

Activation of the Human Superior Temporal Gyrus during Observation of Goal Attribution by Intentional Objects

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Abstract

■ Previous functional imaging experiments in humans showed activation increases in the posterior superior temporal gyrus and sulcus during observation of geometrical shapes whose movements appear intentional or goal-directed. We modeled a chase scenario between two objects, in which the chasing object used different strategies to reach the target object: The chaser either followed the target's path or appeared to predict its end

position. Activation in the superior temporal gyrus of human observers was greater when the chaser adopted a predict rather than a follow strategy. Attending to the chaser's strategy induced slightly greater activation in the left superior temporal gyrus than attending to the outcome of the chase. These data implicate the superior temporal gyrus in the identification of objects displaying complex goal-directed motion. ■

INTRODUCTION

A well-studied phenomenon of visual perception in humans is the ability to recognize the movements of moving living beings, even if these movements are presented in impoverished displays such as the moving dots of Johansson's point-light displays (Johansson, 1973). But a single moving dot can also appear animate. Depending on the way it moves, it can even appear intentional, wanting something, or courting another object (Klin, 2000; Blythe, Todd, & Miller, 1999; Bassili, 1976; Heider & Simmel, 1944). Some characteristics that are necessary for a moving object to appear animate have begun to emerge from behavioral studies in children and adults. When the object's movement does not appear to be explainable by simple physical rules such as gravity, conservation of the movement quantity, or magnetic force, the object appears self-propelled, which makes it more likely to appear animate (Scholl & Tremoulet, 2000). The impression of animacy increases if the object appears to move contingently with the movements of a human (Johnson, 2003). A particularly important factor appears to be goal-directed motion, defined as a "type of autonomous movement in which the agent contingently directs its movement toward (or away from) another object, state or location" (Csibra, 2003; Opfer, 2002).

Psychophysical studies suggest that detection of biological motion is probably effected by very flexible

mechanisms under the influence of learning, different from those involved in the detection of other forms of complex motion (Giese & Poggio, 2003; Neri, Morrone, & Burr, 1998). Neuroimaging and neurophysiological data suggest that the cortex surrounding the posterior part of the superior temporal sulcus and gyrus can be activated by biological motion (Puce & Perrett, 2003; Bonda, Petrides, Ostry, & Evans, 1996; Perrett et al., 1985) such as point-light displays of moving humans and animals. Neuroimaging experiments show that this region is also activated by simple moving objects whose interactions appear causal, goal-directed, or intentional (Blakemore, Boyer, et al., 2003; Schultz et al., 2003; Blakemore, Fonlupt, et al., 2001; Castelli, Happe, Frith, & Frith, 2000), and also during more cognitive processes such as attribution of mental states to others (Saxe & Kanwisher, 2003; Frith & Frith, 1999). Observation and imitation of goal-directed human actions also elicit activation increases in this region of the brain (Grezes, Armony, Rowe, & Passingham, 2003; Iacoboni et al., 2001; Winstein, Grafton, & Pohl, 1997).

Recognizing goal-directed motion is a necessary step towards attribution of intentions to other agents and appears to be identified by the brain whether the agent producing it is a human being or an animate-looking moving object. Previous data from our group show that observation of abstract geometrical shapes moving in a goal-directed way induces activation increases in the superior temporal sulcus, activation increases further when the agent appears to act intentionally (Castelli et al., 2000). More recent, unpublished data show that activation in the superior temporal sulcus and gyrus

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increases in relation to the degree of correlated motion between the two abstract moving objects. We hypothesized that observation of a moving geometrical shape chasing another moving shape might induce greater activation increases in the superior temporal gyrus and sulcus when the chasing object appears to understand the goals of the target object and predict its movements rather than simply following the target. Consequently, our chasing object used one of two strategies to catch the target object: It either followed the target on its path (“follow” strategy), or it went directly to the end point of the other object’s trajectory (“predict” strategy), as if it had predicted where the target would go. When the chasing object used the predict strategy rather than the follow strategy, it gave the impression that it was able to infer the goal of the other object’s movement. In the experimental design, this “strategy” factor was crossed with an “outcome” factor: The chase was only successful in 50% of cases, allowing the performance of a second task using the same animations.

Previous studies indicate that activation in the superior temporal gyrus area increases when subjects attend

to more “socially relevant” dimensions of a visual display, such as emotion (Narumoto, Okada, Sadato, Fukui, & Yonekura, 2001), trustworthiness (Winston, Strange, O’Doherty, & Dolan, 2002), and contingency between the movements of two objects (Blakemore, Boyer, et al., 2003). We therefore asked participants in our experiment to perform two different tasks using the same stimuli. In one half of the experiment, participants were asked to decide which strategy the “chasing” object used to catch the “target” object (the “strategy” task); in the other half of the experiment, subjects had to judge whether the chaser was successful in reaching the target objects (the “outcome” task). Examples of conditions in the experiment are displayed in Figure 1.

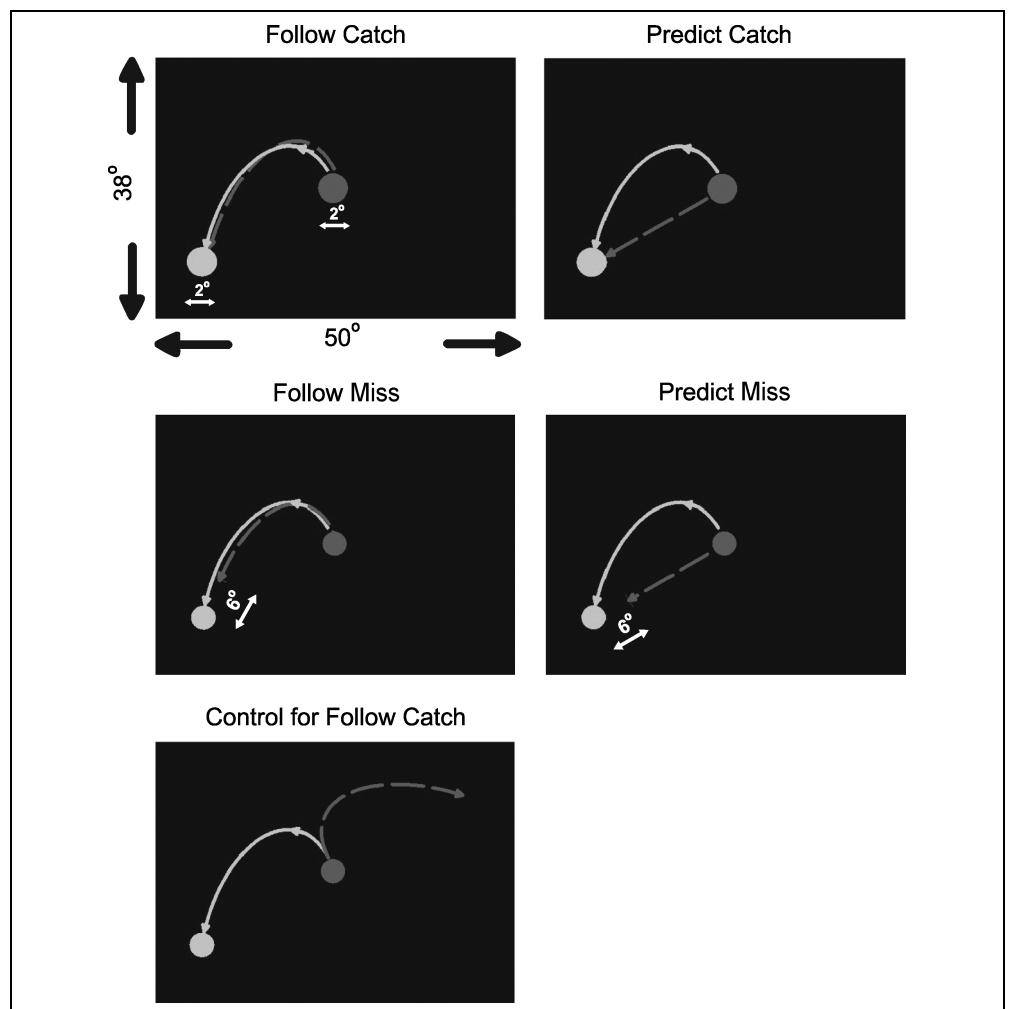
RESULTS

Behavior

Analysis of participants’ ratings from the strategy task and the outcome task performed in the scanner showed that participants performed well in both the strategy

Figure 1. Design and stimuli.

The open light gray arrow indicates time at which the dark gray object started to move. Four experimental conditions come from the combination of two factors in the experiment: predict strategy versus follow strategy and catch outcome versus no catch outcome. Below on the left is the specific control condition for the follow catch condition; such specific control conditions existed for all four experimental conditions, resulting in eight conditions in total. Subjects categorized either the strategy or the outcome of the blue object’s movement in separate tasks on the same animations, therefore the Total number of conditions \times Task combinations in the experiment is 16. The objects moved to any of the four corners of the screen with equal frequency. The object depicted in light gray was presented in red during the experiment, the object depicted in dark gray was blue in the experiment.



and the outcome task. Subjects had to perform the tasks only when a chase between the two objects took place, and they correctly identified the strategy of the chasing object in 94% of “predict” trials and 91% of “follow” trials ($\pm 3\%$ SEM over subjects). Positive outcome (i.e., a successful chase) was identified correctly in 89% of trials (± 4) and negative outcome (i.e., an unsuccessful chase) was identified correctly in 79% of trials (± 5.6). There were no significant differences between ratings of predict and follow trials (paired t test, $p > .05$), but positive outcome trials were more often identified correctly than negative outcome trials (paired t test, $p < .05$). This difference probably stems from subjects responding too quickly and miscategorizing some negative outcome trials as positive outcome trials. This difference does not influence the interpretation of the brain activation analysis because trials with different outcomes were not compared with each other and only served as an implicit task. When asked to describe the stimuli, subjects typically reported that the chasing object “appeared to know where the target object was going” (predict trials), appeared to follow it (follow trials) or to move in opposite directions (control trials). They reported that they tried to find out how the chasers tried to reach their goal in the strategy task and that they tried to judge if the chaser had reached the target in the outcome task. All subjects described both tasks as being quite easy.

fMRI Data

Voxelwise Analysis in the Superior Temporal Sulcus and Gyrus

We used the factorial design of this experiment to test for activation differences due to the strategy used by one object to chase another object and to test how these activation differences were affected by the attentional task the subject performed. To discount object motion effects, we assessed interaction-sensitive activations as the difference between the activation increases due to a predict versus a follow strategy in chase trials and the same activation increases in the equivalent movement control trials. Based on previous studies of biological motion and interacting geometrical shapes, we were particularly interested in the activation of the cortex in the posterior part of the superior temporal sulcus and gyrus of both hemispheres.

Effects of Strategy

Activation increases were found in the superior temporal gyrus and the superior temporal sulcus of both hemispheres when subjects observed a chasing object with a predict strategy compared to observation of a chasing object with a follow strategy (Figure 2). This was tested formally with a two-way interaction between

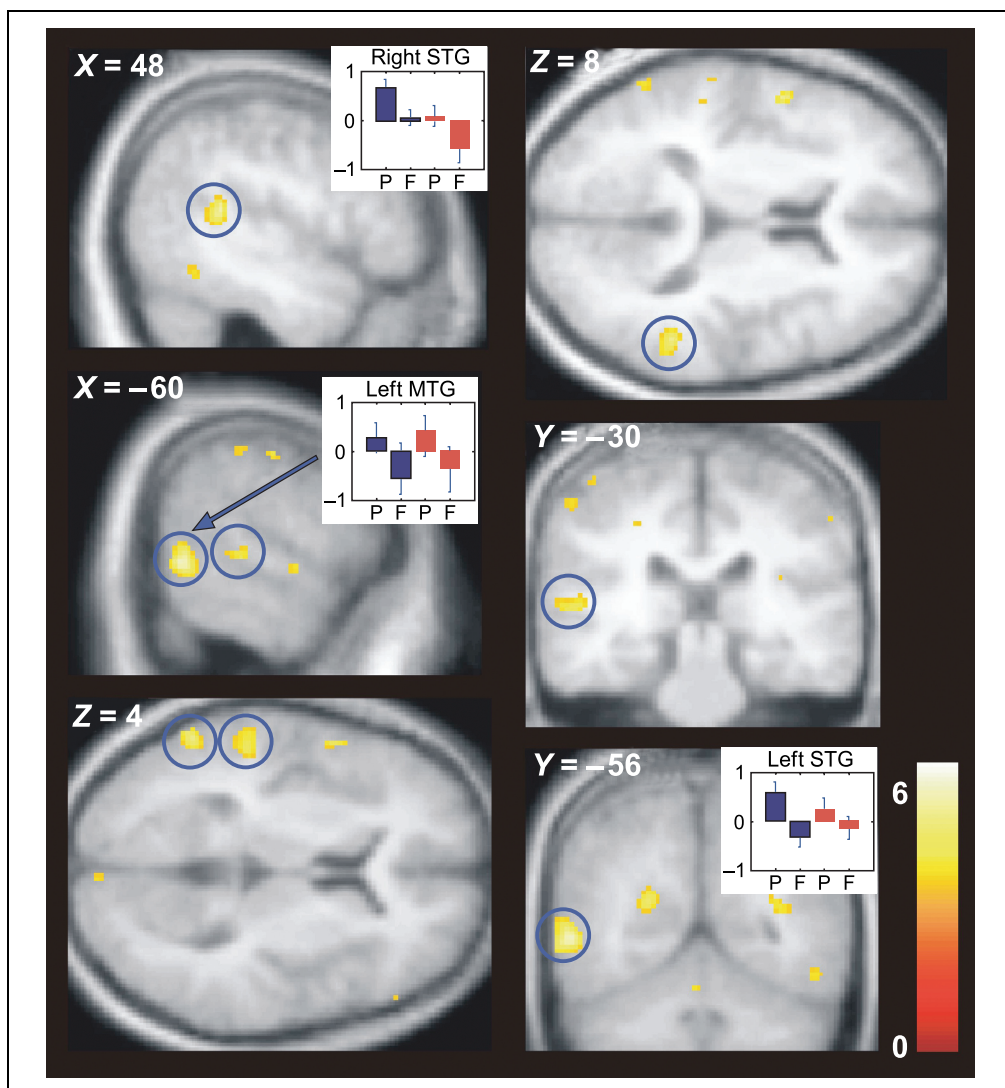
predict versus follow strategies and chase versus control trials to discount differences in object movement. The opposite contrast yielded no significant activation increases in the superior temporal sulcus or gyrus. Neither contrast yielded activation in the medial prefrontal cortex or the temporal poles, even at a relatively low significance threshold ($p < .01$, uncorrected, $T > 2.65$).

Effects of Task on Strategy. When tested as interactions between strategy and task, no cluster showed significantly different activation depending on the task the subjects performed. This was tested by the following three-way interactions: interaction between task (strategy vs. outcome), strategy (predict vs. follow), and chase versus control trial, and interaction between task (outcome vs. strategy), strategy (predict vs. follow), and chase versus control trial. However, a cluster of voxels in the left posterior superior temporal sulcus was found whose activation was greater during observation of a predict versus a follow strategy when subjects performed the strategy categorization task, but was not significantly activated when subjects performed the outcome task. When we masked the results of the comparison in the strategy task with those of the outcome task, the cluster in the left posterior superior temporal sulcus identified in the strategy task remained significantly activated (Figure 3A; exclusive mask, threshold $p = .05$; activation remains significant with all thresholds below $p = .15$). This suggests that voxels in this cluster respond only when subjects performed the strategy task. Masking the results of the comparison in the outcome task with those of the strategy task yielded a cluster of voxels in the right middle temporal gyrus, located caudal and ventral to the cluster of activation in the posterior superior temporal sulcus mentioned above. This cluster was not located within the superior temporal sulcus and gyrus search regions (Figure 3B; exclusive mask, threshold $p = .05$; similar results with all thresholds below $p = .15$). Again, there were no significant activations in either the medial prefrontal cortex or temporal poles, even at the lower threshold of $p < .01$ uncorrected.

Activation Time Courses

Activation time courses in the voxels of the superior temporal sulcus and gyrus with strongest activation increase during observation of a predict versus a follow strategy confirmed the results of the voxelwise analysis. In the superior temporal sulcus in the left hemisphere, activation during the initial phase of the trial was higher in predict trials than in follow trials, but only when subjects performed the strategy task [two-way ANOVA: interaction between strategy and time: $F(1,13) = 7.8$, $p = .015$]. In the right hemisphere, activation during the whole trial was higher in predict trials than in follow trials when subjects performed the strategy task [main

Figure 2. Clusters in the superior temporal sulcus and gyrus whose activation was significantly greater during observation of a predict strategy than a follow strategy. Tested formally with a two-way interaction between predict versus follow strategies and chase versus control trials. For details, see Table 1. For display, the image is thresholded at $p < .001$, uncorrected for multiple comparisons. Clusters surviving a threshold of $p < .05$, corrected for multiple comparisons across anatomical search regions, are circled in blue, listed in Table 1, and discussed in the text. Parameter estimates from the voxels of maximum intensity from these clusters are displayed (Left STG, Right STG, and MTG). P and F represent predict and follow conditions, and colors blue and red represent strategy and outcome tasks, respectively. Parameter estimates shown are from chase conditions from which the parameter estimates of the matched control conditions have been subtracted. Error bars represent *SEM* over subjects. The brain slices used for display are the average image from the subjects' normalized structural brain scans (see Methods). Coordinates are in MNI reference space. The color bar refers to activation intensity expressed in *t* values.



effect of strategy: $F(1,13) = 4.9, p = .045$], and was only initially higher when subjects performed the outcome task [interaction between strategy and time: $F(1,13) = 5.6, p = .035$].

DISCUSSION

This study shows that activation in the superior temporal gyrus and in the cortex surrounding the superior temporal sulcus increases when a simple object appears to chase another object by understanding the target's goal and predicting its movement instead of simply following it. Directing attention to the object's strategy

rather than to the outcome of its chase increased activation differences in the left superior temporal sulcus.

Attribution of Intentions and Goal-Directed Movements and the Superior Temporal Sulcus and Gyrus

A number of studies have shown activation increases in the posterior part of the superior temporal sulcus and gyrus (together with the temporal poles and medial prefrontal cortex) during attribution of mental states to other agents, also called mentalizing or theory of mind (Frith & Frith, 1999, 2003). The exact mechanism on which this ability is based is not fully determined yet,

but intuitively, a necessary first step towards the attribution of mental states to an agent could be the attribution of goals to this agent. When moving objects appear to follow goals, they are more likely to be considered animate by human observers (Csibra, 2003; Opfer, 2002). Previous studies show that activation in the superior temporal sulcus and gyrus increases during observation of geometrical shapes if their movements appear goal-directed or intentional (Castelli et al., 2000). Recent unpublished data show that activation in this part of the cortex increases parametrically with the amount of interactive motion of two objects. These data suggest that this part of the cortex is sensitive to movement characteristics associated with living entities, especially goal-directed movements. In our present study, participants observed an object understanding the goals of another object and predicting its movements or simply following it in order to catch it. As predicting the movements of a target object is a characteristic associated with a potential agent, the greater activation in the superior temporal sulcus and gyrus when the chasing object predicted the movements of

the target object compared to simply following it suggests that this brain region plays a role in the identification of intentional agents.

Attention Effects

The cluster identified in the left superior temporal gyrus showed greater activation increases in predict trials compared to follow trials when subjects tried to identify the strategy of the chaser than when they assessed the outcome of the chase (Figure 3A). As discussed in the Introduction, activation increases in the superior temporal gyrus area have been reported in the right hemisphere when attending to the emotion or the trustworthiness of faces, and in the left hemisphere when attending to contingency between the movements of abstract objects (Blakemore, Boyer, et al., 2003). Blakemore and colleagues suggested that the attention effects they observed could be due to top-down effects related to the search for agents, rather than bottom-up detection on the basis of visual cues. In our case, attending to the strategies used by the objects to reach their goal cued subjects into paying attention to cognitive aspects of the objects' movements. This task is much closer to searching for agents than simply comparing the positions of the chaser to the position of the target at the end of the trial in the outcome task. We suggest that the active process of searching either for agents or for characteristics of their movements can increase or prolong neural responses in areas already sensitive to intentional agents.

Time Course: Early Activations versus Constant

In the left hemisphere, activation during the initial phase of the trial was higher in predict trials than in follow trials when subjects performed the strategy task; in the right hemisphere, a similar pattern was observed during the outcome task (Figure 4). Activation in the right hemisphere was higher in predict trials than in follow trials during the whole trial when subjects performed the strategy task. In the two cases where the activation was only higher in predict than in follow trials at the beginning of the trial, plots of the data show that the activation difference was present at 6.75 sec after trial onset (Figure 4, top left and bottom right), which is compatible with a neural event occurring at the onset of the trial. At the next sampled time point (11.25 sec), the activation difference in the left hemisphere was less important and it disappeared in the right hemisphere. We suggest that this reflects an initial response of the cortex to our animations, which is increased and/or prolonged when subjects pay attention to a socially relevant dimension of the objects' movement. The time course analyses suggest that this response is stronger in the right hemisphere, but as the statistical parametric map (SPM) analyses do not confirm this tendency, we cannot argue strongly in favor of hemispheric specialization in this task.

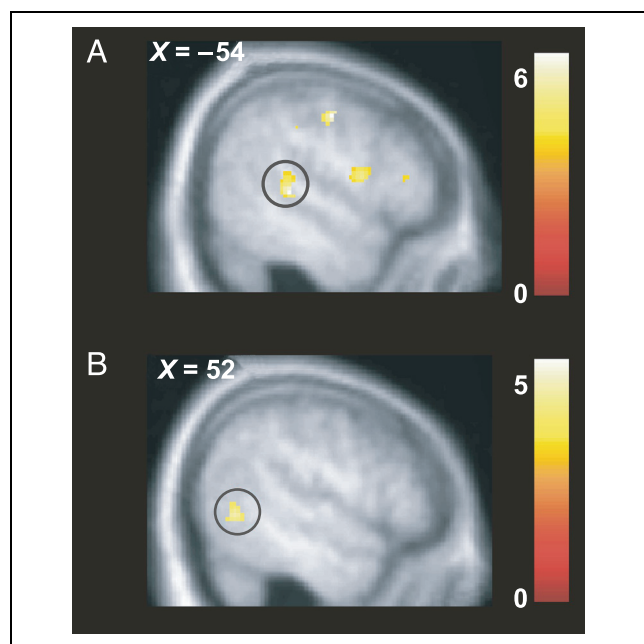
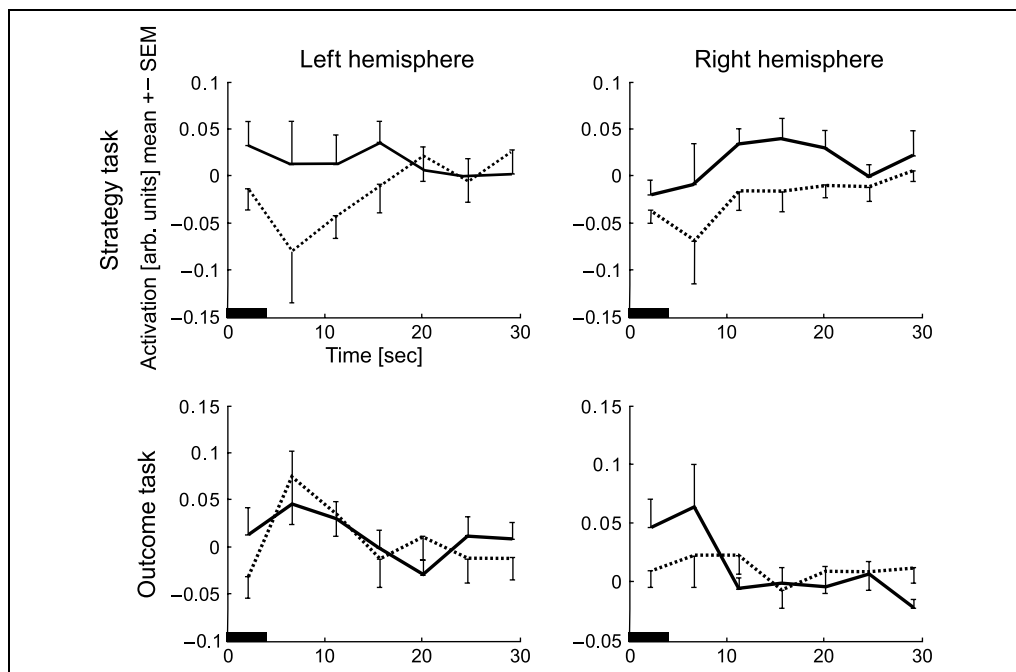


Figure 3. Clusters in the superior temporal sulcus and gyrus whose activation was significantly greater during observation of a predict strategy than a follow strategy and was affected by the subjects' task. (A) Activations in the strategy task masked with activation in the outcome task (exclusive mask, threshold of mask: $p = .05$, uncorrected). (B) Activations in the outcome task masked with activation in the strategy task (exclusive mask, threshold of mask: $p = .05$, uncorrected). The cluster circled in panel A survived a threshold of $p < .05$, corrected for multiple comparisons across anatomical search regions, was listed in Table 1 and discussed in the text. The cluster circled in panel B was activated to a similar degree but was not located within the search regions. The brain slices, coordinate system, and color bar index are similar to Figure 2.

Figure 4. Activation time courses in the superior temporal gyrus in both strategy and outcome tasks. Solid lines refer to trials in which the chasing object used a predict strategy, dotted lines refers to trials in which the chasing object used a follow strategy. The thick black line on the horizontal axis represents the duration of the animation. Activation is displayed in arbitrary units, 0 refers to average activation during the whole course of the experiment. Error bars represent standard errors of the mean across subjects. In the left hemisphere, activation during the initial phase of the trial was higher in predict trials than in follow trials, but only when subjects performed the strategy task [two-way



ANOVA: interaction between strategy and time: $F(1,13) = 7.8, p = .015$). In the right hemisphere, activation during the whole trial was higher in predict trials than in follow trials when subjects performed the strategy task [main effect of strategy: $F(1,13) = 4.9, p = .045$], and was only initially higher when subjects performed the outcome task [interaction between strategy and time: $F(1,13) = 5.6, p = .035$]. Data are from the peaks of activation (coordinates: left hemisphere: $-54 -34 4$, right hemisphere: $48 -44 12$, MNI reference frame) of the significant clusters in the superior temporal gyrus, identified with the predict versus follow * chase versus control contrast.

No Activation Increases in the Medial Prefrontal Cortex

It is interesting to note that we did not find significant activation increases in the medial prefrontal cortex or the temporal poles in all the contrasts we tested, areas which, together with the superior temporal sulcus, are thought to be involved in the attribution of mental states (Frith & Frith, 2003). Previous PET and fMRI studies using complex animations leading to attribution of mental states have shown activation in these areas (Schultz et al., 2003; Castelli et al., 2000), but studies using simple animations have not (Blakemore, Boyer, et al., 2003; Blakemore, Fonlupt, et al., 2001). The latter studies used animations with objects interacting causally, appearing animate, and/or interacting contingently, which are not thought to lead to attribution of mental states. In our present study, observers watching an object attributing a goal to another object did not show a significantly greater activation in the medial prefrontal cortex than when watching an object following another object, regardless of the task the subjects were performing. We suggest that subjects solved this simple task with only a small mentalizing effort or none at all, which was not sufficient to induce activation in the medial prefrontal cortex. Although activation increases in the superior temporal sulcus could be related to mentalizing, we would rather suggest that these are due to detection of

intentional entities, which could explain why activation in the other areas involved in mentalizing was not increased. This view is consistent with informal behavioral reports from our subjects and the results and interpretation of a previous study (Blakemore, Boyer, et al., 2003).

Differences in Movement Paths

A possible alternative explanation of activation differences caused by the observation of objects with different movement paths could be the difference in complexity between the paths. In the present experiment, this was controlled by matched control conditions in which the paths of both chasing and target objects were identical to the paths in the chasing trials except for the fact that the chasing object did not move towards the target object but in the opposite direction. This control condition only affected the contingency between the objects' paths and not the movement paths themselves. Objects moving in opposite directions could be seen to be avoiding instead of approaching each other, and therefore represent another form of social interaction, which could also induce activation in the superior temporal sulcus. Although this is a very valid possibility, in addition to observing activation increases in the superior temporal sulcus and gyrus in the interaction between chase versus

control and predict versus follow strategy, we also found activation in these clusters of activated voxels to be higher in predict than in follow trials when we subtracted activation in the corresponding control conditions from the chase trial activation (see parameter estimate plots in Figure 2). These data support our interpretation suggesting that observation of goal attribution by the chaser induces activation increases in the superior temporal sulcus and gyrus, and that attention to the object's strategy further increases this effect.

Specialization along the Superior Temporal Sulcus?

The cortex in the superior temporal sulcus and gyrus responds to (i) the attribution of mental states to others, (ii) the identification of biological motion, and (iii) the response to animate-looking, moving geometrical shapes. Whether different parts of the cortex in the sulcus and gyrus are specialized for each of these functions is not yet known. Against the idea of specialization is the fact that activation increases during observation of biological motion have been found all along the superior temporal sulcus (Puce & Perrett, 2003) and do not appear organized in a particular way. Instead, a number of studies of all three types of processes have all yielded activation in the same area of the superior temporal gyrus and sulcus (Figure 5). The activation increases found in the present study are also located in this area. This suggests

that this region of the cortex could be involved in a common aspect of these three tasks, for example, the response to goal-directed movements, whether expressed by moving abstract shapes or human beings.

METHODS

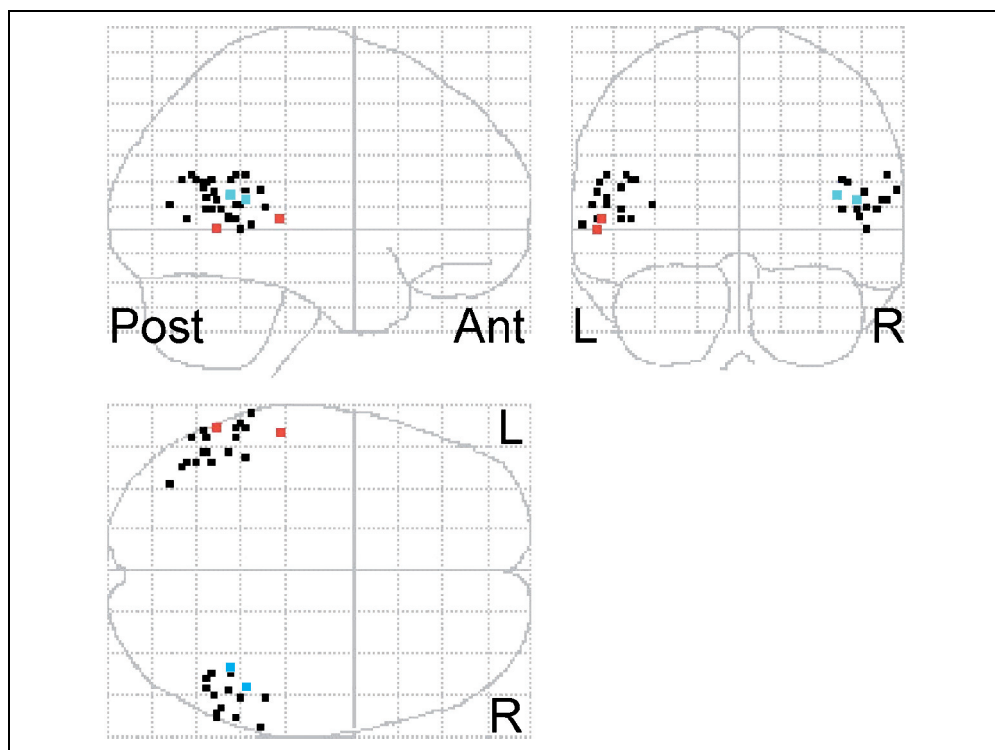
Subjects

Fourteen right-handed participants (8 men and 6 women, aged 19–40) participated in the study. All subjects gave full written informed consent and the study was approved by the local ethics committee.

Stimuli, Animations, Design, and Tasks

Participants in the scanner watched short animations (4.2 sec per animation) in which two moving disks appeared to be either interacting or to move independently from each other (Figure 1). The moving objects were two disks or balls, with a width on the screen in the scanner of 2° of visual angle (Figure 1, top left). One was colored bright red, the other bright blue, and the background was black. The movement trajectories of the two disks were determined prior to the experiment by an equation of motion implemented in Matlab (The MathWorks, Natick, MA). The visual display was controlled by in-house presentation software (Cogent 2000, www.vislab.ucl.ac.uk/Cogent2000/index.html) imple-

Figure 5. Comparison of results of the current study with 16 previous studies of mentalizing, biological motion, and moving geometrical shapes. In red and cyan are results of the current study in the left and right hemispheres, respectively. In black are results of the following previous studies: Schultz et al., 2003; Campbell et al., 2001; Vogetley et al., 2001; Brunet, Sarfati, Hardy-Bayle, & Decety, 2000; Castelli, Happe, Frith, & Frith, 2000; Downar, Crawley, Mikulis, & Davis, 2000; Gallagher, Happe, Brunswick, Fletcher, Frith, & Frith, 2000; Grossman et al., 2000; Hoffman & Haxby, 2000; Grezes & Costes, 1998; Puce, Allison, Bentin, Gore, & McCarthy, 1998; Wicker, Michel, Henaff, & Decety, 1998; Bonda, Petrides, Ostry, & Evans, 1996; Fletcher et al., 1995; Goel, Grafman, & Hallett, 1995. Displayed on Maximum Intensity Projection glass brain with SPM2.



mented in Matlab. Animations were projected onto an opaque surface in the scanner by an LCD projector, subjects viewed them through a mirror mounted on the headcoil.

Design, Conditions, And Tasks

In this experiment, we wanted to test whether moving objects elicit stronger activation in the posterior superior temporal sulcus and gyrus when they appear to attribute goals to a target object than they appear to chase their target without attributing goals to it. We used a chasing situation where one object tried to catch another object by using one of two strategies. The chasing object appeared to attribute a goal to the target object by heading towards the end point of the target's position, or simply followed it (no goal attribution). We used matched control conditions without chasing for each experimental condition to control for differences in object motion across conditions. We also wanted to test whether activation changes happen only when subjects pay attention to the strategy used by the objects or also when they perform another, incidental task. In the strategy task, subjects categorized the chaser's strategy into "following" or "using prediction of the trajectory end point." In the outcome task (the incidental task), they had to decide whether the chaser caught the target at the end of the trial or not. During the control trials, subjects were asked to press one of the two response buttons at random. We therefore used a factorial design with the following four factors: (1) two strategies for the chasing object: predicting or following; (2) two outcome levels: target caught or missed; (3) two task levels: judging strategy or judging outcome; and (4) two condition levels: chase and control (no chase). Combinations of all these factors resulted in 16 different trial types, each repeated 24 times during the experiment, for a total scanning time of 19.5 min. Subjects responded by pressing one of two buttons on a keypad with the corresponding finger of the right hand. Button presses and brain activation were recorded simultaneously during the experiment. On these two types of dependent variable we assessed the effects of strategy and the interaction between task and strategy.

Animation Details

In all the animations, the red object (the target) started to move first, describing an arc from the center of the screen that ended in one of the four corners of the screen (the example shown in Figure 1 ends in the bottom left corner; during the experiment, an equal number of trials with end point in each corner were shown). The blue object (the chaser) started 0.93 sec after the red object, and in half the trials it tried to catch it (chasing trials), in the other half of the trials it moved in the opposite direction from the red object (control

trials). When trying to catch the red object, the blue object either simply followed the target's trajectory or it went directly to the end point of the target's movement, as if it had known the end point of the red object's trajectory. In half of the chasing trials the blue object caught the red object, in the other half of the trials it missed it by 6°.

Image Acquisition

A Shimadzu-Marconi ECLIPSE scanner (Shimadzu, Japan; Marconi, London, UK), operating at 1.5 T was used to acquire both T1-weighted anatomical images and gradient-echo echo-planar T2*-weighted MRI images with blood oxygenation level dependent (BOLD) contrast. The scanning sequence was an echo-planar imaging sequence with repetition time of 4500 msec, an echo time of 45 msec, a flip angle of 90°, a field of view of 256 × 256 mm and a matrix size of 64 × 64. Each functional image comprised 36 axial slices, with a thickness of 3 mm and a 1-mm interval between slices, and was positioned to cover the whole brain. For each subject, 260 functional images were acquired in one session of 19.5 min, including five subsequently discarded "dummy" volumes at the start of the session to allow for T1 equilibration effects. A high-resolution structural MR image was acquired for each subject with a T1-weighted sequence.

fMRI Data Analysis

Statistical analysis was carried out using the General Linear Model framework (Friston et al., 1995) implemented in the SPM2 software package (Wellcome Department of Imaging Neuroscience, www.fil.ion.ucl.ac.uk/spm). To correct for subject motion, the functional images were realigned with the first functional image and resliced (Friston et al, 1995). Images were then normalized into a standard EPI T2* template with a resampled voxel size of 2 mm³ (Friston et al., 1995). To enhance the signal-to-noise ratio and enable intersubject functional anatomical comparison, the images were smoothed by convolution with a 6-mm full width at half maximum (FWHM) gaussian kernel. A high-pass filter (using a cutoff of 128 sec) and a correction for temporal autocorrelation in the data (AR 1 + white noise) were applied to accommodate serial correlations.

A mixed-effects analysis was adopted, using a two-stage procedure. First, a fixed-effects analysis was applied separately to the preprocessed data of each subject using the general linear model implemented in SPM2. This consists of fitting the data with a linear combination of regressors in a design matrix, to produce 3-D maps of parameter estimates. These parameter estimates represent the contribution of a particular regressor to the data, and can be transformed to percent BOLD signal change with respect to the average global signal across

conditions and voxels. The design matrix used in this experiment consisted of 32 regressors. There were 16 conditions in the experiment, engendered by crossing the following factors: (i) following or predicting strategy of the chaser, (ii) successful or unsuccessful outcome, (iii) task (strategy categorization or outcome categorization), or (iv) animations with chasing or controls. Two regressors were created for each condition in the following way: The duration from stimulus presentation onset to the subject's button press was modeled by a series of delta ("stick") functions, then convolved by a canonical hemodynamic response function (HRF) as implemented in SPM2 (first regressor for this condition) and its first temporal derivative (second regressor for the condition). To correct for movement-related artifacts not eliminated during realignment, differential realignment parameters were modeled as additional regressors of no interest.

For each subject, linear contrasts of parameter estimates were used to assess the effects of following factors: (i) predictive strategy versus following strategy of the chasing object, controlling for nonspecific object motion effects (interaction between predictive vs. following strategy and chase vs. control trials) and (ii) effect of task on the previous comparison (interaction between predictive vs. following strategy, chase vs. control trials, and strategy task vs. outcome task). As an additional measure of the effect of task on the observation of chasing strategy, we assessed separately the interaction between predictive versus following strategy and chase versus control trials in the strategy task and in the outcome task. We then masked the results of this contrast in the strategy task with the results of the same contrast in the outcome task with an exclusive masking procedure implemented in SPM2. The threshold of the mask used in the figures was the standard $p = .05$; similar results were obtained with all thresholds below $p = .15$.

One-sample t tests were performed on the above contrast images to give second-level or random effects

SPMs, after further smoothing the weighted maps by convolution with an 8-mm FWHM gaussian kernel to account for anatomical differences across subjects.

On the basis of published work on perception of biological motion, abstract moving agents, and theory-of-mind tasks reported in the Introduction, we expected changes in activation to occur in the cortex surrounding the posterior part of the superior temporal sulcus and in the superior temporal gyrus of both hemispheres. We therefore defined anatomical search regions that we used to perform a correction for multiple comparisons across all voxels of each of these search regions (Poline, Worsley, Evans, & Friston, 1997). The voxels corresponding to these search regions were defined on the basis of the subjects' structural scans and an anatomical atlas of the human brain (Duvernoy, 1999), and were drawn using MRICro software (Rorden & Brett, 2000) (www.cla.sc.edu/psyc/faculty/rorden/mricro.html). To test specifically for activation in the medial prefrontal cortex, we defined search regions that encompass all studies of mentalizing cited in a recent review (Frith & Frith, 2003). Clusters of more than four voxels in extent and with a p value of $<.05$ after correction for multiple comparisons across all voxels in the search region were considered to be significantly activated and are reported in Table 1 and Figures 2 and 3. The search region in the right posterior part of the superior temporal sulcus extended from -68 to -52 mm in the x dimension, from -66 to -34 mm in the y dimension, and from $+2$ to $+30$ mm in the z dimension. The region in the right superior temporal sulcus extended from $+50$ to $+70$ mm in x , from -65 to -37 mm in y , and from -2 to $+29$ mm in z . Volumes were 6049 mm³ (left) and 7284 mm³ (right). The region in the left superior temporal gyrus extended from -71 to -46 mm in x , -54 to $+23$ mm in y , and -31 to $+21$ mm in z . The region in the right superior temporal gyrus extended from $+42$ to $+72$ mm in x , -52 to $+25$ mm in y , and -34 to $+31$ mm in z . Volumes were $33,935$ mm³ (left) and $45,896$ mm³

Table 1. Brain Activation Data, Voxelwise Analysis

Structure	Coordinates			Size (mm ³)	Z score
<i>Predict > Follow strategy * Chase versus Control</i>					
R superior temporal gyrus	48	-44	12	600	4.48
L middle temporal gyrus	-60	-56	4	176	3.83
L superior temporal gyrus	-56	-30	4	584	3.58
<i>Predict > Follow strategy * Chase versus Control, Strategy task only</i>					
L superior temporal gyrus	-54	-34	4	936	4.2
<i>Predict > Follow strategy * Chase versus Control, Strategy task masked by Outcome task</i>					
L superior temporal gyrus	-54	-34	4	784	4.2

Significant clusters in the comparisons of interest, surviving a threshold of $p < .05$, corrected for multiple comparisons across voxels in the superior temporal sulcus or gyrus (see Methods).

(right). The search regions in the left medial prefrontal cortex extended from -18 to $+0$ in the x dimension, from $+20$ to $+60$ in the y dimension, and from 2 to 52 in the z dimension. The region in the right medial prefrontal cortex extended from $+0$ to $+16$ in the x dimension, from $+14$ to $+60$ in the y dimension, and from $+4$ to $+54$ in the z dimension. Volumes were $12,112 \text{ mm}^3$ (left) and $12,448 \text{ mm}^3$ (right).

Peristimulus time courses were obtained by extracting data from the peaks of activation in the superior temporal gyrus of both hemispheres, isolated in the interaction between predict versus follow strategy and chase versus control. Coordinates of the activation peaks were $-54 \ 34 \ 4$ and $48 \ -44 \ 12$. Data from all time points were tested for normality by comparison to a normal distribution with one-sample Kolmogorov–Smirnov tests (all $p > .1$). Two-way ANOVAs were used to assess differences on activation over time between trials with predictive and outcome strategy for each task and each hemisphere.

Image Used for Display

The mean image used for display in the figures was calculated by averaging the 12 subjects' structural images that were previously coregistered with the mean functional image of the same subject and normalized to the standard Montreal Neurological Institute (MNI) space. Anatomical structures were identified with brain atlases by Duvernoy (1999).

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The data reported in this experiment have been deposited in the fMRI Data Center (<http://www.fmridc.org>). The accession number is 2-2004-116RA.

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