

# Activation in Posterior Superior Temporal Sulcus Parallels Parameter Inducing the Percept of Animacy

Johannes Schultz,<sup>1,\*</sup> Karl J. Friston,<sup>1</sup>  
John O’Doherty,<sup>1</sup> Daniel M. Wolpert,<sup>2</sup>  
and Chris D. Frith<sup>1</sup>

<sup>1</sup>Wellcome Department of Imaging Neuroscience  
12 Queen Square  
London WC1N 3BG  
United Kingdom

<sup>2</sup>Sobell Department of Motor Neuroscience  
Institute of Neurology  
Queen Square  
London WC1N 3BG  
United Kingdom

## Summary

An essential, evolutionarily stable feature of brain function is the detection of animate entities, and one of the main cues to identify them is their movement. We developed a model of a simple interaction between two objects, in which an increase of the correlation between their movements varied the amount of interactivity and animacy observers attributed to them. Functional magnetic resonance imaging revealed that activation in the posterior superior temporal sulcus and gyrus (pSTS/pSTG) increased in relation to the degree of correlated motion between the two objects. This activation increase was not different when subjects performed an explicit or implicit task while observing these interacting objects. These data suggest that the pSTS and pSTG play a role in the automatic identification of animate entities, by responding directly to an objective movement characteristic inducing the percept of animacy, such as the amount of interactivity between two moving objects.

## Introduction

For living beings, including humans, it is important to identify other animate entities, as these could be prey, predators, or mates. The movement of an animate entity is one of the most important visual cues to identify it as animate. Interestingly, in certain animations, moving abstract shapes are consistently and spontaneously described by humans as “being alive,” “wanting something,” or even “courting each other” (Blythe et al., 1999; Dittrich, 1993; Heider and Simmel, 1944; Johnson, 2003; Opfer, 2002).

Neuroimaging and neurophysiological data suggest that the neurons in the superior temporal sulcus can be activated by presentations of biological motion (Giese and Poggio, 2003; Puce and Perrett, 2003) such as point-light displays of moving humans and animals. Recent neuroimaging experiments show that this region (also known as the temporo-parietal junction in the hu-

man, or TPJ) is also activated by simple moving objects whose interactions appear causal or intentional (Blakemore et al., 2001; Blakemore et al., 2003; Castelli et al., 2000; Schultz et al., 2004; Schultz et al., 2003). Neurons in the cortex of the posterior superior temporal gyrus and sulcus (pSTS/pSTG) might therefore be involved in the identification of animate entities by their movement.

As yet, it is not known which characteristics of an object’s movement induce attribution of animacy in observing children or adults, nor which movement characteristics trigger neural structures that respond more to animate than to inanimate motion. Previous behavioral studies identified certain characteristics that might play a role in inducing the percept of animacy. Isolated objects whose movement is not explainable by simple “newtonian” mechanics seem to be self-propelled, which increases the appearance of animacy (Scholl and Tremoulet, 2000; Tremoulet and Feldman, 2000). An object interacting contingently with a human is also likely to appear animate to an observing child (Johnson, 2003). Furthermore, destroying the contingency between the movements of two interacting objects can eliminate any attribution of intentionality (Bassili, 1976). But a thorough review of studies of animacy attribution by Opfer (Opfer, 2002) indicated that self-propelled motion provided observers only with “weak” and “uncompelling” animacy cues, while a stronger cue could be goal-directed motion, understood in the following sense: “a type of autonomous movement in which the agent contingently directs its movement toward (or away from) another object, state, or location.”

In the present study, we aimed to test in a tightly controlled way the association between goal-directed motion and the percept of animacy, by creating an algorithm in which the amount of goal-directed motion or interactivity was controlled by one mathematical parameter. Furthermore, we tested the hypothesis that the brain regions responding during observation of animate motion respond directly to variations of the parameter inducing the percept of animacy. This approach should help us to understand which characteristics of biological movements induce the percept of animacy and to understand how brain structures identify animate motion.

Our mathematical algorithm was used to create short animations of two moving disks or balls with different colors that changed direction and speed in an unpredictable but smooth manner (Figures 1A and 1B). The objects’ movements did not seem to follow any obvious physical law, making the objects appear self-propelled (Scholl and Tremoulet, 2000). The percept of goal-directed movement was evoked by inducing interactions between the objects such that one object appeared to chase the other, which tried to escape. This interaction was determined by the cross-correlation between the movements of the objects, which was linearly varied across conditions during the experiment.

\*Correspondence: johannes.schultz@tuebingen.mpg.de

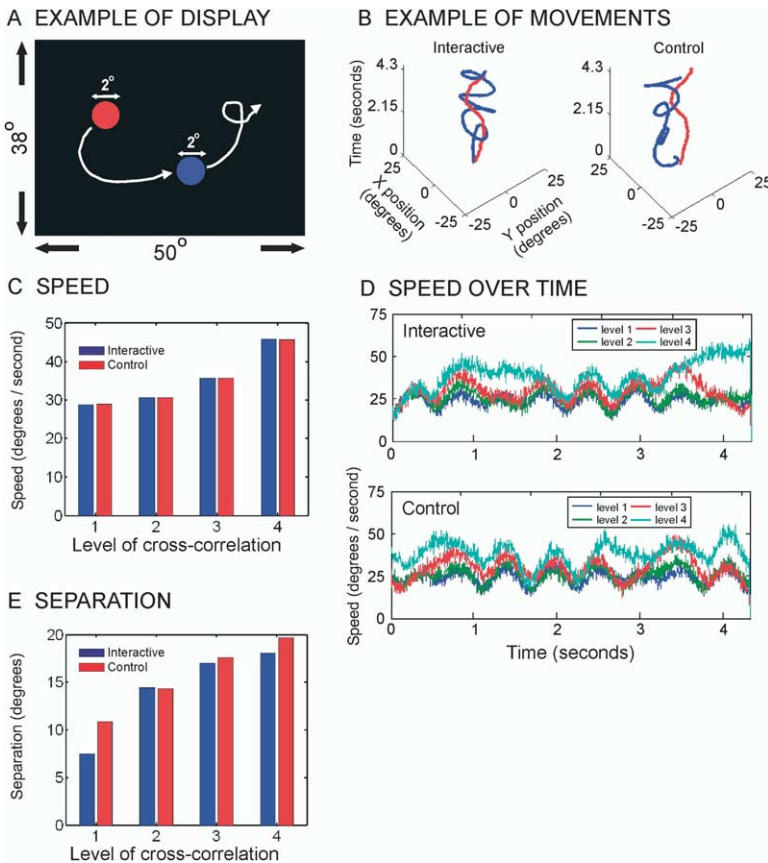


Figure 1. Example and Statistics of the Stimuli

(A) Example of the visual aspect of the animations (white arrows represent a segment of the object's motion and were not shown during the experiment).

(B) Example of the object's motion in time in an Interactive and in a Control trial: the movement of the red object was kept identical across these trials, but the movement of the blue object was changed in the Control conditions, destroying the interactivity between the two objects but conserving the speed of both objects.

(C) Average speed of both objects in the eight different types of animations used in the experiment. Speed increased with the level of the cross-correlation parameter but was almost identical in the Interactive and Control trials.

(D) Average speed of both objects over time in all trials of each level of the cross-correlation parameter and in their Control conditions: the speed profile over time was very similar in the Interactive and the Control trials.

(E) Average distance (instantaneous separation) between the two objects in the eight different types of animations used in the experiment. Distance increased with the level of the cross-correlation parameter, but there was no significant difference between Interactive and Control conditions. See [Experimental Procedures](#) section on stimuli for statistics.

All other parameters of the equation were kept constant across conditions. To control as much as possible the low-level stimulus characteristics across variations of the cross-correlation parameter, we created matched control conditions with similar but uncorrelated movements. Compared with the interactive conditions, in these matched control conditions the speed of both objects was identical and the average instantaneous separation between the objects was closely matched (Figures 1C and 1E).

We assessed how the percept of animacy changed with respect to variations of the cross-correlation parameter and, furthermore, how changes in this parameter affected brain activity. On the basis of the neurophysiological and neuroimaging data mentioned above, we were expecting activation changes in the cortex surrounding the posterior part of the superior temporal sulcus. Furthermore, as the detection of animate entities can be a life-saving process when it alerts an observer to the presence of prey or predators, we were interested in determining if changes in brain activity induced by variations in our parameter were automatic or task dependent. We therefore asked our participants to perform two different tasks in the scanner, using the same animations. In one half of the experiment, participants were asked to decide how much the "chasing" object tried to catch the "target" object (the "interactivity-rating" task); in the other half of the experiment,

subjects had to judge how fast both objects were moving (the "speed-rating" task).

## Results

### Behavioral Pilot

A preliminary behavioral study showed that six subjects could easily perceive the amount of goal-directed interactions in the movements of the objects in our animations (Figure 2), with results indicating a gradual increase in the percept of interactivity with an increase in the cross-correlation parameter [ $F(1,5) = 261$ ,  $p < 0.001$ , repeated-measures one-way ANOVA]. On the basis of these results, four linearly spaced levels of cross-correlation were chosen for further behavioral testing and for the fMRI experiment (indicated by the inverted arrowheads in Figure 2).

### Animacy Ratings

Analysis of the results of the animacy-rating test performed outside of the fMRI scanner indicated that Interactive animations (where the movements of the two objects were correlated) appeared more animate than the Control animations [ $F(1,11) = 11.3$ ,  $p < 0.01$ ; repeated-measures two-way ANOVA, within-subject factors Cross-correlation level and Interact versus Control, between-subjects factor gender] and, importantly, that animacy ratings increased more with the cross-correlation level

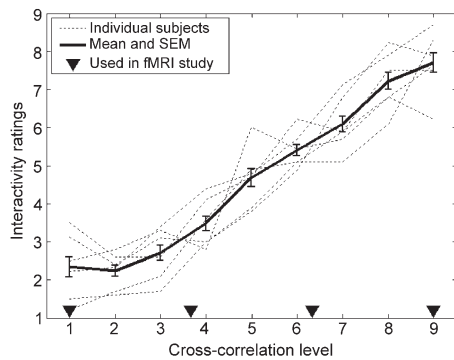


Figure 2. Results from Behavioral Pilot Study

Results from a behavioral pilot study using nine different linearly spaced levels of the cross-correlation parameter. Six naive subjects were tested with ten animations of each level of the cross-correlation parameter (fully randomized design as in the fMRI experiment, but no control animations) and were asked to rate the amount of interactivity (“how much does the red disk appear to follow the blue disk?”) between the two disks on a scale from 1 to 9. As can be seen, a gradual increase in cross-correlation level induced on average an increasing percept of interactivity, particularly in the middle range of values (3 to 7). On the basis of these results, four linearly spaced values were chosen within the tested range for the fMRI experiment (indicated by the triangles). Values plotted represent individual ratings (dashed lines) and mean over subjects with standard error of the mean (continuous line).

in the Interactive conditions compared to the Control conditions [interaction,  $F(1,11) = 24.3, p < 0.001$ ] (Figure 3A). There was no difference due to gender [ $F(1,11) = 0.001, p > 0.5$ ] and no influence of gender on either contrast [interaction Interactive versus Control by gender:  $F(1,11) = 0.1, p > 0.5$ ; three-way interaction:  $F(1,11) = 1.2, p > 0.2$ ]. No significant change over repetitions of trials from a given condition was found (repeated-measures ANOVA with factors: cross-correlation level (1 through 4), Interactive versus Control, gender (m/f), and repetition (1 through 10)). These data suggest that increasing the dependency between the movements of our two objects such that they appeared

to chase each other more increased the percept of animacy.

### Interactivity and Speed Ratings

Analysis of participants’ ratings from the interactivity-rating task and the speed-rating task performed during the fMRI experiment revealed the following effects (Figures 3B and 3C). In the Interactive trials, subjects rated the objects as increasingly interactive with increasing cross-correlation between their movements [ANOVA,  $F(1,11) = 502.7, p < 0.001$ ; repeated-measures two-way ANOVA, within-subject factors Cross-correlation level and Interact versus Control]. However, subjects also considered the objects’ speed to be increasing with increasing cross-correlation [ $F(1,11) = 446.8, p < 0.001$ ]. Matched control animations, in which the correlation between the objects’ movements was destroyed but the speed and instantaneous separation between objects were closely matched (see Experimental Procedures and Figures 1C–1E), were rated by the subjects as displaying much less interactivity than the Interactive animations [interaction between cross-correlation level and Interactive versus Control animations,  $F(1,11) = 29.4, p < 0.001$ ] but as having the same speed [ $F(1,11) = 1.0, p > 0.3$ ]. These data suggest that increasing the dependency between the movements of our two objects increased the percept of interaction.

### Eye Movements

We tested for variations in eye movements during the fMRI experiment by measuring the total excursion of the eye in the vertical and horizontal axes during the different conditions and by calculating the average size of saccades (see Experimental Procedures).

The degree of correlation between the objects’ movements did not influence total eye movements [ANOVA,  $F(1,8) = 0.7, p > 0.4$ ; repeated-measures three-way ANOVA, within-subject factors Cross-correlation level, Interact versus Control and interactivity-rating versus speed-rating task], and there were no differences in eye movements between Interactive and Control trials [ $F(1,8) = 2.0, p = 0.2$ ]. The only factor that significantly

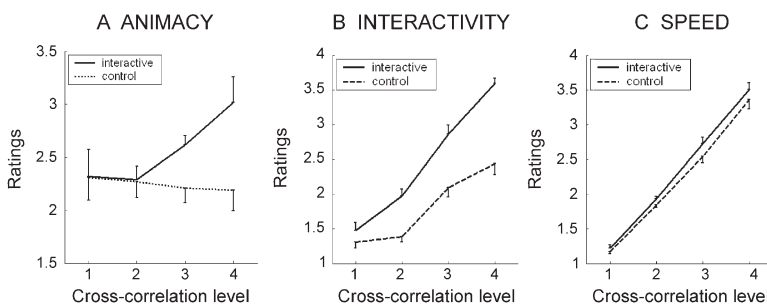


Figure 3. Behavioral Results

Results of three different tasks performed on the stimuli used in the fMRI experiment. (A) Ratings of animacy from 12 subjects who were naive to the experimental manipulations and tested outside of the scanner. These volunteers were asked to indicate how alive the two interacting disks appeared; they were instructed to use any criteria they wished for their rating. (B and C) Ratings of interactivity and speed from 12 subjects, acquired during the fMRI experiment. On the X axis of all panels are the different levels of the cross-correlation parameter that controlled the interactivity between the objects’ movements from 1 (minimum) to 4 (maximum). Broken and unbroken lines correspond, respectively, to Interactive conditions (with interactive motion) and to their matched Control conditions (where the interactivity between the movements was destroyed, see Experimental Procedures). On the Y axis of all panels are the mean and standard errors of the mean (over subjects) of the subjects’ ratings: 1 corresponds to the minimum animacy, interactivity, or speed; 4 corresponds to the maximum. Animacy and interactivity ratings of the Interactive animations (continuous line) increased more with the cross-correlation parameter than the ratings of the Control animations [Animacy:  $F(1,11) = 23.9, p < 0.001$ ; Interactivity:  $F(1,11) = 29.4, p < 0.001$ ; two-way ANOVA, interaction between cross-correlation and Interactive versus Control]. This difference was not seen in the Speed ratings [ $F(1,11) = 1.0, p > 0.3$ ].

parameter that controlled the interactivity between the objects’ movements from 1 (minimum) to 4 (maximum). Broken and unbroken lines correspond, respectively, to Interactive conditions (with interactive motion) and to their matched Control conditions (where the interactivity between the movements was destroyed, see Experimental Procedures). On the Y axis of all panels are the mean and standard errors of the mean (over subjects) of the subjects’ ratings: 1 corresponds to the minimum animacy, interactivity, or speed; 4 corresponds to the maximum. Animacy and interactivity ratings of the Interactive animations (continuous line) increased more with the cross-correlation parameter than the ratings of the Control animations [Animacy:  $F(1,11) = 23.9, p < 0.001$ ; Interactivity:  $F(1,11) = 29.4, p < 0.001$ ; two-way ANOVA, interaction between cross-correlation and Interactive versus Control]. This difference was not seen in the Speed ratings [ $F(1,11) = 1.0, p > 0.3$ ].

influenced total eye movements was the task performed by the subjects: subjects moved their eyes less in the speed-rating task than in the interactivity-rating task [interactivity-rating task versus speed-rating task:  $F(1,8) = 5.8, p = 0.04$ ]. As we did not compare directly the two tasks, this difference in eye movements did not influence the interpretation of the brain activation analysis.

The average saccade size was not significantly influenced by the cross-correlation parameter [ANOVA,  $F(1,8) = 0.153, p > 0.9$ , same factors and design as used for total eye movements], and there were no differences in average saccade size between Interactive and Control conditions [ $F(1,8) = 0.9, p > 0.3$ ] or between tasks [ $F(1,8) = 0.3, p > 0.5$ ]. There were no significant interactions between any combinations of these factors (all  $p > 0.3$ ). Similar, nonsignificant results were obtained when using different eye speed thresholds for the isolation of saccades (see [Experimental Procedures](#)).

### fMRI Data

We used the parametric, factorial design of this fMRI experiment to test for activation increases in relation to increases in interactivity displayed by the two objects and to test how these interaction-dependent responses were affected by the attentional task the subject performed. To discount speed effects, we assessed interaction-sensitive activations as the difference between the regression of brain responses on interaction level and the equivalent speed control trials. Responses to object speed were assessed as a control.

### Effects of a Linear Increase of Interactive Motion

The following regions showed response increases with the increase in correlation between the objects' movements in the Interactive condition but no increases in the Control conditions: the right posterior, ascending branch of the superior temporal sulcus in the inferior parietal cortex, the left superior temporal gyrus, the medial occipital cortex in both hemispheres, the right fusiform gyrus, the caudal part of the anterior cingulate gyrus, and the posterior paracingulate gyrus ([Figure 4](#) and [Table 1](#)). This was tested formally with a two-way interaction between a linear increase in the cross-correlation factor and the Interactive versus Control factor.

### Effects of Task on Observation of Interacting Movements

We found only one cluster in the whole brain that showed significantly different activation depending on the task the subjects performed. This was tested in three different ways:

(1) The most relevant test for evaluating task effects was the three-way interaction between Cross-correlation level, Interactive versus Control, and interactivity-versus speed-rating task. This tested for task effects on the response to a linear increase in interactive motion while controlling as much as possible for responses to low-level stimulus properties. This comparison did not reveal any significantly activated cluster of voxels in the whole brain.

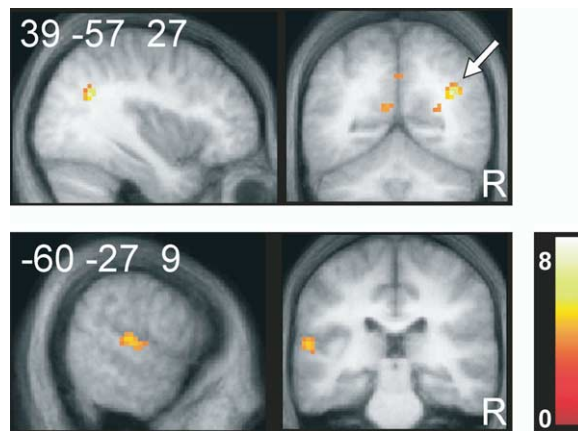


Figure 4. Activation in Posterior Superior Temporal Gyrus and Sulcus

Clusters of voxels in the posterior superior temporal gyrus and sulcus in right and left hemispheres (top and bottom panels, respectively), whose activation increased linearly with the amount of interactive motion. Tested by the interaction between a linear increase in the cross-correlation parameter and Interactive versus Control trials. For details and other regions showing similar activation increases, see [Table 1](#). The image is thresholded at  $p < 0.05$ , corrected for multiple comparisons across the whole brain at the cluster level (see [Experimental Procedures](#)). The brain slice used for display is the average image from the subjects' normalized structural brain scans (see [Experimental Procedures](#)). Coordinates are in Montreal Neurological Institute (MNI) reference space. The color bar refers to activation intensity expressed in T values.

(2) Differences between tasks: comparing all conditions in both tasks directly with each other yielded one cluster of voxels that was more active when subjects performed the Interactivity than when they performed the Speed task, in the caudal part of the anterior cingulate gyrus (MNI coordinates:  $X = -6, Y = -12, Z = 36$ ;  $Z$  score = 4.1, size =  $1161 \text{ mm}^3$ ), probably corresponding to the caudal cingulate zone in Picard and Strick's terminology (Picard and Strick, 2001). This activation is to be interpreted with caution, however, because the design of the experiment was not optimized to compare directly the two tasks with each other, but rather to test interactions between task and the conditions of the experiment while minimizing task-switching effects. As a consequence, each task was performed as one block, with only one task switch in the middle of the experiment. Therefore, the results of a direct comparison of these two blocks with each other could be influenced by slow changes over time, such as scanner signal drift, subject fatigue, or changes in concentration. Some of these effects were probably removed during preprocessing, but remaining artifactual effects might still be present. We will therefore discuss this activation only briefly.

(3) Two-way interactions between Interactive versus Control trials and interactivity- versus speed-rating task, and between Cross-correlation level and task type: these comparisons did not yield any significantly activated cluster of voxels anywhere in the brain.

Table 1. Brain Activation Data, Whole-Brain Voxelwise Analysis

Structure	Coordinates			Size (mm <sup>3</sup> )	Z Score	Brodmann Area
	X	Y	Z			
Effects of a linear increase of interactive motion						
R asc. post. superior temporal sulcus/ supramarginal gyrus	39	-57	27	1323	4.5	39
L superior temporal gyrus	-60	-27	9	1080	3.6	41
L medial occipital cortex	-6	-69	0	4941	4.8	18
R medial occipital cortex	15	-72	-9		4.3	18
Medial occipital cortex	0	-66	18	2187	4.0	23
R fusiform gyrus	30	-63	-6		4.2	19
R caudal part of ant. cingulate	3	0	45	1674	4.0	24
Posterior paracingulate	0	-48	39	1053	3.5	31
Task effects (Interactivity-rating task vs. Speed-rating task)						
L caudal part of ant. cingulate	-6	-12	36	1161	4.1	23
Effects of object speed						
L&R medial occipital cortex	0	-84	3	71361	5.9	17-18-19
L post lat occipital (MT/V5)	-45	-75	3	837	3.7	19

Significant clusters showing (1) a greater linear increase in activation with contingency in the experimental conditions than in the control conditions or (2) greater activation during the interactivity-rating task than the speed-rating task or (3) a linear increase in activation proportional to increases in object speed. All clusters survive a threshold of  $p < 0.05$  corrected for multiple comparisons (see [Experimental Procedures](#)). L and R refer to left and right hemispheres, respectively, and pSTS and pSTG refer to posterior superior temporal sulcus and gyrus, respectively. Empty fields in the "Size" column indicate subclusters within the cluster listed immediately above in the column.

### Effects of Increase in Object Speed

As a control, we evaluated the activation response to variations in object speed, by testing for increases in activation to an increase in the cross-correlation parameter, pooling over interactive and control trials. This test yielded extensive activation in bilateral medial occipital cortex and in a cluster located in lateral occipital cortex most likely corresponding to left area MT/V5 (see [Table 1](#); the cluster in lateral occipital cortex survived correction across a small search volume centered around coordinates commonly associated with area MT/V5, see [Experimental Procedures](#)). None of the other tests performed and described above yielded significant activation increases located in the MT/V5 search volumes.

### Discussion

This study shows that activation in the superior temporal gyrus and in the cortex surrounding the superior temporal sulcus increases linearly with the interactivity between the movements of two abstract, self-propelled objects. Directing attention to the interactions rather than to their speed had no significant impact on activation increases in the temporal cortex. These cortical structures are known to respond during observation of biological motion, such as point-light walkers ([Allison et al., 2000](#); [Pelphrey et al., 2003](#)). As this study also shows that increasing interactivity between the movements of two abstract objects makes the objects appear more animate, this suggests a link between activation in the posterior superior temporal sulcus and gyrus and the detection of animate entities. Similarity between the results of the behavioral analysis and the fMRI data is shown in [Figures 5A–5C](#).

### Does the Cortex in the Superior Temporal Sulcus and Gyrus Respond to Objective Characteristics of Animate Motion or to Categorical Percepts?

In previous studies using abstract moving "agents," a human controlled the movements of the abstract shapes to create the desired effects ([Blakemore et al., 2003](#); [Blythe et al., 1999](#); [Castelli et al., 2000](#); [Heider and Simmel, 1944](#); [Schultz et al., 2003](#)). Observers can reliably identify which behavior an animator intends to give to the objects he controls ([Blythe et al., 1999](#)). Animated cartoons on television also speak to the capacity to reliably evoke the impression of complex intentional behavior in abstract moving shapes. Although it is very interesting that such stimuli induce activation in the superior temporal region and in the fusiform gyrus ([Blakemore et al., 2001](#); [Blakemore et al., 2003](#); [Castelli et al., 2000](#); [Schultz et al., 2003](#)), it is not clear whether (or which of) these structures respond to objective characteristics of the objects' movements that indicate they might be alive (such as parameters of self-propelled or goal-directed motion) or whether these regions simply respond to anything that appears animate. In our study, we selectively increased the interactivity between the movements of two abstract objects (for graphical information on the stimuli, see [Figures 1 and 6](#)). Our results show that activation in certain parts of the superior temporal gyrus and the cortex surrounding the superior temporal sulcus increases in proportion to the amount of interactivity. Our results further indicate that these activation increases are probably not due to differences in instantaneous separation between the objects or to differences in speed (speed increases induced proportional activation increases in left area MT/V5, among other regions) or to differences in eye movements. We therefore propose that our data suggest an involvement of the superior temporal sulcus re-

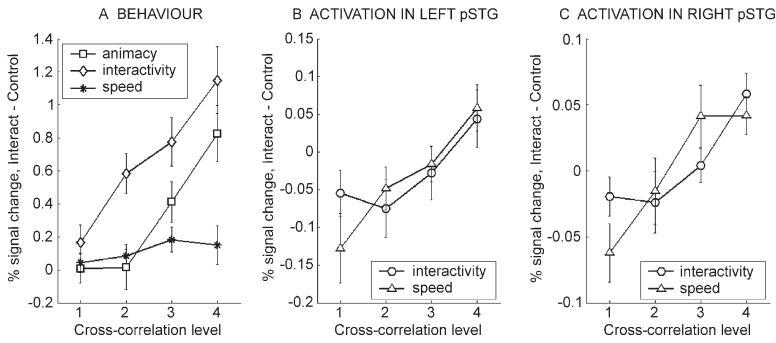


Figure 5. Similarity between Behavior and Activation in the Posterior Superior Temporal Sulcus and Gyrus

(A) Differences between ratings of Interactive and Control animations for all four levels of cross-correlation, for the three tasks (averages and standard errors of the mean across ratings of Animacy, Interactivity, and Speed). The differences in ratings increased with the cross-correlation parameter in the Animacy and Interactivity tasks, but not in the Speed task. (B and C) Differences between activation in Interactive and Control trials, for all four levels of cross-correlation, for the two tasks performed in the scanner (Inter-

activity rating and Speed rating). Data are percent signal change (mean and standard error of the mean) in voxels of the clusters in the posterior superior temporal sulcus (pSTS) and posterior superior temporal gyrus (pSTG) identified in the SPM analysis. The differences in activation increase relatively linearly with the cross-correlation level in both brain regions and in both tasks.  $n = 12$  in all panels. Note: Interactivity and Speed ratings were collected simultaneously with the fMRI data.

gion in processing movement characteristics that characterize living beings rather than simply responding to the presence of living beings.

### Superior Temporal Sulcus Region and Social Information

Together with the amygdala, the fusiform gyrus, and the orbital and the medial frontal cortex, the superior temporal sulcus region is thought to be part of a network forming the “social brain” (Adolphs, 2003; Brothers, 1990). Neurophysiological recordings in the posterior superior temporal area of monkeys revealed cells that respond during observation of biological motion, such as a walking person, moving parts of a face such as mouth and eyes, or whole faces (Bruce et al., 1981; Desimone, 1991; Hasselmo et al., 1989; Oram and Perrett, 1994; Perrett et al., 1985). Neuroimaging studies of human volunteers yielded similar results (for review, see Puce and Perrett, 2003). Pictures and words referring to animals also induce activation increases in the superior temporal area (Kanwisher et al., 1997; Martin et al., 2000). But this area of the brain is also associated with higher cognitive functions, such as the attribution of mental states to other living organisms, also known as mentalizing or theory-of-mind (Frith and Frith, 1999, 2003; Samson et al., 2004; Saxe and Kanwisher, 2003),

and even to moving abstract shapes (Blakemore et al., 2001, 2003; Castelli et al., 2000; Schultz et al., 2003). Activity in the posterior superior temporal sulcus region has previously been found during imitation of human actions (Iacoboni et al., 2001), which is performed mostly by imitating an action’s goals rather than the actual movements (Koski et al., 2003; Wohlschlaeger et al., 2003). This brain region is also thought to extract intentional cues from goal-oriented human behavior (Toni et al., 2001). Our results show that this region is engaged by the observation of objects moving in a self-propelled and interactive way, which are movement characteristics that increase the percept of animacy. Therefore, our results are compatible with a role of the superior temporal region in identifying animate agents in the environment based on their movement, a necessary step in the processing of social information.

### Task Effects

Our results show that there was no significant difference in activation of the pSTS/pSTG between the two tasks our volunteers had to perform, while activation in the posterior part of the anterior cingulate gyrus was greater when subjects performed the interactivity-rating rather than the speed-rating task. These results suggest that the response of the pSTS/pSTG during

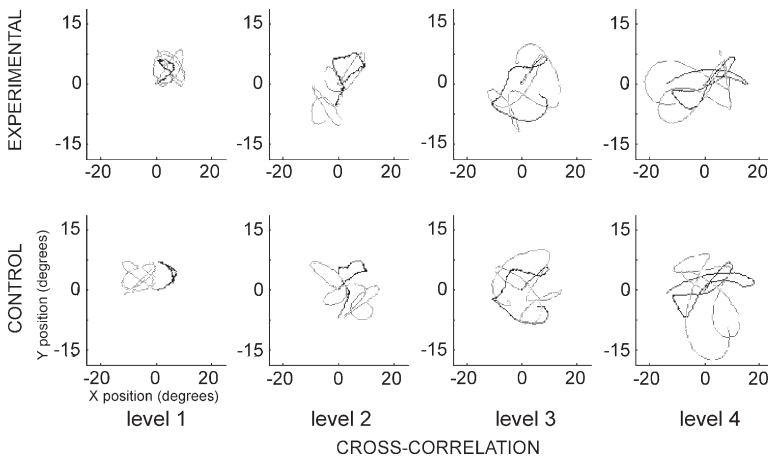


Figure 6. Sample Trajectories of Moving Objects

Sample trajectories (X and Y positions collapsed over time) for all eight types of animations used in the fMRI experiment and in the animacy-rating task. Black and gray lines correspond, respectively, to the trajectories of the red and blue objects. X and Y coordinates are indicated in degrees from center of screen.

observation of moving abstract objects interacting in very simple ways is task independent. This could be interpreted as an automatic role of these brain regions in the detection of animate-looking motion, which is not modulated by directing attention to the movement characteristics related to the percept of animacy (goal-directedness in the objects' motion in the present study) or to irrelevant movement characteristics (speed in the present study).

Previous studies indicate that both recognition of biological motion and activation in the superior temporal gyri and sulci can be influenced by attention and the task performed by the subjects (Blakemore et al., 2003; Thornton et al., 2002). In a previous study using simple, abstract moving objects performing a chasing scenario, we also found differences in activation of the pSTG due to the task performed by our volunteers (Schultz et al., 2004). In this previous study, two moving objects performed a more complex chasing scenario in which we varied the strategy used by the chaser to catch its target. The subjects' tasks were to identify which strategy the chaser used to catch the target (either simply following the target or predicting its destination) or to determine if the chase was successful or not. Stronger activation was found in the pSTG when subjects had to identify the chaser's strategy rather than the outcome of the chase. We proposed that paying attention to the chaser's strategy cued subjects into thinking about characteristics that are often associated with agents (for example, goals and ways to reach them). Thinking about such characteristics could be considered a simplified form of mental state attribution, which is known to induce activation in the pSTS (Frith and Frith, 2003). Such processes probably don't happen either when judging the outcome of a chase as in the previous study, or, as in the present study, when rating how much two objects appear to chase each other or how fast they move. Therefore, we propose that the absence of task effects on pSTS activation in the present study is due to the fact that the tasks performed by our subjects did not differ in the amount of mentalizing involved.

We did find a cluster of voxels in the posterior part of the anterior cingulate cortex (ACC) whose activation was greater when subjects rated the interactivity of the objects compared to rating their speed, irrespective of the stimulus presented. (Note: this result is to be taken with caution, as the design of our experiment was not optimized to compare directly these two tasks, as we were aiming to test for the effect of task on observation of interactive motion; see Results for a short discussion of this issue.) As discussed above, we propose that the two tasks used in this experiment did not differ in terms of the mentalizing involved, and therefore we do not think that the cluster in the posterior ACC represents activation changes related to mentalizing. In favor of this interpretation is the fact that our cluster is located far posterior (about 55 mm) to the medial prefrontal cortex region previously associated with mentalizing (Frith and Frith, 2003). To understand the increase in activation in the posterior ACC would require further studies using adapted experimental designs that are beyond the scope of the present study.

### Other Regions Engaged by Interacting Objects: Fusiform Gyrus and Medial Occipital Cortex

Significant activation increases corresponding to increasing interactivity were also found in the fusiform gyrus and the medial occipital cortex. Previous studies showed activation increases in the fusiform gyrus during presentation of pictures of faces (Haxby et al., 1994; Kanwisher et al., 1997; Puce et al., 1995) and of living beings (Chao et al., 1999a, 1999b) and during observation of moving, abstract "agents" (Castelli et al., 2000; Schultz et al., 2003). Activation in the medial occipital cortex is also known to increase during observation and naming of pictures of animals, but not tools (Damasio et al., 1996; Martin et al., 1996, 2000; Perani et al., 1995). Lesions of the medial occipital lobe (particularly in the left hemisphere) are associated with a specific semantic knowledge deficit for animals (Nielsen, 1958; Tranel et al., 1997). As reviewed above, goal-directed motion and self-propelled movement appear to be the main cues for the attribution of animacy to abstract objects, and our data show an association between interactivity and the percept of animacy. It is therefore possible that activity in the fusiform gyrus and the medial occipital cortex increased with increasing interactivity because the moving objects appeared increasingly animate and animal-like.

### Conclusion

Our results show that objects that appear to move in a self-propelled and interactive way appear more animate with increasing goal-directed interactivity and that the superior temporal gyrus and sulcus, the fusiform gyrus, and the medial occipital cortex show activity varying in parallel with the amount of interactivity. This shows that one characteristic of the movements of animate entities can induce the percept of animacy and can also induce activation in brain areas known to respond to biological and animate-looking motion. Interestingly, many of the brain areas isolated in the present experiment are thought to be involved in social cognition and to constitute a "social brain" (Adolphs, 2003). Our results suggest that these regions are already involved in a very early process required for engaging in all social interactions: the visual identification of animate entities in the environment.

### Experimental Procedures

#### Subjects

Twelve right-handed participants (eight males and four females, aged 19–35, average age 25.6) participated in the study. All subjects gave full written informed consent, and the study was approved by the ethics committee of the Institute of Neurology, University College London, UK.

#### Stimuli and Animations

Subjects watched short animations (4.3 s per animation) in which two moving disks appeared to be either interacting or moving independently from each other. The moving objects were two disks or balls, 2° wide on the screen (Figure 1A). One was red, the other 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, Inc., Natick, MA) and detailed below. This equation made the objects move in a way that appeared biological and, in addition, allowed parametric control of the interactivity between the two objects by varying the

correlation between their movements. The visual display was controlled by in-house presentation software (Cogent 2000, <http://www.vislab.ucl.ac.uk/Cogent2000/index.html>) implemented in Matlab. For the fMRI experiment, animations were projected onto an opaque surface in the scanner by an LCD projector; subjects viewed them through a set of mirrors mounted on the headcoil.

### Pilot Study

In order to assess the variation of the percept of interactivity induced by variations of the correlation between the movements of the two disks, six right-handed participants watched animations created with the equations of motion, using nine different, linearly spaced levels of the cross-correlation parameter. Subjects were tested with ten animations of each level of the cross-correlation parameter (fully randomized design) and were asked to rate the amount of interactivity (“how much does the red disk appear to follow the blue disk?”) between the two disks on a scale ranging from 1 to 9. On the basis of these results, four linearly spaced values were chosen within the tested range for the fMRI experiment (indicated by the triangles in Figure 2).

### Design, Conditions, and Tasks

In this experiment, we wanted to identify regions whose responses increased in relationship with the amount of interactivity. We also wanted to test whether these activation changes happen only when subjects pay attention to the interactions between the objects or also when they perform another, incidental task. We therefore used a factorial design with the following three factors: (1) four linearly increasing levels of interactive motion, (2) two condition levels (Control and Interactive), and (3) two task levels (an interactivity- and a speed-rating task). Combinations of the first two factors resulted in eight different animation types (for samples, see Figure 6), and together with the two tasks, there were 16 different trial types in the fMRI experiment, each repeated ten times. The four levels of interactivity were created by manipulating a cross-correlation parameter, which controlled the dependence between object movements. Increasing this parameter increased the objective and subjective interactivity and their speed. We therefore used a matched Control condition for each interactivity level, in which speed was identical but interactivity was destroyed (see below). Subjects performed the two tasks on the same stimuli: in the interactivity-rating task, subjects were asked “how much does the red object follow the blue object, one being the minimum and four the maximum?” In the speed-rating task, the instructions were “how fast do the objects move, one being the minimum and four the maximum?” They responded by pressing one of four buttons on a keypad with the corresponding finger of the right hand. Ratings, eye movements, and brain activation were recorded simultaneously during the experiment. On these three types of dependent variable, we assessed the effects of interactivity and the interaction between task and interactivity. In addition, we assessed the effects of subjects’ task and object speed on the fMRI data.

### Movement Equation

The equations of motion specified a time-series of positions for each object, where the new position of each object was determined by the previous position of both using a multivariate autoregressive process (MAR). The influence of the objects on one another was parametrically varied according to a cross-correlation parameter, whereas the influence of previous positions of the same object was kept constant. Both objects had their own movement characteristics, such that the blue ball always moved faster than the red ball. The movement equation consisted of a set of differential equations with a cross-correlation matrix containing terms controlling the influence of each object’s previous coordinate on its new coordinates (these terms were kept constant during the experiment), and terms controlling the influence of the other object’s previous coordinates on the new coordinates of each object. These equations were integrated using matrix exponentials to give a MAR time-series. The cross-correlation parameters were identical for the two objects except for their opposite sign, which made one object appear as the chaser and the other as the target. To give the objects a basic movement that appeared biological, the

equations of motion included an exogenous component (combination of sine waves with different periods and a small random term). The update equation for each time step was

$$x(t + \Delta t) = \exp(J\Delta t)x(t) + \sum_i \beta_i \sin(t\omega_i) + W\epsilon(t)$$

$$J = \begin{bmatrix} -0.01 & 0 \\ 0 & -0.01 \end{bmatrix} \otimes \begin{bmatrix} 1 & \rho \\ -\rho & 1 \end{bmatrix}$$

Our exogenous driving terms were controlled by  $\beta = \{1/7, 1/10, 1/2, 2/3\}$  and  $\omega = \{1/100, 1/200, 1/50, 1/40\}$ . In this equation,  $x(t)$  are the coordinates of both objects,  $x(t - 1)$  are their previous coordinates,  $J$  is the system’s Jacobian controlling the dependencies,  $W$  is a constant that scales the random term  $\epsilon(t) \sim N(0, \Delta t)$  and  $\Delta t$  is the time step between two successive positions.  $J$  was based on a cross-correlation matrix containing the cross-correlation coefficient  $\rho$ , which was modified across conditions and increased the amount of interactivity. This resulted in the impression of the red ball chasing the blue ball, in a parametric fashion.

### Matched Control Conditions

Increases of the cross-correlation parameter also increased the speed of both stimuli (speed depends on value of the cross-correlation parameter). To control for speed differences and other low-level characteristics of the animations due to changes of the cross-correlation parameter, we created matched Control conditions, where the interactivity between the objects was removed but the average speed of the objects and their average instantaneous separation were closely matched: there was no significant difference in measured speed or separation between objects relative to the Interactive trials [Speed:  $t(1,3) = 0.0, p = 1$ ; separation:  $t(1,3) = -1.8, p > 0.1$ ; both paired samples  $t$  tests. See Figures 1C–1E]. These Control stimuli were created by reversing the path of the blue object in time, swapping the X and Y coordinates, and reversing left and right (Figure 1B). This manipulation destroyed the dependency between the objects but retained almost exactly the same motion dynamics otherwise (see Figures 1C–1E).

### Pulling versus Goal Directedness

The fact that the movements of both objects were not only determined by each other’s positions but also had their own movement characteristics reduced the impression of one object “pulling” or “pushing” the other. The absence of a pulling or pushing motion is known to reinforce the sense of goal-directed motion (Opfer, 2002). Pulling and pushing can be reduced by (1) a delay between a movement of the target and the movement of the follower and (2) the follower changing its direction differently than the target (Opfer, 2002). Our stimuli conformed to both these factors and therefore increased the impression of interactive movements. Possible contributions of the separation between the objects to the percept of pushing were similar in control and interactive conditions, as separation was not found to be significantly different in these two types of condition.

### Animacy and Interactivity

Based on previous behavioral studies, we had postulated for this study that two moving abstract objects that appeared to interact with each other would appear animate and also that the stronger the interactivity percept would be, the more animate the objects would appear. As our parameter controlling the amount of animacy in the observed animations was relatively abstract and the stimulus development process was long and involved many steps, it was necessary to make sure that the final animations still appeared animate. To this end, we used the same animations as in the fMRI experiment and asked 12 volunteers (6 male and 6 female, aged 23–36) who were unaware of the different experimental conditions, of the parameters used, and of the aim of the experiment to judge how “alive” the objects appeared, on a scale of 1 to 4. Volunteers were completely free to use any movement criteria for their animacy judgement.



### Eye Movement Recording and Analysis

Subjects were allowed to move their eyes freely during the fMRI experiment. To evaluate potential confounds due to eye movement differences between conditions, we recorded eye movements using an infrared eye-tracking system recording at 60 Hz (ASL Model 504, Applied Science Laboratories, Bedford, MA), with remote, custom-adapted optics for use in the scanner. Reliable eye tracking data throughout the whole scanning session were only available in 9 out of 12 subjects, as the remaining 3 subjects wore contact lenses, which created artifacts in the eye tracker. Eye blinks were removed by eliminating all differences in successive time points more than 3 standard deviations away from the mean difference, which were replaced by the average of the positions immediately before and after the replaced time point. To yield a measure of total eye movements for each trial, the data were mean corrected, squared, and then summed. Saccades were identified as periods of eye movements faster than 50°/s (as this value was chosen somewhat arbitrarily, other thresholds between 30° and 120°/s were used for the isolation of saccades and yielded similar results), and their amplitudes were calculated as the difference in eye position before and after each saccade. These amplitudes were calculated and averaged for each condition. Total eye movements and saccade amplitudes were analyzed with the same tests as those used in the analysis of the subjects' ratings (see [Results](#)).

### Image Acquisition

A Siemens VISION System (Siemens, Erlangen, Germany), operating at 2 Tesla, was used to acquire both T1-weighted anatomical images and gradient-echo echoplanar T2\*-weighted MRI images with blood oxygenation level-dependent (BOLD) contrast. The scanning sequence was a trajectory-based reconstruction sequence with repetition time of 2736 ms and echo time of 35 ms. Each volume, positioned to cover the whole brain, comprised 36 axial slices, with an isotropic in-plane resolution of 3 mm, a slice thickness of 3 mm, and a 1 mm interval between slices. For each subject, 315 volumes were acquired in one session of 14.5 min, including 5 subsequently discarded "dummy" volumes at the start of the session to allow for T1 equilibration effects. A structural MR image was acquired for each subject (modified MP RAGE sequence [[Deichmann et al., 2000](#)]; parameters were TR = 11 ms, TE = 4 ms, flip angle 12°, image matrix 256 pixels [Read] × 224 pixels [Phase], voxel size 1 × 1 × 1 mm, 176 slices per volume).

### 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, <http://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 3 mm<sup>3</sup> ([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 cut-off of 128 s) 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 3D 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 effects in the experiment, engendered by crossing the three factors above: (1) task (interactivity-rating or speed-rating), (2) value of cross-correlation parameter (1, 2, 3, or 4), (3) condition (Interactive or Control trials). Two regressors were created for each condition, in the following way: the time period 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). We also included two covariates, made by convolving the average speed of both objects during each trial with both the HRF (first covariate) and the temporal derivative of the HRF (second covariate). This enabled us to model separately the effect of the average object speed on the brain activation, which was not an effect of interest in the analysis. 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 the following factors: linear increase of the cross-correlation parameter, and the difference between Interactive (i.e., animations with interactive motion) and Control trials (where interactive motion was destroyed). The contrasts of greatest interest were the effects of interactivity controlled for other movement characteristics (tested by the interaction between a linear increase in the cross-correlation parameter and Interactive versus Control trials) and the effects of performing different tasks on animations with increasingly interactive motion (tested by the three-way interaction between the linear increase of cross-correlation, Interactive versus Control trials, and interactivity-rating versus speed-rating task).

One-sample *t* tests were performed on the above contrast images to give second-level or random-effects statistical parametric maps (SPMs), after further smoothing the weighted maps by convolution with an 8 mm FWHM (full-width at half-maximum) Gaussian kernel to account for anatomical differences across subjects. Significantly activated regions are reported in [Table 1](#) and [Figure 4](#). These comprise clusters of more than four voxels in extent (voxel size was 3 × 3 × 3 mm = 27 mm<sup>3</sup>) with a *p* value of <0.05 corrected for multiple comparisons ([Kiebel et al., 1999](#)), with inference at the cluster level ([Poline et al., 1997](#)).

Anatomical search volumes were used to test for responses to motion in area MT/V5. These search volumes were defined as 20 mm diameter spheres centered around the following MNI coordinates. Left hemisphere: [-43, -70, -4], right hemisphere: [46, -67, -10] (average coordinates from following studies: [Buchel et al., 1998](#); [Kourtzi et al., 2002](#); [Rees et al., 2000](#); [Watson et al., 1993](#)).

### Image Used for Display

The mean image used for display in the figures was calculated by averaging the twelve 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 \(1999\)](#).

### Acknowledgments

J.S. would like to thank Wolfram Schultz for discussions and useful comments on an earlier version of the manuscript. K.J.F. and C.D.F. are supported by the Wellcome Trust; J.S. is supported by the Wellcome Trust, the British Council, and the James S. McDonnell Foundation. The contents of this study are solely the responsibility of the authors and do not necessarily represent the official views of the James S. McDonnell Foundation.

Received: July 14, 2004

Revised: November 22, 2004

Accepted: December 17, 2004

Published: February 16, 2005

### References

- Adolphs, R. (2003). Cognitive neuroscience of human social behaviour. *Nat. Rev. Neurosci.* 4, 165–178.
- Allison, T., Puce, A., and McCarthy, G. (2000). Social perception from visual cues: role of the STS region. *Trends Cogn. Sci.* 4, 267–278.

- Bassili, J.N. (1976). Temporal and spatial contingencies in the perception of social events. *J. Pers. Soc. Psychol.* 33, 680–685.
- Blakemore, S.J., Fonlupt, P., Pachot-Clouard, M., Darmon, C., Boyer, P., Meltzoff, A.N., Segebarth, C., and Decety, J. (2001). How the brain perceives causality: an event-related fMRI study. *Neuroreport* 12, 3741–3746.
- Blakemore, S.J., Boyer, P., Pachot-Clouard, M., Meltzoff, A., Segebarth, C., and Decety, J. (2003). The detection of contingency and animacy from simple animations in the human brain. *Cereb. Cortex* 13, 837–844.
- Blythe, P.W., Todd, P.M., and Miller, G.F. (1999). How motion reveals intention: categorising social interactions. In *Simple Heuristics that Make Us Smart*, G. Gigerenzer and P.M. Todd, eds. (Oxford: Oxford University Press), pp. 257–285.
- Brothers, L. (1990). The social brain: a project for integrating primate behaviour and neurophysiology in a new domain. *Concepts in Neuroscience* 1, 27–151.
- Bruce, C., Desimone, R., and Gross, C.G. (1981). Visual properties of neurons in a polysensory area in superior temporal sulcus of the macaque. *J. Neurophysiol.* 46, 369–384.
- Buchel, C., Josephs, O., Rees, G., Turner, R., Frith, C.D., and Friston, K.J. (1998). The functional anatomy of attention to visual motion. A functional MRI study. *Brain* 121, 1281–1294.
- Castelli, F., Happe, F., Frith, U., and Frith, C. (2000). Movement and mind: a functional imaging study of perception and interpretation of complex intentional movement patterns. *Neuroimage* 12, 314–325.
- Chao, L.L., Haxby, J.V., and Martin, A. (1999a). Attribute-based neural substrates in temporal cortex for perceiving and knowing about objects. *Nat. Neurosci.* 2, 913–919.
- Chao, L.L., Martin, A., and Haxby, J.V. (1999b). Are face-responsive regions selective only for faces? *Neuroreport* 10, 2945–2950.
- Damasio, H., Grabowski, T.J., Tranel, D., Hichwa, R.D., and Damasio, A.R. (1996). A neural basis for lexical retrieval. *Nature* 380, 499–505.
- Deichmann, R., Good, C.D., Josephs, O., Ashburner, J., and Turner, R. (2000). Optimization of 3-D MP-RAGE sequences for structural brain imaging. *Neuroimage* 12, 112–127.
- Desimone, R. (1991). Face-selective cells in the temporal cortex of the monkey. *J. Cogn. Neurosci.* 3, 1–8.
- Dittrich, W.H. (1993). Action categories and the perception of biological motion. *Perception* 22, 15–22.
- Duvernoy, H.M. (1999). *The Human Brain* (Vienna: Springer Verlag).
- Frith, C.D., and Frith, U. (1999). Interacting minds—a biological basis. *Science* 286, 1692–1695.
- Frith, U., and Frith, C.D. (2003). Development and neurophysiology of mentalizing. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 358, 459–473.
- Friston, K.J., Holmes, A.P., Worsley, K.J., Poline, J.B., Frith, C.D., and Frackowiak, R.S. (1995). Statistical parametric mapping in functional imaging: a general linear approach. *Hum. Brain Mapp.* 2, 189–210.
- Giese, M.A., and Poggio, T. (2003). Neural mechanisms for the recognition of biological movements. *Nat. Rev. Neurosci.* 4, 179–192.
- Hasselmo, M.E., Rolls, E.T., Baylis, G.C., and Nalwa, V. (1989). Object-centered encoding by face-selective neurons in the cortex in the superior temporal sulcus of the monkey. *Exp. Brain Res.* 75, 417–429.
- Haxby, J.V., Horwitz, B., Ungerleider, L.G., Maisog, J.M., Pietrini, P., and Grady, C.L. (1994). The functional organization of human extrastriate cortex: a PET-rCBF study of selective attention to faces and locations. *J. Neurosci.* 14, 6336–6353.
- Heider, F., and Simmel, M. (1944). An experimental study of apparent behaviour. *Am. J. Psychol.* 57, 243–259.
- Iacoboni, M., Koski, L.M., Brass, M., Bekkering, H., Woods, R.P., Dubeau, M.C., Mazziotta, J.C., and Rizzolatti, G. (2001). Reafferent copies of imitated actions in the right superior temporal cortex. *Proc. Natl. Acad. Sci. USA* 98, 13995–13999.
- Johnson, S.C. (2003). Detecting agents. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 358, 549–559.
- Kanwisher, N., McDermott, J., and Chun, M.M. (1997). The fusiform face area: a module in human extrastriate cortex specialized for face perception. *J. Neurosci.* 17, 4302–4311.
- Kiebel, S.J., Poline, J.B., Friston, K.J., Holmes, A.P., and Worsley, K.J. (1999). Robust smoothness estimation in statistical parametric maps using standardized residuals from the General Linear Model. *Neuroimage* 10, 756–766.
- Koski, L., Iacoboni, M., Dubeau, M.C., Woods, R.P., and Mazziotta, J.C. (2003). Modulation of cortical activity during different imitative behaviors. *J. Neurophysiol.* 89, 460–471.
- Kourtzi, Z., Bulthoff, H.H., Erb, M., and Grodd, W. (2002). Object-selective responses in the human motion area MT/MST. *Nat. Neurosci.* 5, 17–18.
- Martin, A., Wiggs, C.L., Ungerleider, L.G., and Haxby, J.V. (1996). Neural correlates of category-specific knowledge. *Nature* 379, 649–652.
- Martin, A., Ungerleider, L.G., and Haxby, J.V. (2000). Category specificity and the brain: the sensory/motor model of semantic representations of objects. In *The new cognitive neurosciences*, M.S. Gazzaniga, ed. (Cambridge, MA: MIT Press), pp. 1023–1036.
- Nielsen, J.M. (1958). *Memory and Amnesia* (Los Angeles: San Lucas Press).
- Opfer, J.E. (2002). Identifying living and sentient kinds from dynamic information: the case of goal-directed versus aimless autonomous movement in conceptual change. *Cognition* 86, 97–122.
- Oram, M.W., and Perrett, D. (1994). Responses of anterior superior temporal polysensory area (STPa) neurons to ‘biological motion’ stimuli. *J. Cogn. Neurosci.* 6, 99–116.
- Pelphrey, K.A., Mitchell, T.V., McKeown, M.J., Goldstein, J., Allison, T., and McCarthy, G. (2003). Brain Activity Evoked by the Perception of Human Walking: Controlling for Meaningful Coherent Motion. *J. Neurosci.* 23, 6819–6825.
- Perani, D., Cappa, S.F., Bettinardi, V., Bressi, S., Gorno-Tempini, M., Matarrese, M., and Fazio, F. (1995). Different neural systems for the recognition of animals and man-made tools. *Neuroreport* 6, 1637–1641.
- Perrett, D.I., Smith, P.A., Mistlin, A.J., Chitty, A.J., Head, A.S., Potter, D.D., Broennimann, R., Milner, A.D., and Jeeves, M.A. (1985). Visual analysis of body movements by neurones in the temporal cortex of the macaque monkey: a preliminary report. *Behav. Brain Res.* 16, 153–170.
- Picard, N., and Strick, P.L. (2001). Imaging the premotor areas. *Curr. Opin. Neurobiol.* 11, 663–672.
- Poline, J.B., Worsley, K.J., Evans, A.C., and Friston, K.J. (1997). Combining spatial extent and peak intensity to test for activations in functional imaging. *Neuroimage* 5, 83–96.
- Puce, A., and Perrett, D. (2003). Electrophysiology and brain imaging of biological motion. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 358, 435–445.
- Puce, A., Allison, T., Gore, J.C., and McCarthy, G. (1995). Face-sensitive regions in human extrastriate cortex studied by functional MRI. *J. Neurophysiol.* 74, 1192–1199.
- Rees, G., Friston, K., and Koch, C. (2000). A direct quantitative relationship between the functional properties of human and macaque V5. *Nat. Neurosci.* 3, 716–723.
- Samson, D., Apperly, I.A., Chiavarino, C., and Humphreys, G.W. (2004). Left temporoparietal junction is necessary for representing someone else’s belief. *Nat. Neurosci.* 7, 499–500.
- Saxe, R., and Kanwisher, N. (2003). People thinking about thinking people. The role of the temporo-parietal junction in “theory of mind”. *Neuroimage* 19, 1835–1842.
- Scholl, B.J., and Tremoulet, P.D. (2000). Perceptual causality and animacy. *Trends Cogn. Sci.* 4, 299–309.
- Schultz, R.T., Grelotti, D.J., Klin, A., Kleinman, J., Van der Gaag, C., Marois, R., and Skudlarski, P. (2003). The role of the fusiform face area in social cognition: implications for the pathobiology of autism. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 358, 415–427.

Schultz, J., Imamizu, H., Kawato, M., and Frith, C. (2004). Activation of the human superior temporal gyrus during observation of goal attribution by intentional objects. *J. Cogn. Neurosci.* *16*, 1695–1705.

Thornton, I.M., Rensink, R.A., and Shiffrar, M. (2002). Active versus passive processing of biological motion. *Perception* *31*, 837–853.

Toni, I., Thoenissen, D., and Zilles, K. (2001). Movement preparation and motor intention. *Neuroimage* *14*, S110–S117.

Tranel, D., Damasio, H., and Damasio, A.R. (1997). A neural basis for the retrieval of conceptual knowledge. *Neuropsychologia* *35*, 1319–1327.

Tremoulet, P.D., and Feldman, J. (2000). Perception of animacy from the motion of a single object. *Perception* *29*, 943–951.

Watson, J.D., Myers, R., Frackowiak, R.S., Hajnal, J.V., Woods, R.P., Mazziotta, J.C., Shipp, S., and Zeki, S. (1993). Area V5 of the human brain: evidence from a combined study using positron emission tomography and magnetic resonance imaging. *Cereb. Cortex* *3*, 79–94.

Wohlschlaeger, A., Gattis, M., and Bekkering, H. (2003). Action generation and action perception in imitation: an instance of the ideomotor principle. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* *358*, 501–515.