



Understanding actors and object-goals in the human brain

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ABSTRACT

When another person takes £10 from your hand, it matters if they are a shopkeeper or a robber. That is, the meaning of a simple, goal-directed action can vary depending on the identity of the actors involved. Research examining action understanding has identified an action observation network (AON) that encodes action features such as goals and kinematics. However, it is not yet known how or where the brain links actor identity to action goal. In the present paper, we used a repetition suppression paradigm during functional magnetic resonance imaging (fMRI) to examine the neural representation of actor identity within the context of object-directed actions. Participants watched video clips of two different actors with two different object-goals. Repeated presentation of the same actor suppressed the blood oxygen level-dependent (BOLD) response in fusiform gyrus and occipitotemporal cortex. In contrast, repeated presentation of an action with the same object-goal suppressed the BOLD response throughout the AON. Our data reveal an extended brain network for understanding other people and their everyday actions that go beyond the traditional action observation network.

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Introduction

In the final scene of an action movie, someone fires a gun. Understanding what happens next depends on linking the identity of the gunman (hero or villain) to that action. Similarly, appreciating the meaning of social interactions depends crucially on an understanding to whom you are interacting with. The current paper uses functional magnetic resonance imaging (fMRI) to examine how the human brain encodes the object-goals of other people's actions and the identities of the actors involved.

An extensive literature has identified an action observation network (AON) in the human brain that responds when an individual observes someone else performing an action (Buccino et al., 2001; Decety and Grèzes, 1999; Grèzes and Decety, 2001). This AON includes the inferior frontal gyrus (IFG) and inferior parietal lobule (IPL), which make up the mirror neuron system (Rizzolatti and Craighero, 2004), and also the middle temporal gyrus and superior temporal sulcus regions (MTG/STS) that respond to the observation of biological motion (Puce and Perrett, 2003). The AON encodes action features such as goals and kinematics (Hamilton and Grafton, 2006, 2007, 2008), as well as actions in context (Iacoboni et al., 2005; Liepelt et al., 2008, 2009; Newman-Norlund et al., 2007). However, it is not known how this information is integrated with other critical action information, such as actor identity. A recent study found that AON activity was similar whether or not an actor's face was visible, which

suggests that other brain regions must be involved in encoding actor identity (Turella et al., 2009).

Past studies of person identity have linked face recognition processes to brain areas such as the fusiform face area (FFA) (Kanwisher et al., 1997; Winston et al., 2004), and body recognition processes to the fusiform body area (FBA) and extrastriate body area (EBA) (Downing et al., 2001; Peelen and Downing, 2005; Urgesi et al., 2007). However, these studies did not examine person identity in the context of action, and used only static images of static people. The purpose of the current experiment was to link these different fields and investigate how the brain encodes the identity of actors performing object-directed action.

Investigating the AON in more complex, realistic social situations has implications for theories about the role of the AON in social cognition: how much does this network take on and what is done elsewhere? Some authors have attributed a wide range of social abilities to the AON or mirror system, including action understanding and theory-of-mind (Gallese, 2005, 2007), whilst others have made the argument that processes and brain regions beyond the AON are necessary to understand other people's actions (Csibra, 2007; Goldman and de Vignemont, 2009; Wood and Hauser, 2008). In the present experiment, we examined whether the identity of an actor performing an object-directed action is encoded in or influences the AON.

Studying actor identity in social contexts also has implications for the problem of knowing *who* is acting. This has been previously studied in the context of agency and self-other discrimination. Several studies suggest that the AON does not discriminate between self and other since a robust blood oxygen level-dependent (BOLD) signal is recorded for actions performed by the self and for actions of another

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human (Etzel et al., 2008; Gazzola and Keysers, 2009; Grèzes and Decety, 2001) or robot (Gazzola et al., 2007). These results led Georgieff and Jeannerod (1998) to posit the problem of *who*—how does the brain represent who is acting? Neuroscientific investigations have examined how self-agency is represented in the brain, with numerous brain regions implicated (David et al., 2006; Farrer and Frith, 2002; Fink et al., 1999; Ruby and Decety, 2001). However, in social situations the problem of *who* is broader than just discriminating between self and other; distinguishing between other and other is often critical. The current paper provides an initial attempt to address this problem.

We use an established repetition suppression (RS) paradigm to investigate the brain regions encoding actor identity and action goal (as defined by the object grasped). Participants watched video clips of two different actors with two different object-goals, arranged in an RS design during fMRI. RS is grounded on the principle that the presentation of a repeated stimulus will result in a reduced BOLD response in brain regions that encode that stimulus (Grill-Spector and Malach, 2001). Consistent with previous work, we predicted RS for object-goal in aIPS and the wider AON (Hamilton and Grafton, 2006, 2007). In addition, if actor identity is also encoded within the AON we expected RS for actor within this network of regions. Alternatively, if actor identity is encoded outside the AON, then RS for actor will be seen in face- and body-identity regions located in fusiform gyrus (FFA, FBA) and occipitotemporal cortex (EBA) (Downing et al., 2001; Kanwisher et al., 1997; Peelen and Downing, 2005).

Materials and methods

Twenty-five participants (8 male, mean age 24 years, one left-handed) gave their informed consent to complete the experiment in accord with the local ethics board. One participant was excluded due to excessive head movement. During fMRI scanning, participants viewed sets of movies separated by a blank screen. Each movie comprised a pair of same-sex actors, one of whom would step forward and take one of two objects (a tool or a food) from a table (Fig. 1). Movie clips were presented in sets of 9, pseudorandomly ordered to obtain RS for actor and object-goal in a one-back RS design. Each set began with a 'new' movie followed by 8 movies, each defined in relation to the previous movie as either novel Actor-novel Object-Goal (nAnO-G), repeated Actor-novel Object-Goal (rAnO-G), novel Actor-repeated Object-Goal (nArO-G), or repeated Actor-repeated Object-Goal (rArO-G). Movie clip durations ranged from 5 to 8 s according to the natural length of the event, but were constant within each set. After the set, participants answered an unpredictable yes–no question about the content of the last movie in order to keep participants attentive during scanning. Questions covered all aspects of the observed videos and instructions were simply to watch the movies and answer the question with a button press. Each participant completed 4 functional runs with 8 sets of movies in each run giving 256 RS trials, which evenly filled a 2×2 factorial design for actor and object-goals, novel and repeated (Fig. 1). Six different pairs of actors, whom participants did not know, and twelve different tool-food pairs of objects were presented over the four runs. All stimuli were presented with Cogent running under Matlab 6.5 permitting synchronisation with the scanner and accurate timing of stimuli presentation.

The experiment was performed in a 3 T Phillips Achieva scanner using an 8 channel-phased array head coil with 40 slices per TR (3 mm thickness); TR: 2500 ms; TE: 40 ms; flip angle: 80°; field of view: 19.2 cm, matrix: 64×64 . For each functional run 240 images were collected and stored. Data were realigned, unwrapped and normalised to the MNI template with a resolution of $2 \times 2 \times 2$ mm using SPM2 software. A design matrix was fitted for each subject with one regressor for each trial type (nAnO-G, rAnO-G, nArO-G, rArO-G, new and question) in each set of movies. Each trial was modelled as a boxcar with the duration of that movie convolved with the standard

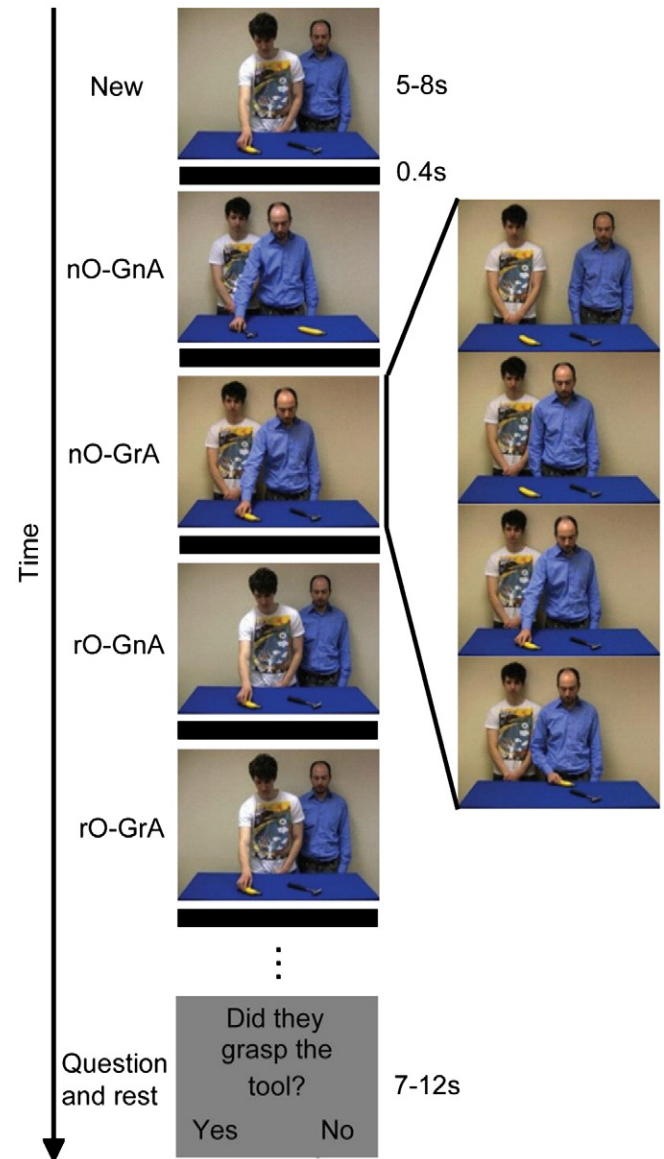


Fig. 1. Stimuli and experimental setup. The left side shows five movies from a typical sequence viewed by participants. Each movie sequence began with a new movie followed by 8 experimental clips. Movies were sequenced to achieve one-back repetition suppression for actor and object-goal. Therefore, each movie was defined with respect to the previous movie. For each experimental clip the observed actor and object-goal could be the same (repeated) or different (novel) with respect to the previous movie. In doing so, each clip fell evenly into a 2×2 factorial design for actor and object-goal, novel and repeated (abbreviations are: n = novel, r = repeated, A = actor, OG = object-goal). Following a sequence, participants answered a yes–no question regarding the previous movie. The right side shows four scenes from one movie clip. An actor would step forward, take one of two objects (a tool or a food) and place it closer to them.

haemodynamic response function. To reduce the impact of movement artifacts each design matrix weighted every raw image according to its overall variability (Diedrichsen and Shadmehr, 2005). After estimation, 9 mm smoothing was applied to the beta images.

In order to localise brain regions showing RS for actor and RS for object-goal, we focussed our search volume onto *a priori* regions of interest, which included the AON and person identity areas. To do so, we used an anatomical mask made of overlapping 20 mm diameter spheres that covered bilateral IFG, IPL, and posterior temporal brain regions, which included STS, MTG, fusiform gyrus and occipitotemporal cortex (Cross et al., 2009). Spheres were centred in both hemispheres but coordinates are only reported for the left hemi-

Table 1
Brain regions showing RS for actor and RS for object-goal.

Region	Number of voxels	T	P cluster corrected	Montreal Neurological Institute coordinates		
				x	y	z
<i>Actor</i>						
Right fusiform gyrus extending into occipitotemporal cortex (EBA)	1288	6.21	<0.001	36	−68	−14
				34	−48	−22
				52	−82	−4
Left posterior fusiform gyrus extending into occipitotemporal cortex (EBA)	697	4.39	0.006	−44	−80	−18
				−52	−82	0
				−42	−90	0
<i>Object-goal: main effect</i>						
Left inferior/middle temporal gyrus	1268	4.53	0.001	−42	−60	−6
				−50	−66	−16
				−54	−50	−26
Left inferior frontal gyrus	544	4.31	0.042	−46	8	22
				−38	8	30
<i>Object-goal: simple effect</i>						
Right intraparietal sulcus	722	4.89	0.008	36	−44	50
				36	−30	40
				36	−12	58
Left inferior/middle temporal gyrus	1355	4.78	<0.001	−40	−58	−6
				−34	−60	−14
				−46	−54	−12

Note. Only regions surviving a voxel-level threshold of $p < 0.005$ and 50 voxels and a cluster-corrected level threshold of $p < 0.05$ are reported. Subpeaks more than 8 mm from the main peak in each cluster are listed. Abbreviations: EBA, extrastriate body area.

sphere. The IFG/premotor cortex ($x = -44$, $y = 8$, $z = -3$; $x = -44$, $y = 9$, $z = 18$; $x = -44$, $y = -3$, $z = 30$) and IPL ($x = -44$, $y = -42$, $z = 39$; $x = -47$, $y = -42$, $z = 35$) coordinates were taken from the meta-analysis by Grèzes and Decety (2001), and the temporal region coordinates ($x = -54$, $y = -47$, $z = 11$; $x = -57$, $y = -50$, $z = 16$) were based on the works of Pelphrey et al. (2004) and Iacoboni et al. (2005) (for more details, see Cross et al., 2009). Subsequently, only voxels within this mask were used in data analysis. Contrasts for the main effect of Actor (novel > repeated) and Object-Goal (novel > repeated) were calculated across all movies. For comparison

with previous research that did not manipulate actor (Hamilton and Grafton, 2006, 2007, 2008), the simple effect of Object-Goal was calculated across movies where the actor did not vary ($rAnO-G > rArO-G$). 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) by applying an uncorrected voxel-level threshold of $p < 0.005$ and 50 voxels, and then a cluster-level correction of $p < 0.05$. Brain regions that survived the cluster-corrected threshold for RS for actor and RS for object-goal are reported in Table 1.

Results

Two brain regions showed RS for actor, bilaterally: fusiform gyrus and occipitotemporal cortex/EBA (Table 1). In Fig. 2 the pattern of response in bilateral fusiform gyrus and EBA is depicted with parameter estimate plots showing that irrespective of object-goal, the response to a novel actor was suppressed when the identical actor performed the task a second time.

RS for object-goal was found in two brain regions: left inferior/middle temporal gyrus (I/MTG) and left IFG (Table 1). In Fig. 3A the pattern of response in both regions is depicted with parameter estimate plots showing that irrespective of actor, the response to a novel object-goal was suppressed when the identical object-goal was performed for a second time. For comparison with previous results (Hamilton and Grafton, 2006), the simple effect of RS for object-goal (with no change in actor: $rAnO-G > rArO-G$) was calculated and RS was found in two regions: left I/MTG and right intraparietal sulcus (IPS) (Fig. 3B). There were no interactions between RS for actor and RS for object-goal at the corrected significance level.

Discussion

Our results demonstrate that the observation of the same actor repeatedly performing an object-directed action suppresses the BOLD response in fusiform gyrus and occipitotemporal cortex, whilst observation of a novel actor performing the action results in a release from suppression in this region. In contrast, brain regions within the AON (IFG, IPL and MTG) showed RS for the object-goal of the performed action. These findings have important implications for theories of how we understand other people's actions.

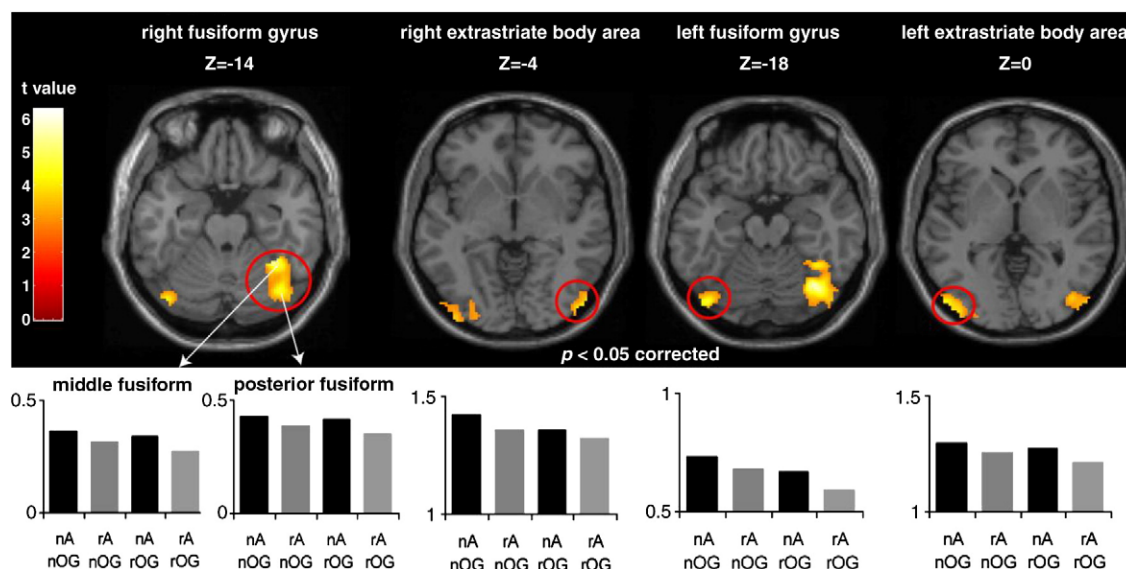


Fig. 2. Brain regions showing RS for actor. Significant suppression ($p < 0.05$ corrected, $t > 2.81$) was seen for repeated actor (grey bars) compared to novel actor (black bars) in bilateral fusiform gyrus and extrastriate body area. Parameter estimates (SPM betas) are plotted for each region (abbreviations are: n = novel, r = repeated, A = actor, OG = object-goal).

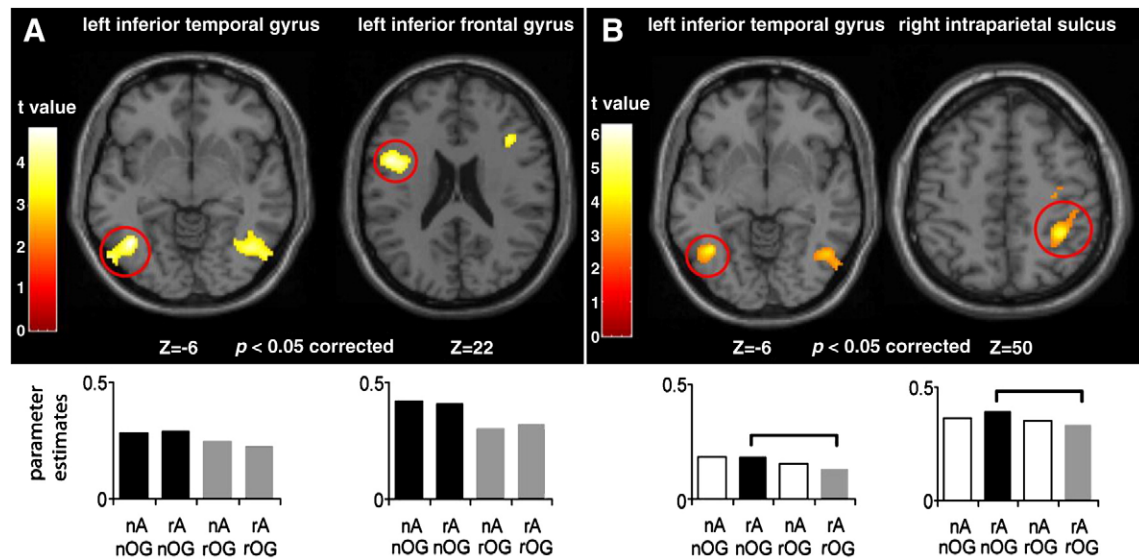


Fig. 3. Brain regions showing RS for object-goal. (A) Brain regions showing the main effect of RS for object-goal (nOG > rOG). Significant suppression ($p < 0.05$ corrected, $t > 2.81$) was seen for repeated goals (grey bars) compared to novel goals (black bars) in left inferior temporal gyrus and left inferior frontal gyrus. (B) Brain regions showing the simple effect of RS for object-goal (rAnO-G > rArO-G). Significant suppression ($p < 0.05$ corrected, $t > 2.81$) was seen for repeated goals (grey bars) compared to novel goals (black bars) in left inferior temporal gyrus and right intraparietal sulcus. Parameter estimates (SPM betas) are plotted for each region (abbreviations are: n = novel, r = repeated, A = actor, OG = object-goal).

Actor identity

Our study is the first investigation of the brain systems that encode the identity of an actor performing an object-directed action. We find evidence of RS for actor identity in fusiform and occipitotemporal brain regions, which have previously been shown to respond selectively to faces, bodies and body parts (Downing et al., 2001; Kanwisher et al., 1997; Peelen and Downing, 2005). Although we did not functionally localise face and body regions, the peak coordinates of our RS for actor findings correspond closely with previous work that localised FFA (Kanwisher et al., 1997), FBA (Peelen and Downing, 2005) and EBA (Downing et al., 2001) (see Table 1). Therefore, we are confident that these responses reflect person identity processes. These data develop our understanding of the functional processes that occur in brain regions that encode person identity. Previous work most commonly studied person identity regions, such as FFA, FBA and EBA with static images of motionless people. Our data suggest that similar person identity regions are also recruited in more social and dynamic contexts; they distinguish between two intentional agents who are acting in a goal-directed fashion. This demonstrates that regions beyond the traditional AON are critical in understanding actions that occur in everyday social situations.

The absence of RS for actor within the AON, even at lenient statistical thresholds, suggests that the AON is less sensitive to actor identity than fusiform and occipitotemporal brain regions. However, there was a simple effect of object-goal in right IPS when actor was held constant but not a main effect of object-goal. A main effect would demonstrate object-goal encoding independent of actor. This pattern of results hints at a subtle sensitivity to actor in right IPS, but to positively confirm this, an interaction between RS for actor and RS for goal is needed. Such an interaction was not found, even at lower statistical thresholds. Thus, the current dataset does not provide any clear evidence for actor encoding within the AON. Rather, our data suggest that a brain network outside of the AON processes actor-related features of observed actions, which complement other action features that are processed within the AON. Further research will be needed to investigate possible interactions between actor identity and object-goals, within and beyond the AON.

The finding that, at most, there is only a subtle sensitivity to actor identity in the AON is consistent with recent evidence that showed the AON responds similarly to observed actions whether or

not the actor's face is seen, suggesting that other brain regions encode actor identity (Turella et al., 2009). In addition, IPL and IFG regions in human and monkey give similar responses when an action is performed by self or other, further suggesting the AON to be agent-neutral (Etzel et al., 2008; Fogassi et al., 2005; Gallese et al., 1996; Gazzola and Keysers, 2009; Grèzes and Decety, 2001). By contrast, other datasets show dissimilar responses throughout the AON for tasks involving self–other distinctions (Dinstein et al., 2007; Schütz-Bosbach et al., 2009; Schütz-Bosbach et al., 2006; Uddin et al., 2007; Uddin et al., 2005), which suggests the AON is involved in distinguishing self from other. Our data do not resolve this debate regarding self–other agency, but complement it by demonstrating that the AON shows minimal sensitivity to ‘other–other’ distinctions.

Thus, our data may have relevance for the problem of agency and understanding the *who* of a social situation. Previously, it has been suggested that a “who” system is needed to resolve the problem of agency (Georgieff and Jeannerod, 1998). Discussion of this “who” system has been limited to the problem of deciding if the agent is the self or somebody else (de Vignemont and Fournier, 2004; Georgieff and Jeannerod, 1998; Jeannerod and Pacherie, 2004). Similarly, neuroscientific investigations of the problem of agency have focussed on the representation of self-agency in the brain (David et al., 2006; Farrer and Frith, 2002; Fink et al., 1999; Ruby and Decety, 2001), and numerous brain regions have been implicated. Data from the current experiment show that brain regions beyond the AON predominantly distinguish between two different ‘others,’ which suggests that a “who” system might also be needed for encoding the identity of different actors. Our results implicate fusiform and occipitotemporal brain regions in this critical process.

It has recently been shown that perception of unusual actions involves brain regions beyond the AON (Brass et al., 2007), suggesting limits to the social competence of this action network. Our data add to this idea and show that in order to distinguish between two different actors in a social scene, brain regions beyond the AON are involved. This is compatible with the hypothesis that the AON alone is not sufficient for the complete understanding of observed actions (Csibra, 2007; Wood and Hauser, 2008). Further, it supports the suggestion that different, although complementary, brain networks are involved in action understanding in social contexts (Keysers and Gazzola, 2007; Uddin et al., 2007).

Action goals

The observation of an action with a repeated object-goal suppressed the BOLD response in IFG, IPS and I/MTG, regions that are part of the AON (Decety and Grèzes, 1999; Gazzola and Keysers, 2009; Grèzes and Decety, 2001; Rizzolatti and Craighero, 2004). These data add to the wealth of evidence that the AON is involved in understanding the goals of other people's actions. Previous RS studies localised the neural representation of simple object-goal-directed actions to the left aIPS (Hamilton and Grafton, 2006, 2007), whereas viewing more complex outcomes resulted in RS throughout the IPL and IFG (Hamilton and Grafton, 2008). Similarly, IFG has been shown to respond more to goal-directed actions than actions without an explicit goal (Koski et al., 2002) and to code actions in context (Iacoboni et al., 2005).

Limitations

In the movie stimuli for this study, each actor maintained a constant starting position and stepped forward to the table in the same way. This means actor identity co-varied with actor location and walking direction. As each actor stepped forward to the centre of the table before reaching and grasping the object, the kinematics of the reach and grasp were not impacted by the actor location. This experimental design was necessary to avoid change blindness for actor identity, since previous work has shown that it is often difficult to keep track of strangers over location changes (Simons and Levin, 1998). In addition, behavioural data show that participants find it hard to detect changes in actors when two unfamiliar individuals swap locations (Ramsey et al., in preparation). Given that our primary objective was to examine actor identity rather than change blindness, we had to maintain a constant actor starting location in the movie stimuli. However, if our results were to be explained by the observation of biological motion as actors approach the table (and not identity) then we would expect STS, a key biological motion region which responds robustly to the observation of walking people (Pelphrey et al., 2003), to be engaged. Instead, we found RS for actor in brain regions known to represent person identity (EBA and fusiform gyrus), which suggests that the actor walking direction did not substantially interfere with our results.

One further possible confound to our interpretation of these data concerns the focus of attention. Some might suggest that the sequence of novel and repeated stimuli may have engaged attention or task-switching mechanisms but we argue that this interpretation of the data is not convincing. Participants performed the same basic orienting task throughout the experiment (see *Materials and methods*), which rules out a task-switching account of the data. The spatial organisation of the scene and the objects was consistent between movies, which renders spatial or object-focussed attention mechanisms implausible explanations of the data. Prior studies using RS have shown that focussing participant's attention onto different aspects of the observed scene (i.e., object type, weight, location and grip type) did not influence RS (Hamilton and Grafton, 2007), which means that RS is distinct from visual attention. For these reasons, we argue that brain responses to novel and repeated actors and object-goals measured in the current study are not a consequence of more general attention or task-switching processes (Grafton, 2009).

Future directions

There are several ways in which this research could be expanded in the future. Our study used actors who were unknown to the participants and could be distinguished only by their physical features. But, understanding the meaning associated with who is acting often requires more than identifying only physical character-

istics. For example, if the villain grabs the gun in the final scene of an action movie, your prediction of what will happen next draws on your knowledge of the character and motivation of that individual. Research has already shown that neurons in temporal regions respond to the perception of familiar individuals (Quiroga et al., 2005), whilst knowledge about the 'fairness' of other people modulates empathy-related brain responses (Singer et al., 2006).

All these factors are part of situating action understanding within a broader context, where an action is not just an isolated hand movement but is part of a socially relevant scene. Previous work on the role of context in action understanding has revealed effects within the AON. For example, right IFG shows stronger responses to actions in a scene than to isolated actions (Iacoboni et al., 2005), whilst IFG and IPL show larger responses in a non-imitative, complementary context than an imitative context (Newman-Norlund et al., 2007). Furthermore, Liepelt et al. (2009) showed that environmental constraints in a scene modulate responses of the AON. Specifically, they measured lateralised readiness potentials whilst participants prepared finger responses to the presentation of a static hand. They showed that motor-related readiness potential components were modulated when the observed hand had a mechanical clamp on the corresponding finger to the response finger. All these results reveal that the AON is not driven purely by the sight of hand actions, but that activation is often substantially modulated by the context within which these actions occur. Our results extend this position, showing that brain regions within and beyond the AON are involved in making sense of actions in the context of more than one actor. Future work investigating action context could explore how the brain represents action goals and actor identity when the character and motivation of other agents are known and contextually meaningful to the observed action (Frith and Frith, 2006).

Distinct, but complementary, representations of actor and of object-goal in the human brain are useful in interpreting social situations, but it may also be helpful to have some mechanism to 'bind' the representation of actor identity with the representation of action goal. This 'binding problem' is ubiquitous throughout perception and action representations (Hommel, 2004; Treisman, 1996; 1998; 1999), and rests on our ability to integrate information across time, space, attributes and ideas to produce a coherent understanding of our experiences (Treisman, 1999). In the current experiment, there was no significant interaction between actor and object-goal. Therefore, it remains an open question how or where the brain links actors to object-goals. RS research may find progress in pursuing interactive effects using methods that specifically aim to identify independent and shared processing between stimulus features (Drucker et al., 2009). In addition, the exact physiological mechanism underlying RS is still not well known (Grill-Spector et al., 2006) so further investigation is necessary to aid the interpretation of RS studies more generally.

Conclusion

The capacity to rapidly understand who is the perpetrator in goal-directed behaviour is an essential feature of human social cognition, but the problem of identifying actors and binding actors to actions has seldom been addressed in social cognition research. Our findings show that when observing goal-directed actions, actor identity is encoded in brain regions typically associated with face- and body-identity whilst object-directed action goals are encoded in the AON. This suggests that different, although complementary, brain networks process actor-related and object-goal-related aspects of observed actions. In doing so, these results support the hypothesis that understanding other people's everyday actions requires brain systems both within and beyond the AON (Csibra, 2007; Wood and Hauser, 2008).

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