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Brief communication

Triangles have goals too: Understanding action representation in left aIPS

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ABSTRACT

Humans freely interpret moving shapes as being "alive" and having social intentions, such as beliefs and desires. The brain systems underpinning these processes are the same as those used to detect animacy and infer mental states from human behaviour. However, it is not yet known if the brain systems that respond to human action-goals also respond to the action-goals of shapes. In the present paper, we used a repetition suppression paradigm during functional magnetic resonance imaging (fMRI) to examine brain systems that respond to the action-goals of shapes. Participants watched video clips of simple, geometrical shapes performing different 'take-object' goals. Repeated presentation of the same goal suppressed the blood oxygen level-dependent (BOLD) response in left anterior intraparietal sulcus (aIPS), a brain region known to distinguish the goals of human hand actions. This finding shows that left aIPS shows similar sensitivity to the action-goals of human and non-human agents. Our data complement previous work on animacy perception and mental state inference, which suggest components of the social brain are driven by the type of action comprehension that is engaged rather than by the form of the acting agent (i.e., human or shape). Further, the results have consequence for theories of goal understanding in situations without access to biological form or motion.

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1. Introduction

A striking feature of human cognition is the liberal way thoughts, feelings and intentions are attributed to human and non-human entities (Heider & Simmel, 1944). Numerous brain imaging studies have identified a 'social brain' that responds when understanding and engaging with other people. Components of this network also respond to the motion of simple, computer generated shapes, when these shapes are perceived as behaving in a human-like fashion. Here we test whether parts of the social brain known to encode the goals of human hand actions also encode the goals of actions performed by non-human shapes.

Past research on the perception of animate entities shows that multiple brain areas are involved in this process (Table 1). An initial step towards perceiving animacy is the detection of biological form and motion (Johansson, 1973), which activates the superior temporal sulcus (STS) in the human brain (for a review see Blake & Shiffrar, 2007). STS is also activated if interactions between simple moving objects appear causal or intentional (Blakemore et al., 2003; Schultz, Friston, O'Doherty, Wolpert, & Frith, 2005). In an fMRI experiment, Schultz et al. (2005) presented two moving circles on a screen and found that increasing the correlation between the shapes' movement increased participants' percept of animacy and brain activity in bilateral STS. Thus, STS is activated by the perception of moving animate agents, whether they have human or non-human form.

However, perceiving animacy does not provide access to an agent's goal or intention, information which is important for social understanding and interaction (Frith & Frith, 1999). In contrast to STS, when animated shapes take part in more complex behaviours, a second broader network is involved. Medial prefrontal cortex (mPFC) and temporoparietal junction (TPJ) respond when one attributes mental states, such as thoughts, beliefs and desires, to other people (Frith & Frith, 1999). This 'mentalising' network also responds when mental states are attributed to non-human shapes. Castelli, Happe, Frith, and Frith (2000) showed participants computer animations of two triangles that moved around a screen in a self-propelled manner (cf. Heider & Simmel, 1944). If the triangles' movements could be interpreted in terms of beliefs and intentions then mPFC and TPJ were activated. Similarly, observation of simple shape movements lead to greater activation in mPFC and TPJ if the context of the scene enabled participants to perceive the shape as an animate agent (Wheatley, Milleville, & Martin, 2007). Hence, it is widely argued that the attribution of mental states to human and non-human entities involves mPFC and TPJ. As summarised in Table 1, these studies suggest that independent of stimulus form (human or shape), STS responds to animate motion, while mPFC and TPJ are driven by mental state inference.

In contrast, a separate brain network in the inferior frontal gyrus (IFG) and inferior parietal lobule (IPL) responds to the observation

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Table 1
Literature summary.

		Action type		
		Moving/walking	Goal-directed action	Mentalising
Actor	Human form	MTG and STS	aIPS, IPL and IFG	mPFC and TPJ
	Animate shapes	MTG and STS	?	mPFC and TPJ

Abbreviations: MTG, middle temporal gyrus; STS, superior temporal sulcus; aIPS, anterior intraparietal sulcus; IPL, inferior parietal lobule; IFG, inferior frontal gyrus; mPFC, medial prefrontal cortex; TPJ, temporoparietal junction.

of human actions, in particular goal-directed hand actions (Grèzes & Decety, 2001). This frontoparietal network (FPN) is also active when participants perform and imitate hand actions and is sometimes referred to as the human mirror neuron system (Rizzolatti & Craighero, 2004). Unlike STS, mPFC and TPJ, activation of the FPN may be specific to human actions. Some evidence suggests that IFG is activated only by perception of humans, not non-human agents (Tai, Scherfler, Brooks, Sawamoto, & Castiello, 2004). Similarly, behavioural evidence using a motor interference task, which is likely to involve the FPN, show interference from observation of human but not robotic actions (Kilner, Paulignan, & Blakemore, 2003). However, other neuroimaging evidence shows equivalent activation of the FPN for actions performed by a human and a humanoid robot (Gazzola, Rizzolatti, Wicker, & Keysers, 2007). Thus, claims for activation of the FPN by non-human agents are mixed, and the response of the FPN to observation of goal-directed actions performed by non-human shapes is unknown (see ? in Table 1). The current paper addresses this gap in the literature.

Previously, we have shown that part of the FPN, left anterior intraparietal sulcus (aIPS), distinguishes the goal of object-directed hand actions (Hamilton & Grafton, 2006, 2007). Here, we use a similar paradigm to test if the same brain region encodes the goals of non-human shapes. We predict that, if the perception of social stimuli is driven by the type of action or mental state rather than the form of stimulus (human or shape), then aIPS should be sensitive to the goals of non-human shapes. In contrast, if aIPS and the wider FPN respond only to the observation of human actions, then the goals of non-human shapes should be processed elsewhere in the brain.

2. Materials and methods

Twenty-eight participants (14 male, mean age 25.9 years) gave informed consent. Participants watched movie clips showing an animated shape move around an obstacle towards one of two objects, pause and return to the start location with the object (Fig. 1). The two objects comprised one food (e.g., cookie) and one non-food item (e.g., keys) in order to distinguish two possible goals (i.e., 'take-cookie' or 'take-keys'), while the obstacle consisted of four circles. The shape's trajectory had a linear velocity profile unlike biological motion, which has a minimum-jerk trajectory (Hogan, 1984). To induce the perception of animacy the shapes appeared self-propelled and included small variations in size and movement direction (Premack, 1990; Tremoulet & Feldman, 2000; supplemental video S1). Three shapes (purple star, turquoise triangle, blue diamond) performed as 'actors' in each of three functional runs. Movies were 4 s long and 640 pixels wide by 480 pixels high. All stimuli were created in Microsoft Powerpoint and presented with Cogent running under Matlab 6.5.

Movies were sequenced to obtain one-back repetition suppression (Fig. 1) and for comparison with studies of brain systems for human goal-directed action, scanning and data analysis were performed using near-identical procedures (Hamilton & Grafton, 2006, 2007). Sequences of nine movies always started with a 'new' clip followed by eight clips depicting a novel (n) or repeated (r) goal (G) or trajectory (T). Following a sequence, participants answered a question to maintain alertness. Each participant completed 168 RS trials, which evenly filled a 2×2 factorial design for Goal and Trajectory, novel and repeated. Scanning was performed in a 3T 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°; FOV: 19.2 cm, matrix: 64×64. 132 brain images were stored on each of 3 functional runs. Data were realigned, unwarped, normalised to the MNI template with a resolution of 3 mm × 3 mm × 3 mm and spatially smoothed (8 mm) using SPM8 software. A design matrix was fitted for each participant with regressors for each movie type (nGnT, nGrT, rGnT, rGrT, new and question). Each trial was modelled as a boxcar with the duration of that movie convolved with the standard hemodynamic response function.

The main effect of Goal was calculated (novel > repeated; nGnT + nGrT – rGrT – rGnT) in a random effects analysis. Consistent with our *a priori* hypothesis, a small volume correction was applied using a 10 mm sphere localised on the peak coordinate for left aIPS found previously (Hamilton & Grafton, 2006). Correction for multiple comparisons was performed at the cluster level (Friston, Worsley, Frackowiak, Mazziotta, & Evans, 1994), using a voxel-level threshold of $p < 0.005$ and 10 voxels and a cluster-level correction of $p < 0.05$. In addition, the main effect of Trajectory (novel > repeated) and the interaction between goal and trajectory were calculated.

3. Results

Left aIPS showed significant RS for the identity of the object-goal taken by a shape: the response to a novel goal was suppressed when the next movie showed the same goal, even with a different motion trajectory (Fig. 2). The cluster-peak was 5 mm (Hamilton & Grafton, 2007) and 10 mm (Hamilton & Grafton, 2006) from peaks previously found for human hand actions and no other brain region met corrected thresholds (Table 2). No brain regions showed RS for trajectory at the corrected threshold and only one region – the left frontal eye fields – met the uncorrected threshold (Table 2).

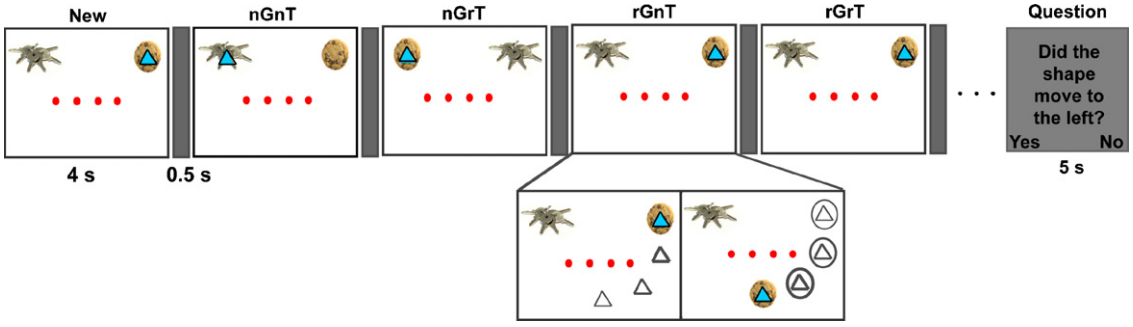

Fig. 1. Stimulus sequencing. Each video showed an animated shape move around an obstacle (four red circles) towards one of two objects, pause and return to the start location with the object. Target objects were always one food item and one non-food item. In the example shown, a triangle takes keys or a cookie in each clip. Sequences of nine movies always started with a 'new' clip followed by eight clips depicting a novel (n) or repeated (r) goal (G) or trajectory (T). Novelty was defined relative to the previous movie in a one-back design. Following a sequence, participants answered a question to maintain alertness. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

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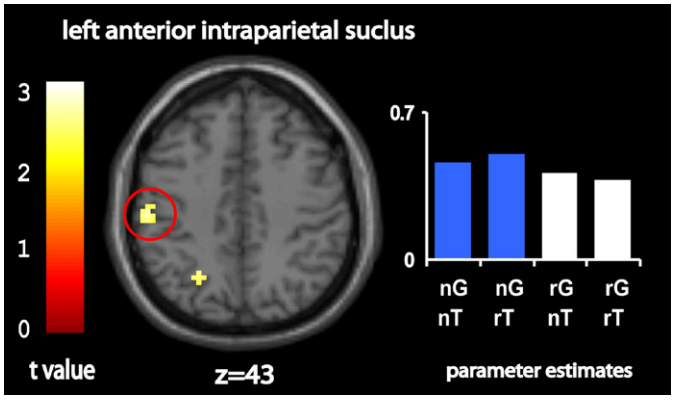

Fig. 2. Repetition suppression for goal. Significant suppression ($p < 0.05$ corrected, $t > 2.77$) was seen for repeated goal (white bars) compared to novel goal (blue bars) in left anterior intraparietal sulcus. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

Table 2
Brain regions showing RS for goal and RS for trajectory.

Region	Number of voxels	*T*	MNI coordinates		
			x	*y*	*z*
Goal					
Right superior parietal lobule extending into intraparietal sulcus	10	3.68	30	−67	61
Left postcentral gyrus	10	3.48	−51	−25	22
Left precentral gyrus	11	3.48	−57	2	37
Left anterior intraparietal sulcus	**34**	**3.31**	**−54**	**−22**	**43**
			−48	**−31**	**34**
Left middle intraparietal sulcus	11	3.13	−24	−58	43
Trajectory					
Left frontal eye fields	33	3.83	−21	−4	43
			−24	−13	46

Note: Only regions surviving a whole-brain voxel-level threshold of $p < 0.005$ and 10 voxels are reported. Subpeaks more than 8 mm from the main peak in each cluster are listed. Bold indicates regions that survive a cluster-corrected threshold at $p < 0.05$ within the *a priori* region of interest (left anterior intraparietal sulcus, at −52, −32, 44).

No brain regions showed the interaction between object-goal and trajectory, even at the uncorrected threshold.

4. Discussion

Our result shows that left aIPS distinguishes the goals of actions performed by non-human shapes. The pattern and location of this activation closely matches that previously found, in a similar paradigm, for observation of human goal-directed hand actions (Hamilton & Grafton, 2006, 2007). In the following discussion, we consider what these data mean for aIPS function, for how the human brain interprets the movements of animated shapes, and the implications for theories of social information processing.

4.1. The role of aIPS

Human neuroimaging studies associate aIPS with the control of hand shaping to grasp objects and grasp comprehension (Culham, Cavina-Pratesi, & Singhal, 2006). These findings are consistent with studies of the homologous region in the monkey brain (AIP), which contains neurons selective for object- and hand-shape (Gardner et al., 2007). However, recent studies in social cognition have suggested a more abstract role for aIPS that relates to action-goals (Tunik, Rice, Hamilton, & Grafton, 2007). Transcranial magnetic stimulation over aIPS has been shown to impair the ability of participants to achieve action-goals (Tunik, Frey, & Grafton, 2005). Further, using fMRI, aIPS has also shown sensitivity to the object-goal of an observed reaching action (Hamilton & Grafton, 2006, 2007). These latter results extends the function of aIPS beyond hand shaping into the domain of understanding and controlling simple action-goals (Tunik et al., 2007).

The current findings develop the idea that one function of aIPS is to support actor-object interactions at a higher level of abstraction than matching hand shape with object size. We show that aIPS responds to the observation of 'agent takes object' action-goals even when the agent has no human form or motion. Two limitations to this interpretation warrant discussion. First, we did not test observation of human hand actions in the same participants because adding a different trial type would either reduce power in our primary analyses or make the scanning time excessively long. Thus, it is not known if exactly the same neural regions respond to goal-directed hand actions and goal-directed actions performed by shapes. Future work could use more intensive scanning of selected brain regions or other methods to boost signal, and attempt to identify cross-actor repetition suppression.

Second, the full repeat condition in this type of RS design involves showing the identical stimulus twice in a row and this could be a 'special' stimulus in attentional terms and drive the effects observed. However, this interpretation is not convincing for three reasons. First, consistent with the main effect, aIPS shows the simple effect of RS for goal (nGnT – rGnT), although at a lower statistical threshold. Second, if full repeats were special, we might expect an interaction between RS for goal and RS for trajectory, reflecting suppression only in the full repeat condition. No brain regions showed the interaction between goal and trajectory, even at lenient statistical thresholds. These analyses affirm our conclusion that left aIPS is sensitive to object-goal, independent of the shape's trajectory. Third, in a series of previous studies, we have shown RS for goals in left aIPS (Hamilton & Grafton, 2006), RS for more complex actions in right IPL (Hamilton & Grafton, 2008), and RS for kinematic features in IFG and middle temporal gyrus (Hamilton & Grafton, 2007). All these studies involved full repeat conditions, but each yielded reliable RS in a distinct brain region. This suggests there is no brain region which detects 'full repeats' independent of the other conditions in a study.

The current results clearly show that left aIPS is sensitive to the object-goals of non-human agents, just like it is sensitive to the same goals of human agents (Hamilton & Grafton, 2006). Considering the numerous functions associated with aIPS and cytoarchitectonic evidence for anatomical subdivisions (Choi et al., 2006), separating which subportions perform which processes would be a valuable future direction for research.

4.2. Brain systems for understanding animate actors

The close correspondence in brain activity for the perception of human and animated shape behaviour complements a range of previous studies (Table 1). STS responds to human motion (Blake & Shiffrar, 2007) and interactive motion of shapes (Schultz et al., 2005), whereas mPFC and TPJ respond when reasoning about the beliefs and desires of other humans (Frith & Frith, 1999) and animated shapes (Castelli et al., 2000). Complementing this work, we show that aIPS, a brain region known to process the object-goals of human hand actions (Hamilton & Grafton, 2006, 2007), is also sensitive to the object-goals of animated shapes. This extends previous findings of sensitivity in the FPN to robotic movement (Gazzola et al., 2007) to shapes with no humanoid form. Importantly, the shapes in the present study moved with a linear trajectory (unlike biological motion) and did not have hands or any parts that could

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'grasp' the object. Taken together, these studies suggest that brain activation is determined by the type of action or mental state that is engaged, not by the form of the actor (human or shape).

Our results contrast with reports suggesting the FPN is specifically accessed by human and not robotic action (Kilner et al., 2003; Tai et al., 2004). However, these latter studies used actions without a salient goal, which may contribute to the discrepant literature. Tai et al. (2004) found IFG responded to robotic arms moving wooden blocks, but not IPL or aIPS, whereas Kilner et al. (2003) found no movement interference from watching robotic arm movements that had no obvious goal. Our results are consistent with a hierarchical model of action understanding (Hamilton, 2008; Hamilton & Grafton, 2007), in which aIPS represents actions at the goal level, which is independent of human form, while IFG represents actions at the kinematic level. Thus, actions of an animate shape can be encoded at the goal level, but in the absence of body parts, a shape might not engage kinematic representations in the IFG.

4.3. Broader implications

The current results have implications for models of how social information is processed in the human brain. More specifically, the findings constrain a debate over how other people's actions are understood (Csibra, 2007). Direct-matching accounts argue that actions are understood by directly matching observed actions onto one's own motor system, specifically the FPN (Rizzolatti & Craighero, 2004). An alternative account proposes that direct-matching is not sufficient to understand actions in social contexts; instead actions are evaluated in relation to environmental constraints (Csibra, 2007).

A direct-matching mechanism could contribute to the perception of goal-directed human hand actions (Hamilton & Grafton, 2006, 2007) and even of humanoid robots (Gazzola et al., 2007). However, a mechanism that matches biological form and motion cannot apply to the current findings because the shapes that served as actors had neither hand-like body parts nor biological motion trajectories. Therefore, the present result demonstrates that the parietal node of the FPN is sensitive to goals in the absence of human form or motion. This is consistent with the possibility that goals rather than body kinematics are encoded in the FPN (Gazzola, Aziz-Zadeh, & Keysers, 2006; Gazzola et al., 2007). Further, it is consistent with the idea that action comprehension can occur without access to biological form or motion (Csibra, 2007; Hamilton & Grafton, 2007). Our findings implicate a role for aIPS in this type of goal understanding.

5. Conclusion

We demonstrate that left aIPS, a brain region known to distinguish the goals of human hand actions, also distinguishes the goals of actions performed by triangles. This result is compatible with hierarchical models of goal understanding (Hamilton, 2008; Hamilton & Grafton, 2007) and the idea that goals can be understood without simulation of human form and motion (Csibra, 2007). The data complements previous work on perception of animacy and mental state attribution, and suggests that activation of different components of the social brain is driven more by different types of action comprehension than by the form of the acting agent.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.neuropsychologia.2010.04.028.

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