How are the actions of triangles and people processed in the human brain?

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Abstract

Comprehension of actions is a core social skill. Here we provide a critical review of the dominant mirror neuron theory of action comprehension. Recent data demonstrate that parts of the mirror system respond to actions performed by non-human shapes, and are insensitive to actor identity. Regions beyond the mirror system are also important for action comprehension. We suggest this data is not compatible with a strong mirror system hypothesis, and outline alternative theories.

1. Introduction

Humans invest a large proportion of their time acting and interacting with other people, and as such are social animals. A central feature of social interaction is reciprocal non-verbal understanding: individuals must make sense of each other's actions in order to interact appropriately. For example, if a mother and child are building a sand castle, each must interpret the other's actions of scooping sand or tapping the bucket in order to coordinate their own actions and achieve their joint goal. The ability to understand other people's actions is a key feature of human social cognition. The present paper focuses on the cognitive and brain mechanisms that underpin how adults make sense of other people's actions and goals.

Making sense of others' actions is not a unitary cognitive process, but multifaceted. An observed action encompasses features at multiple different levels of description, including kinematics (e.g., grip type), target objects (e.g., the type of object grasped) and broader motivations (e.g., deceit). Although it is important to keep track of all these levels during social interaction, the major theme of the current paper is the relationship between actions and target objects, which we refer to as object-goals. As we carry out our daily activities, we frequently observe other people performing object-directed actions, which commonly achieve specific goals. Different types of object are normally associated with different goals. For example, a person who grasps a banana is likely to want to eat, while one who grasps a hammer is more likely to hit a nail and not likely to eat. Thus, interpretation of even simple object-grasping actions can help us to predict future actions, to learn from them and to interact appropriately. The present paper reviews a series of neuroimaging studies, which examine the cognitive and brain processes that allow us to interpret other people's goal-directed actions.

The chapter is organized into three parts. In the first part, we outline an account of goal understanding that has dominated the literature in the past 15 years, which is based on directly matching observed actions onto one's own motor system; a process linked to the human Mirror Neuron System, or henceforth MNS (Rizzolatti, Fogassi and Gallese 2001). We further consider some limitations of this framework, and of past research into brain systems for goal understanding.

In the second part we review a series of studies from our laboratory that take inspiration from developmental psychology, and are designed to examine how actions and goals are processed in the adult human brain. We consider how different brain systems may represent two features of observed actions: 1) the target object of an action (object-goal) and; 2) the identity of the agent performing an action. In particular, we suggest that one specific brain region within the MNS - anterior intraparietal sulcus (aIPS) - is sensitive to the target object of an action (food vs. tool) but does not distinguish agent identity. Responses in aIPS are the same for two different human agents, and even for a human agent compared to an animated geometric shape that is devoid of human-like form and motion.

Finally, we consider the implications of these findings in relation to claims that the MNS is tuned only to human actions, and that actions are understood by a direct-matching mechanism within the MNS (Rizzolatti et al. 2001). We suggest that activation of the MNS is driven by the behaviour and interpretation of an animate actor rather than by its form, and that strong direct-matching theories cannot account for these results. Further, we suggest that brain systems beyond the MNS are required to interpret who is performing an action and to understand unusual actions, implying that the MNS is not the sole brain network for action comprehension. We further consider some future directions for research into goal understanding. We suggest a multidisciplinary approach, comprising developmental, social and cognitive psychology with the addition of neuroscience methods as a good starting point.

2. Background

2.1. Brain systems for action understanding

A dominant view in the action cognition literature is that we understand other people's actions by matching observed actions onto our own motor repertoire (Rizzolatti et al. 2001). Evidence for this proposal has mainly been provided by the discovery of mirror neurons in ventral premotor cortex (di Pellegrino, Fadiga, Fogassi, Gallese and Rizzolatti 1992; Gallese, Fadiga, Fogassi and Rizzolatti 1996) and inferior parietal lobule (Fogassi et al. 2005). These neurons respond when a monkey performs a specific action, such as a precision grip to a piece of food, or observes the same action performed by another monkey or a human.

Since the discovery of mirror neurons in the monkey brain, cognitive neuroscientists have used neuroimaging techniques, such as functional magnetic resonance imaging (fMRI), to examine whether analogous regions in the human brain responded in a similar manner. In general, results have been consistent with findings in the monkey brain: inferior frontal gyrus as well as adjacent ventral premotor cortex and inferior parietal lobule respond to performed and observed actions in a similar manner (for meta-analyses see (Grèzes and Decety 2001; Caspers, Zilles, Laird and Eickhoff 2010). Based on these findings, it has been claimed that the activity in the observer's brain "mirrors" that of the performer's brain. Further, it is this matching or mirroring process that results in comprehension of the observed action, which is a primary component of social interaction (Rizzolatti et al. 2001; Gallese, Keysers and Rizzolatti 2004).

One limitation is that human neuroimaging and monkey neurophysiology experiments have used a variety of definitions for what it is to "understand" an action (Hickok 2009). When one sees a child grasp an apple, the brain is able to rapidly process many different types of action information, including the kinematic features of the action (the speed of the hand and shape of the grasp), object-goal information (the hand grasps an apple) and broader motivations (he wants the reddest apple on the tree) (Grafton and Hamilton 2007). In a conventional fMRI experiment, which employs a subtraction design, it is not easy to separate these different components and to define if a particular brain region responds to action kinematics, object-goals, broader motivations or even some combination of these.

One study manipulated context in an attempt to identify brain regions that are sensitive to the goals or intentions underlying observed actions. Iacoboni and colleagues (2005) showed a hand grasp a teacup from a messy or a tidy table. The authors reasoned that in the former case the action was suggestive of the goal 'cleaning', whereas in the latter case the action was suggestive of the goal 'drinking'. When participants observed actions in a context compared to equivalent actions with no context, stronger responses were found in Inferior frontal gyrus (IFG) and adjacent ventral premotor cortex (PMv). Furthermore, these authors reported stronger activity in this region for 'drinking' actions compared to 'cleaning' actions. Thus, the authors argued that the inferior frontal node of the MNS performed a context sensitive mirroring process to understand the goals behind other people's actions (Iacoboni et al. 2005). Making such claims from these data, however, are problematic for several reasons. First, differences in context covary with other features, such as visual scene complexity, task difficulty, movement kinematics and saliency (Grafton and Hamilton 2007). Second, there is no reason to predict that 'drinking' should lead to stronger brain activity than 'cleaning'. And finally, the process by which one could "mirror" a context has not been clearly specified, as yet (Uithol, van Rooij, Bekkering and Haselager 2011a). Considering these limitations, it is difficult to claim that the observed response in IFG is a mirroring process responsible for goal inference.

A second study attempted to localize brain systems that are sensitive to goals and intentions of other people's actions by comparing brain responses when observing an object-directed action to responses when observing an identical action towards empty space (Pelphrey, Morris and McCarthy 2004). This study found that posterior superior temporal sulcus (pSTS) showed stronger responses when the action was directed to an empty space compared to an object. The authors suggest that reaching to an empty location (when a target object is available) violates our expectations about how intentional agents will behave, and thus suggest that pSTS is sensitive to the intentionality of observed actions. While it is possible that this pSTS response reflects the interpretation of an unusual action, it is difficult to argue that this region encodes object-goals or intentions during actions that we typically observe, such as those directed towards objects.

One common feature of these two early attempts to localize brain regions that are sensitive to the goals served by actions is that they both used subtraction as an experimental design. Subtraction designs in neuroimaging have been criticized on broad theoretical grounds (Friston et al. 1996). More specifically, in the case of action goal perception, it does not seem to be possible to create an optimal subtraction between a stimulus with a goal and a matched stimulus without a goal. As previously mentioned, these two conditions also typically vary in other features, such as context, visual scene complexity, kinematics or similar confounds (Grafton and Hamilton 2007). To circumvent this issue, the studies we describe from our laboratory have used a different approach, which is inspired by work in developmental psychology.

2.2. Repetition suppression

In a seminal infant study of action comprehension (Woodward 1998), Amanda Woodward showed that 6 month olds are sensitive to the object-goals of other people's actions. She first habituated infants to the sight of an actor reaching toward a ball on the left thereby ignoring a teddy on the right. At test, the infants look longer if the actor reaches toward the teddy, even when located on the left, but did not look longer at reaches toward the ball, even when located on the right. Thus, infants were sensitive to the identity of the object-goal but not to the direction of the hand motion. For the purposes of neuroimaging, the critical feature of this experimental design is that infant sensitivity to an object-goal can be revealed by testing how the infant responds to a change in the target object from ball to teddy.

Similarly, many regions of the human cortex are highly sensitive to changes in a sequence of stimuli. For example, if a participant in an fMRI study observes the same stimulus twice in a row, the blood oxygen level dependent (BOLD) response in brain regions that encode that stimulus is weaker for the second trial, but recovers when a novel stimulus is shown. This phenomenon is termed repetition suppression (RS), but also known as fMRI-adaptation (Grill-Spector and Malach 2001; Naccache and Dehaene 2001). RS has been shown to be a general property of the human cortex across many domains, including processing of objects (Grill-Spector et al. 1999), faces (Winston, Henson, Fine-Goulden and Dolan 2004), numbers (Naccache and Dehaene 2001) and syntax (Noppeney and Price 2004), as well as with memory (Buckner et al. 1998) and motor performance tasks (Hamilton and Grafton 2008b). Although there is some debate about the neural mechanism underlying RS (Grill-Spector, Henson and Martin 2006), there is agreement that the presentation of a repeated stimulus feature results in suppression of the BOLD signal, whereas presentation of novel a stimulus feature results in a release from suppression.

There are a number of advantages of RS paradigms over conventional subtraction designs. First, RS is sensitive to specific features of a stimulus, and permits independent analysis of each feature. For example, a movie of an everyday action typically includes both object-goals (take cookie) and kinematic features (move left). In a sequence of stimuli for an RS experiment, we can control the repetition of each feature independently (Figure 1 – top row). Consider the trial sequence [1. take-cookie-right] [2. take-disk-right] [3. take-disk-left]. On trial 2, the goal of the action (disk) is novel relative to trial 1 but the direction of movement (right) is repeated. Thus, we would predict RS in any brain regions sensitive to movement direction, but no suppression in any brain regions sensitive to goal. On trial 3, the goal (disk) is now repeated relative to trial 2, while the direction of movement (left) is novel. Thus, we would predict RS in brain regions encoding goal but a robust response in regions encoding movement direction. By presenting different sequences of stimuli, we can test for sensitivity to repeated kinematic features or repeated goal features independently, and distinguish these features within the brain. (Figure 1 – middle rows).

Second, RS designs are well balanced for attention and low-level features. All of our studies use a 'one-back' RS paradigm, whereby each video is coded as novel or repeated (in terms of a specific stimulus feature) relative to the previous video that was presented (Figure 1). One-back RS designs differ from other work on RS or adaptation that show multiple repeats in order to 'adapt' participants to a certain stimulus feature, such as leftward gaze (Calder et al. 2007). Specifically, within the one-back RS design, the same stimulus movie can appear in different repetition contexts, which means that conditions are balanced for the precise details of the movies. While observing videos, participants typically perform an incidental task, such as answering simple questions about the videos they have been watching. This means that the participants' task during scanning is always constant and they are unaware of the structure of novel and repeated stimulus features.

Third, RS studies can potentially be interpreted in terms of the tuning of neuronal populations within specific brain regions. The dominant neurophysiological explanation of RS suggests that populations of neurons within a brain region encode particular stimulus features. When a feature is repeated, the neuronal population that encodes that feature may respond with different timing, a sharper response tuning curve or a weaker overall firing rate (Grill-Spector et al. 2006; but see Sawamura, Orban and Vogels 2006). These changes in the population response are believed to cause the weaker BOLD signal on repeated trials. Thus, finding RS for a particular stimulus feature in a particular brain region implies that distinct populations of neurons encode that feature within the same brain region (Naccache and Dehaene 2001). Consequently, compared to conventional subtraction fMRI designs, RS can reveal what populations of neurons are coding within a brain area and not just between brain areas.

Fourth, as described above, the RS method has conceptual parallels with the habituation methods commonly used in developmental psychology. Experimental designs and stimuli that have been developed for infant habituation can often be used for adult RS studies and vice versa, allowing parallel study of the adult and developing cognitive system. It is not yet clear how the neural and cognitive mechanisms underlying changes in looking time in infants relate to the brain responses seen in adults. Nevertheless, the possibility of using equivalent paradigms in infants and adults can enhance the links between these two often-unrelated literatures.

In the following section we turn to empirical evidence. Several studies will be outlined that have used RS-fMRI to examine the neural foundations of human action understanding.

3. RS-fMRI studies of action understanding

3.1. Perception of human action kinematics, object-goals and outcomes

In an initial study using the RS method, Hamilton and Grafton (2006) adapted the work of Woodward (1998) to investigate which regions of the human brain are sensitive to the object-goals of observed hand actions (Hamilton and Grafton 2006). Participants saw short videos in which two distinct objects were visible on a table, and a human hand reached to one of the objects, grasped it and moved it back to the starting location. The objects were matched for size and shape in order to afford a similar grasp configuration, but they were from distinct object categories: tool (e.g., hammer) and food (e.g., banana). This meant the two objects have very distinct semantic associations and likely future actions. The goal of the action was defined in terms of the target object grasped by the actor (tool vs. food), and could be manipulated independent of the reach trajectory of the action (left vs. right) (Figure 1).

Brain regions showing RS for the object-goal were those regions that showed suppression when the same object was grasped repeatedly, but release from suppression when a novel object was grasped (novel > repeated object-goal). One brain region, left aIPS, showed this response pattern at cluster-corrected significance levels (Figure 2A). By contrast, RS for trajectory was found in lateral occipital and superior frontal brain areas. This result demonstrates that left aIPS is sensitive to the object-goal of an observed reaching action, irrespective of reach trajectory. It also served as a proof-of-principle by demonstrating that RS could be used with fMRI to separate different features of observed actions independently.

Two follow-up studies applied the same experimental design to separate other features of perceived actions, such as hand grip (fingertip vs. whole-hand), action means (push vs. pull) and action outcome (open vs. close a box). First, Hamilton and Grafton (2007) showed participants movies of an actor grasping a wine-bottle or a dumbbell. Each object could be grasped with a whole-hand grip or a fingertip grip. RS for the object-goal of the action was found in left aIPS, which replicates the previous result (Hamilton and Grafton 2006). RS was also evaluated for the two different grip configurations. When novel grips were compared to repeated grips (regardless of object-goal), RS for grip was found in occipital regions, IFG, supplementary motor area, middle frontal gyrus and middle IPS. There was no response in aIPS or in IPL for the grip contrast. These data are consistent with other RS studies that show sensitivity in IFG adjacent to PMv to perceived hand kinematics (Kilner, Neal, Weiskopf, Friston and Frith 2009) and the relationship between hand-grip and object type (Johnson-Frey et al. 2003).

In a second study, the outcome of observed actions was separated from the means used to achieve the outcome (Hamilton and Grafton 2008a). For example, opening or closing a box (outcome) could be achieved by pulling the lid with the fingers or pushing with the thumb (means). Sensitivity to action outcome was found in right IFG, right IPL and left aIPS. By contrast, RS for means was observed in lateral occipital cortex, STS and middle IPS. This result suggests that when actions are more complex than just taking a single object, right IFG and right IPL are engaged more. Further, across all three experiments visual areas in occipitotemporal cortex provide an analysis of trajectory, grip and means, thus supporting a role for visual brain systems in action perception.

The studies reviewed thus far have demonstrated how different regions of the human brain are specifically sensitive to different features of observed actions, including kinematics (IFG), object-goals (left aIPS) and outcomes (left aIPS and right IFG and IPL). The next challenge is to explore the cognitive processes that underlie these responses. A key prediction of the direct-matching hypothesis is that it should only be possible to employ direct-matching for stimuli that have human features that relate one's own motor system, such as human form and motion (Kilner, Paulignan and Blakemore 2003; Press 2011). In the next section, we outline an experiment that tests if human features are necessary for object-goal sensitivity in aIPS, by using simple, geometric shapes as agents instead of human hands (Ramsey and Hamilton 2010c).

3.2. Triangles have goals too

Developmental studies suggest that in some but not all circumstances, infants can attribute goals to non-human agents (Gergely, Nadasdy, Csibra and Biro 1995; Gergely and Csibra 2003; Csibra 2008). For example, 12-month-old infants look longer (i.e., they're surprised) when a circle violates the most efficient means of achieving a desired goal (Gergely et al. 1995). The authors interpret these findings as evidence that infants at around 1 year of age are able to treat circles as intentional agents that have goals (but see Paulus, Hunnius, van Wijngaarden et al. 2011). In contrast, Woodward (1998) showed that 5-, 6- and 9-month-old infants treat a human hand as goal-directed but did not respond in the same way if an inanimate rod or claw performed the same actions. This suggests that not all movements toward an object are equivalent for infants, but that contextual features or the form of the actor impact the interpretation of the action as goal-directed. However, it is not clear from these infant studies if the same cognitive and brain mechanisms are used to interpret the goal directed actions of human and non-human agents. Neuroimaging studies allow us to address this question with adult participants.

Studies of human brain responses to observation of animated shapes have often shown overlap between the processing of shapes and the processing of human stimuli. Superior temporal sulcus (STS) is known to respond to biological motion (Blake and Shiffrar 2007), in particular walking human figures and eye / head movements (Allison, Puce and McCarthy 2000). This region is also engaged when participants observe interacting spheres with increasing animacy (Schultz, Friston, O'Doherty, Wolpert and Frith 2005), and when they observe shapes moving in a context that makes them seem human (Wheatley, Milleville and Martin 2007). When the behaviour of animated shapes is more complex, such that typical observers attribute mental states to the shapes (Heider and Simmel 1944), activation is seen in temporoparietal junction (TPJ) and medial prefrontal cortex (mPFC) (Castelli, Happe, Frith and Frith 2000). This same brain network is engaged when participants consider the mental states of other people (Frith and Frith 2003)

In all these studies, the same brain systems respond to humans and shapes if participants interpret the action they see as animate or if participants engage in mentalising. Thus, brain responses seem to be determined by the participants' interpretation of the stimuli rather than the form of the agent. In contrast, it is widely believed that responses of the MNS are specifically tuned to human actions (Press 2011). These human actions have particular low level features, namely the shape of the hand and characteristic biological motion trajectory, which seem to engage the MNS. For example, stronger MNS engagement has been reported for actions with biological (rather than linear) movement trajectories (Shimada 2010), for actions which obey the 2/3rds power law (Casile et al. 2010) and for observation of a human hand rather than a robot hand (Perani et al. 2001; Tai, Scherfler, Brooks, Sawamoto and Castiello 2004). These and other findings have been used to argue that MNS regions are specifically tuned to human actions, and that this tuning reflects a direct-matching process.

Our study aimed to determine which brain systems respond to the perception of simple shapes performing object-directed actions (Ramsey and Hamilton 2010c). The design of the study was the same as used previously to study the perception of human goal-directed actions (Hamilton and Grafton 2006). Short videos were sequenced to systematically manipulate goal (target object: tool vs. food) and trajectory (left vs. right). Importantly, instead of a human hand as the agent, geometric shapes (e.g., a triangle, star and diamond) were animated to act as agents (Figure 1 – bottom row). The shapes did not possess two key features of human stimuli: biological form and motion. Specifically, the shapes *did not* look like human hands nor did they move with the minimum-jerk trajectory, which is typical of human hand movements (Hogan 1984); instead, they moved according to a linear velocity profile.

Despite this lack of low-level human features, the shapes did behave in a manner that induces the percept of animacy. Their motion was object-directed, which acts a potent cue to animacy (Opfer 2002). Second, the shapes appeared self-propelled and would grow or shrink as they made contact with the target objects, as well as when they returned to the start location (Tremoulet and Feldman 2000). Third, a barrier (four red circles) was placed between the animated shape and the two target objects (cookie and keys) because moving shapes appear more goal-directed when they negotiate barriers (Csibra 2008). Overall, the shape stimuli behaved as if 'alive' but did not have any low-level perceptual cues of human action such as a hand-like form or hand-like biological motion. This means that kinematic features of the stimuli, such as form and motion, could not be directly matched onto the observer's own motor system.

Twenty eight participants observed the movies depicting animated shapes during fMRI. As before, we searched for brain regions showing a stronger response to novel object-goals compared to repeated object-goals. This pattern of response was found in left aIPS (Figure 2B). There was no evidence for object-goal sensitivity in other brain regions of specific interest, such as IFG adjacent to PMv. These findings suggest that left aIPS distinguishes the object-goals of actions performed by simple geometric shapes. The pattern and location of this response closely matches that observed previously with human hand actions (Hamilton and Grafton 2006; 2007), and suggests that aIPS shows similar sensitivity to object-goals, independent of the agent's form.

One possible limitation of our study is that the participants did not observe any videos of human hand actions, and thus our conclusion that the same brain region processes both human and shape actions is based on a comparison across studies, rather than a comparison within participants. However, it is also an advantage that participants did not see human action videos, because it means that these participants were not primed within the experiment to make analogies between the movement of the shapes and the behavior of a human hand.

The results of this study raise two critical questions. First, how can we interpret these data in relation to the large number of previous studies that claim the MNS is specifically tuned to human biological motion? Second, if the response of aIPS is the same for people and triangles, what brain systems distinguish who is acting? Recent data allow us to consider each of these questions in turn.

3.3. A human-specific MNS?

Numerous studies suggest that the response of the human MNS is stronger when observing human actions (Press 2011). That is, actions performed by a human body and using typical human movement profiles such as minimum jerk trajectories for reaching actions and the 2/3rd power law for curved movements.

The results of the triangles study suggests that brain regions that encode object-goals of human actions can also encode object-goals when the actor is a triangle and lacks low-level human features. This demonstrates that goal-encoding is not specific to human actors. However, our results do not allow us to test if the response to human goal-directed actions is greater than the response to goal-directed actions performed by nonhuman actors, because participants did not view both types of action within a single experiment.

A recent study by Cross and colleagues did directly address this question (Cross et al. in press). Using a conventional factorial design, Cross and colleagues tested how the human brain responds to seeing a person or a robotic figure dance in a smooth human style or a jerky robotic style. Surprisingly, responses in both parietal and premotor MNS brain regions were stronger when participants observed the robotic dance style. There were no differences in these regions when viewing a real human form compared to a humanoid robot. These results run counter to the dominant claim that the MNS is tuned only to natural human motion (Press 2011), and suggest that responses within these brain systems are more flexible than previously considered.

One possible account of these results focuses on how participants interpret or categorize a stimulus, rather than its low-level features. As hinted above, in other regions of the social brain, activation seems to be determined by how a stimulus is interpreted. Thus, seeing a variety of animate, moving agents engaged MTG and STS, regardless of the specific form of the agent (Schultz et al. 2005; Wheatley et al. 2007). Similarly, when the actions of an agent can be interpreted in terms of mental states, TPJ and mPFC are engaged (Castelli et al. 2000). This response can even be seen when the agent's behaviour does not change at all, for example, TPJ and mPFC are active when participants believe they are interacting with a person compared to an identical condition where participants believe they are interacting with a computer (Gallagher, Jack, Roepstorff and Frith 2002).

The same principle might apply across the MNS. That is, if an action is perceived as directed toward an object-goal, aIPS is engaged regardless of whether the actor is a human or a triangle. Similarly, if a figure is perceived as dancing, the MNS is engaged regardless of whether the figure has human or robotic form or motion. Under this model, responses of the MNS are not tuned specifically to human or biological features, but are driven more by the top-down interpretation of the stimulus. Further experiments will be required to test if this idea is valid.

3.3. Who is acting?

If responses of the MNS to observed actions do not distinguish whether the actor is a human, an animated triangle (Ramsey and Hamilton 2010c) or a robot (Cross et al. in press), which cognitive and brain systems distinguish *who* is acting? Addressing this question is critical for many social interactions. For example, 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. We recently used an RS paradigm to separate the brain systems that code actor identity from the action goal performed (Ramsey and Hamilton 2010b). Participants watched video clips of two different actors with two different object-goals, arranged in an RS design during fMRI. We calculated RS for repeated compared to novel actor-identity as well as object-goal.

Our results demonstrated 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 these regions. In contrast, brain regions within IFG, IPL and MTG showed RS for the object-goal of the performed action. Previous work on person identity most commonly examined the BOLD response in fusiform gyrus and occipitotemporal cortex using static images of motionless faces or body-parts (Kanwisher, McDermott and Chun 1997; Downing, Jiang, Shuman and Kanwisher 2001). Our data suggest that similar cortical regions that have previously been associated with person identity are also recruited in more social and dynamic contexts; they distinguish between two intentional agents who are acting in a goal-directed fashion. These results demonstrate that regions beyond the MNS are critical for distinguishing between different actors in a social scene and thus understanding actions that occur in everyday social situations.

These data have relevance for the problem of understanding the *who* of a social situation. Previously, it has been suggested that if performed and observed actions are represented in the same brain systems then an additional "who" system is needed to resolve distinguish between self and other (Georgieff and Jeannerod 1998). Discussion of this "who" system has been limited to the problem of deciding if I am acting or another person is acting (Georgieff and Jeannerod 1998; de Vignemont and Fourneret 2004). The current experiment considers the problem of distinguishing between two distinct other people, and shows the MNS does not discriminate between two other agents. Rather, a "who" system encoding the identity of different actors might be needed and our results implicate fusiform and occipitotemporal brain regions in this process. These results mean that the MNS is not the sole brain system responsible for comprehending actions, but that other brain networks respond to the broader social context of the action.

3.4. Summary of empirical evidence

In sum, we have presented a series of fMRI experiments using RS that have examined how different brain systems process others' actions in a social context. We have shown that left aIPS is sensitive to the object-goal of an action, regardless of whether the actor is a human hand or a simple geometric shape that is devoid of human form and motion. Further studies have shown that the MNS responds to the actions of both human and robotic figures, and that it does not distinguish between two different human actors. These results are compatible with the claim that the MNS encodes actions but is not tuned to particular actors or agents. We suggest that other brain systems are required to encode actor identity. In the next section we outline and evaluate several interpretations of this finding in aIPS and discuss the resulting implications for cognitive theories of goal understanding.

4. Theoretical implications

These new findings lead us to consider two questions. First, what aspect of an action or observed action is represented in aIPS? And second, how is the visual image on the retina transformed into this representation?

4.1. What is represented in aIPS?

Traditional accounts of aIPS focused on the role of this region in encoding performed hand grasps. Single neurons in the AIP region of the macaque brain encode different hand shapes (Sakata, Taira, Murata and Mine 1995; Murata, Gallese, Luppino, Kaseda and Sakata 2000) and sensitivity to hand shape has also been detected in human aIPS (Króliczak, Quinlan, McAdam and Culham 2006). However, these studies tend to use meaningless objects as stimuli, which are differentiated only by their shape. The data from our series of studies show that when object shape is matched but object identity changes, aIPS is sensitive to the identity of the object-goal (Hamilton and Grafton 2006; 2007). This encoding is independent of hand shape information, because the same pattern of response was seen when the action was performed by an animated triangle with no human grasp or biological motion trajectory.

Other studies also suggest that aIPS encodes a more abstract representation of action than just hand grasp. Jastorff and colleagues showed that aIPS is sensitive to the direction that other people move objects (i.e., towards vs. away from the body), irrespective of whether the person performed the action with their hand, foot or mouth (Jastorff, Clavagnier, Gergely and Orban 2010). They suggest that for actions typically performed by the hand, such as moving small objects, we may process these actions in hand-centred space, even when a different effector is being used, such as a foot or mouth. This result is consistent with our data showing actor independence in aIPS (See also Sommerville & Loucks, this volume).

Parietal cortex is also sensitive to the difference between typical and unusual person-object relationships (Newman-Norlund, van Schie, van Hoek, Cuijpers and Bekkering 2010). Specifically, bilateral parts of IPL distinguished between typical effector-object relations (a hand touching a phone) compared to atypical effector-object relations (a foot touching a phone). Finally, a study using multivoxel pattern analysis to search for overlapping neuronal representations of goal-directed actions performed by the self and other found that left aIPS was one of the few regions encoding the goal of actions for both self and other (Oosterhof, Wiggett, Diedrichsen, Tipper and Downing 2010).

These results could be considered within a framework of intentional relations (Barresi and Moore 1996). This framework defines an intentional relation as a three-way link between an agent, a directed activity and an object. Such relationships can involve real objects, such as observing somebody grasp an apple, and more complex mental relations, which involve beliefs and desires directed towards imaginary objects or world states. Barresi and Moore (1996) proposed that these intentional relationships form the basis of how social interactions are understood and processed.

The response profile we have demonstrated in aIPS could be interpreted as a very simple type of intentional relationship. aIPS is sensitive to the object (Hamilton and Grafton 2006; Ramsey and Hamilton 2010c) and also to the type of action (Jastorff et al. 2010; Newman-Norlund et al. 2010; Oosterhof et al. 2010). While this region does not discriminate between different actors (Ramsey and Hamilton 2010b; Ramsey and Hamilton 2010c), it is likely that the presence of an animate agent is required to engage aIPS. Further study will be needed to determine how the representation of actions and object-goals within aIPS fits into broader frameworks for social cognition.

4.2 How are goal representations calculated?

If aIPS represents the object-goal of an action, possibly in the form of a simple intentional relationship, it is then useful to know how this representation is achieved. How can the moving visual image on the retina be transformed to a representation of an action on an object? The dominant model of action understanding within the human brain is based on the idea of direct-matching. This is the claim that an observed action can be 'directly-matched' onto a motor representation in the observer's own motor system. A strong version of this direct-matching hypothesis might require matching at the level of kinematics (Rizzolatti, Fadiga, Fogassi and Gallese 1999). However, more recent variants suggest direct-matching could occur primarily at the level of goals (Gazzola, Rizzolatti, Wicker and Keysers 2007), or there could be two separate routes for direct-matching and goal-processing within the MNS (Rizzolatti and Sinigaglia 2010).

An alternative to the direct-matching account is a teleological reasoning theory, which proposes that actions can be understood using visual inference alone, without the involvement of the motor system (Gergely and Csibra 2003; Csibra 2007). This mechanism considers the rationality of the action in relation to a desired goal-state and environmental constraints. The data described above provide us with new insights into which of these mechanisms might lead to a goal representation.

First, our data allow us to rule out a strong version of the direct matching hypothesis. This is the idea that an observed action must be first matched to a kinematic motor representation of hand shape and movement in the MNS in order for a goal to be calculated (Rizzolatti et al. 2001). Such a direct-matching mechanism could contribute to the perception of goal-directed human hand actions (Hamilton and Grafton 2006) and even of humanoid robots (Gazzola et al. 2007; Cross et al. in press). 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 goal representations in aIPS can be achieved without a strong form of direct matching.

This result is also consistent with the idea that action comprehension can occur without access to biological form or motion (Csibra 2007). In doing so, this empirical evidence raises a challenge to the MNS theories of action understanding, which has previously been raised on theoretical grounds (Uithol, van Rooij, Bekkering and Haselager 2011b): namely, what does the mirror neuron system "mirror"?

More recent theories of direct-matching do not make such strong claims, and suggest that the primary role of the MNS is to encode goals rather than kinematics (Gazzola et al. 2007). Under this account, any intentional agent, independent of form and motion, can be incorporated into the MNS. Once an observed agent is deemed intentional and object-directed, aIPS could subsequently treat it *as if* it were a human hand, and process object-goals in a similar manner. In this sense the shapes in our study may have been treated like hands, in a functional sense, in that they can manipulate objects. It is important to note that we did not present hands and shapes in the same study in order to reduce the likelihood that participants would interpret the shapes as hands, but we cannot rule out that participants did this spontaneously.

However, these direct-matching accounts, by abstracting away from motor-kinematic features of an action and suggesting matching of 'goals', lose a lot of the power of the original mirror hypothesis. A 'goal' is not necessarily a motor representation, so a visual input could be matched to a goal by means of visual processing, without any contribution from the motor system. Thus, these variants on the direct-matching hypothesis do not have much unique predictive power, and can be hard to distinguish from visual or teleological hypotheses.

The core claim of the teleological reasoning hypothesis is that actions are interpreted with reference to whether that action is rational (Gergely and Csibra 2003). Under a teleological approach, a goal is assigned to an action by evaluating the efficiency of the agent's action with respect to environmental constraints on goal attainment (Gergely and Csibra 2003). Evidence for teleological processing of actions can be found in both infant and adult research. Typical infants look longer at irrational actions (Gergely et al. 1995; Csibra, Gergely, Bíró, Koós and Brockbank 1999) and imitate actions rationally (Gergely, Bekkering and Kiraly 2002; but see Paulus, Hunnius, Vissers and Bekkering 2011). In the adult brain, TPJ and mPFC distinguish rational from irrational actions (Brass, Schmitt, Spengler and Gergely 2007; Marsh and Hamilton 2011). The teleological account can explain the response of aIPS to actions performed by triangles, because motor or kinematic representations are not required for teleological processing.

Distinguishing between the teleological and direct-matching accounts of goal understanding will be an important focus in future research. Critical differences between the models emerge when we consider the impact of experience and of rationality on each. The direct-matching model predicts that the ability to understand a goal should be closely linked to one's experience of performing that goal-directed action (Kanakogi and Itakura 2010; Paulus, Hunnius, Vissers and Bekkering 2011). In contrast, the teleological model predicts that understanding of goals should be related to judgments of whether that goal is rational given current environmental constraints (Csibra 2003). Current data do not conclusively distinguish between these models yet.

5. Broader implications and future directions

5.1. The variety of goal

The majority of this chapter has discussed evidence for one very simple type of action goal, an object goal, which is defined by the identity of the object manipulated by an agent. But there are many other types of goal that can be served by action (Jacob and Jeannerod 2005; Uithol et al. 2011a). These range along a continuum from concrete, tangible actions, which can be performed over a relatively short period of time (seconds and minutes), such as grasping a teapot and pouring tea, to longer-term, intangible goals, such as planning a holiday for next summer or striving for a promotion. However, the relationship between goal inference from specific concrete actions and from processing longer-term thoughts, desires and beliefs is not yet clearly specified.

Some studies claim that the motor system, specifically the MNS, plays a more sophisticated role in the perception of action than processing kinematic features and simple goals, by showing sensitivity to the context surrounding an action (Iacoboni et al. 2005; Liepelt and Brass 2009). For example, Liepelt and Brass (2009) showed that motor-related readiness potentials were modulated if participants observed a finger action imposed by a mechanical clamp, instead of under free control. Similarly, Iacoboni et al. (2005) suggests that responses in the IFG to observed action are modulated by the context of the action.

Other work has suggested the social competence of MNS is limited, and instead, a growing body of fMRI studies implicate brain regions associated with mentalizing / theory-of-mind in the perception of action (Grèzes, Frith and Passingham 2004a; 2004b; Brass et al. 2007; Ramsey and Hamilton 2010a; Spunt, Satpute and Lieberman 2010; Marsh and Hamilton 2011). Recent fMRI studies have shown that the mentalising network is sensitive to the perception of irrational actions (Brass et al. 2007; Marsh and Hamilton 2011) as well as when the observed actor's knowledge state is different to the perceiver's knowledge state (Ramsey and Hamilton 2010a). In these studies, no instructions were given to consider the mental states of the observed actors, but the mentalizing network still showed sensitivity to aspects of observed actions.

Together this work suggests that the diverse range of goals that actions can serve are processed by a distributed brain network comprising, but not restricted to, brain areas associated with the MNS and mentalizing network (Keysers and Gazzola 2007; Uddin, Iacoboni, Lange and Keenan 2007). We suggest that future work should aim to further delineate the contributions to goal understanding made by the MNS, mentalizing network and other social brain systems. Specifically, it will be pertinent to examine how these systems work together during social interactions. Approaches from motor control, developmental, cognitive and social psychology as well as neuroscience methods will be needed to fully examine human goal understanding and its neural substrates.

5.2. Linking actions and actors

To make sense of other people's actions, it is not sufficient to only process action features, such as kinematics, objects-goals and broader motivations. It is also important link the identity of the agent to these action features. Our data suggest that MNS regions, specifically aIPS, are agent-neutral. These regions do not discriminate between different human actors (Ramsey and Hamilton 2010b) and show similar responses to human and non-human actors (Ramsey and Hamilton 2010c). This insensitivity to actor form is consistent with brain imaging work using animated shapes during biological motion and mentalizing tasks (Castelli et al. 2000; Schultz et al. 2005). In all these studies, the BOLD response is determined by the type of social processing engaged, such as mental state reasoning, animacy perception or object-goal perception, rather than the form of the actor.

However, in real social interactions, it matters immensely who you are interacting with, because each different actor is likely to have different beliefs, desires and motivations. Initial work has shown different brain responses to individuals associated with positive and negative behaviour (Singer, Kiebel, Winston, Dolan and Frith 2004) and different social stereotypes (Krendl, Macrae, Kelley, Fugelsang and Heatherton 2006). The question of how these types of actor information are linked to and integrated with information about an individual's current goal-directed behaviour will be an important area for future research.

Conclusion

This paper reviews evidence that the human MNS is finely tuned to goal-directed hand actions, and encodes the identity of the object that an actor reaches for. In contrast, these brain systems are insensitive to actor identity, showing equivalent responses to different people and animated shapes. These results imply that a strong direct-matching account of action comprehension is implausible, and highlight the importance of future research into comprehension of different types of goals and actors as well as the links between them.

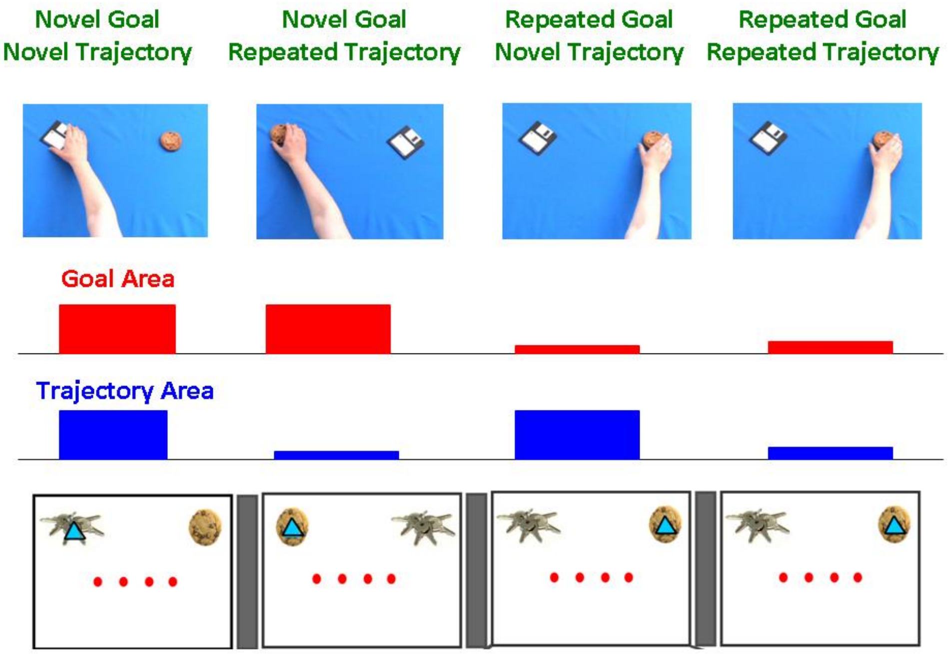
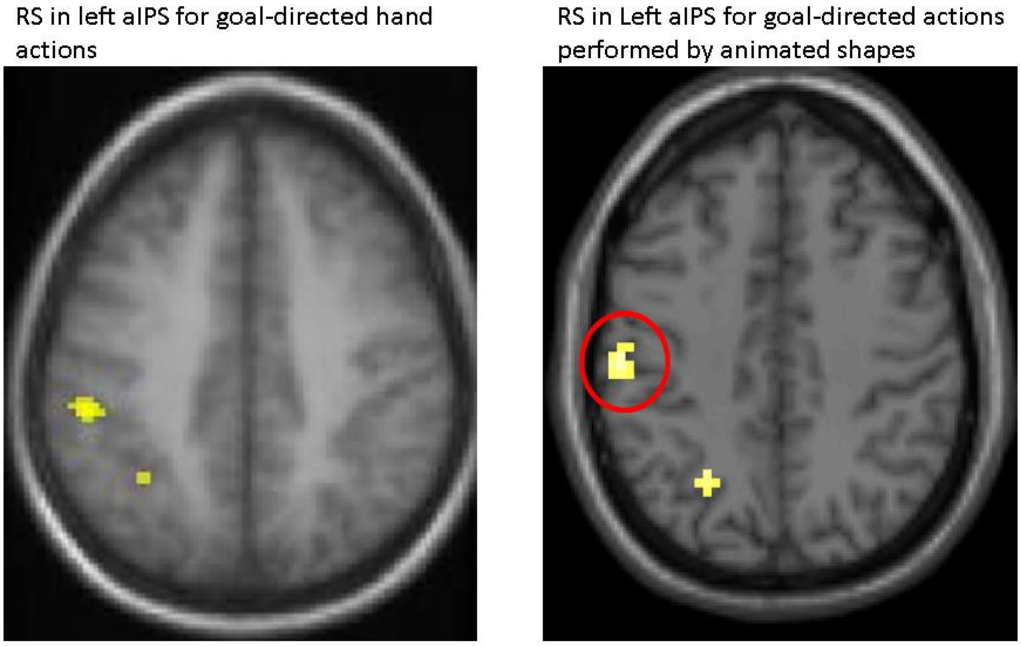


Figure 1 Stimulus sequences for repetition suppression studies of goal-directed actions performed by a human hand or an animated triangle. *Top row* – sample sequence of movies for the hand action study. *Middle rows* – predicted BOLD signal in brain regions encoding goal and trajectory. *Bottom row* – sample sequence of movies for the animated triangles study.

Figure 2. Brain regions showing RS for goal directed hand actions (left) and for goal directed actions performed by animated shapes (right). Both studies found engagement of left anterior intraparietal sulcus (aIPS) in this contrast).



RS in left aIPS for goal-directed hand actions

RS in Left aIPS for goal-directed actions performed by animated shapes

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