Neural correlates of social perception: The posterior superior temporal sulcus is modulated by action rationality, but not animacy

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Abstract

Recent research has investigated the neural basis of social perception, the ability to make high-level social inferences from perceptual information. The right posterior superior temporal sulcus (pSTS) has been identified as a candidate region for this ability, but the specific processes to which the pSTS contributes remain unclear. In the present study, we investigated the neural correlates of social perception using simple animated geometric shape stimuli, separately manipulating the perceived animacy, goal-directedness, and path rationality in the animations. We did not find an increased pSTS response to animate or goal-directed animations. However, we found that across conditions, the pSTS response tracked path rationality, with stronger responses to irrational paths. This is consistent with prior neuroimaging research on the perception of human actions, and supports the claim that the pSTS is involved in action understanding.

Keywords: social perception, fMRI, superior temporal sulcus

Introduction

Humans have a remarkable ability to infer the dispositions and intentions of other agents from perceptual information, and specifically from motion patterns such as hand and body motion, gaze shifts, and facial motion. This ability, termed social perception, comprises a number of subprocesses: the detection of agents in an environment, perceptual analysis of their motion, inference about social properties from the agent's actions and their context, and prediction of future actions based on these properties.

Recent research has begun to probe the neural basis of these processes, although the relevant brain regions and their specific functional role is still debated. One line of research has pointed to the right posterior superior temporal sulcus (pSTS) as a critical region for social perception (Allison, Puce, & McCarthy, 2000). This region responds more strongly to (human) biological motion than motion of inanimate objects (e.g. Grossman et al., 2000; Pelphrey et al., 2003). These responses might relate to the detection or perceptual analysis of biological motion, to higher-level processing of the intentions underlying the actions, or to some combination thereof.

Another set of studies indicates that the pSTS response to human actions is modulated by inferred intentions. Specifically, actions that violate inferred intentions in a given context, such as twisting empty space next to a gear rather than a gear itself, elicit a stronger pSTS response than the expected actions, across a range of contexts and specific actions (Brass, Schmitt, Spengler, & Gergely, 2007; Pelphrey, Morris, & McCarthy, 2004; Pelphrey, Singerman, Allison, & McCarthy, 2003; Saxe, Xiao, Kovacs, Perrett, & Kanwisher, 2004; Vander Wyk, Hudac, Carter, Sobel, & Pelphrey, 2009). Such actions have been referred to as incongruent, irrational, or unexpected.

This effect has been interpreted as evidence that the pSTS is sensitive to the goals or intentions underlying human motion. For instance, Pelphrey et al. (2004) argued that the pSTS is involved in predicting actions in a given context based on an "intentional stance," in which actions are determined by a goal state and an assumption that the agent will choose the most efficient means to achieve the goal given situational constraints. They proposed that when this prediction is violated, the pSTS must engage in extra processing to explain the observed action in other terms, which would explain its stronger response to unexpected actions.

Another line of research supporting the role of pSTS in action understanding as employed animations of simple geometric shapes as stimuli (Castelli, Happé, Frith, & Frith, 2003; Gobbini, Koralek, Bryan, Montgomery, & Haxby, 2007). These studies have found a stronger pSTS response to animations depicting social interactions between animate shapes, compared with animations of shapes moving as inanimate physical objects. This demonstrates that the role of the pSTS extends to animations that lack the form and motion kinematics of humans, but imply intentional action. However, such comparisons have been largely visually uncontrolled, and could also reflect one of a number of processes: detecting agents, processing of their motion or intentions, or processing of interactions between multiple agents.

The present study aimed to investigate the neural correlates of social perceptual processes, using geometric shape stimuli. In particular, we use dot-chain stimuli perceived as slithering snakes or worms, which provide a strong percept of animacy without the need for multiple, interacting agents (Gao, New, & Scholl, 2011). This ensures that any effects observed do not relate to processing interactions between agents (c.f. Centelles, Assaiante, Nazarian, Anton, & Schmitz, 2011). To investigate each of the subprocesses listed above, we separately manipulated the perceived animacy, goal-directedness, and path rationality (or expectedness) of the animations. We first performed a behavioral study, eliciting judgments about these animations on various dimensions. The animations were then used as stimuli for an fMRI experiment, to investigate the response of the pSTS, as well as motion-sensitive area MT+, as a control region.

Methods

Experiment 1: Behavioral study

Participants For the behavioral study, responses were gathered using Amazon Mechanical Turk. There were 16 types of animation per condition, and 15 responses were elicited for each animation, yielding a total of 240 responses per condition. Participants were constrained to be from the United States, and to have a minimum 95% approval rating from prior Turk studies. The survey included several foil questions (e.g., what is the color of the dots?), and responses with incorrect answers to these questions were rejected.

Stimuli The stimuli consisted of a set of 4s-long animations of dots (i.e. circles) and dot-chains moving within a square-shaped environment, with walls present in some conditions as obstacles. For the head dot of the snake, motion was determined using the chase-subtlety algorithm from Gao, Newman, & Scholl (2009). In this algorithm, the velocity of the dot has a fixed magnitude, with a direction that updates periodically (every 5 frames or .167s, in the present study). The direction is chosen probabilistically: if the angle that directs the dot toward its goal is denoted α and the subtlety parameter is denoted γ, the new direction is chosen from a uniform distribution over the interval $[\alpha-\gamma,\alpha+\gamma]$, where $\gamma=\pi/12$ in this study. This results in a dot that takes a slightly winding path toward a goal. Tail dots in the chain, if present, followed the path taken by the head dot with a slight lag.

Conditions 1-4 were intended to manipulate animacy and goal-directedness in a 2x2 design (see figure 1 for a schematic depiction of each condition). Animacy was modulated by the presence or absence of six tail dots, leading to the percept of a worm or snake. Goal-directedness was modulated by the presence of a goal-dot at the end of the trajectory.

Conditions 5-8 were intended to manipulate path rationality. Stimuli in conditions 5-7 were considered animate and goal-directed, but involved trajectories with a bend, which was either around a wall or around nothing. These conditions were 5) rational (full wall), 6) semi-rational (half of a wall), and 7) irrational (no wall). As a visual control, walls were added to conditions 1-4 and 7-8, which were not relevant to the paths. In condition 8 (wander), the dot-chain had no goal and increased subtlety ($\gamma=\pi/4$), leading to a percept of a randomly wandering snake, intended as a highly irrational, unexplainable action.

For each condition, 4 specific animations were designed with distinct trajectories; these stimuli were rotated 0°, 90°, 180°, and 270° to create 16 animations per condition. Two visual confounds should be noted: the animate condition had more dots and therefore more motion than the inanimate condition; and the wander condition had more changes in motion than all other conditions. These issues are further discussed below.

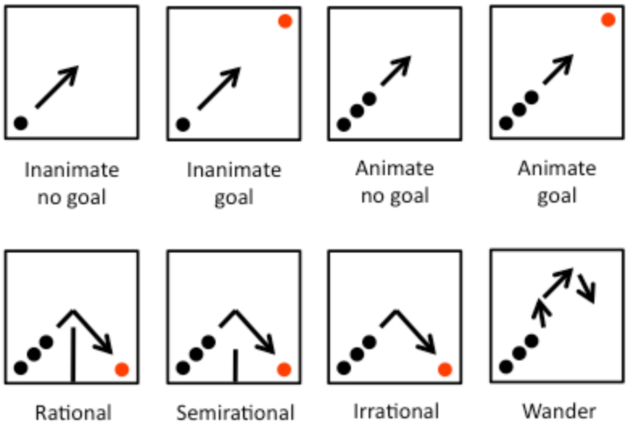


Figure 1: Schematic illustrations of the animation stimuli (not to scale). Note that the actual trajectories were not straight lines, but winding paths (see Methods section).

Behavioral measures Participants viewed the animations and were asked to respond to the following questions on a seven-point scale: 1) How much did the moving dot look like a living, animate thing, as opposed to an inanimate physical object? 2) To what extent did the moving dot appear to have a goal or goals? 3) To what extent did the dot's path seem strange or irrational? Additionally, several foil questions were asked to ensure meaningful responses.

Data analysis We performed several planned unpaired two-sample *t*-tests to test the specific effects of interest. We first tested the effect of having a tail (conditions 3 and 4 versus 1 and 2) on animacy ratings. We then tested the effects of having a goal dot (2 and 4 versus 1 and 3), of path irrationality (7 versus 5), and of wandering over irrationality (8 versus 7), on both goal-directedness and irrationality ratings. Additionally, we performed a post-hoc test for the effect of having a goal dot for animations with a tail (4 versus 3) on animacy ratings.

Experiment 2: fMRI study

Participants 20 subjects (aged 19-28, mean 23.1; 10 female) were recruited for the fMRI study. All participants had normal or corrected-to-normal vision and no history of neurological or psychiatric disorders, and gave written, informed consent in accordance with the requirements of the MIT institutional review board.

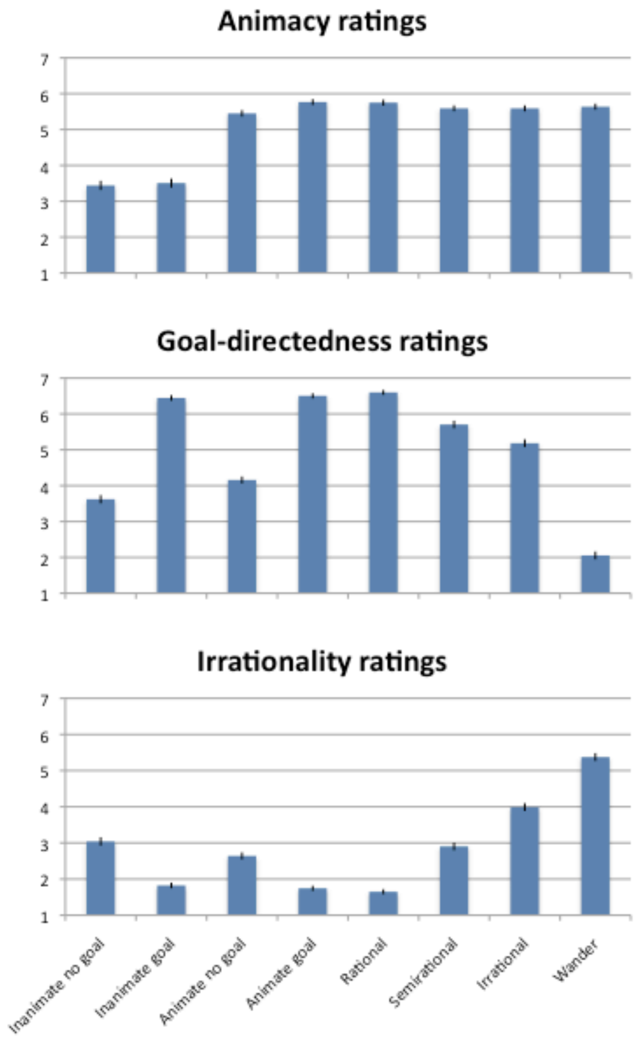
Stimuli The animations used in the fMRI experiment were the same as those used in the behavioral study. Stimuli were presented in a jittered, event-related design, with a variable inter-stimulus interval of 0-15 seconds, during which a central fixation cross was presented. The experiment comprised 8 blocks lasting 9 minutes and 44 seconds, each containing 8 stimuli per condition, for a total of 64 stimuli per condition. Participants performed a one-back task on animations during the scan, to maintain attention; repeat trials were not included in the analysis.

Additionally, each subject received a localizer scan intended to define the pSTS and motion-sensitive area MT. This consisted of three conditions in a blocked design: biological motion (point-light displays [PLDs] depicting human motion; cf Grossman et al. 2000), scrambled motion (PLDs with initial dot positions scrambled), and static luminance change (static dots changing in luminance). Each subject received 2 or 3 runs lasting 7 minutes and 24 seconds each, and comprising 6 12s-long blocks per condition separated by a 12s interstimulus interval. Participants performed a one-back task on individual animations within the blocks, to maintain attention.

fMRI Data Acquisition Data were acquired on a 3T Siemens Tim Trio scanner, with a 32-channel head coil. Following high-resolution anatomical scans, functional images were acquired with an echo planar imaging pulse sequence sensitive to blood-oxygen-dependent (BOLD) contrast (repetition time [TR] = 1s, echo time [TE] = 30ms, flip angle = 70°, voxel size 3x3x3mm, matrix 64x64, 16 axial slices). Because of our interest in specific brain regions, we used a sequence with limited coverage (of visual cortex and the STS), but a TR of 1s for increased power and temporal resolution. The first four volumes of each acquisition were discarded to allow the system to reach steady state. For localizer scans, a similar pulse sequence was used, but with TR=2 and full brain coverage (32 axial slices).

fMRI Data Analysis Preprocessing and analysis of fMRI data was carried out using the FMRIB Software Library (FSL) version 4.1.8, supplemented with Freesurfer 4.5. Preprocessing steps included rigid-body motion correction, correction for interleaved slice timing, brain extraction, spatial smoothing (5mm FWHM Gaussian kernel), and highpass temporal filtering (100s cutoff). Functional images were registered to anatomical images using Freesurfer's bbregister; anatomical images were in turn normalized to MNI space using FSL's nonlinear registration image registration tool (FNIRT).

For data analysis, whole-brain general linear model-based analyses were initially performed for the main task and localizer, for the purpose of defining regions-of-interest (ROIs) in individual subjects. Regressors were defined as boxcar functions with nonzero values during the duration of the stimuli; these were then convolved with a canonical double-gamma hemodynamic response function. FSL's FILM prewhitening was applied to account for residual autocorrelation. Statistical maps were thresholded with an initial cutoff of $Z > 2.3$, followed by Gaussian random field theory-based thresholding with a cluster-wise threshold of $P < .05$, to correct for multiple comparisons.


Animacy ratings

Goal-directedness ratings

Irrationality ratings

Figure 2: Behavioral responses. Plot of responses to three questions—regarding animacy, goal-directedness, and irrationality—for the eight conditions. Error bars give standard error.

To define the right pSTS, the main task was used rather than the localizer, because the latter did not consistently yield pSTS responses in individual subjects. The contrast of all conditions versus rest in the main task was used to define the pSTS, because this contrast is orthogonal to any balanced between-condition comparison. As a control, we investigated responses in right MT+, a motion-sensitive region thought include retinotopic areas MT, MST, and possibly others (Amano, Wandell, & Dumoulin, 2009). This was defined using the localizer scan, by contrasting scrambled motion with static luminance change. Regions were defined as all active voxels within a 7.5mm-radius sphere around the peak coordinate within an anatomical search space, intersected with a gray matter mask derived using Freesurfer. The search spaces consisted of the STS (for pSTS), and lateral occipito-temporal cortex (for MT+).

Mean betas values across the ROI were extracted for each subject. Planned, paired two-sample t-tests were performed for each ROI, testing for effects of 1) animacy (conditions 3 and 4 vs 1 and 2), 2) goal-directedness (2 and 4 vs 1 and 3), 3) irrationality (7 vs 5), and 4) wandering over irrationality (8 vs 7). Responses were averaged when combining two conditions. Additionally, a post-hoc test assessed the effect of goal-directedness for animations with a tail (condition 4 versus 3) on the pSTS response.

Results

Behavioral results

The behavioral results are shown in figure 2. As predicted, the presence of a tail or dot-chain significantly increased the percept of animacy ($t[958] = 19.43$, $p < 10^{-70}$). In spontaneous post-scan self-reports from subjects who participated in the fMRI experiment (a separate group of subjects), many described the dot-chain stimuli as either a “worm,” “snake,” or “tadpole,” that was “swimming” or “wiggling.” Additionally, we observed that for stimuli with tails, animations that contained a visible goal dot were rated as more animate than those without. A post-hoc test of this difference was significant ($t[478] = 2.56$, $p < .02$).

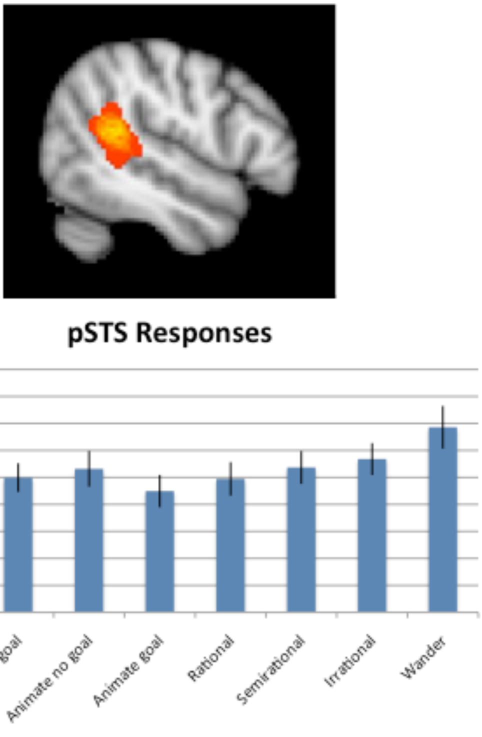
Ratings of goal-directedness were increased by the presence of a goal dot, as expected ($t[958] = 25.40$, $p < 10^{-108}$). Additionally, goal-directedness ratings were lower for irrationality than rational stimuli ($t[478] = -13.86$, $p < 10^{-36}$), and for wandering than irrational stimuli ($t[478] = -24.79$, $p < 10^{-87}$).

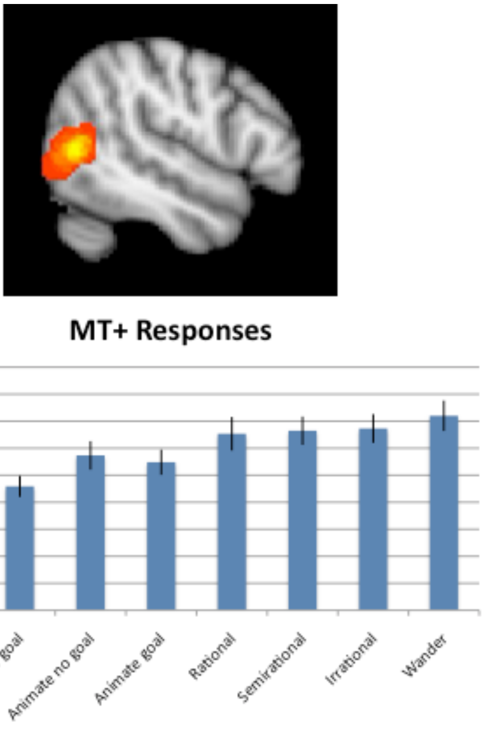
Ratings of irrationality were higher for irrational than rational paths, as expected ($t[478] = 18.00$, $p < 10^{-54}$). Additionally, they were higher for wandering than irrational paths ($t[478] = 8.96$, $p < 10^{-17}$). The presence of a goal dot also influenced irrationality ratings, with higher ratings for stimuli without a visible goal ($t[958] = -11.27$, $p < 10^{-27}$). Thus, we found an inverse relationship between ratings of goal-directedness and irrationality: namely, animations depicting an efficient path toward a clear goal were rated as highly goal-directed and rational, while paths that lacked a clear goal or used an inefficient trajectory were rated as less goal-directed and more irrational.

fMRI results

Results from the right pSTS ROI analysis are shown in figure 3. The ROI was found in 19 out of 20 subjects. We found no effect of the animacy manipulation ($t[18] = -.03$, $p = .98$), nor the goal dot manipulation ($t[18] = -1.17$, $p = .26$). However, the pSTS did respond more strongly to irrational than rational stimuli ($t[18] = -2.25$, $p < .05$), and to wandering than irrational stimuli ($t[18] = 3.03$, $p < .01$).

Additionally, we observed that among animate stimuli, or stimuli with a tail, the pSTS had a lower response to animations with a visible goal dot. A post-hoc test for this comparison was significant ($t[18] = -2.30$, $p < .05$). Thus, the pSTS response to animate stimuli tracked behavioral ratings of irrationality, but did not correspond to ratings of animacy or goal-directedness.





Figures 3 (above) and 4: Mean beta values extracted from right posterior superior temporal sulcus (pSTS, figure 3) and right MT+ (figure 4) regions of interest (ROIs). Error bars give standard error. The images above the bar plots show the locations of ROIs across subjects: for each voxel, the value plotted is the fraction of subjects whose ROI contained this voxel.

Results from the right MT+ ROI analysis are shown in figure 4. The ROI was found in 19 out of 20 subjects. For this ROI, there was a main effect of the animacy manipulation ($t[18] = 5.57, p < 10^{-4}$). This is to be expected for a retinotopic region, insofar as the dot-chain stimuli occupied more of the visual field than the individual dot stimuli, and therefore this difference may not reflect the processing of animacy.

There was no effect of goal-directedness ($t[18] = .52, p = .61$) or irrationality ($t[18] = .97, p = .34$) on the MT+ response. These comparisons were tightly controlled for the magnitude and direction of motion, so no differences relating to motion processing were expected.

There was an effect of wandering over irrational stimuli in MT+ ($t[18] = 2.71, p < .02$). This effect may also result from motion processing. Although the magnitude of motion is equated across wander and irrational conditions, the direction and derivatives thereof are not controlled. A larger number of changes in motion direction in the wander condition may have lead to decreased adaptation of direction-specific neural responses in MT+, and therefore an increased BOLD signal.

Discussion

We have shown behaviorally that dot-chain stimuli governed by a simple motion algorithm can evoke a strong percept of animacy, and in certain conditions, goal-directedness, replicating and extending the findings of Gao et al. (2011). Furthermore, we found that the right pSTS response to these stimuli is not stronger for stimuli rated as animate or goal-directed. However, this response was modulated by path irrationality: for conditions 3-8 (the conditions rated as highly animate), pSTS activity corresponds well with irrationality ratings, as can be seen by comparing figures 2 and 3. By comparison, activity in right MT+ was not generally modulated by irrationality, instead tracking the amount of motion and change in motion in the stimuli, as expected.

Several results of interest came from our behavioral analysis. We found that ratings of goal-directedness and path irrationality had an inverse relationship. Straight paths without goal dots were rated as more irrational than those with visible goals, and inefficient trajectories toward a goal were rated as less goal-directed than efficient trajectories. Thus, these ratings may have both derived from a common implicit quantity, perhaps corresponding to the extent to which an action can be explained in terms of perceptible goals and environmental constraints (e.g. Gergely & Csibra, 2003).

Furthermore, we found that for dot-chain stimuli, which were perceived as highly animate, the presence of a goal dot had a small but significant influence on ratings of animacy. This is consistent with the hypothesis that goal-directedness provides a cue to animacy (e.g. Shultz and McCarthy, 2011). This result was unexpected and assessed with a post-hoc test, and thus should be independently replicated; however, we note that we have another, unpublished dataset consisting of Mechanical Turk responses to similar stimuli, in which this effect was also observed.

Our imaging results show that with these stimuli, the pSTS response is not modulated by a large difference in perceived animacy between dot-chain and individual dot stimuli. This result appears inconsistent with claims that the pSTS is generally involved in the detection of agents or animate beings (e.g. Gobbini et al., 2011; Shultz and McCarthy, 2011). This finding is not directly inconsistent with any prior empirical result in the literature, to our knowledge, because prior contrasts involving animacy (e.g. faces versus nonfaces, biological motion versus scrambled motion, Heidel-Simmer animations versus control animations) have been confounded with other factors (such as specific static or dynamic visual properties, the presence of a human, or the presence of an interaction), and thus cannot be considered pure animacy contrasts.

Another interpretation of these data is that the pSTS is involved in the detection of animacy, but relies on local cues such as the motion of individual dots in our animations, which are similar for the animate and inanimate conditions. This interpretation must invoke other processes to explain the large behavioral difference in animacy judgments for dots and dot-chains. However, this explanation appears inconsistent with the fact that the pSTS response to human motion is modulated by global form, and not just local cues (e.g. Grossman et al. 2000), unless this modulation relates to a process separate from agent detection.

The pSTS response in our data was also not increased by perceived goal-directedness. This is consistent with findings that the right pSTS responds similarly to intentional and externally caused human movements (Morris, Pelphrey, & McCarthy, 2008), and to goal-directed and non-goal-directed actions by robots (Shultz and McCarthy, 2011). This result might be interpreted as evidence against a role of pSTS in processing action goals. However, given the inverse relationship observed between ratings of goal-directedness and irrationality, there is another potential explanation. This region may apply an assumption that actions by animate beings are intentional, and attempt to explain all such actions. In this case, actions with a visible goal may be easier to explain, and thus evoke a weaker pSTS response, as observed for animate stimuli.

While the pSTS response in the present study did not increase with animacy or goal-directedness, it did track the perceived irrationality of the actions depicted. This is consistent with prior findings of irrationality effects during the perception of human actions, as described above, and extends these results to nonhuman agents depicted by simple geometric shape animations. Thus, whatever computations underlie this irrationality effect are likely similarly applied to the actions of human and nonhuman agents.

We note that animations in the rational, irrational, and semirational conditions were perfectly controlled for visual motion; therefore motion cannot be driving the differences observed. The wander condition did have a motion change confound, as noted above. However, given the similar pSTS response to animate and inanimate conditions, which had a substantial difference in visual motion, we consider it implausible that the high response to the wander condition in this region results from motion properties.

As discussed above, the irrationality effect has been interpreted as supporting a role of the pSTS in action understanding, or inferring goals of actions and predicting future actions based on these goals. There are a number of interpretations of the irrationality effect consistent with this claim. For instance, this response might relate to the inference of a more complex goal structure underlying irrational actions. On this hypothesis, the pSTS tries to rationalize all actions, including ostensibly irrational ones, and simply requires a more complex explanation for the latter, perhaps positing extra goals that weren't immediately inferred from the context. Another possible interpretation is that this response constitutes an error detection signal for actions. On this hypothesis, the pSTS response doesn't reflect a reappraisal of the causal structure behind an irrational action, but simply reflects a signal indicating that the inferred structure was not correct. Future research should attempt to distinguish between these hypotheses.

Another question is of the specificity of this effect to actions. Does the right pSTS respond to any unexpected event, or more specifically, to unexpected visual motion events? While our current data doesn't speak to this question, Saxe et al. (2004) showed that while the pSTS responds more strongly when a walking human pauses behind a bookshelf than when he walks without pause, this isn't the case for gliding objects. This provides some preliminary evidence that this effect is specific to intentional actions, but this question should be followed up in subsequent studies.

In sum, we have shown that the pSTS response to animations of geometric shape motion is not increased by animacy or goal-directedness, but is modulated by action rationality. Future research should explore the computations that underlie this effect, and their precise contribution to action understanding.

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