Animations of simple geometric shapes are readily interpreted as animate agents engaged in meaningful social interactions. Such animations have been shown to activate brain regions implicated in the detection of animate motion, in understanding the intentions of others as well as areas commonly linked to the processing of social and emotional information. However, attribution of animacy does not occur under all circumstances and the precise conditions under which specific regions are activated remains unclear. In a functional magnetic resonance imaging study we manipulated viewers’ perspective to assess the part played by selective attention. Participants were cued to attend either to spatial properties of the movements or to the kind of social behavior it could represent. Activations that occurred to the initial cue, while observing the animations themselves and while responding to a postpresentation probe, were analyzed separately. Results showed that activity in the social brain network was strongly influenced by selective attention, and that remarkably similar activations were seen during film viewing and in response to probe questions. Our use of stimuli supporting rich and diverse social narratives likely enhanced the influence of top-down processes on neural activity in the social brain.

**Keywords:** amygdala, animacy, autism, dorsomedial prefrontal cortex, social cognition

**Introduction**

Animated movements of abstract geometric shapes can readily be interpreted as depicting social events in which animate agents are engaged in intentional activity such as pursuit, play, or fighting (Heider and Simmel 1944; Scholl and Tremoulet 2000; Barrett et al. 2005). That these simple graphical renderings give rise to intricate conceptual meanings has attracted considerable interest from social neuroscientists. Such animations provide an ideal platform for investigating brain areas involved in the perception of animate motion versus its mechanical counterparts as well as those areas involved in the understanding of causality, of “Theory of Mind” and of social interactions that are associated with particular movement dynamics.

Several studies have shown that brain areas linked to biological motion processing, social perception, the processing of the intentions of others, emotional information, and social knowledge can be activated when viewing Heider-Simmel animations. They include the lateral fusiform gyrus (FG), the temporoparietal junction (TPJ), the amygdala, the posterior cingulate cortex (PCC), the temporal poles (TPs) and the medial prefrontal cortex (Castelli et al. 2000, 2002; Martin and Weisberg 2003; Schultz et al. 2003; Ohnishi et al. 2004), consistent with the idea of a distributed social brain network (Brothers 1990). The nature of the activations is nevertheless subject to considerable variation. Regional activation varies as a function of the precise kinetic properties of the animations (e.g., Blakemore et al. 2003), and with the nature of the viewing task itself (e.g., Schultz et al. 2003). The typical patterns of activation to animations usually interpreted as having social content can also be markedly reduced in some individuals—most notably those with autistic spectrum disorders (Castelli et al. 2002). There is also evidence that Heider-Simmel animations, being ambiguous, do not of necessity invoke social interpretations. For example, Martin and Tversky (2003) have shown that healthy individuals, on initial exposure interpret Heider-Simmel animations as involving mechanical rather than intentional movements (see Epley et al. 2007 for review).

Here, we focus on the role of selective attention in the interpretation of animate motion and in the preparatory and response phases that precede and follow the viewing itself. Our aim is to clarify the part played by top-down influences on regional activation. There is mounting evidence of the importance of top-down influences in the interpretation of ambiguous material within areas linked to the processing of social stimuli. Kingstone et al. (2004) presented healthy participants with ambiguous pictures and obtained different patterns of activation when they were biased to see the images as an inanimate entity (a car) or as an animate one (eyes and a hat). The right superior temporal sulcus (STS) was only observed to activate in the latter condition. In the context of economic games, Gallagher et al. (2002) and Rilling et al. (2004) found different patterns of neural activity when participants thought they were playing with/against another person or a computer. In McCabe et al. (2001) and Gallagher et al. (2002) this difference was restricted to the dorsomedial prefrontal cortex (DMPFC), whereas in Rilling et al. (2004) increases were seen in DMPFC, PCC, TPJ, and STS. Kumaran and Maguire (2005) found increased activity in FG, STS, TPJ, PCC, TP, and DMPFC when people thought about the social, rather than spatial, relations between the same individuals (see also Mitchell et al. 2004).

Research specifically using Heider-Simmel style animations has also involved a range of task conditions. Several studies have relied on the most unconstrained form of task in which observers passively view animations (Castelli et al. 2000, 2002; Martin and Weisberg 2003; Ohnishi et al. 2004). In 1 previous study, Castelli et al. (2000) did provide prior knowledge of the type of animation about to be encountered (“Theory of Mind,” “Goal Directed,” or “Random Motion”) on 50% of occasions. They found no significant differences in activation as a function of that prior knowledge.
Other studies suggest a role for top-down influences on patterns of activation. Schultz et al. (2003) presented "Theory of Mind" animations and asked their participants either to decide whether the animated shapes were friends or not, or to pretend that the shapes were cars and decide whether they shared the physical property of being equally heavy. Whereas a contrast between the physical and social decisions revealed activation only in the dorsal bank of the intraparietal sulcus, the opposite contrast between attention to social and physical properties showed more widespread activation in the FG, amygdala, TP, STS, and DMPFC. Schultz et al. (2004) created animations depicting a pursuit scenario between 2 objects, in which the chasing object used different strategies to reach the target object. Attending to the pursuer's strategy induced slightly greater activation in the left superior temporal gyrus than attending to the outcome of the chase. Blakemore et al. (2003) developed animations that varied both whether the movement of abstract figures had animate properties and the contingencies that held between the movement of 2 figures. Viewers' attention was either directed at the contingencies that held between the 2 figures or left undirected. Right middle frontal gyrus and the left STS were only engaged when attention was directed to the contingent nature of the movement patterns. However, Blakemore et al. (2003) found no evidence of differential engagement of TPs, amygdala, right STS, or DMPFC when attention was directed at salient intentional contingencies. One possibility is that these areas only respond when animations contain cues that support the formation of schematically rich representations of mental states of others interacting in social ways, and then only when attention is directed towards salient features.

Given the ambiguous nature of Heider–Simmel animations, and findings suggesting that "social" brain areas such as STS are also activated in the processing of nonsocial motion processing (Frith and Frith 2003; Dakin and Frith 2005), together with uncertainty as to the relative roles of bottom-up versus top-down social processing deficits in autism (Behrmann et al. 2006; Bird et al. 2006), there is a pressing need to acquire more data on regional brain activation under circumstances where identical animations are viewed from different observational perspectives, conditions required to rule out simple stimulus-driven effects. Our study therefore sought to extend previous work by focusing on the effects of top-down attentional perspective, in the context of relatively rich animation scenarios of simple shapes that are open to interpretation in terms of intentional and emotional attributes.

Our attentional manipulation was realized by directly cueing the participants to pay attention to social or spatial aspects of the figures' behavior and then probing them after viewing the animations with a question about either the social behavior of the figures or their use of physical space. The animations were developed to sample movement patterns characteristic of affiliative, antagonistic, and indifferent behaviors (e.g., approach, avoidance, contact strength—Michotte 1950) in order to ensure that when asked about social attributes they would have attended to both interpersonal and affective dimensions. In order to further clarify the role of top-down processes, we scanned the participants while attending to the initial cue and when responding to the final probe, in addition to "on-line" viewing of the animations. By drawing attention to the social attributes of schematically rich behaviors, we predicted that, the full spectrum of brain areas implicated in social cognition

Figure 1. Schematic representation of the sprites and sprite world.

In the affiliative animations, the 2 sprites entered from different sides of the sprite world. They approached each other and touched or moved in a mutually coordinated way throughout. They then left the sprite world together at a gentle pace. In the antagonistic animations, the 2 sprites entered from different sides of the sprite world and approached each other. In this case, they initially kept at a small distance from each other, while moving around slowly. In one half of the animations, the circles then repeatedly approached each other, made brief contact and retreated rapidly, a pattern suggesting physical aggression. In the other half they never actually touched each other, but moved in close proximity to each other suggestive of suspicion. At the end of the sequence, the 2 sprites left the scene in different directions.

In the indifferent animations, the 2 sprites again entered from different sides of the sprite world and passed each other without interacting. The sprites continued to move around, sometimes stopping and changing direction, but never approaching each other or moving in any way that might suggest an influence of one on the other. As with the antagonistic animations, the sprites left the scene independently at a gentle pace.

**Tasks**

During scanning, each animation was preceded by a cue word, either Behavioral or Spatial, specifying the nature of the probe that would follow the next animation, thereby constraining the perspective from which the animations were to be viewed. For the Behavioral cue, participants were instructed to identify what kind of interaction might be happening between the 2 circles. For the Spatial cue, participants were instructed to pay attention to various aspects of the motion of the 2 circles, such as their speed, trajectory, position of entering/exiting the scene, etc. After the presentation of each animation, a probe statement appeared describing the contents of the animation, and the participant had to decide (true/false) if the statement could appropriately describe the behavior in the animation just viewed. Examples of Behavioral statements included "Soldiers engaged in hand to hand combat," "People were shopping in a supermarket," and "An old lady was helped by a friend to carry her bags." Examples of Spatial statements included "The circles passed each other only once" and "The blue circle collided with one of the lines." Behavioral and Spatial probe statements were matched for number of words and syllables and had been pretested to reliably elicit either a true or false response to the particular animation to which it referred. Each animation and each probe statement was presented only once, with 56% true and 44% false responses to the probes. The cue word was presented for 1.8 s, the animation for 14 s, and the probe statement for 7.5 s. In addition, a baseline fixation condition was used. In this condition, the cue word Cross appeared, followed by a fixation cross for 14 s, and then a statement saying that the participants should press either the left or right response button. Temporal jitter was introduced between the cue, animation and probe statement phases to ensure they could be modeled separately. There were 12 examples of each of the animations in each of the 2 conditions (Behavioral or Spatial cue) plus baseline condition, presented in pseudorandom order. The experiment took an average of 16.3 min to complete.

**Post-task Ratings**

Participants were invited to return to do a follow-up ratings task. They were asked to classify the behavior shown in each of the animations they had seen in terms of the extent to which the sprites appeared animate or alive, and the emotional valence associated with the animation, using visual analogues scales with lines 11.5 cm long. For the animacy judgment, ratings were made by marking a point on the line, anchored by the terms "not alive" at one end and "fully alive" at the other. For valence ratings, the scale ranged from "positive" at one end through "indifferent" labeled at the center point of the line, to "negative" at the other end.

**Image Acquisition**

Blood oxygenation level-dependent contrast functional images were acquired with echo-planar $T_2^*$-weighted (EPI) images using a Medspec (Bruker, Ettlingen, Germany) 3-T MR system with a head coil gradient set. Each image volume consisted of 21 interleaved 4-mm thick slices (interslice gap: 1 mm; in-plane resolution: 2.2 × 2.2 mm; field of view: 20 × 20 cm; matrix size: 90 × 90; flip angle: 74°; echo time: 27.5 ms; voxel bandwidth: 143 kHz; repetition time 1.6 s). Slice acquisition was transverse oblique, angled to avoid the eyeballs, and covered most of the brain. Six hundred and ninety-five volumes were acquired, and the first 6 volumes were discarded to allow for $T_1$ equilibration.

**Image Analysis**

Neuroimaging data were analyzed using statistical parametric mapping software (Wellcome Trust Centre for Neuroimaging, London, UK). Standard preprocessing was conducted, comprising slice timing correction, realignment, undistortion (Cusack et al. 2003), and mask normalization of each participant’s EPI data to the Montreal Neurological Institute (MNI) International Consortium for Brain Mapping template (Brett, Leff, et al. 2001). Images were resampled into this space with 2-mm isotropic voxels and smoothed with a Gaussian kernal of 8-mm full-width at half-maximum. For the epochs of the animations and probe statements, condition effects were estimated for each participant at each voxel using boxcar regressors for the 14-s animation period and 7.5-s probe statement period, respectively, convolved with a canonical hemodynamic response function (HRF) in a general linear model, with spatial realignment parameters included as regressors to account for residual movement-related variance. Activation to the cue word was modeled using a canonical HRF, plus time and dispersion derivatives. A high-pass filter was used to remove low-frequency signal drift, and the data were also low-pass filtered with the canonical HRF. Activation contrasts between conditions were estimated for each participant at each voxel, producing statistical parametric maps. Random-effects analysis was conducted to analyze data at a group level.

We used small volume correction (SVC) (Worsley et al. 1996) for multiple comparisons applied at $P < 0.05$ (family-wise error), following an initial thresholding of $P < 0.002$ (uncorrected). Amygdala, TP, and PCC regions of interest (ROIs) were defined using structural templates derived by automated anatomic labeling (Tzourio-Mazoyer et al. 2002). The TP ROI resulted from the sum of the middle and superior TPs structural templates. Spherical ROIs (10-mm radius spheres) were created for the remaining ROIs. For the lateral FG (central coordinates $-12, -49, -19; 40, -48, -16$), TPJ $(-56, -56, 17; 57, -53, 17)$, DMPCP (BA 9/10/32) ($4, -50, 7; 55, 28$), and ventromedial prefrontal cortex ($42, -8, 12$), by computing the average of the reported activation coordinates for these regions across previous imaging studies of animate motion (Castelli et al. 2000, 2002; Martin and Weisberg 2003; Schultz et al. 2003; Ohnishi et al. 2004). For the STS we used the coordinates $(54, -34, 4)$ taken from Schultz et al. (2003). For the dorsolateral prefrontal cortex (DLPFC) $(54, 36, 24)$, dorsal anterior cingulate cortex (dACC) $(4, 14, 36)$, and parietal cortex $(37, -53, 40)$ we used coordinates from Duncan and Owen (2000). For the frontal eye fields (FEF) we used the coordinates $(352, -2, -47)$ from Silvanto et al. (2006), and for the motion-selective homolog of macaque area MT (hMT) we used the coordinates $(352, -60, 5)$ from Blakemore et al. (2001).

For anatomical labeling purposes, activation coordinates were transformed into the Talairach and Tournoux (1988) coordinate system using an automated nonlinear transform (Brett, Christoff, et al. 2001) and labeled with reference to the Talairach Demon database (http://ric.uthscsa.edu/projects/talairachdaemon.html). For visualizing activations, group maps are overlaid on the ICBM 152 structural template, an average $T_1$-weighted image of 152 individuals coregistered to MNI space. Activations are reported using $(x, y, z)$ coordinates in MNI standardized space.

**Results**

**Behavioral and Rating Data**

Participants took an average of 3.3 s to respond to the probes and the times to respond showed no main effects of scenario (affiliative, antagonistic, and indifferent) $F_{1, 12} = 0.84, P = 0.46$,
task (Behavioral, Spatial) \( F_{1,12} = 0.03, P = 0.87 \), or response (true, false) \( F_{1,12} = 0.20, P = 0.66 \) and there were no interactions between category, type of statement, and task. Participants provided the expected response to 92% of the probes and error rates were comparable across the types of animations (affiliative, antagonistic, and indifferent) \( \chi^2 = 2.9, df = 2, P = 0.24 \), for the 2 viewing tasks (Behavioral, Spatial) \( \chi^2 = 0.072, df = 1, P = 0.79 \) and for the 2 responses (true, false) \( \chi^2 = 0.129, df = 1, P = 0.72 \). There was therefore no evidence to indicate that the Behavioral and Spatial probe questions differed in difficulty.

The post-task visual analogue scale based valence ratings (see methods section under “post-task ratings”) confirmed that the films were rated as intended (affiliative—positive; antagonistic—negative; indifferent—neutral). There was however, some evidence that the animated materials differed in the nature of their most likely interpretation. The indifferent set of animations was rated as less alive than the affiliative (Z = −3.01, \( P < 0.01 \)) and antagonistic animations (Z = −3.01, \( P < 0.01 \)), which did not differ from each other (affiliative mean 9.5 SD 2.24; antagonistic mean 9.3 SD 2.19, indifferent mean 5.2 SD 2.09).

fMRI Data

Preparatory Cues

When the response in the ROIs to each of the Behavioral and Spatial cues was compared with fixation, there was significant activation in hMT (Behavioral: 48, −68, 2, Z = 3.56, \( P_{SVC} = 0.024 \); Spatial: −50, −68, 6, Z = 3.75, \( P_{SVC} = 0.012 \) and 48, −68, 2, Z = 3.53, \( P_{SVC} = 0.023 \)); in the posterior parietal ROI (Behavioral: −28, −52, 46, Z = 3.26, \( P_{SVC} = 0.053 \); Spatial: −30, −52, 48, Z = 4.08, \( P_{SVC} = 0.004 \) and 30, −56, 44, Z = 3.19, \( P_{SVC} = 0.055 \)); and in FEFs (Behavioral: −26, −2, 54, Z = 5.07, \( P_{SVC} < 0.001 \) and 24, −4, 52, Z = 4.72, \( P_{SVC} < 0.001 \); Spatial: −24, −4, 52, Z = 4.95, \( P_{SVC} < 0.001 \) and 24, −4, 52, Z = 4.55, \( P_{SVC} < 0.001 \)) (Fig. 2).

When the response in the ROIs to the Behavioral cue was compared with that of the Spatial cue, there was no significant activation in any of our ROIs.

For the opposite contrast (Spatial > Behavioral cue), there was increased activity in the posterior parietal ROI (−30, −50, 42, Z = 3.85, \( P_{SVC} = 0.01 \)); DLPFC (−34, 46, 24, Z = 4.07, \( P_{SVC} = 0.005 \) and 30, 42, 24, Z = 3.89, \( P_{SVC} = 0.009 \)); dACC (0, 16, 44, Z = 3.57, \( P_{SVC} = 0.022 \); and FEFs (−40, 2, 52, Z = 3.21, \( P_{SVC} = 0.055 \)).

Animation Viewing

Regions showing increased activation during viewing of interactive animations (affiliative and antagonistic) rated as strongly animate, relative to noninteractive (indifferent) animations rated as more ambiguously animate. When contrast- viewer activity for the highly interactive scenarios, rated as highly animate (affiliative and antagonistic) relative to the indifferent scenarios, rated as more weakly animate, there was increased activity in FG (bilaterally) (−42, −40, −24, Z = 3.84, \( P_{SVC} = 0.011 \) and 48, −48, −20, Z = 3.89, \( P_{SVC} = 0.009 \)), right TPJ (54, −16, 12, Z = 3.54, \( P_{SVC} = 0.029 \)), right STS (56, −40, 2, Z = 4.64, \( P_{SVC} = 0.001 \)), amygdala (−18, 0, −20, Z = 4.06, \( P_{SVC} = 0.002 \) and 24, 0, −24, Z = 3.19, \( P_{SVC} = 0.026 \)), and hMT (48, −60, 6, Z = 3.81, \( P_{SVC} = 0.012 \) and −48, −62, 6, Z = 3.46, \( P_{SVC} = 0.032 \)).

Regions showing increased activation during viewing when animations are preceded by the Behavioral cue, compared with the Spatial cue. All of the social brain ROIs showed increased activation when animation viewing followed the Behavioral cue relative to the Spatial cue: right FG, amygdalae (bilaterally), PCC (bilaterally), right TPJ, right STS, DMPFC (bilaterally), and TP (bilaterally) (Fig. 3, Table 1). Activation in right TPJ, right STS, right TP, right amygdala, bilateral FG, and right PCC was also increased when comparing animation viewing following the Behavioral cue relative to baseline, as was activation in posterior parietal cortex, DLPFC, hMT, and FEFs (see online Supplementary Table 1).

Does the modulatory effect of task cue (Behavioral vs. Spatial) depend on the manifest emotionality of the animations? When comparing the emotionally valenced (affiliative and antagonistic) animations relative to the neutral, indifferent animations for the Behavioral > Spatial contrast, there was no significantly increased activity in any of our predefined ROIs, suggesting that increased activation for the Behavioral > Spatial contrast cannot be due to the indirect influence of the manifest emotionality of the animations.

Figure 2. Regional activations to the Behavioral and Spatial cue events relative to the fixation cue. (A) Activation in the FEF. (B) Activation in hMT. Cross-hair centered on group-average location of hMT reported in Downing et al. (2007).
Regions showing increased activation during film viewing when films are preceded by the Spatial cue, compared with the Behavioral cue. For the contrast Spatial > Behavioral, increased activity was seen in the posterior parietal cortex (−32, −48, 42, Z = 3.87, \(P_{\text{SVC}} = 0.009\) and 38, −44, 46, Z = 3.09, \(P_{\text{SVC}} = 0.07\)), DLPFC (−34, 38, 32, Z = 3.37, \(P_{\text{SVC}} = 0.037\) and 38, 40, 32, Z = 4.03, \(P_{\text{SVC}} = 0.005\)), dACC (2, 18, 44, Z = 3.60, \(P_{\text{SVC}} = 0.02\)), and FEFs (−30, 2, 46, Z = 5.47, \(P_{\text{SVC}} < 0.0001\) and 32, −4, 54, Z = 3.48, \(P_{\text{SVC}} = 0.027\)), but not in hMT. This difference did not vary as a function of animation type. Activation in all these regions, and also in the vicinity of hMT was increased when comparing animation viewing following the Spatial cue relative to fixation (data not presented).

**Probe Statements**

Regions showing increased activation in response to Behavioral probe statements, compared with the Spatial probe statements. All social brain ROIs showed increased activation in response to Behavioral probes relative to Spatial probes: right FG, amygdala (bilaterally), PCC (bilaterally), STS (bilaterally), right TPJ, TPs (bilaterally), and DMPFC (bilaterally) (Fig. 4, Table 2). There were no significant differences in these ROIs when comparing probes related to the emotional versus the indifferent, neutral animations.

**Table 1**

Neural regions showing increased activation to the animations during selective attention to Behavioral versus Spatial properties

<table>
<thead>
<tr>
<th>Brain regions</th>
<th>MNI coordinates</th>
<th>Z score</th>
<th>(P_{\text{SVC}})</th>
</tr>
</thead>
<tbody>
<tr>
<td>PCC</td>
<td>−6 −52 22</td>
<td>3.33</td>
<td>0.029</td>
</tr>
<tr>
<td></td>
<td>13 −52 30</td>
<td>3.28</td>
<td>0.026</td>
</tr>
<tr>
<td>DMPFC</td>
<td>−8 60 24</td>
<td>4.06</td>
<td>0.005</td>
</tr>
<tr>
<td></td>
<td>4 56 20</td>
<td>4.25</td>
<td>0.003</td>
</tr>
<tr>
<td>TPJ</td>
<td>54 −50 14</td>
<td>4.52</td>
<td>0.001</td>
</tr>
<tr>
<td>STS</td>
<td>50 −30 −4</td>
<td>4.08</td>
<td>0.005</td>
</tr>
<tr>
<td>TP</td>
<td>−44 8 −30</td>
<td>4.43</td>
<td>0.004</td>
</tr>
<tr>
<td></td>
<td>40 26 −24</td>
<td>3.74</td>
<td>0.042</td>
</tr>
<tr>
<td>Amygdala</td>
<td>26 0 −24</td>
<td>3.34</td>
<td>0.016</td>
</tr>
<tr>
<td>FG</td>
<td>42 −54 −18</td>
<td>3.86</td>
<td>0.009</td>
</tr>
</tbody>
</table>

Note: NB for abbreviations see Figures 3 and 4.

**Table 2**

Neural regions showing increased activation to Behavioral relative to the Spatial probes

<table>
<thead>
<tr>
<th>Brain regions</th>
<th>MNI coordinates</th>
<th>Z score</th>
<th>(P_{\text{SVC}})</th>
</tr>
</thead>
<tbody>
<tr>
<td>PCC</td>
<td>0 −50 26</td>
<td>4.52</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>2 −50 28</td>
<td>4.45</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>DMPFC</td>
<td>−8 58 34</td>
<td>5.44</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td></td>
<td>2 58 28</td>
<td>5.26</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>TPJ</td>
<td>−52 −64 22</td>
<td>3.19</td>
<td>0.06</td>
</tr>
<tr>
<td>STS</td>
<td>58 −60 22</td>
<td>4.16</td>
<td>0.004</td>
</tr>
<tr>
<td></td>
<td>−52 −32 2</td>
<td>3.65</td>
<td>0.018</td>
</tr>
<tr>
<td>TP</td>
<td>−44 26 −20</td>
<td>3.95</td>
<td>0.019</td>
</tr>
<tr>
<td>Amygdala</td>
<td>44 20 −30</td>
<td>4.53</td>
<td>0.003</td>
</tr>
<tr>
<td></td>
<td>−20 −8 −16</td>
<td>4.33</td>
<td>0.001</td>
</tr>
<tr>
<td>FG</td>
<td>30 4 −28</td>
<td>3.92</td>
<td>0.003</td>
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<tr>
<td></td>
<td>42 −48 −22</td>
<td>4.31</td>
<td>0.002</td>
</tr>
</tbody>
</table>

**Figure 3.** Regional activations to the animations following the Behavioral relative to the Spatial cue. (A) PCC and DMPFC. (B) Right TPJ and anterior STS. (C) Amygdala. (D) FG. (E) Parameter estimates.

**Figure 4.** Regional activations to the Behavioral relative to the Spatial probe statements. (A) PCC and DMPFC. (B) Right TPJ and anterior STS/TPs. (C) Amygdala. (D) FG. (E) Parameter estimates.
Amygdala, left FG, left STS, TPJ, TP, and DMPFC were also more active when comparing response to the Behavioral probes relative to the control condition (online Supplementary Table 2).

**Regions showing increased activation in response to Spatial probe statements, compared with the Behavioral probe statements.** For the opposite contrast (Spatial > Behavioral probes) only the left posterior parietal cortex ROI showed increased activation (−36, −48, 44, \(Z = 4.72, P_{\text{FWE}} = 0.001\)).

Relative to baseline, both the Spatial and Behavioral probes produced increased activation in posterior parietal cortex, dACC and FEFs (online Supplementary Table 3).

For each of the 3 phases (cue, animation, probe statements), regions surviving a threshold of \(P < 0.05\), whole brain corrected (family-wise error), with a cluster extent minimum of 5 voxels, for the Behavioral versus Spatial and Spatial versus Behavioral contrasts are presented in Table 3. The only region outside our predefined ROIs more active for the Behavioral versus Spatial contrast was the right parahippocampal gyrus, during the response to the probe statements.

**Discussion**

We examined the influence of manipulating observers’ selective attention, on brain activity in preparation for, during, and in response to probe questions concerning animations of simple geometric shapes that could be interpreted as animate agents engaged in meaningful social interactions. This was achieved by precueing participants to attend either to the social behavior underlying their interaction or to the spatial aspects of their movement patterns. Our design allowed us to analyze separately brain activity to the cue, to the animations, and to the probe statements. Several novel findings emerged.

**Activations during the Preparatory Cue Period**

Relative to the control Cross condition, presentation of both the Behavioral and Spatial cue words lead to increased activation in the FEF and posterior parietal cortex, as well as in motion sensitive area hMT. Relative to the Behavioral cue, the Spatial cue produced increased activation in posterior parietal cortex, the vicinity of the FEF, the DLPFC, and dACC. These results are consistent with prior studies on the preparatory deployment of spatial attention and attention to motion (e.g., Luks and Simpson 2004; Caplan et al. 2006). The same frontoparietal regions have also been implicated in nonspatial orienting, for example to semantic categories (Cristescu et al. 2006), and may underpin a general purpose attentional orienting network (Corbetta and Shulman 2002).

Notably, there was a lack of Behavioral cue-related activity in social brain regions. This relative lack of preparatory activity might relate to Raichle and colleagues’ notion of a default brain state (Raichle and Gusnard 2005)—in particular the idea that social brain regions form part of a default mental state involved in constantly monitoring for self-relevant events (Iacoboni et al. 2004). If this is indeed the default state then there is little need for a “baseline shift”—these systems are constantly “primed,” ready for action, as part of our default mode of interacting with the world. Alternatively, the Behavioral cue might be more indeterminate than the Spatial cue, and hence not trigger specific preparatory processes beyond those involved in motion processing and perceptual event segmentation (Zacks et al. 2001) (i.e., hMT, FEF), which have been argued to play important roles in social perception (Michotte 1950; Newton 1980; Premack and Premack 1995; Baldwin and Baird 2001).

**Activations during Animation Viewing**

Again, during film viewing, and comparing both cues, there was increased activity in regions implicated in motion processing, event segmentation, sustained attentive tracking, and spatial working memory, including the posterior parietal cortex, hMT, FEFs, and DLPFC (Culham et al. 1998). Increased activity following the Spatial relative to the Behavioral cue was found not only in the posterior parietal cortex (Schultz et al. 2003), but also in DLPFC, FEF, and dACC. This suggests an increased demand on sustained attentional tracking and spatial working memory processes in the Spatial condition, presumably as participants could rely on “gist”-based knowledge to answer the Behavioral probe statements, rather than encoding the full detail of sprite motion. Notably, there was no difference in activity in area hMT between the 2 conditions, consistent with a role for motion cues in the perception of intention and social behaviors.

When comparing activation to the highly interactive, strongly animate (antagonistic and affiliative), relative to the more weakly animate (indifferent) animations, regardless of attentional set, we saw activity in regions previously implicated in processing biological motion and animacy (see introduction). These included TPJ, STS, FG and amygdala, as well as activity in motion processing areas including hMT, but not in DMPFC, PCC, or TP, consistent with the former, but not the latter, areas in detecting animacy/social interactivity from perceptual/motion cues (Allison et al. 2000; Schultz et al. 2003; Heberlein and Adolphs 2004; Frith and Frith 2006). However, the animations also differed in emotional valence, and so this comparison cannot unambiguously disentangle responses to animacy from those due to manifest emotion.

More importantly, similar to Schultz et al. (2003), when comparing animation viewing following the Behavioral versus the Spatial cue, there was increased activity in all our social brain ROIs: the amygdala, PCC, right FG, right TPJ, right STS, TPs, and DMPFC, demonstrating that activity in all these areas is

<table>
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<tr>
<td>Neural regions showing increased activation at (P &lt; 0.05) whole brain corrected, cluster minimum 5 voxels for key contrasts</td>
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<tr>
<th>Brain regions</th>
<th>MNI coordinates</th>
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<td>Cues</td>
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<td>Behavioral versus Spatial No suprathreshold voxels</td>
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<tr>
<td>Spatial versus Behavioral Cerebellum</td>
<td>10 −61 −10</td>
<td>5.42</td>
<td>0.007</td>
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<tr>
<td>Animations</td>
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<tr>
<td>Behavioral versus Spatial DMPFC</td>
<td>12 50 36</td>
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<td>0.036</td>
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<tr>
<td>Spatial versus Behavioral Middle frontal gyrus</td>
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<td>5.47</td>
<td>0.005</td>
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<td>Phrases</td>
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<tr>
<td>Behavioral versus Spatial Amygdala</td>
<td>26 −12 −11</td>
<td>5.38</td>
<td>0.006</td>
</tr>
<tr>
<td>DMPFC</td>
<td>−8 56 29</td>
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<td>0.004</td>
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<tr>
<td>Parahippocampal Gyrus</td>
<td>2 57 23</td>
<td>5.26</td>
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<tr>
<td>Spatial versus Behavioral No suprathreshold voxels</td>
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<td>Parahippocampal Gyrus</td>
<td>16 −33 −7</td>
<td>5.54</td>
<td>0.002</td>
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strongly influenced by selective attention to the social meanings of the movements. In Schultz et al. (2003), different films were used for the social and physical decisions, and so an influence of stimulus material on those findings cannot be excluded. Our results extend those findings by showing that, for identical stimulus materials, a manipulation of selective attention towards social meaning increases activity in essentially all areas implicated in social processing. This strikingly demonstrates the widespread influence of goal-directed selective attention, and supports the idea of a distributed social brain network (Brothers 1990).

Wheatley et al. (2007) have very recently reported similar widespread increases in activity throughout the social brain when people were biased to interpret the same moving shapes as either animate (e.g., ice-skater) or inanimate (e.g., spinning top), although they did not find differences in the TPs. Their study manipulated the background context in which the shapes appeared. It is logically however, possibly, that the background contexts themselves contained certain stimuli that could drive areas of the social brain in a bottom-up fashion. In our study, all perceptual inputs were identical in both social and nonsocial conditions.

Our results and those of Wheatley et al. (2007; see also Kumaran and Maguire 2005) contrast with previous studies manipulating social attention reporting relatively focal top-down influences, notably in DMPFC (see Introduction). Sugase et al. (1999) argue that the ability of neurons in visual temporal cortex to make fine social perceptual distinctions depends on feedback from more anterior regions including prefrontal cortex and amygdala. Frith and Frith (2006) argue that activity in DMPFC is concerned with the “set” appropriate to social tasks and is the source of top-down signals that modify signal processing in more posterior brain regions such as STS, concerned with the analysis of social signals. Although our results are consistent with these suggestions, they suggest there may be multiple neural sources of social attention.

One issue with interpreting the main effect of cue (Behavioral vs. Spatial) when viewing the animations is that some of the scenarios depicted were emotional—one could argue that differences in brain activity for this contrast activity reflect a “side-effect” of increased attention to emotion in the social condition. Importantly, we found no significant differences in activity in any ROI, for the manifestly emotional scenarios relative to the neutral scenarios, suggesting that manifest emotion per se is not driving differential activation in these regions under the Behavioral cue (see also Martin and Weisberg 2003).

Activations during Probe Statements
A key feature of our experimental design was the investigation of the brain responses to probe statements concerning the social interactions depicted in the animations, in the absence of activity triggered by the stimuli themselves. Relative to a low-level decision baseline, activation was seen to both Behavioral and Spatial probe statements in the posterior parietal cortex, FEF and dACC. These joint activations likely reflect activity in a system responsible for the planning and execution of reading saccades (Leff et al. 2000). As with the processing of the cue and when viewing the animations, there was increased activity in the posterior parietal cortex for the Spatial probes relative to the Behavioral probes, consistent with the well known involvement of parietal regions in spatial cognition, including spatial imagery, reasoning, problem solving, and memory (Cabeza and Nyberg 2000).

With regard to our primary focus, the Behavioral versus Spatial contrast, with exception of the left TPJ and left FG, all remaining social brain ROIs showed increased activation. This suggests modulation of all these regions in the absence of any direct perceptual input, including regions linked to bottom-up elements of social perception (Allison et al. 2000; Frith and Frith 2006) and social behavior (Amaral 2003), when participants respond to probe statements concerning the social meaning of the interactions. That is, merely thinking about the social properties of a remembered stimulus seems to be sufficient to engage all these brain regions (Bargh 2006). These activations were also seen relative to a low-level baseline condition, suggesting they are not the result of relative deactivations to the Spatial probes, but are true activations (Pessoa et al. 2005).

A notable feature of the probe statements is that they did not ask explicitly about complex mental states, such as beliefs, but rather required participants to consider the interactions of the figures in terms of rather generic situations involving social agents sampled across quite diverse domains (e.g., shopping, playing, fighting, visiting an art gallery, business activities, etc.). Activation in certain brain regions, for example, TPJ could result from the spontaneous use of component Theory of Mind processes (Saxe 2006). Additionally, to answer the rather generic Social probe statement, as opposed to the much more referentially specific Spatial probe statements, participants presumably utilize higher-order knowledge structures such as models, scripts, schemas, narratives, or context frames that represent generic knowledge. People understand their social worlds via schemas for personalities, selves, roles, groups (stereotypes), social events, emotional episodes, and narratives, which guide encoding, remembering, and responding (Parkinson 1995; Fiske 2004).

The anterior TPs have been argued to play a critical role in social concept processing (Zahn et al. 2007), in narrative processing (Maguire et al. 1999), in social schemas (Frith and Frith 2003), and in emotional context frames (together with the parahippocampal cortex) (Mobbs et al. 2006). The amygdala has been linked to emotional gist memory (Adolphs et al. 2005). The DMPFC has also been implicated in schema-level knowledge representation. For example, Heberlein and Saxe (2005) found that DMPFC was activated when participants made personality judgments, whereas Teasdale et al. (1999) found increased DMPFC activation when viewing pairs of pictures and captions which when combined formed a coherent (emotional) schematic model of “implicational meanings” (Teasdale and Barnard 1993). DMPFC and PCC have also been implicated in autobiographical memory retrieval and prospection (Svoboda et al. 2006; Buckner and Carroll 2007). There are strong narrative and schematic influences on both autobiographical memory recall and prospective memories (Eldridge et al. 1994), suggesting an interesting reason for such overlap. We are currently examining how individual differences in schema elaboration modulate activity in these regions to social animations.

Our data confirm a role for TPs, DMPFC, and PCC in higher-level aspects of social cognition, perhaps related to representation of complex social knowledge structures, but additionally suggest that a rather broad network of structures is activated when participants access and utilize social knowledge,
including FG and STS, regions often argued to support social perception rather than social knowledge (Allison et al. 2000), as well as social behavior (e.g., amygdala) (Amaral 2003). As mentioned above, it is likely that activation in sensory regions results from top-down feedback from structures like DMPPC, PCC, TP, and amygdala. According to certain models of semantic cognition (McLelland and Rogers 2003) semantic knowledge arises from the interactive activation of modality-specific representations of perceptual attributes (such as patterns of movement, etc.)—these different modality-specific representations communicate with one another through a common set of amodal representations coded in the anterior temporal lobes. Our results are also consistent with the influence of priming social knowledge structures on perception, motivation, and behavior (Bargh 2006).

Although related studies of “spontaneous” social understanding based on animate motion have not shown engagement of TPs (Wheatley et al. 2007), it is likely that the increased complexity and richness of the animations we used played a key role. Our animations were not only relatively rich in perceptual terms (Mar et al. 2007) but also in terms of the potential for assigning highly varied meanings to the scenarios in our sprite world (Iacoboni et al. 2004), and this likely resulted in our findings of activation throughout so many areas of the social brain, including anterior TPs, when participants were instructed to attend to the social meaning of the interactions.

An important topic for future research will be to determine whether activity in “social” brain regions is specific to social stimuli, or could be similarly active for certain nonsocial stimuli (Mitchell 2007). For example, it has been proposed that schematic representations of self, others, and world are all encoded at an abstract, generic level of representation that integrates over both cognitive and affective dimensions derived from multimodal inputs and the interpretation of referentially specific meanings (Teasdale and Barnard 1993). Such a position would be consistent with extensive evidence that key areas of the social brain integrate over multimodal sources (Pandya and Yeterian 2001). Similarly, Ochsner et al. (2004) argue that regions such as DMPPC respond to stimuli “for which an attributed meaning is a meta-level emergent property of multiply interpretable inputs, that in and of themselves, do not directly imply a single interpretation”.

Summary and Conclusions

In an fMRI study we manipulated the viewers’ perspective to assess the part played by top-down attentional influences on neural activity to animations of simple geometric shapes that can be interpreted as animate agents engaged in social interactions with meaningful properties. Our results highlight that widespread structures throughout the social brain are strongly influenced by social processing goals, consistent with them operating as a common processing network. Such influences did not appear to depend on there being manifest emotional content in the animations. Notably, very similar patterns of neural activation were seen when viewing films and when remembering and responding to them. This indicated that activity in regions, such as the FG, linked to perceptual processing of social stimuli, does not need to be perceptually triggered, but can be re-activated as a result of input from top-down social attention and knowledge systems, consistent with several current “interactionist” theoretical models of social knowing. Our results also emphasize the close relationship between social knowledge structures, perception, motivation, and behavior. Finally, our use of stimuli supporting the generation of rich and diverse social narratives in this study likely enhanced the influence of top-down processes on neural activity in key areas of the social brain, such as the TPs.

Supplementary Material

Supplementary material can be found at: http://www.cercor.oxfordjournals.org/

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