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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.

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).

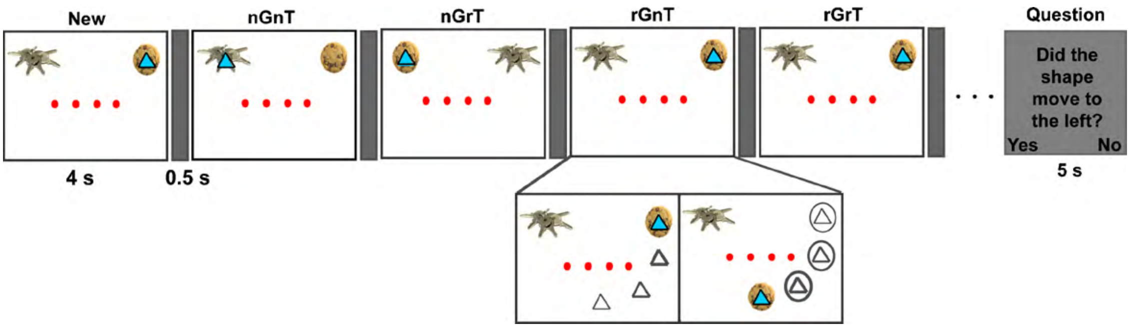

Fig. 1. Stimulus sequencing. Each video showed an animated shape move around an obstacle (four red circles) towards one of two objects, pause and return to the start location with the object. Target objects were always one food item and one non-food item. In the example shown, a triangle takes keys or 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.)