

Exploring the neural correlates of goal-directed action and intention understanding

Elizabeth J. Carter^{a,b,*}, Jessica K. Hodgins^{b,c}, David H. Rakison^a

^a Department of Psychology, Carnegie Mellon University, Pittsburgh, PA, USA

^b Robotics Institute, Carnegie Mellon University, Pittsburgh, PA, USA

^c Department of Computer Science, Carnegie Mellon University, Pittsburgh, PA, USA

ARTICLE INFO

Article history:

Received 13 April 2010

Revised 24 August 2010

Accepted 31 August 2010

Available online 9 September 2010

Keywords:

fMRI

Posterior superior temporal sulcus

Biological motion

Goals

Intention

Animation

ABSTRACT

Because we are a cooperative species, understanding the goals and intentions of others is critical for human survival. In this fMRI study, participants viewed reaching behaviors in which one of four animated characters moved a hand towards one of two objects and either (a) picked up the object, (b) missed the object, or (c) changed his path halfway to lift the other object. The characters included a human, a humanoid robot, stacked boxes with an arm, and a mechanical claw. The first three moved in an identical, human-like biological pattern. Right posterior superior temporal sulcus (pSTS) activity increased when the human or humanoid robot shifted goals or missed the target relative to obtaining the original goal. This suggests that the pSTS was engaged differentially for figures that appeared more human-like rather than for all human-like motion. Medial frontal areas that are part of a protagonist-monitoring network with the right pSTS (e.g., Mason and Just, 2006) were most engaged for the human character, followed by the robot character. The current data suggest that goal-directed action and intention understanding require this network and it is used similarly for the two processes. Moreover, it is modulated by character identity rather than only the presence of biological motion. We discuss the implications for behavioral theories of goal-directed action and intention understanding.

© 2010 Elsevier Inc. All rights reserved.

Introduction

Throughout evolution, primates have developed unique social interaction abilities to survive as groups and individuals, including comprehending the goal-directed actions and intentions of others. Goal-directed action encompasses behaviors that occur in a causal relationship with particular goals rather than by coincidence (Csibra and Gergely, 2007). It has also been described as a voluntary movement with direct consequences that is performed to bring about a specific future state (D'Andrade, 1987; Woodward, 1998). Thus, goals themselves drive motor behaviors that are organized by an action hierarchy for optimal achievement (Grafton and Hamilton, 2007). Humans seem to be remarkably motivated to interpret behaviors in terms of goal states, a tendency called the functional stance (Csibra and Gergely, 2007). Information about the actor's mental states is not required for goal-directed action understanding, but these two types of knowledge converge to form a building block for intention understanding.

Intention has come to be used in a folk psychological sense as a derivative of the verb intend and implies doing something purposefully (Feldman and Reznick, 1996). Anscombe (1957) used intentional action to describe a behavior directed at bringing about some state of

affairs. The intentional quality is applied to an agent's actions when an observer believes that the actions are deliberate and based on a specific, expressed attitude towards an object. Thus, people view others as having intentions when drawing upon mental state information to understand the motivation underlying behaviors, which include but are not limited to goal-directed actions.

Neuroimaging research, particularly functional magnetic resonance imaging (fMRI), has begun to explore the neural correlates of these processes. Thus far, the focus has been on two brain networks: the right posterior superior temporal sulcus (pSTS) network and the mirror neuron system. The right pSTS has been implicated in processing biological motion (e.g., Bonda et al., 1996; Pelphrey et al., 2003a; Puce et al., 1998). This region also processes the goal of actions, such that when greater attention is applied to the goal-directedness of movements, the response is increased (Hoffman and Haxby, 2000). Moreover, this region is more active when seemingly goal-directed actions fail to meet the viewers' expectations, such as when an animated character reaches (Pelphrey et al., 2004) or looks (Pelphrey et al., 2003b) away from a target. These studies suggested increased processing was required when expected goals were not achieved. Vander Wyk et al. (2009) had an actress look at one of two objects, make either a positive or a negative facial expression, and then reach for one of the objects. This design created expectations that the actress either would reach towards the appealing object or would not reach for the disgusting object. When these predictions were violated, the right pSTS response increased, suggesting a role in intention

* Corresponding author. Robotics Institute, Carnegie Mellon University, 5000 Forbes Avenue, Pittsburgh, PA 15213, USA. Fax: +1 412 268 6436.

E-mail address: lizcarter@cmu.edu (E.J. Carter).

understanding (Vander Wyk et al., 2009). The right pSTS has been proposed to be part of a protagonist-monitoring network along with medial frontal cortex and the right temporoparietal junction (TPJ) (Mason and Just, 2006, 2009). Medial frontal cortex performs a variety of social tasks, including action monitoring, person perception, and mentalizing (for review, see Amodio and Frith, 2006). The right TPJ is involved in reasoning about the minds of others (Saxe and Kanwisher, 2003).

The mirror neuron system consists of the inferior frontal gyrus (IFG) and inferior parietal lobule (IPL) and is active during both observation and performance of actions (for review, see Rizzolatti and Craighero, 2004), including mouth movements (Buccino et al., 2004), finger movements (e.g., Iacoboni et al., 1999), communicative hand gestures and object-directed hand motions (Montgomery et al., 2007), and limb movements (Buccino et al., 2001). Iacoboni et al. (2005) investigated goal-directed action processing in the mirror neuron regions by modifying context information surrounding images of grasping to imply varying goals rather than changing the action itself. They showed pictures of a grasping hand in isolation, images of the hand that included contexts such as cleaning up or setting a table, and images of those contexts without the hand. The IFG showed an increased response to scenes of grasping in context relative to viewing the action or context alone. When using a repetition suppression paradigm to explore the effects of how an object was gripped on mirror neuron activity, Grafton and Hamilton (2007) found increased right IFG activity when the grip changed. Buccino et al. (2007) examined the brain response for actions done on purpose, or intentionally, compared to accidental movements in the absence of clear goals and reported increases in IPL and premotor regions, but not right pSTS. A study of object-directed actions revealed that all of the movements increased activity equally in the bilateral IPL, but the bilateral IFG differentiated between meaningful and meaningless actions (Newman-Norlund et al., 2010).

Various behavioral theories have been proposed to account for goal-directed action and intention understanding. Brain research can assist with the assessment of these theories, particularly when what is known about neural networks aligns with the proposed behavioral mechanisms. Among the theories that have been put forth for goal-directed action understanding and pairing actions with goals are teleological reasoning and simulation theory. Csibra and Gergely (1998) suggested that a teleological stance is taken by individuals in order to analyze the relationships between actions, goals, and constraints to determine rational actions. A principle of rational action assesses the efficiency of behaviors in context so that one could use action information to determine what end state could be efficiently achieved through such means or predict selection of an efficient course of action to achieve a known goal (Csibra and Gergely, 1998; Csibra et al., 2003; Gergely and Csibra, 2003). Based on what is known about the right pSTS network, it is possible that these processes occur there by relying on the pSTS for goal detection and the medial frontal cortex for agent identification and action monitoring.

Alternatively, simulation theory accounts for goal-directed action understanding by stating that viewers could use their own minds to simulate the minds of others by putting themselves in the other's position and determining what actions and goals are available and likely in the same situation (Gallese and Goldman, 1998; Stich and Nichols, 1993). This relies on an assumption of equivalency between the self and other. Simulation theory proponents have benefited from the discovery of mirror neurons because they provide evidence of a neural substrate in which the actions of both the self and others are processed, and many have suggested that this is where simulation occurs (e.g., Gallese and Goldman, 1998; Gallese et al., 2004).

In addition to the two potential mechanisms for goal-directed action understanding, two mechanisms have been proposed to underlie intention understanding. One of these is a folk psychology or "theory theory of mind" that has been advanced as an alternate

method of intention understanding that uses mental state information. Proponents of theory theory posit that observers assess the mental states of others using a set of heuristics and laws about why and how people behave (Gopnik and Meltzoff, 1997; Gopnik and Wellman, 1994; Perner and Davies, 1991; Wellman, 1990; see Leslie, 2000, for a review). According to this structure, inferences about the intentions of others result from comparisons of the viewer's internal set of behavioral laws with external stimuli. This might occur in the right TPJ of the right pSTS network. The other proposed theory for the mechanism underlying intention understanding is the same simulation theory that was put forth as a mechanism for goal-directed action understanding (Gallese and Goldman, 1998; Stich and Nichols, 1993). In this version of the theory, the viewer simulates the actors in order to determine mental states as well as corresponding actions and goals.

The previously discussed pSTS and mirror neuron studies have been interpreted consistently as intention research by the authors. However, if analyzed from the perspective of a developmental psychologist, the majority of the work only addresses goal-directed action, and the two processes have been conflated. For example, no knowledge of mental states is required to form the expectation that an individual will act towards an object rather than away from it (e.g., Montgomery et al., 2007; Pelphrey et al., 2003b, 2004). Thus far, only two of the studies have examined intentions by requiring mental state assignment (Buccino et al., 2007; Vander Wyk et al., 2009). The purpose of the current study was to differentiate the neural underpinnings of goal-directed action and intention understanding to determine whether mental state assignment affects brain processing.

To directly compare these two processes, we created stimuli that included both goal-directed actions that did not require mental states and those that did and therefore were intentional. Notably, prior work examined brain responses to missing a goal (e.g., Pelphrey et al., 2004) but never to changing the goal—a shift that introduces mental state attribution by giving the impression that the actor is changing his mind. Additionally, previous research included only human actors, who are likely to be assigned goals and mental states. An actor without a brain does not have mental states; thus, it cannot act intentionally. Moreover, it is unknown whether the goal-directed action and intention effects are related to biological motion instead of human identity if only human characters are studied. Because of these numerous issues, we decided to manipulate whether actions were perceived as goal-directed or intentional both by altering motion trajectories and by using a variety of animated characters.

Twelve types of video stimuli were created, with each of 4 actors performing 3 motions. Three reaching behaviors were exhibited by each actor. In the Goal Stay condition, the actor would reach forward towards one of the two objects placed on the table in front of him, lift, and replace it. This condition was to be a baseline to elicit activity in motion processing regions and served as a successful goal-directed action. The actors in the Goal Miss condition moved their arms at an angle that resulted in an end position between the two objects and then raised and lowered their empty hand. In this condition, brain activity reflected processing when a failure to achieve any obvious goal occurred. Lastly, the Goal Shift condition consisted of the actor setting out towards one of the two objects but then shifting paths towards the other object midway, lifting and resetting it instead. This condition explored processing when a target is reached, but not the original target, suggesting a shift in intention.

The different animated actors included a man, a humanoid robot, a set of boxes with an articulating human-like arm, and a machine with a grasping claw (Fig. 1). The man (Human condition) was used to examine the brain regions involved in perceiving human motion made by a human form. The second character, a humanoid robot (Robot condition), performed the same biological motion as the human while appearing obviously mechanical and thus without mental states. Third, the boxes actor (Boxes condition) consisted of four stacked cubes and an attached arm that followed the same

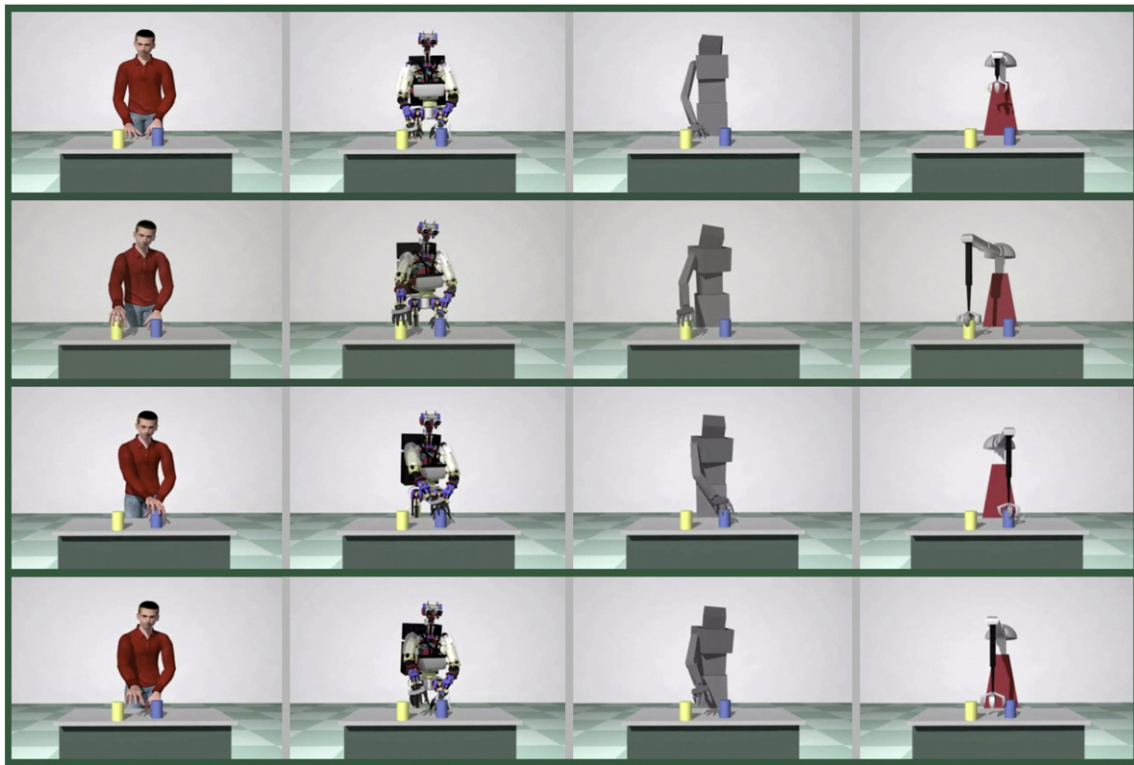


Fig. 1. Characters and conditions. Row 1: The Human, Robot, Boxes and Claw characters at rest. Row 2: The characters picking the original target object (Goal Stay). Row 3: The actors grasp the alternate object (Goal Shift). Row 4: The characters miss the objects altogether (Goal Miss).

motion patterns as the Human and Robot; however, it was even less human in appearance. Lastly, a mechanical claw (Claw condition) was created that had no biological characteristics and moved in an organized but non-biological fashion. Thus, we created actors who had varying levels of biological motion and capacity for mental states.

Method

Participants

Seventeen adults were recruited from the university and local populations who successfully participated in this research (age range = 18 to 41 years, mean = 27.5 years, SD = 5.8, 8 females, 15 right-handed). All had normal or corrected-to-normal vision. Data from an additional three participants were discarded due to excessive head motion and not included in analyses. All participants gave written informed consent to participate in this research, which was approved by the Institutional Review Boards of Carnegie Mellon University and the University of Pittsburgh, and they were compensated for their time.

fMRI

Imaging took place at the Brain Imaging Research Center shared by Carnegie Mellon University and the University of Pittsburgh. The MRI scanner used was a 3 T, head-only Siemens Allegra (Siemens, Erlangen, Germany). High-resolution structural images included a T1-weighted, 3D MPRAGE sequence to be used for structural morphometry and for coregistration with functional images (224 slices, TR = 1630 ms, TE = 2.48 ms, FOV = 20.4 cm, $\alpha = 8^\circ$, matrix size = 256^2 , voxel size = $0.8 \times 0.8 \times 0.8$ mm). A single-shot, gradient-recalled, echo-planar pulse sequence was used for the collection of whole-brain functional images sensitive to blood-oxygenation-level-dependent contrast (35 slices, TR = 2000 ms, TE = 30 ms, FOV = 20.4 cm, $\alpha = 73^\circ$, matrix size = 64^2 , voxel size = $3.2 \times 3.2 \times$

3.2 mm). The five functional runs included the acquisition of 344 volumes, not including 2 discarded RF excitations at onset to achieve steady-state equilibrium. Participants viewed the movies within the scanner bore during functional data acquisition using mirrored glasses and a projector and screen set up behind the scanner. All participants were able to describe the various conditions after scan session completion.

Data analysis

BrainVoyager QX (Brain Innovation, Maastricht, Netherlands) was used for preprocessing and analyzing the imaging data. Automated preprocessing consisted of the following steps: (1) slice time correction; (2) slice alignment and 3D motion correction using sinc interpolation; (3) spatial smoothing with a 4-mm Gaussian kernel; (4) linear trend removal; (5) temporal high-pass filtering; and (6) removal of serial correlations in residuals. If head motion was found to have surpassed a 2-mm threshold, the data were discarded. Data from 6 runs (1 each from 6 participants) was discarded, leaving a total of 79 runs in the analysis of all participants. Then, functional and structural data sets for each person were coregistered and manually marked for transformation into Talairach space by BrainVoyager (Talairach and Tournoux, 1988).

Once these data were transformed, all participants' functional data were overlaid on a standard brain for multi-subject statistical analyses. This multiple linear regression, general linear model was calculated from the 79 successful runs of data collection (5 each from 11 participants, 4 each from 6 participants due to motion loss). Event predictors were modeled based on the initial 2-s periods of reaching in each video, using an idealized boxcar model of hemodynamic response (Friston et al., 1998). Linear contrasts using *t*-statistics were calculated in order to determine response differences to each event condition. Time courses consisted of averaged percent BOLD signal change across all trials of each condition for all participants. The multi-participant, random-effects statistical maps were visualized on

the Talairach-transformed template brain with a threshold of $q < .01$ to correct for false discovery (Genovese et al., 2002), and no activation consisting of fewer than 8 contiguous voxels was considered.

Paradigm

Each movie lasted 6 s. Video clips were separated by 10-s intervals of a black screen. Twelve conditions (4 movers \times 3 movements) were created in total, and each was displayed 20 times over the course of five runs. The video clips for each trial were merged into the final runs using iMovie, and the final videos were 720 by 480 pixels. Each run lasted approximately 11.5 min and included four trials of each of the 12 trial types in a semi-randomized order such that neither type of reach nor type of actor was repeated more than twice in a row. Participants were instructed simply to remain still and watch the movies.

Stimulus creation

Animated stimuli were used to create control conditions in which humans and machines followed identical movement patterns. Rather than using a standard animation software package, which often results in unnatural- or impossible-looking motions, videos were made using motion capture data in the Graphics Laboratory at the Robotics Institute at Carnegie Mellon University. This results in superior animation of dynamic human motion. Please see the Supplemental Methods section for more detail.

The size and motion information were registered to 3 types of models, including a human male (Human condition), a humanoid robot (Robot), and a box-like machine (Boxes) (see Fig. 1). The box-like machine consisted of stacked rectangular prisms of the same approximate size as the head, chest, and lower torso regions of the human with a reaching arm that could move in a similar fashion to the actor's body. This figure was registered to the same motion pattern as the Human and Robot, based on the actor's movements. Lastly, a fourth machine condition (Claw) was created that moved in a way that would be impossible for a human or animal. The machine had an outreached horizontal arm with a joint to another, vertical, extendable arm ending in a grasping claw (similar to the popular arcade game). Thus, the Claw was able to reach towards objects in a unique, non-human fashion. Although the overall motion path used to approach the objects on the table was the same, the Claw movements were unique rather than overlaid on the motion capture data. These 4 categories of movers were created to examine the pSTS responses to biological motion performed by a human (Man), biological motion performed by a humanoid robot (Robot), biological motion performed by a less-humanoid machine (Boxes), and non-biological motion performed by a machine (Claw).

The target objects for the reaching movements were cylinders of identical sizes and weights but different colors, placed on a table in front of the mover. During motion capture, the two objects were positioned such that object A was located at a distance of 16 in and an angle of approximately 20° from center line of the table, at the end of which the actor's hands were originally placed. Object B was positioned at a distance of 11.3 in and 25°. To reach for A, the actor took a direct, 16-inch path. To get object B, he followed the first 8 in of the path towards A, but then the motion turned at a 90-degree angle to travel another 8 in to grasp B. Upon grasping one of the two objects, the actor lifted it 10 in straight up and then replaced it in its original position. Lastly, a condition was created in which the actor appeared to set out for Object A, but missed. He still proceeded to lift his arm 10 in and lower it, as in the other conditions. Additionally, the grasping action of the hand was kept consistent throughout all conditions in order to ensure that perceived intentions would not be affected by hand position (Ansuini et al., 2006; Becchio et al., 2008). These three trial types were labeled Goal Stay, Goal Shift, and Goal

Miss. In all three trial types, the actor returned his hand to the starting position by following a direct, straight-line path to the center of the edge of the table closest to him. Each trial lasted 6 s: 2 s for the initial reach, 2 s for the lift and replacement, and 2 s to return to the starting position.

Because the movements of the Claw were not registered with the actor's motion capture data, these trials were created separately. The base of the mechanical claw was positioned in the same location behind the table as the figures created using the actor. The "hand" was made up of four jointed talons located at 90-degree angles from each other. A large, stable, horizontal branch connected to the top of the base. It expanded and retracted in the manner of a radio antenna to cover the horizontal distance to each object. Once the claw was vertically aligned above the final location (over one of the target objects or empty space in the case of missing an object), it was lowered on a vertical branch to the height of the object, the claw clenched and was raised partway again to lift or miss the object in a way similar to the other actors. Then, the claw loosened its grip and rose back up to the horizontal arm, which then retracted to its original starting position. Thus, the same horizontal distances and paths were covered in the same amount of time, but neither a biological figure nor biological motion occurred.

Results

The results are organized by brain network for the right pSTS and the mirror neuron system. Other results are listed in Supplemental Table 1. We did whole-brain analyses and examined all findings. Notably, no regions outside of these two networks showed systematic variations in response by character or reaching condition. All reported findings are significant at the level of $q < .01$, corrected for false discovery rate (Genovese et al., 2002), unless otherwise noted. Reported regions of interest consist of a minimum of eight contiguous voxels.

The right pSTS network: RpSTS, RTPJ, and medial frontal cortex

First, we determined which regions were more sensitive to biological motion than non-biological motion to ensure replication of prior work. To do this, we compared the averaged response to all of the Human, Robot, and Boxes conditions to the response to the Claw conditions. The right pSTS was more sensitive to biological motion than to non-biological motion, similar to prior reports (e.g., Bonda et al., 1996; Pelphrey et al., 2003a). (See Fig. 2, left panel.) This was also true when only the Goal Stay conditions for each character were used and the activity in this condition for the Human, Robot, and Boxes was collapsed and compared to the Goal Stay response for the Claw, ensuring that violations of goal-directed action and intention were not driving the effect. With the Human, Robot, and Boxes characters still collapsed to look at all biological motion, we then examined the responses to the various reaching conditions. When Goal Miss (violation of goal-directed action) was compared to Goal Stay (consistent action), the response was greater in the right pSTS. Goal Miss elicited a similar pattern of activity relative to Goal Shift (change in goal object), with increased activity in the right pSTS. No right pSTS increase was found for Goal Shift relative to Goal Stay or to Goal Miss for all of the biological motion characters.

We then considered each character independently. For the Human, the response to Goal Miss was greater than that to Goal Stay in the right pSTS. The right pSTS was again active for Goal Shift more than for Goal Stay, and the increased response was in the same location as in the previous contrast. (See Fig. 2, center panel.) In fact, direct comparisons between the Goal Miss and Goal Shift reaching conditions for the Human found no difference in the right pSTS. The contrasts examining where the Goal Stay response was greater than to Goal Miss or to Goal Shift did not reveal any effects in this network for

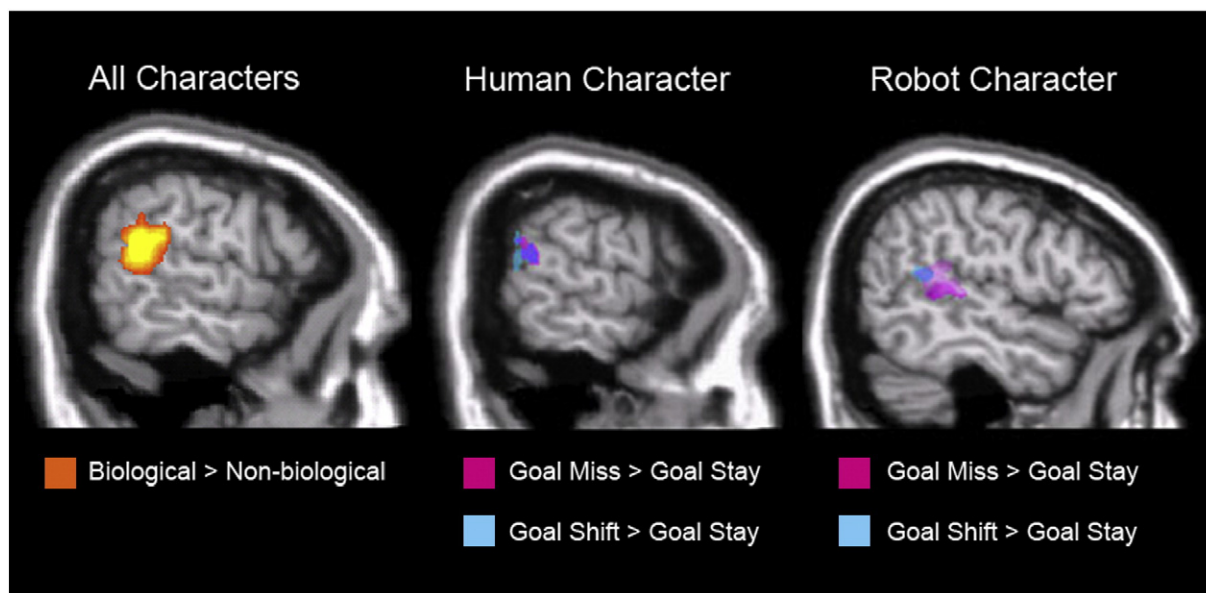


Fig. 2. Right pSTS response patterns. Left panel: Biological motion > Non-biological motion in the Right pSTS. Center panel: Goal Miss > Goal Stay (violation of goal-directed action expectation) ($q < .01$) and Goal Shift > Goal Stay (shift in intention) ($q < .01$) for the Human character only. Right panel: Goal Miss > Goal Stay ($q < .01$) and Goal Shift > Goal stay ($q < .05$) for the Robot character only.

the Human character. The Robot showed a similar pattern of effects (See Fig. 2, right panel.). Goal Miss elicited more activity than Goal Stay in the right pSTS. The response was greater to Goal Shift than to Goal Stay to a lesser but still significant degree in the right pSTS ($q < .05$). The right pSTS did not differentiate between Goal Shift and Goal Miss. Again, there were no areas in this network where the response was greater to Goal Stay than to Goal Miss or Goal Shift. Despite being created with the same biological motion characteristics as the Human and Robot, there was no significant or trending differentiation between any of the reaching conditions in the right pSTS for the Boxes character. The only differentiation seen in the right pSTS network for this character was that Goal Miss elicited more activity than Goal Shift in a small area of medial frontal cortex. Less surprisingly, there were no differences in this network among any comparisons of the three reaching conditions for the Claw. This was expected because the character was created with non-biological motion and did not require processing in this network relative to fixation. Waveforms for all characters and reach conditions in the pSTS are available in Fig. 3.

Unlike the right pSTS, the medial frontal cortex differentiated between characters instead of individual reaching behaviors. The medial frontal cortex response was greater to the Human than to the Robot and greater for the Robot than the Boxes. Given that the motion characteristics were the same for all three characters, the medial frontal cortex response is thought to be modulated by appearance. The right TPJ was not found to be differentially active to any characters or reaches at a significant or trend level. Results for the right pSTS network are reported in Table 1.

The mirror neuron system: inferior frontal gyrus and inferior parietal lobule

Portions of the IFG and IPL have been identified as human mirror neuron regions that respond to both performed and observed actions (e.g., Buccino et al., 2001; Chaminade and Decety, 2002; Decety et al., 2002; Fadiga et al., 1995; Grezes et al., 2003; Iacoboni et al., 1999, 2005; Montgomery et al., 2007; Pieroni et al., 2006). We examined the brain responses in these structures to our various characters and reaching conditions with the assumption that these regions should be activated because the participants were observing actions. The

response in the bilateral IFG was greater for biological (Human, Robot, and Boxes) motion than for non-biological (Claw) motion, but no difference was seen in the IPL. When the reaching conditions were examined for the collapsed biological motion from the three characters, the right IFG and right IPL activity was greater for Goal Miss than for either Goal Stay or Goal Shift. Additionally, the left IPL was greater for Goal Miss than for Goal Shift. No significant differences in these regions were found when Goal Shift and Goal Stay were directly compared for the combined Human, Robot, and Boxes characters.

Next, each character's reaching motions were considered independently. For the Human, the right IPL response was greater to Goal Shift than to Goal Stay. There was no area of greater response in the IFG or IPL for Goal Stay relative to Goal Shift. A different area of right IPL was more active to Goal Stay than to Goal Miss, as were areas of left IPL and right IFG, but there were no significant IFG or IPL results where Goal Miss was greater than Goal Stay. No differences in these regions were found between Goal Shift and Goal Stay or Goal Miss and Goal Shift. Among the comparisons for the Robot and Boxes reaching conditions, no IPL or IFG response differences were found. Additionally, no differentiation was found in this network when looking at each character in comparison to other characters. In the absence of localizer scans, we compared local maxima in our results and previous reports. The IPL and IFG responses recorded in these numerous motion and appearance contrasts did not align with the areas of these structures that were previously identified by other researchers as parts of the mirror neuron system in similar studies (e.g., Iacoboni et al., 2005; Montgomery et al., 2007; Pieroni et al., 2006). Additionally, we ensured that there were no results with a trend towards significance in the previously identified areas. We have included an illustration of locations from our results along with those of the mirror neuron system in Fig. 4 and report results for the complete anatomical structures in Table 2.

Discussion

In this study, we sought to directly compare the neural correlates of goal-directed action and intention understanding. To do so, we created four animated characters that each performed three different reaching behaviors. Striking similarities were observed in the

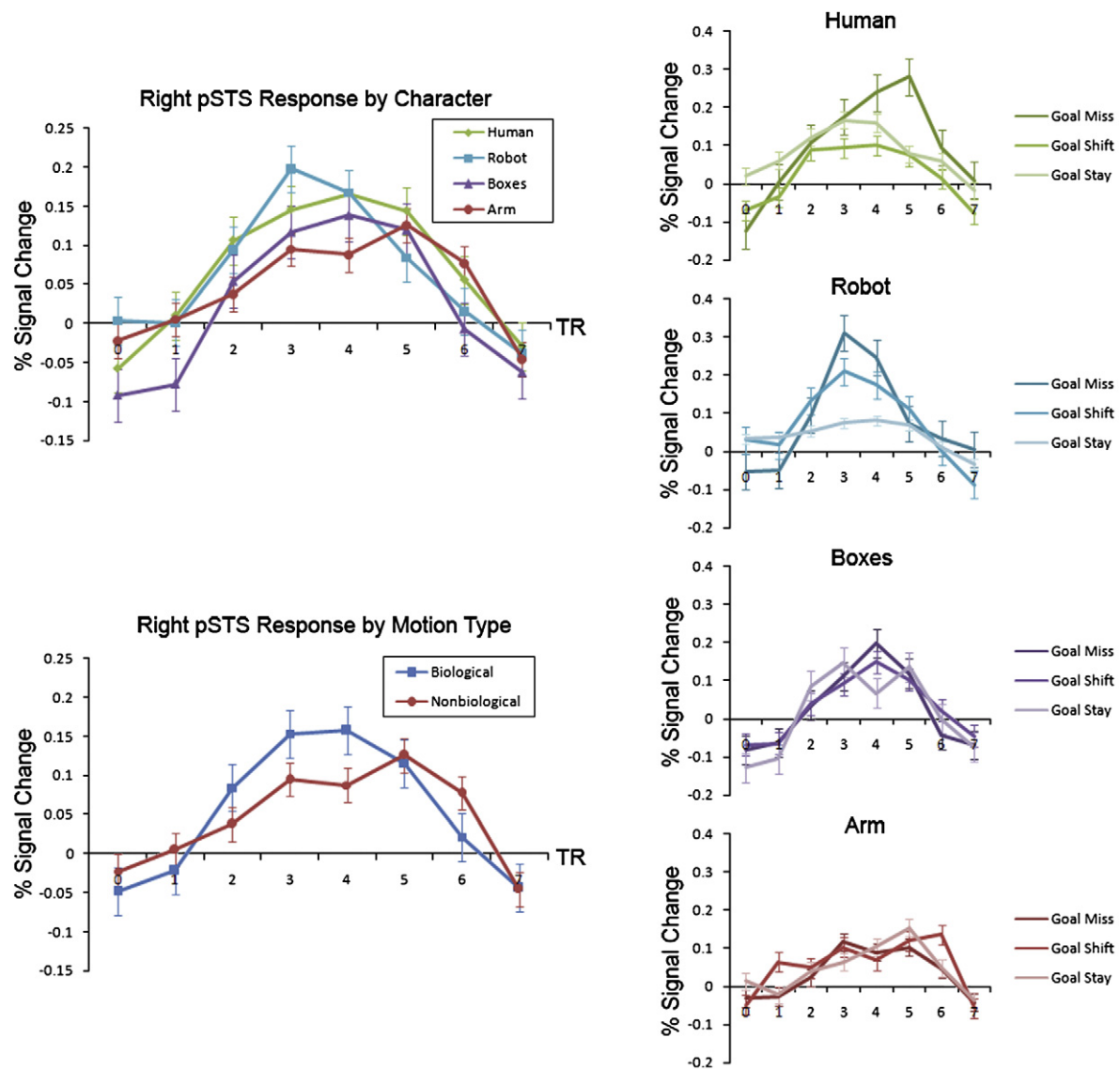


Fig. 3. Hemodynamic response in the right pSTS to each condition. We used the right pSTS, as shown in the left panel of Fig. 2, as an area of interest and show the hemodynamic response within this region to the various conditions. In the top left panel, the responses to each character for all reaching conditions are shown. The bottom left panel shows the hemodynamic response to all of the biological motion conditions (Human, Robot, Boxes) combined and the non-biological motion condition (Arm). The right panels are graphs of the individual responses in the right pSTS to the three reaching conditions for each character.

processing for both violations of goal-directed action and intention expectations in the right pSTS network when the character was a human or humanoid robot. These findings suggest a role for character appearance as well as for motion properties in determining how and when neural network components are recruited for social processing. Moreover, they offer support for certain behaviorally derived theories regarding these processes.

The right pSTS network

Consistent with previous research (Pelphrey et al., 2004), the right pSTS responded more when a human's reaching behaviors resulted in missing a target object than obtaining it. This area was found within the larger area of the right pSTS that responded to biological motion. This experiment was the first to introduce an alternative reaching behavior: shifting during the reach to obtain a new goal instead of the original goal. Thus, a goal was still achieved, but it was not the original target. Again, the right pSTS was more active when participants viewed a human shifting his goals relative to obtaining the original

goal. This motion pattern went beyond basic goal-directed action understanding, potentially eliciting mental state attributions via a physical indication of changing one's mind.

In the prior work on misdirected reaches, the increased brain activity in response to missed goals was interpreted as indicative that more processing is required in response to violations of expectations (Pelphrey et al., 2003b, 2004). This same explanation was offered when a greater right pSTS response was found when emotional displays did not match up with subsequent actions (Vander Wyk et al., 2009). The striking similarity in brain response in both cases here suggest that there is one subarea of the larger right pSTS region implicated in biological motion that is responsible for monitoring goal-directed movements. Notably, our data suggest that this sub-region tracks success only as it pertains to the original target, rather than an updated goal.

The different animated characters were created to examine the effects of similarity to humans on the motion processing of actors. Prior research had only assessed brain response in the pSTS to human reaches, and it failed to address the potential issue that this region

Table 1
Responses in the right pSTS network: RpSTS, RTPJ, and medial frontal cortex.^a

Category	Contrast	RpSTS	RTPJ	medFr
Biological motion	Human, Robot, Boxes>Claw	✓	–	–
Human, Robot, Boxes	Goal Miss>Goal Stay	✓	–	–
	Goal Shift>Goal Stay	–	–	–
	Goal Miss>Goal Shift	✓	–	–
	Goal Shift>Goal Miss	–	–	–
Human	Goal Miss>Goal Stay	✓	–	✓
	Goal Shift>Goal Stay	✓	–	–
	Goal Miss>Goal Shift	–	–	–
	Goal Shift>Goal Miss	–	–	–
Human>Robot	All Human>All Robot	–	–	✓
Robot	Goal Miss>Goal Stay	✓	–	–
	Goal Shift>Goal Stay	✓(q<.05)	–	–
	Goal Miss>Goal Shift	–	–	–
	Goal Shift>Goal Miss	–	–	–
Robot>Boxes	All Robot>All Boxes	✓	–	✓
Boxes	Goal Miss>Goal Stay	–	–	–
	Goal Shift>Goal Stay	–	–	–
	Goal Miss>Goal Shift	–	–	✓
	Goal Shift>Goal Miss	–	–	–

^a All reported responses are significant at the $q < .01$ level unless otherwise noted.

Table 2
Responses in the mirror neuron system: IFG and IPL.^a

Category	Contrast	RIFG	LIFG	RIPL	LIPL
Biological motion	Human, Robot, Boxes>Claw	✓	✓	–	–
Human, Robot, Boxes	Goal Miss>Goal Stay	✓	–	✓	–
	Goal Shift>Goal Stay	–	–	–	–
	Goal Miss>Goal Shift	✓	–	✓	✓
	Goal Shift>Goal Miss	–	–	–	–
Human	Goal Miss>Goal Stay	–	–	–	–
	Goal Shift>Goal Stay	–	–	✓	–
	Goal Miss>Goal Shift	–	–	–	–
	Goal Shift>Goal Miss	✓	–	✓	✓
Human>Robot	All Human>All Robot	–	–	–	–
Robot	Goal Miss>Goal Stay	–	–	–	–
	Goal Shift>Goal Stay	–	–	–	–
	Goal Miss>Goal Shift	–	–	–	–
	Goal Shift>Goal Miss	–	–	–	–
Robot>Boxes	All Robot>All Boxes	–	–	–	–
Boxes	Goal Miss>Goal Stay	–	–	–	–
	Goal Shift>Goal Stay	–	–	–	–
	Goal Miss>Goal Shift	–	–	–	–
	Goal Shift>Goal Miss	–	–	–	–

^a All reported responses are significant at the $q < .01$ level.

might not be specific to humans but instead to biological motion (Carter and Pelphrey, 2006; Pelphrey et al., 2003a). The inclusion of the Robot and Boxes conditions functioned as a replication of the biological motion of the animated Human with non-human actors. The Robot elicited a similar pattern of right pSTS responses to the various reaches as the Human. Although the Boxes character performed a reaching pattern that was identical to that of the Human and Robot, no right pSTS differences were observed when comparing either the Goal Shift or Goal Miss to the Goal Stay condition for the Boxes. It is likely that the right pSTS, widely acknowledged to be part of the social perception network (e.g., Allison et al., 2000; Pelphrey and Carter, 2008), was not active because the Boxes character was not considered to be a social other given its unusual appearance. Previous research suggested that the pSTS is modulated by whether portrayed humans are shown in video or animated form (Mar et al., 2007), indicating that there is an important role for perceived humanness in this region. The Claw character failed to engage the right pSTS for any movements and did not elicit differential responses to the various reaches. This confirms prior findings that the right pSTS is specific for biological motion (e.g., Bonda et al., 1996; Carter and Pelphrey, 2006; Pelphrey et al., 2003a).

Other brain responses related to human similarity could be observed by comparing the characters regardless of reach condition.

The medial frontal cortex was most active to the Human character, followed by the Robot and then the Boxes. This region has been previously implicated in self-other comparisons, action monitoring, and mentalizing (for review, see Amodio and Frith, 2006). Mason and Just (2006, 2009) described medial frontal cortex as part of a protagonist-monitoring network, along with the right pSTS and the temporoparietal junction (TPJ). Thus, it might be that the animated human was interpreted as more similar to the self and more likely to be a protagonist, followed by the Robot. Further support for this comes from research comparing live-action video of humans and animals with cartoons wherein the medial frontal cortex was found to respond more strongly to the videos than to the animations (Han et al., 2005, 2007). Medial frontal cortex could be recruited based on a hierarchy of similarity to live humans.

In turn, the medial frontal cortex response could modulate pSTS activity. The medial frontal response to the Robot was greater than it was to the Boxes, and the Boxes failed to recruit the pSTS differentially to the various reaches despite identical reaching behaviors. Dissimilarity in appearance to a live human could result in a failure of a character to be interpreted as a protagonist, resulting in low medial frontal cortex response and therefore no recruitment of the right pSTS despite biological motion. Future work could explore a single actor moving in both a biological and a non-biological fashion

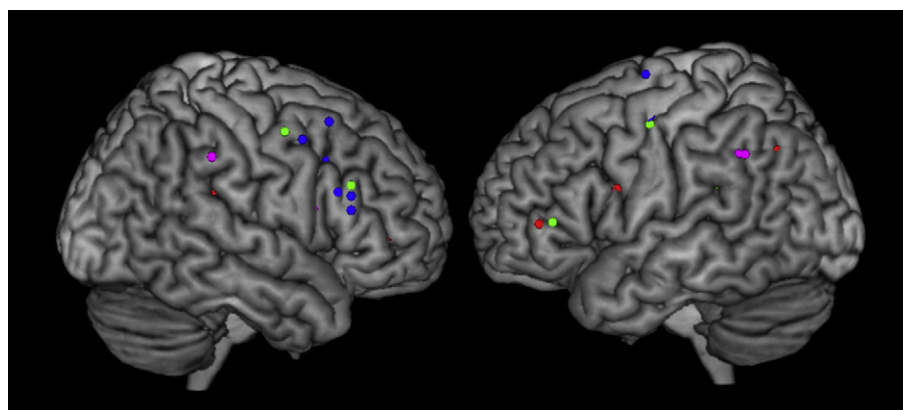


Fig. 4. Comparison of locations of response in IFG and IPL with previous reports of mirror neuron sites. We mark results from our experiment in red, Pierno et al. (2006) in green, Iacoboni et al. (2005) in blue, and Montgomery et al. (2007) in violet. For the previous research, these points indicate the local maxima reported in the areas that were indicated as mirror neuron regions. Locations of these reported peaks were marked with spheres at the exact coordinates and then visualized on a standard 3D brain template using MRICron software (Rorden and Brett, 2000).

to examine the interaction of appearance and motion for character identification.

Mirror neurons

The mirror neuron system was not engaged differentially by the various actors and reaches presented in this experiment. Although there were some contrasts that resulted in activity in the IPL and IFG, the areas did not align with reported centroids of activation from prior research (Buccino et al., 2001; Gazzola et al., 2006; Iacoboni et al., 2005; Pierro et al., 2006). Various explanations could be proposed for these results, which confirm some prior findings. Buccino et al. (2007) suggested that the mirror system is more active for surprising actions, though it was previously found to be more active for actions which the viewer has experience performing (Fadiga et al., 1995; Sakreida et al., 2005), and the increases might cancel each other out in the Buccino and colleagues research comparing surprising versus previously experienced actions. Alternatively, goals and intentions might not be analyzed in this region; similar prior studies did not report activity in mirror neurons (e.g., Pelphrey et al., 2003b, 2004). If the mirror neuron system is processing motion without consideration for context and goal achievement, the failure in differentiation could result from the physical similarity of the various reaches in terms of total motion. However, it is notable that these were passive viewing tasks and the lack of engagement of mirror neuron regions could be a task effect. Lastly, this lack of differentiation could be an effect of our stimuli. Previous work on the mirror neuron system has produced controversial results as to whether it responds more to humans than robots (Kilner et al., 2003; Tai et al., 2004) or equivalently to both (Gazzola et al., 2007; Oberman et al., 2007; Perani et al., 2001). Additionally, mirror neuron system responses are reduced overall in response to computer-generated or televised stimuli (Gu & Han, 2007; Shimada & Hiraki, 2006).

Theoretical implications: goal-directed action

Prior research implicated the pSTS in goal-directed action understanding (e.g., Pelphrey et al., 2003b, 2004). According to the teleological stance, rational actions are determined via analysis of actions, goals, and constraints (Csibra and Gergely, 1998; Gergely and Csibra, 2003). Violations could necessitate increased processing in the brain regions used in goal-directed action monitoring, including the pSTS. The teleological stance includes a role for assignment for agency (Csibra and Gergely, 2007). In the current study, brain differentiation between missing and achieving the goal was found in the pSTS only for the Human and Robot. Higher levels of agency could have been assigned to these characters via a network that includes the medial frontal areas as well as pSTS. Altogether, the data fit the predictions of the teleological stance.

Many proponents of simulation theory have suggested that the mirror neuron system is responsible for determining goals from motions and predicting actions from goal information because it processes actions made both by the self and others (Gallese and Goldman, 1998; Rizzolatti et al., 2001; Rizzolatti and Craighero, 2004). If this were so, one would expect that the mirror neuron system would differentiate between reaching behaviors that achieve or miss a goal. The latter condition violates the original goal expectation and is highly unusual. Similarly, if the mirror neuron system were using motion patterns to predict goals and infer intentions, it should discriminate between achieving an original goal and shifting direction to obtain another target instead. It would be required to reinterpret the goal and alter predictions to match the new circumstances. In both cases, the need for reassessment of the situation would presumably result in differing levels of mirror neuron system recruitment during processing. The absence of such differentiation in the current results argues against this substrate for simulation theory underlying goal-

directed action and intention understanding. More recently, Mitchell et al. (2006) identified a region of ventral medial prefrontal cortex that responds to both self-referential thought and judgments about similar others and suggested it as a substrate for simulation theory. If our results are interpreted using this perspective, the differential activity in this region for the various characters would therefore not rule out a role for simulation theory entirely. However, this region differentiated systematically between characters, but not between reaches. The results from reach comparisons were primarily in the pSTS. The pSTS cannot plausibly be a substrate for simulation theory because it processes the actions of others but not those performed oneself (Emery and Perrett, 2000). This suggests that though there might be a role for simulation in medial frontal cortex in character identification, it cannot be the only process at work.

Theoretical implications: intention

The Goal Shift versus Goal Stay comparison was created to examine intention understanding by introducing a behavior in which the actor appears to change his goal, and therefore his intent. The pattern of pSTS results for this contrast of the Human and Robot was largely the same as for the Goal Miss versus Goal Stay comparison. Two explanations are possible for these results: either intention understanding in the brain builds upon goal-directed action understanding and therefore uses the same substrates or intention understanding was not elicited by the Goal Shift stimuli. In the first case, this pattern of results would be assessed in relation to theories of intention understanding, such as simulation theory and theory theory. Simulation theory has similar problems for intention understanding as those addressed previously for goal-directed action. Proponents of theory theory posit that observers use sets of rules and heuristics to attribute mental states to others. Shifting paths towards a different goal would either necessitate quick formulation of a new expectation about the intention of the actor or simply substantiate a violation of original expectations about intent; either of these could result in the increased processing and higher activity seen in the pSTS.

However, it remains possible that the similarities between the results for the Goal Miss (goal-directed action violation without intention) and Goal Shift (altered intentions) arose instead from a lack of recruitment of intention understanding. This is a higher-level process than goal-directed action comprehension, but might not have been drawn upon because of simplicity of the stimuli, repetitiveness, or lack of realism. Specifically, the lack of differential activity in the right TPJ could indicate that mental states were not assigned to the various actors. If it is the case that intention understanding was not required, all conditions might have been processed in terms of goal-directed action and therefore only need to be accounted for by theories of goal-directed action understanding. When including the additional Goal Shift conditions, these data still do not rule out the use of the teleological stance. The increased pSTS activity to the Goal Shift condition relative to Goal Stay could be a result of either a violation of expectation or a need to revise original assumptions about the goal and form a new prediction. Either explanation could account for the similarity between the pSTS results for the Goal Miss and Goal Shift contrasts.

In all, the current data can be accounted for by the teleological stance on goal-directed action. This research suggests that simulation theory alone cannot adequately address these findings. Future studies should address more complex intention understanding requiring a wider variety of mental states.

Supplementary materials related to this article can be found online at doi: [10.1016/j.neuroimage.2010.08.077](https://doi.org/10.1016/j.neuroimage.2010.08.077).

Acknowledgments

This study was funded by NSF Grant 0811450, "Exploring the Uncanny Valley", and a grant from the Microsoft Corporation awarded

to JKH. We thank Dr. Marcel Just, Dr. Diane Williams, and Elinora Hunyadi for their valuable input throughout this project. Autodesk, Inc., donated the Maya software package used for animation. We also thank our participants.

References

- Allison, T., Puce, A., McCarthy, G., 2000. Social perception from visual cues: role of the STS region. *Trends Cogn. Sci.* 4 (7), 267–278.
- Amodio, D., Frith, C., 2006. Meeting of minds: the medial frontal cortex and social cognition. *Nat. Rev. Neurosci.* 7, 268–277.
- Anscombe, G.E.M., 1957. *Intention*. Cornell University Press, Ithaca.
- Ansuini, C., Santello, M., Massaccesi, S., Castiello, U., 2006. Effects of end goal on hand shaping. *J. Neurophysiol.* 95, 2456–2465.
- Becchio, C., Sartori, L., Bulgheroni, M., Castiello, U., 2008. Both your intention and mine are reflected in the kinematics of my reach-to-grasp movement. *Cognition* 106 (2), 894–912.
- Bonda, E., Petrides, M., Ostry, D., Evans, A., 1996. Specific involvement of human parietal systems and the amygdala in the perception of biological motion. *J. Neurosci.* 16 (11), 3737–3744.
- Buccino, G., Binkofski, F., Fink, G.R., Fadiga, L., Fogassi, L., Gallese, V., et al., 2001. Action observation activates premotor and parietal areas in a somatotopic manner: an fMRI study. *Eur. J. Neurosci.* 13 (2), 400–404.
- Buccino, G., Lui, F., Canessa, N., Patteri, I., Lagravinese, G., Benuzzi, F., et al., 2004. Neural circuits involved in the recognition of actions performed by nonconspecifics: An fMRI study. *J. Cogn. Neurosci.* 16 (1), 114–126.
- Buccino, G., Baumgaertner, A., Colle, L., Buechel, C., Rizzolatti, G., Binkofski, F., 2007. The neural basis for understanding non-intended actions. *Neuroimage* 36 (Suppl 2), T119–T127.
- Carter, E.J., Pelphrey, K.A., 2006. School-aged children exhibit domain-specific responses to biological motion. *Soc. Neurosci.* 1 (3–4), 396–411.
- Chaminade, T., Decety, J., 2002. Leader or follower? Involvement of the inferior parietal lobule in agency. *NeuroReport* 13 (15), 1975–1978.
- Csibra, G., Gergely, G., 1998. The teleological origins of mentalistic action explanations: a developmental hypothesis. *Dev. Sci.* 1 (2), 255–259.
- Csibra, G., Gergely, G., 2007. 'Obsessed with goals': functions and mechanisms of teleological interpretation of actions in humans. *Acta Psychol. (Amst)* 124 (1), 60–78.
- Csibra, G., Biro, S., Koos, O., Gergely, G., 2003. One-year-old infants use teleological representations of actions productively. *Cogn. Sci.* 27 (1), 111–133.
- D'Andrade, R., 1987. A folk model of the mind. In: Holland, D., Quinn, N. (Eds.), *Cultural Models in Language and Thought*. Cambridge University Press, Cambridge, UK, pp. 113–147.
- Decety, J., Chaminade, T., Grezes, J., Meltzoff, A.N., 2002. A PET exploration of the neural mechanisms involved in reciprocal imitation. *Neuroimage* 15 (1), 265–272.
- Emery, N.J., Perrett, D.I., 2000. How can studies of monkey brains help us understand 'theory of mind' and autism in humans? In: Baron-Cohen, S., Tager-Flusberg, H., Cohen, D.J. (Eds.), *Understanding other minds: Perspectives from developmental cognitive neuroscience*, pp. 274–305. Oxford, UK: Oxford University Press.
- Fadiga, L., Fogassi, L., Pavesi, G., Rizzolatti, G., 1995. Motor facilitation during action observation: a magnetic stimulation study. *J. Neurophysiol.* 73 (6), 2608–2611.
- Feldman, R., Reznick, S., 1996. Maternal perception of infant intentionality at 4 and 8 months. *Infant Behav. Dev.* 19 (4), 483–496.
- Friston, K.J., Fletcher, P., Josephs, O., Holmes, A., Rugg, M.D., Turner, R., 1998. Event-related fMRI: characterizing differential responses. *Neuroimage* 7 (1), 30–40.
- Gallese, V., Goldman, A., 1998. Mirror neurons and the simulation theory of mind-reading. *Trends Cogn. Sci.* 2 (12), 493–501.
- Gallese, V., Keysers, C., Rizzolatti, G., 2004. A unifying view of the basis of social cognition. *Trends Cogn. Sci.* 8 (9), 396–403.
- Gazzola, V., Aziz-Zadeh, L., Keysers, C., 2006. Empathy and the somatotopic auditory mirror system in humans. *Curr. Biol.* 16 (18), 1824–1829.
- Gazzola, V., Rizzolatti, G., Wicker, B., Keysers, C., 2007. The anthropomorphic brain: the mirror neuron system response to human and robotic actions. *Neuroimage* 35, 1674–1684.
- Genovese, C.R., Lazar, N.A., Nichols, T., 2002. Thresholding of statistical maps in functional neuroimaging using the false discovery rate. *Neuroimage* 15 (4), 870–878.
- Gergely, G., Csibra, G., 2003. Teleological reasoning in infancy: the naive theory of rational action. *Trends Cogn. Sci.* 7 (7), 287–292.
- Gopnik, A., Meltzoff, A.N., 1997. *Words, Thoughts, and Theories*. MIT Press, Cambridge, MA.
- Gopnik, A., Wellman, H.M., 1994. The theory theory. In: Hirschfeld, L., Gelman, S. (Eds.), *Domain Specificity in Cognition and Culture*. Cambridge University Press, New York, pp. 257–293.
- Grafton, S.T., Hamilton, A.F.de.C., 2007. Evidence for a distributed hierarchy of action representation in the brain. *Hum. Mov. Sci.* 26 (4), 590–616.
- Grezes, J., Armony, J.L., Rowe, J., Passingham, R.E., 2003. Activations related to "mirror" and "canonical" neurones in the human brain: an fMRI study. *Neuroimage* 18 (4), 928–937.
- Gu, X., Han, S., 2007. Attention and reality constraints on the neural processes of empathy for pain. *Neuroimage* 36, 256–267.
- Han, S., Jiang, Y., Humphreys, G.W., 2007. Watching cartoons activates the medial prefrontal cortex in children. *Chinese Science Bulletin* 52 (24), 3371–3375.
- Han, S., Jiang, Y., Humphreys, G.W., Zhou, T., Cai, P., 2005. Distinct neural substrates for the perception of real and virtual visual worlds. *NeuroImage*, 24, 928–935.
- Hoffman, E.A., Haxby, J.V., 2000. Distinct representations of eye gaze and identity in the distributed human neural system for face perception. *Nat. Neurosci.* 3 (1), 80–84.
- Iacoboni, M., Woods, R.P., Brass, M., Bekkering, H., Mazziotta, J.C., Rizzolatti, G., 1999. Cortical mechanisms of human imitation. *Science* 286 (5449), 2526–2528.
- Iacoboni, M., Molnar-Szakacs, L., Gallese, V., Buccino, G., Mazziotta, J.C., Rizzolatti, G., 2005. Grasping the intentions of others with one's own mirror neuron system. *PLoS Biol.* 3 (3), e79.
- Kilner, J.M., Paulignan, Y., Blakemore, S.J., 2003. An interference effect of observed biological movement on action. *Curr. Biol.* 13, 522–525.
- Leslie, A.M., 2000. How to acquire a "representational theory of mind". In: Sperber, S., Davis, S. (Eds.), *Metarepresentation*. Oxford University Press, Oxford, UK, pp. 197–223.
- Mar, R.A., Kelley, W.M., Heatherton, T.F., Macrae, C.N., 2007. Detecting agency from the biological motion for veridical vs animated agents. *Soc. Cogn. Affect Neurosci.* 2, 199–205.
- Mason, R.A., Just, M.A., 2006. Neuroimaging contributions to the understanding of discourse processes. In: Traxler, M., Gernsbacher, M.A. (Eds.), *Handbook of Psycholinguistics*. Elsevier, Amsterdam, pp. 765–799.
- Mason, R.A., Just, M.A., 2009. The role of the theory-of-mind cortical network in the comprehension of narratives. *Lang. Linguist. Compass* 3, 157–174.
- Mitchell, J.P., Macrae, C.N., Banaji, M.R., 2006. Dissociable medial prefrontal contributions to judgments of similar and dissimilar others. *Neuron* 50, 655–663.
- Montgomery, K.J., Isenberg, N., Haxby, J.V., 2007. Communicative hand gestures and object-directed hand movements activated the mirror neuron system. *Soc. Cogn. Affect Neurosci.* 2 (2), 114–122.
- Newman-Norlund, R., van Schie, H.T., van Hoek, M.E.C., Cuijers, R.H., Bekkering, H., 2010. The role of inferior frontal and parietal areas in differentiating meaningful and meaningless object-directed actions. *Brain Res.* 1315, 63–74.
- Oberman, L.M., McCreery, J.P., Ramchandran, V.S., Pineda, J.A., 2007. EEG evidence for mirror neuron activity during the observation of human and robot actions: toward an analysis of the human qualities of interactive robots. *Neurocomputing* 70, 2194–2203.
- Pelphrey, K.A., Mitchell, T.V., McKeown, M.J., Goldstein, J., Allison, T., McCarthy, G., 2003a. Brain activity evoked by the perception of human walking: controlling for meaningful coherent motion. *J. Neurosci.* 23 (17), 6819–6825.
- Pelphrey, K.A., Singerman, J.D., Allison, T., McCarthy, G., 2003b. Brain activation evoked by perception of gaze shifts: the influence of context. *Neuropsychologia* 41 (2), 156–170.
- Pelphrey, K.A., Morris, J.P., McCarthy, G., 2004. Grasping the intentions of others: the perceived intentionality of an action influences activity in the superior temporal sulcus during social perception. *J. Cogn. Neurosci.* 16 (10), 1706–1716.
- Pelphrey, K.A., Carter, E.J., 2008. Charting the typical and atypical development of the social brain. *Dev Psychopathol.* 20 (4), 1081–102.
- Perani, D., Fazio, F., Borghese, N.A., Tettamanti, M., Ferrari, S., Decety, J., et al., 2001. Different brain correlates for watching real and virtual hand actions. *Neuroimage* 749–758.
- Perner, J., Davies, G., 1991. Understanding the mind as an active information processor: do young children have a "copy theory of mind"? *Cognition* 39 (1), 51–69.
- Pierro, A.C., Becchio, C., Wall, M.B., Smith, A.T., Turella, L., Castiello, U., 2006. When gaze turns into grasp. *J. Cogn. Neurosci.* 18 (12), 2130–2137.
- Puce, A., Allison, T., Bentin, S., Gore, J.C., McCarthy, G., 1998. Temporal cortex activation in humans viewing eye and mouth movements. *J. Neurosci.* 18 (6), 2188–2199.
- Rizzolatti, G., Craighero, L., 2004. The mirror-neuron system. *Annu. Rev. Neurosci.* 27, 169–192.
- Rizzolatti, G., Fogassi, L., Gallese, V., 2001. Neurophysiological mechanisms underlying the understanding and imitation of action. *Nat. Rev. Neurosci.* 2 (9), 661–670.
- Rorden, C., Brett, M., 2000. Stereotaxic display of brain regions. *Behav. Neurol.* 12 (4), 191–200.
- Sakreida, K., Schubotz, R.I., Wolfensteller, U., von Cramon, D.Y., 2005. Motion class dependency in observers' motor areas revealed by functional magnetic resonance imaging. *J. Neurosci.* 25 (6), 1335–1342.
- Saxe, R., Kanwisher, N., 2003. People thinking about thinking people: The role of the temporo-parietal junction in "theory of mind". *NeuroImage* 19, 1835–1842.
- Shimada, S., Hiraki, K., 2006. Infants' brain responses to live and televised action. *NeuroImage* 32, 930–939.
- Stich, S., Nichols, S., 1993. Folk psychology: simulation or tacit theory? *Mind Lang.* 7 (1–2), 35–71.
- Tai, Y.F., Scherfler, C., Brooks, D.J., Sawamoto, N., Castiello, U., 2004. The human premotor cortex is 'mirror' only for biological actions. *Curr. Biol.* 14, 117–120.
- Talairach, J., Tournoux, P., 1988. *Co-Planar Stereotaxic Atlas of the Human Brain: 3-Dimensional Proportional System—An Approach to Cerebral Imaging*. Thieme Medical Publishers, New York.
- Vander Wyk, B.C., Hudac, C.M., Carter, E.J., Sobel, D.M., Pelphrey, K.A., 2009. Action understanding in the superior temporal sulcus region. *Psychol. Sci.* 20 (6), 771–777.
- Wellman, H.M., 1990. *The Child's Theory of Mind*. MIT Press, Cambridge, MA.
- Woodward, A.L., 1998. Infants selectively encode the goal object of an actor's reach. *Cognition* 69 (1), 1–34.