention, social cognition, and individual differences. *Psychological Bulletin*, 133(4), 694–724.

- Friston, K. J., Worsley, K. J., Frackowiak, R. S. J., Mazziotta, J. C., & Evans, A. C. (1994). Assessing the significance of focal activations using their spatial extent. *Human Brain Mapping*, 1(3), 210–220.
- Gazzola, V., & Keysers, C. (2009). The observation and execution of actions share motor and somatosensory voxels in all tested subjects: Single-subject analyses of unsmoothed fMRI data. *Cerebral Cortex*, 19(6), 1239–1255.
- Grèzes, J., & Decety, J. (2001). Functional anatomy of execution, mental simulation, observation, and verb generation of actions: A meta-analysis. *Human Brain Mapping*, 12(1), 1–19.
- Grosbras, M.-H., Laird, A. R., & Paus, T. (2005). Cortical regions involved in eye movements, shifts of attention, and gaze perception. *Human Brain Mapping*, 25(1), 140–154.
- Grush, R. (2004). The emulation theory of representation: Motor control, imagery, and perception. *Behavioral and Brain Sciences*, 27(03), 377–396.
- Hamilton, A. F., & Grafton, S. T. (2008). Action outcomes are represented in human inferior frontoparietal cortex. *Cerebral Cortex*, 18, 1160–1168.
- Hietanen, J. K., Nummenmaa, L., Nyman, M. J., Parkkola, R., & Hämäläinen, H. (2006). Automatic attention orienting by social and symbolic cues activates different neural networks: An fMRI study. *NeuroImage*, 33(1), 406–413.
- Hoffman, E. A., & Haxby, J. V. (2000). Distinct representations of eye gaze and identity in the distributed human neural system for face perception. *Nature Neuroscience*, 3(1), 80–84.
- Iacoboni, M., Woods, R. P., Brass, M., Bekkering, H., Mazziotta, J. C., & Rizzolatti, G. (1999). Cortical mechanisms of human imitation. *Science*, 286(5449), 2526–2528.
- Jeannerod, M. (2001). Neural simulation of action: A unifying mechanism for motor cognition. *NeuroImage*, 14(1), S103–S109.
- Johansson, R. S., Westling, G., Backstrom, A., & Flanagan, J. R. (2001). Eye–hand coordination in object manipulation. *Journal of Neuroscience*, 21(17), 6917–6932.
- Keysers, C., Kaas, J. H., & Gazzola, V. (2010). Somatosensation in social perception. *Nature Reviews Neuroscience*, 11(6), 417–428.
- Keysers, C., Wicker, B., Gazzola, V., Anton, J. L., Fogassi, L., & Gallese, V. (2004). A touching sight: SII/PV activation during the observation and experience of touch. *Neuron*, 42(2), 335–346.
- Kilner, J. M., Vargas, C., Duval, S., Blakemore, S. J., & Sirigu, A. (2004). Motor activation prior to observation of a predicted movement. *Nature Neuroscience*, 7(12), 1299–1301.
- Land, M., Mennie, N., & Rusted, J. (1999). The roles of vision and eye movements in the control of activities of daily living. *Perception*, 28(11), 1311–1328.
- Langton, S. R. H., & Bruce, V. (1999). Reflexive visual orienting in response to the social attention of others. *Visual Cognition*, 6(5), 541–567.
- Marsh, L. E., & Hamilton, A. F. d. C. (2011). Dissociation of mirroring and mentalising systems in autism. *NeuroImage*, 56(3), 1511–1519.
- Materna, S., Dicke, P. W., & Thier, P. (2008). Dissociable roles of the superior temporal sulcus and the intraparietal sulcus in joint attention: A functional magnetic resonance imaging study. *Journal of Cognitive Neuroscience*, 20(1), 108–119.
- Morin, O., & Grèzes, J. (2008). What is “mirror” in the premotor cortex? A review. *Neurophysiologie Clinique/Clinical Neurophysiology*, 38(3), 189–195.
- Nummenmaa, L., & Calder, A. J. (2009). Neural mechanisms of social attention. *Trends in Cognitive Sciences*, 13(3), 135–143.
- Perrett, D. I., Smith, P. A. J., 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: Biological Sciences*, 223(1232), 293–317.
- Pierno, A. C., Becchio, C., Tubaldi, F., Turella, L., & Castiello, U. (2008). Motor ontology in representing gaze–object relations. *Neuroscience Letters*, 430(3), 246–251.
- Pierno, A. C., Becchio, C., Wall, M. B., Smith, A. T., Turella, L., & Castiello, U. (2006). When gaze turns into grasp. *Journal of Cognitive Neuroscience*, 18(12), 2130–2137.
- Prinz, W. (1997). Perception and action planning. *European Journal of Cognitive Psychology*, 9(2), 129–154.
- Prinz, W. (2006). What re-enactment earns us. *Cortex*, 42(4), 515–517.
- Ramsey, R., Cross, E. S., & Hamilton, A. F. de C. (2011). Eye can see what you want: Posterior intraparietal sulcus encodes the object of an actor’s gaze. *Journal of Cognitive Neuroscience*, 23(11), 3400–3409.
- Redcay, E., Dodell-Feder, D., Pearrow, M. J., Mavros, P. L., Kleiner, M., Gabrieli, J. D. E., et al. (2010). Live face-to-face interaction during fMRI: A new tool for social cognitive neuroscience. *NeuroImage*, 50(4), 1639–1647.
- Rizzolatti, G., & Luppino, G. (2001). The cortical motor system. *Neuron*, 31(6), 889–901.
- Rizzolatti, G., & Sinigaglia, C. (2010). The functional role of the parieto-frontal mirror circuit: Interpretations and misinterpretations. *Nature Reviews Neuroscience*, 11(4), 264–274.
- Schilbach, L., Wilms, M., Eickhoff, S. B., Romanzetti, S., Tepest, R., Bente, G., et al. (2010). Minds made for sharing: Initiating joint attention recruits reward-related neurocircuitry. *Journal of Cognitive Neuroscience*, 22(12), 2702–2715.
- Schubotz, R. I. (2007). Prediction of external events with our motor system: towards a new framework. *Trends in Cognitive Sciences*, 11(5), 211–218.
- Shepherd, S. V. (2010). Following gaze: Gaze-following behavior as a window into social cognition. *Frontiers in Integrative Neuroscience*, 4.
- Shepherd, S. V., Klein, J. T., Deaner, R. O., & Platt, M. L. (2009). Mirroring of attention by neurons in macaque parietal cortex. *Proceedings of the National Academy of Sciences*, 106(23), 9489–9494.
- Silver, M. A. and S. Kastner (2009). Topographic maps in human frontal and parietal cortex. *Trends in Cognitive Sciences*, 13, 488–495.
- Stadler, W., Schubotz, R. I., von Cramon, D. Y., Springer, A., Graf, M., & Prinz, W. (2011). Predicting and memorizing observed action: Differential premotor cortex involvement. *Human Brain Mapping*, 32(5), 677–687.
- Tipper, S. P. (2010). From observation to action simulation: The role of attention, eye–gaze, emotion, and body state. *Quarterly Journal of Experimental Psychology*, 63, 2081–2105.
- Tomasello, M., Carpenter, M., Call, J., Behne, T., & Moll, H. (2005). Understanding and sharing intentions: The origins of cultural cognition. *Behaviour Brain Science*, 28(5), 675–691.
- Verfaillie, K., & Daems, A. (2002). Representing and anticipating human actions in vision. *Visual Cognition*, 9(1–2), 217–232.
- Williams, J. H., Waiter, G. D., Perra, O., Perrett, D. I., & Whiten, A. (2005). An fMRI study of joint attention experience. *NeuroImage*, 25(1), 133–140.
- Wilson, M., & Knoblich, G. (2005). The case for motor involvement in perceiving conspecifics. *Psychological Bulletin*, 131(3), 460–473.
- Wolpert, D. M., & Flanagan, J. R. (2001). Motor prediction. *Current Biology*, 11(18), R729–R732.
- Wolpert, D. M., & Kawato, M. (1998). Multiple paired forward and inverse models for motor control. *Neural Networks*, 11, 1317–1329.