The detection of contingency and animacy from simple animations in the human brain

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Abstract

Contingencies between objects and people can be mechanical or intentional-social in nature. In this fMRI study we used simplified stimuli to investigate brain regions involved in the detection of mechanical and intentional contingencies. Using a factorial design we manipulated the ‘animacy’ and ‘contingency’ of stimulus movement, and the subject’s attention to the contingencies. The detection of mechanical contingency between shapes whose movement was inanimate engaged the middle temporal gyrus and right intraparietal sulcus. The detection of intentional contingency between shapes whose movement was animate activated superior parietal networks bilaterally. These activations were unaffected by attention to contingency. Additional regions, the right middle frontal gyrus and left superior temporal sulcus, became activated by the animate-contingent stimuli when subjects specifically attended to the contingent nature of the stimuli. Our results help to clarify neural networks previously associated with ‘theory of mind’ and agency detection. In particular, the results suggest that low-level perception of agency in terms of objects reacting to other objects at a distance is processed by parietal networks. In contrast, the activation of brain regions traditionally associated with theory of mind tasks appears to require attention to be directed towards agency and contingency.

Introduction

The ability to detect contingency is fundamental for understanding the world and other people around us. Contingencies between objects and people can be mechanical or intentional-social in nature. Collisions between billiard balls are an example of mechanical causality (Michotte, 1946). By contrast, people's and other agents' interactions with objects or other agents are examples of intentional and social contingency (Watson, 1966). The purpose of the present study was to investigate the neural structures involved in the distinction between mechanical and intentional contingency, in particular in the detection of intentional contingencies between agents.

Both mechanical and intentional contingencies can be specified by simple perceptual cues. Michotte showed that the apparent mechanical causality involving geometrical shapes on a screen is reliably perceived from simple psychophysical cues, to which infants are sensitive from an early age (Michotte, 1946; Leslie & Keeble, 1987; Oakes & Cohen, 1990; Watson, 1966). Using simple Michotte-like launching displays, we previously demonstrated an involvement of the MT/V5 complex and superior temporal sulcus (STS) bilaterally and the left intraparietal sulcus in the perception of mechanical causal contingencies (Blakemore et al. 2001).

The detection of intentional contingencies, or agency, is more complex and may be based either on type of motion or on interaction between objects. In contrast to the linear, constant acceleration, push-pull movements typical of mechanical contingencies (Schlottman & Shanks, 1992), movement that is self-propelled (Premack, 1990) and apparently 'non-Newtonian' in velocity changes (Tremoulet & Feldman, 2000) is perceived as animate movement. Here we use the word 'animate' motion to refer to movement that is self-propelled, but which is not necessarily enacted by human or animal bodies, faces and limbs, which is generally referred to as 'biological' motion (Johansson et al. 1973; Allison et al. 2000). A second feature that yields attribution of agency to an object is the presence of non-mechanical contingency or causation at a distance. An object that follows another object or reacts to its movement is perceived as driven by internal intentions or goals. Such animacy and contingency features lead to attributions of mental states such as agency, intentions and emotions to simple 2-D shapes (Heider & Simmel, 1944; Scholl & Tremoulet, 2000).

The detection of agency on the basis of cues such as movement and contingency might be a precursor of our ability to infer other people's mental states, a component of a 'theory of mind' (Frith & Frith, 1999; Allison et al. 2000; Blakemore & Decety, 2001). Functional neuroimaging studies in which subjects think about other people's intentions and beliefs in stories and cartoons demonstrate activation in the STS, the temporal pole (adjacent to the amygdala) and the medial frontal cortex (Fletcher et al. 1995; Brunet et al. 2000; Gallagher et al. 2000). The same brain regions are activated by simple geometrical shapes whose movement patterns evoked mental state attribution compared with random motion of the same shapes (Castelli et al. 2000).

These studies combined different types of agency cue: [a] self-propelled (animate) movement of the objects, [b] contingencies at a distance between the objects, and [c] similarity with prototypical human interactions. It is difficult to disentangle which among all these cues leads to the attribution of agency and is responsible for the specific brain activations. Furthermore, in previous neuroimaging studies, subjects' attention was explicitly drawn to the mental states of the various characters, which might have affected the way in which such stimuli were processed.

In the present fMRI study, our aim was to investigate the contribution of these factors – animate motion, causation at a distance and attention to contingency – to the neural correlates of the detection of agency. We aimed to disentangle these different aspects of agency detection by using very simple stimuli with tightly controlled psychophysics. We used computer generated animation films with two quasi-geometric shapes that suggested neither 'body' nor 'face' nor any other biologically-relevant morphological feature. These shapes had reduced behaviours: either linear motion, no motion or constant angular velocity rotations. All animations included only two objects in the roles of *Prime Mover* and *Reactive Mover* respectively. In each condition, the Prime Mover moved across the screen at constant speed. What was manipulated was its apparent interaction with Reactive Mover. We used a 2x2x2 factorial design with the following variables (**Figure 1**, see *Methods* for details):

- *Contingency*: whether the behaviour of the Reactive Mover was perceived to be contingent upon the motion of the Prime Mover;
- *Animacy*: whether the movement of the shapes included an animate component (the Reactive Mover moved of its own accord) or not;
- *Attention to contingency*: subjects' attention was drawn either to the physical aspects of motion or to the contingency between the two shapes.

Using this design we were able to characterise brain activation due to contingency and animacy. Furthermore, this design enabled us to investigate the interaction between contingency and animacy, that is whether contingency is processed differently in the context of animate movement versus mechanical motion. Finally, this design also allowed us to investigate the effect of drawing the subject's attention to the contingent nature of the relationship between the shapes on the neural processing of the different types of stimuli.

We had three specific predictions. Firstly, we predicted that the presence of animacy and contingency (in this case, causation at a distance), because of the complex spatial processing necessary to detect causation at a distance, would activate regions of the brain that are involved in processing spatial relations, in particular the superior parietal cortex. Such activations associated with the spatial processing of the animate-contingent displays should be independent of whether subjects are looking out for such contingency. Secondly, we predicted that this bottom-up processing of animate-contingency would be distinct from the higher-level processing of intentions and agency. This difference can be measured by the three-way interaction between stimulus type and attention to contingency. We predicted that animate-contingent stimuli would produce activations of brain regions associated with theory of mind tasks – the medial frontal cortex, temporal pole and STS – primarily when subjects were specifically directed to pay attention to the contingent nature of the interaction. Third, we predicted that such top-down effects of attention to contingency would not apply to the perception of mechanical contingency, which would be processed by the brain's visual motion areas and the intraparietal sulcus, in line with our previous findings.

Materials and Methods

Subjects

10 healthy right-handed volunteers (5 females; age range 18-27 years) took part in the study, which was performed in accordance with the local Ethics Committee (Centre Leon Berard). Written, informed consent was obtained from all subjects prior to participation.

Experimental Design

The experiment was split into two 12-minute sessions. Each subject underwent 180 fMRI scans in each session. In each session stimuli from the following five conditions were presented:

- In the *Animate-Contingent* condition (AC), a ‘Prime Mover’ shape moves across the screen. A ‘Reactive Mover’ shape, which is positioned behind a window in a vertical wall, starts to rotate in the direction of the Prime Mover’s motion at the moment when the Prime Mover moves past the window. The Reactive Mover stops moving when the Prime Mover has moved past the window and is ‘out of view’ (see **Figure 1-AC**). This film was designed so that Reactive Mover appeared to ‘see’ and ‘follow’ the Prime Mover – its movement was ‘contingent’ on the movement of the Prime Mover.
- In the *Animate-Non-contingent* condition (AN) the Prime Mover moves across the screen, as in condition AC. The movement of the Reactive Mover is identical to its movement in condition AC, except for its timing with respect to the movement of the Prime Mover. Instead of moving only when the Prime Mover can be ‘seen’ through the window, it rotates before the Prime Mover reaches the window - when the Prime Mover is ‘out of sight’. The only difference between this and condition AC, then, is that here the movement of the Reactive Mover is not perceived to be contingent on the movement of the Prime Mover (**Figure 1-AN**).

- In the *Inanimate-Contingent* condition (IC), the same Prime Mover as in the Animate conditions moves across the screen and collides with the Reactive Mover, which is positioned in the path of the Prime Mover (**Figure 1-IC**). The Reactive Mover moves off the screen. This condition was designed to appear as if the Prime Mover's movement caused (launched) the movement of the Reactive Mover.
- In the *Inanimate-Non-contingent* (IN) condition, the Prime Mover moves across the screen as in IC but moves past the Reactive Mover, which is positioned to the side of the path of the Prime Mover, so no contact is made between them (**Figure 1-IN**). Thus in this condition there was neither animate motion nor an appearance of contingency between the two shapes. The total amount of movement in the IC and IN conditions was the same.
- The *Baseline* condition comprised a black fixation point in the centre of a white screen.

Each stimulus image consisted of 512x512 pixels and 256 colours and lasted 4 seconds, and the screen was updated at 15 frames per second. The position of the Prime Mover's exit point (top or bottom of the screen), the colour of the shapes (blue, green or red), the form of the shapes (spiked- or smooth-edged) and the direction of motion (horizontal or vertical) were varied. The variation of these factors was counter-balanced between conditions.

Before the experiment each subject was shown an exemplar of each of the five stimulus-types, and instructed to watch the movement of the two shapes in the visual displays. Subjects were informed that they would be asked a question concerning the shapes' movement after each block of stimuli. Within each session there were 15 blocks, comprising 3 repetitions of each of the five conditions. Each block consisted of a set of instructions for the task, which lasted 8 seconds. This was followed by 8 types of stimulus from one condition. After the block of stimuli, a question was presented, which lasted 8 seconds. Subjects made a button-press response during this time. The order of conditions was pseudorandomised and counterbalanced within and between subjects.

Factorial nature of the design

We employed a 2x2x2 factorial design with three factors:

- Stimulus type: Contingency versus no contingency
- Stimulus type: Animate versus inanimate movement
- Task: Attention to contingency ('con') versus no attention to contingency ('mov').

After each block of stimuli in the first session, subjects were instructed to make a response with the index or middle finger of their right hand depending on the velocity or the regularity of motion of the shapes (the *Attention to motion* task; 'mov'). Subjects were asked, "In your opinion, was the movement of the shapes of constant velocity or did the velocity of movement change at all within each film?" and, "In your opinion, was the movement of the shapes smooth or was it irregular within each film?" These questions were designed to be attention-demanding and subjective and they required subjects to watch the objects for the duration of each film. After the first scanning session, subjects were informed that in some of the following displays the movement of one of the shapes might be caused - either directly or indirectly - by the movement of the other shape. They were told that this would constitute a contingent relationship between the shapes, and that this relationship could be either physical or non-physical. Subjects were instructed to look out for contingency between the shapes in the second session. Before the second scanning session began, the experimenter verified that each subject understood the new task. After each block of stimuli in the second session, subjects were instructed to make a response with the index or middle finger of their right hand based on the presence or absence of a causal relationship between the shapes (the *Attention to contingency* task; 'con'). Subjects were asked, "In your opinion, was there a contingent relationship between the shapes in each film?" and, "In your opinion, was the movement of one shape caused, either directly or indirectly, by the movement of the other shape in each film?" The ordering of the tasks was not counterbalanced between sessions in order to avoid biasing subjects' attention towards contingency in the *Attention to motion* task. Although this design may be subject to order effects, it was necessary to investigate the effects of attention to contingency.

Data acquisition

A Philips NT MRI scanner operating at 1.5T was used to acquire both 3D T1-weighted fast-field echo structural images and multi-slice T2*-weighted echo-planar volumes with blood oxygenation level dependent (BOLD) contrast (TR = 4 secs; TE = 45 ms; Matrix = 64x64 mm; FOV = 256x256 mm^2). For each subject, data were acquired in two scanning sessions. A total of 180 volumes were acquired per session, plus 4 'dummy' volumes, subsequently discarded, to allow for T1 equilibrium effects. Each functional brain volume comprised 30 5mm axial slices with in-plane resolution of 4x4 mm positioned to cover the whole brain. The acquisition of a T1-weighted anatomical image occurred between the two sessions for each participant. The total duration of the experiment was around 35 mins per subject.

Data analysis

Behavioural ratings. In the second session, subjects' attention was drawn to the causal relationships between the shapes. Subjects were informed that the movement of one of the shapes might be caused - either directly or indirectly - by the movement of the other shape. They were told that this would constitute a contingent relationship between the shapes, and that this relationship could be either direct or indirect, physical or non-physical. After viewing the four different types of stimulus, subjects were asked to rate the strength of the relationship between the two shapes on an 11-point scale from 0 – 10. Subject responses after each condition were recorded and subsequently analysed. Given the non-normal distribution of scores, we used a non-parametric Wilcoxon signed-ranks test to compare the ratings in the Contingent versus the Non-contingent conditions.

Functional neuroimaging. Functional imaging analysis used the technique of statistical parametric mapping, implemented in SPM99 [http://www.fil.ion.ucl.ac.uk/spm]. For each subject, a set of 360 fMRI scans was realigned to correct for interscan movement and stereotactically normalised using sinc interpolation (Friston et al., 1995), with a resolution of 4x4x5 mm^3, into the standard space defined by the Montreal Neurological Institute template. The scans were then smoothed with a Gaussian kernel of 8 mm full-width half maximum to account for residual inter-subject differences.

The analysis of the functional imaging data entailed the creation of statistical parametric maps representing a statistical assessment of hypothesised condition-specific effects (Friston et al., 1994). The scans corresponding to the instruction and response phase of each block were excluded from the analysis. Condition-specific effects were estimated with the General Linear Model with a delayed boxcar wave-form. Low-frequency sine and cosine waves modelled and removed subject-specific low-frequency drifts in signal, and global changes in activity were removed by proportional scaling. Areas of significant change in brain activity were specified by appropriately weighted linear contrasts of the condition-specific effects and determined using the t-statistic on a voxel to voxel basis.

Statistical analysis was performed to examine the simple effects of the four visual conditions (AC, AN, IC, IN) compared with the baseline stimulus, and the main effects of Contingency versus Non-contingency [(AC+IC)-(AN+IN)] and Animate versus Inanimate movement [(AC+AN)-(IC+IN)]. The interactions between type of stimuli were also modelled: the interaction between animate movement and contingency [(AC-AN)-(IC-IN)] and the interaction between inanimate movement and contingency [(IC-IN)-(AC-AN)]. Finally, the three-way interactions between stimuli and experimental task were modelled: the interaction between animate-contingency and attention to contingency [(ACcon–ANcon) – (ACmov–ANmov)] compared with [(ICcon–INcon) – (ICmov–INmov)], and the interaction between inanimate-contingency and attention to contingency

[(ICcon–INcon) – (ICmov–INmov)] compared with [(ACcon-ANcon) – (ACmov–ANmov)]. Examination of these interactions reflects the statistically significant differential effects of the interaction between stimulus type (animate-contingent or inanimate-contingent) in the context of attention to contingency versus attention to stimulus motion. Maxima of activity are reported that survived a masking procedure in which the three-way contrast was masked with the two-way interaction between stimulus type of attention to contingency at $P<0.05$. The presence of a significant interaction would suggest that stimulus-evoked activation depends on experimental task.

The statistical contrasts were used to create an SPM{t}, which was transformed into an SPM{Z} and thresholded at $P<0.05$ (corrected on the basis of the theory of random Gaussian fields for multiple comparisons across the whole brain volume examined). We report regions that survive correction at $P<0.05$ plus those regions surviving an uncorrected threshold of $P<0.001$ for which we had an a priori hypothesis for their activation.

Behavioural results

In the second half of the experiment, subjects' attention was drawn to the contingent relationships between the shapes. After viewing the four different types of stimuli, subjects were asked to rate the strength of the relationship between the two shapes on an 11-point scale from 0 to 10. **Table 1** shows the mean ratings. A Wilcoxon signed-ranks test demonstrated that subjects rated the relationship between the shapes in the two Contingent conditions as significantly stronger than in the two Non-Contingent conditions: for the animate displays, W(10)=55, $p<0.01$; and the inanimate displays, W(10)=55, $p<0.01$. When asked to describe what they saw in each type of stimulus, subjects reported that they perceived the Reactive Mover in the Animate-Contingent condition to be 'following' or 'watching' the Prime Mover.

Functional imaging results

Data from one subject were excluded from the analysis due to technical problems.

Simple effects of visual conditions compared with baseline

The analysis of the simple effects of each of the four visual conditions (AC, AN, IC and IN) compared with the baseline condition revealed significant activations in cortical regions involved in processing the various aspects of moving, coloured visual stimuli, as would be expected (Zeki et al., 1991) at a threshold of $P<0.05$ (corrected; see **Figure 2**).

Main effects

Animate compared with inanimate motion

The displays in which the Reactive Mover's motion was animate (a self-propelled rotation) activated the right lingual gyrus (bordering the medial fusiform gyrus; 20 –64 –10, Z=6.25) to a significantly greater extent than the displays in which the Reactive Mover was inanimate, regardless of task.

Contingency compared with non-contingency

The displays in which the Reactive Mover's motion was contingent on the Prime Mover's motion activated the left cerebellar cortex (-48 -56 -25, Z=4.73) to a significantly greater extent than the displays in which the Reactive Mover's behaviour was not contingent on the Prime Mover.

Interactions

Interaction between contingency and inanimate movement

The posterior part of the middle temporal gyrus, on the border with the superior temporal sulcus, on the left (–60 –60 10, Z=4.79) and right (60 –52 15, Z=3.92), and the right intraparietal sulcus (64 –40 25, Z=3.85), were activated by contingency in the context of inanimate (as opposed to animate) movement, regardless of task (**Figure 3**).

Interaction between contingency and animacy

The superior parietal cortex (BA 7) on the right (36 –44 65, Z=4.04) and the superior parietal cortex extending to intraparietal sulcus on the left (–20 –52 70, Z=4.40) was activated by contingency in the context of animate (as opposed to inanimate) movement, regardless of task (**Figure 4**).

Interactions between task and stimuli

Interaction between animate-contingent stimuli and attention to contingency

This contrast revealed regions activated by animate-contingent stimuli when subjects specifically attended to the contingent nature of the relationships between the stimuli (as opposed to attending to physical aspects of the shapes' movement). The right middle frontal gyrus (border of BA 8 and

9; MNI coordinates: 24 40 50; Z=4.14; **Figure 5**) and the ventral side of the left superior temporal sulcus (-64 -24 5; Z=3.84; **Figure 6**) were activated by this contrast. The masking procedure and inspection of the activation patterns confirmed that these regions showed the predicted pattern of interaction.

Interaction between inanimate-contingent stimuli and attention to contingency

There was no significant activation resulting from the interaction between inanimate-contingent stimuli and attention to the contingent nature of the relationships between the stimuli. In other words, we found no evidence of a top-down effect of attention to contingency on the neural processing of the inanimate-contingent stimuli.

Discussion

In the present study, perception of mechanical contingency, in which one object is perceived to be launched by another object, and intentional contingency, in which one object is perceived to react at a distance to another object's movement, in simple animations, modulated haemodynamics in different brain regions. Furthermore, attention to the contingent nature of the stimuli influenced the neural processing of intentional – but not mechanical – contingency. These activations occurred as a result of watching animated geometric shapes that lacked animal or human features. Differences between conditions were reduced to different parameters on two psychophysical dimensions: whether a shape moved of its own accord or not and whether its behaviour was contingent upon another shape's movement or not.

Brain activations associated with mechanical causality

A basic type of contingency is that between two inanimate objects in which one collides with and launches the other. In the current study this situation was characterised in the Inanimate-Contingent condition, in which a 'Prime Mover' shape moved across the screen and collided with a 'Reactive Mover,' which then moved off the screen. The interaction between contingency and inanimate movement in the present study activated the posterior regions of the middle temporal gyrus, at the border with the STS, in both hemispheres and the right intraparietal sulcus. In other words, displays in which the shapes collided and one was launched activated these regions to a greater extent than both the inanimate displays in which no collision occurred and displays in which the contingency was 'intentional', occurring between shapes whose movement was animate. These regions are not involved in the processing of contingency per se, as evidenced by their absence in the main effect of contingency, regardless of whether this contingency was intentional or mechanical, which was associated with activation only in the left cerebellar cortex. In contrast, the middle temporal gyrus and the right intraparietal sulcus activations were specific to the perception of contingency when it involved the mechanical launching of one object by another.

The activated regions are a subset of those activated in our previous study of the neural processes involved in billiard ball causality. Notably, in our previous study two distinct regions in the temporal lobe (MT/V5 and the STS) in both hemispheres were activated by billiard ball causality, whereas only one temporal region (the middle temporal gyrus on the border of the STS, in both hemispheres) was activated by inanimate-contingent stimuli in the present study. This may suggest that activations triggered by mechanical causality are affected either by the visual features of the displays (realistically drawn balls vs. novel geometric shapes) or by the contrast conditions (presence of animate movement in the present study), although either interpretation would require additional evidence.

We also investigated whether activation to inanimate-contingent stimuli was modulated by focusing the subjects' attention on the contingent nature of launching displays. This manipulation had no significant effect on the neural processing of such displays. This supports our previous observation – in both studies we found that attention to mechanical causality had no significant top-down influence on the way in which the brain processes such causal stimuli (Blakemore et al., 2001). This supports the claim that the detection of mechanical causation is a low-level mechanism not readily influenced by top-down processes (Michotte, 1946; Schlottman & Shanks, 1992).

Right lingual gyrus responses to animate movement of shapes

The displays in which the Reactive Mover's motion was animate (it rotated in a self-propelled manner), regardless of the presence or absence of contingency, activated the right lingual gyrus (bordering the medial fusiform gyrus) to a significantly greater extent than the displays in which the Reactive Mover was inanimate, regardless of task. This activation might be due to the more complex spatial processing involved in the animate displays, which comprised two shapes moving at some distance away from each other, than the inanimate displays, which comprised motion of nearby shapes. The lingual gyrus is involved in perception of complex visual scenes, particularly those that involve a degree of spatial information processing (Menon et al. 2000). The right lingual gyrus is also activated when subjects attend to the global, as opposed to local, aspect of scenes (Fink et al. 1996).

The motion of the Reactive Mover in the two Animate conditions was a constant angular velocity self-propelled rotation. Although non-mechanical, this motion was not 'biological;' our stimuli were designed so that the geometric shapes suggested no biological feature. We intended to avoid any similarity with biological (human or animal) features of movement, and thus would not expect activation of brain regions that support the perception of biological motion, such as the STS (Allison et al. 2000), in the main effect of animate motion.

The perception of intentional contingency and the superior parietal lobe

A second type of contingency, distinct from the mechanical kind, is intentional or social contingency, which links actions with their distal causes and consequences. The only difference between the contingent and non-contingent animate displays used in the current study was the time at which the Reactive Mover rotated with respect to the Prime Mover's path. In the contingent displays the Reactive Mover's self-propelled rotation coincided with the time at which the Prime Mover passed the window (see **Figure 1-AC**). Despite the fact that the shapes had no biological features, this coincidence produced the perception that the Reactive Mover was 'looking at', or 'following', the Prime Mover, as evidenced by the subjects' ratings and comments on the displays. The interaction between animate movement and contingency was associated with activation of the superior parietal lobe bilaterally. In other words, the superior parietal lobe was activated by contingency in the context of animate movement, regardless of animate movement or contingency per se.

The animate-contingent condition was the only condition in which there was a contingency between the two shapes 'at a distance,' typical of situations where an animate being *attends* to moving objects in its environment. Detection of such contingency engages visual attention in a particular way. Specific regions in the parietal cortex, such as the intraparietal sulcus, superior parietal lobule and precuneus show increased activation with attentive tracking of moving objects (Culham et al. 1998). The concept of attentive tracking is relevant to the animate-contingent condition in the current study because the shapes used in these displays were interacting at a distance. In order to make sense of the scene, it is necessary to track the behaviour of both shapes as they interact with each other. The anterior intraparietal sulcus is activated when subjects search for expected stimuli (coherent motion; Shulman et al. 2001) and the superior parietal lobe and precuneus are activated during attention-shifts (Corbetta et al. 1993) as well as during the detection of targets that combine two different features (Corbetta et al. 1995). Similarly, activity in the superior parietal lobe and anterior part of intraparietal sulcus are modulated by increased attentional load (as a result of increasing the complexity of visual targets to follow; Jovicich et al. 2001). We would suggest that the detection of animate contingency requires increased spatial processing, necessary to process the precise relationship between the two shapes that show contingency 'at a distance'.

The detection of intentional contingency and brain regions involved with 'theory of mind'

In the same way as for the inanimate conditions, we also measured the effects of orienting subjects' attention to the contingent nature of the stimuli on the neural processing of those stimuli. This revealed, firstly, no significant difference between the activation of superior parietal cortex to animate-contingent displays when subjects attended to the contingency between the objects compared with when they focused on physical parameters of the objects' movement. This suggests that the superior parietal lobe is involved in the bottom-up processing of displays that are animate and contingent. In contrast, activity in various other brain regions to the animate-contingent stimuli was significantly affected by where subjects' attention was directed. Our predictions were partly supported. When subjects focussed their attention on the contingent relationships between the objects in the displays, as opposed to physical aspects of the objects' movement, there was significant activation of the right middle frontal cortex (on the border of Brodmann areas 8 and 9; figure 4) and the left STS. It is noteworthy that these are a subset of the regions that are consistently activated by theory of mind tasks, such as inferring a story character's intentions and desires from a description of their actions. Our results are similar in part to those of a previous PET study by Castelli and colleagues, in which subjects were shown animation displays that were interpreted as involving mental states and emotions (Castelli et al. 2000). The stimuli used in the present study, however, were much simpler and the psychophysics of the contingent vs. non-contingent displays were reduced to the timing of one shape's movement. This allows us to hypothesise that the left STS and the right middle frontal cortex are activated by basic shape interactions when specifically attending to animate contingency. These regions might thus exert a top-down influence on the perception of certain movement patterns, including those that are animate and contingent.

The right middle frontal gyrus activations in this study are similar to previous activations reported in theory of mind studies, which tend to occur mainly in the right hemisphere (Brunet et al. 2000; Castelli et al. 2000; Fletcher et al. 1995; Gallagher et al. 2000; Vogeley et al. 2001). This right hemisphere dominance of the frontal activations is interesting in light of the proposal that the right hemisphere is implicated in the attribution of mental states (Happé et al. 1999). Happé et al. found that people who had suffered right hemisphere strokes showed significant specific impairments on theory of mind tasks that involve understanding other people's intentions, desires, false beliefs and so on, compared with age-matched control subjects.

In summary, the activations resulting from the interaction between Animate-Contingent displays and attention to contingency are a subset of the activations in previous theory of mind tasks. Contingency and animacy are two cues to agency. Our results suggest that the explicit detection of these two factors - contingency in displays that contain animate movement - might account for the left STS and right frontal activations found in previous theory of mind studies.

The major differences between our results and previous functional neuroimaging studies of theory of mind is the lack of significant temporal pole, right STS and medial frontal activity in the current study. The right STS is activated by the perception of motion of biological forms such as whole human and animal body movements (see Allison et al. 2000 for review). In our study the stimuli were designed specifically to avoid similarity with real biological forms. The activation of temporal pole, adjacent to the amygdala, in theory of mind studies has been interpreted to reflect the emotional processing inherent in these tasks – previous theory of mind tasks elicit emotional interpretations of a story or cartoon character, to some extent (Frith, 2001). In contrast, our stimuli were designed to avoid any similarity with real human characters or situations, and as such did not elicit emotional interpretations. The lack of emotional content of the displays might account for the lack of temporal pole activity in the current study. The lack of high level mental state attribution to the shapes might also account for the lack of frontal activation at a very medial location in our study. This region seems to be particularly involved in high level tasks such as taking an intentional stance in a competitive game (Gallagher et al. 2002) and making moral judgements (Moll et al. 2002).

Our results help to clarify neural activations previously associated with theory of mind and agency detection. The results suggest that perception of inanimate, mechanical contingency is largely automatic, unaffected by subjects' expectations and attention, and engages regions of the middle temporal gyrus and intraparietal sulcus. The detection of animate contingency also includes automatic, bottom-up neural processing, which is unaffected by attention to contingency, largely confined to parietal networks dedicated to complex visuo-spatial detection. In contrast, activations in the right middle frontal gyrus and left STS appear to be a result of attending to possible agents in animate-contingent displays as opposed to detecting them on the basis of visual cues. An impairment of theory of mind has been proposed to be a central underlying cause of the social interaction difficulties experienced in autism (Baron-Cohen et al. 1985; Frith, 2001). The current results may be of interest in the understanding both of normal theory of mind functions and of their impairment.

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Figure legends

Figure 1

Diagram illustrating the 2x2x2 factorial design employed in the experiment, in which the factors animacy, contingency and attention to contingency were varied. Subjects were presented with four types of visual stimulus. In the *Animate Contingent* (AC) condition, a ‘Prime Mover’ shape moves across the screen. A ‘Reactive Mover’ shape, which is positioned behind a window, starts to rotate in the direction of the Prime Mover’s movement at the moment when the Prime Mover moves past the window and stops moving when the Prime Mover has moved past the window (as indicated by the bold line). In the *Animate Non-contingent* (AN) condition, the Prime Mover moves across the screen, as in condition AC. The movement of the Reactive Mover is identical to condition AC, except for its timing with respect to the movement of the Prime Mover - it rotates when the Prime Mover is out of sight. In the *Inanimate Contingent* (IC) condition, the Prime Mover moves across the screen and collides with the Reactive Mover, which is positioned in the path of the Prime Mover. The Reactive Mover moves off the screen. In the *Inanimate Non-contingent* (IN) condition, the Prime Mover moves across the screen as in IC but moves past the Reactive Mover, which is positioned to the side of the path of the Prime Mover, so no contact is made between them. In all displays the Prime Mover comes into view from off-screen. The third factor in the design, which is not illustrated in the figure, was attention to contingency. During the first scanning session, subjects were asked questions concerning the physical movement of the Prime Mover (No attention to contingency; ‘mov’), whereas during the second session subjects were asked questions concerning the contingency between the two shapes (Attention to contingency; ‘con’).

Figure 2

Sagittal and coronal views through a glass brain showing average group activations in the four visual conditions (AC, AN, IC and IN) compared with the baseline condition, thresholded at T=3.10, depicting activations in parietal cortex, temporal cortex, occipital cortex and fusiform gyrus.

Figure 3

Left middle temporal cortex group activation superimposed on a sagittal section of a T1 image. The middle temporal cortex, posterior to the superior temporal sulcus which is shown on the image, was activated more when contingency was mechanical than when it was intentional (irrespective of the attentional directions to the subject). Plots showing the mean and standard deviation of the condition-specific parameter estimates, which reflect the relative contribution of each condition to the amplitude of the adjusted BOLD signal relative to the fitted mean, are shown for the left middle temporal gyrus (–60 –60 0, indicated by the crossover point of the two lines on the image) in the four visual conditions: Animate-Contingent, Animate-Noncontingent, Inanimate-Contingent and Inanimate-Noncontingent.

Figure 4

Bilateral superior parietal cortex group activations superimposed on a coronal section of a T1 image. The superior parietal cortex was activated more when contingency was intentional than when it was mechanical (irrespective of the attentional directions to the subject). Plots showing the mean and standard deviation of the condition-specific parameter estimates, which reflect the relative contribution of each condition to the amplitude of the adjusted BOLD signal relative to the fitted mean, are shown for the left superior parietal cortex (-20 -52 70, indicated by the crossover point of the two lines on the image) in the four visual conditions: Animate-Contingent, Animate-Noncontingent, Inanimate-Contingent and Inanimate-Noncontingent.

Figure 5

Right middle frontal gyrus (border of BA 8 and 9) activation superimposed on a coronal section of a T1 image. This region was activated by animate-contingent displays to a greater extent when subjects were attending to contingency ('con') than when they were attending to movement parameters ('mov'). Plots showing the mean and standard deviation of the condition-specific parameter estimates, which reflect the relative contribution of each condition to the amplitude of the adjusted BOLD signal relative to the fitted mean, are shown for the right middle frontal gyrus (24 40 50) in the Animate-Contingent and Animate Non-contingent conditions during the attention to movement task and during the attention to Contingency task.

Figure 6

Left superior temporal sulcus group activations superimposed on saggital section of a T1 image, at x = –64. This region was activated by animate-contingent displays to a greater extent when subjects were attending to contingency ('con') than when they were attending to movement parameters ('mov'). Plots showing the mean and standard deviation of the condition-specific parameter estimates, which reflect the relative contribution of each condition to the amplitude of the adjusted BOLD signal relative to the fitted mean, are shown for the left superior temporal sulcus (-64 -24 5) in the Animate-Contingent and Animate Non-contingent conditions during the attention to movement task and the attention to Contingency task.

Table 1

Mean (± standard error) ratings of the strength of the relationship between the two shapes in the four visual conditions.

Condition	Animate contingent	Animate non-contingent	Inanimate contingent	Inanimate non-contingent
Mean (±SE) rating	7.43(0.51)	4.10(0.89)	10(0)	0.6(0.6)

Figure 1

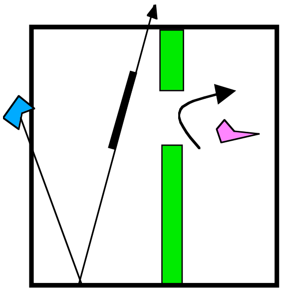
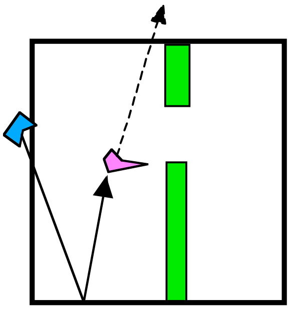
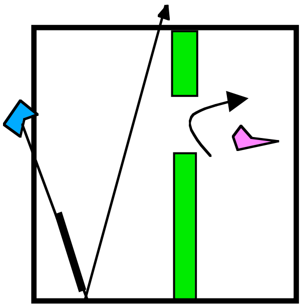
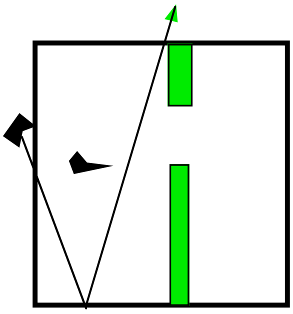
	Animate movement	**Inanimate movement**
Contingent	Animate contingent AC 	Inanimate contingent IC 
Non-contingent	Animate non-contingent AN 	Inanimate non-contingent IN 

Figure 2

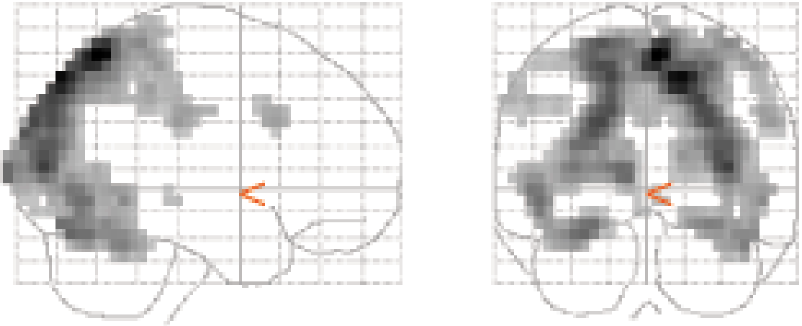


Figure 3

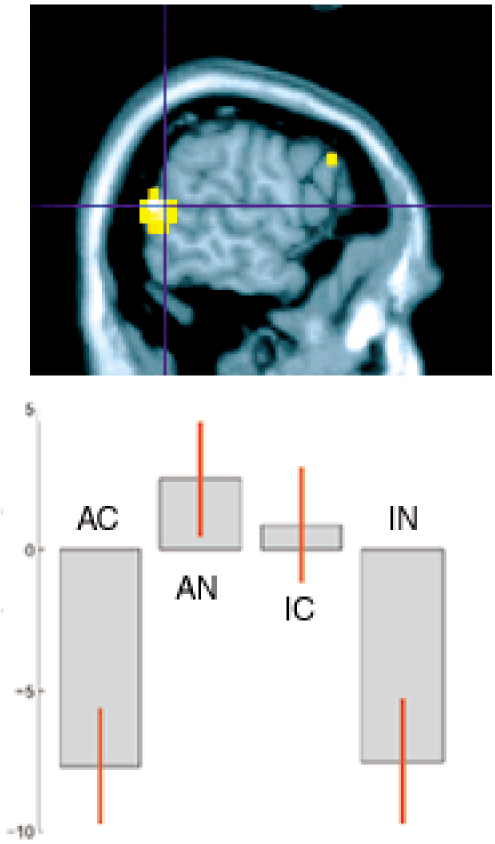


Figure 4

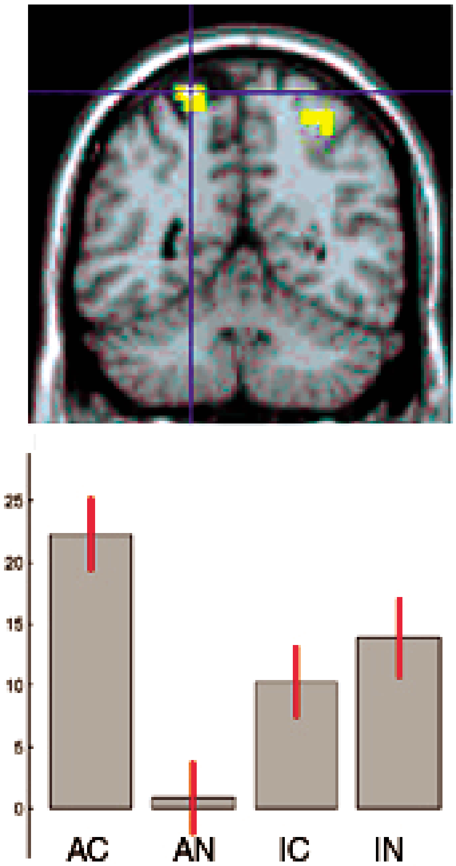


Figure 5

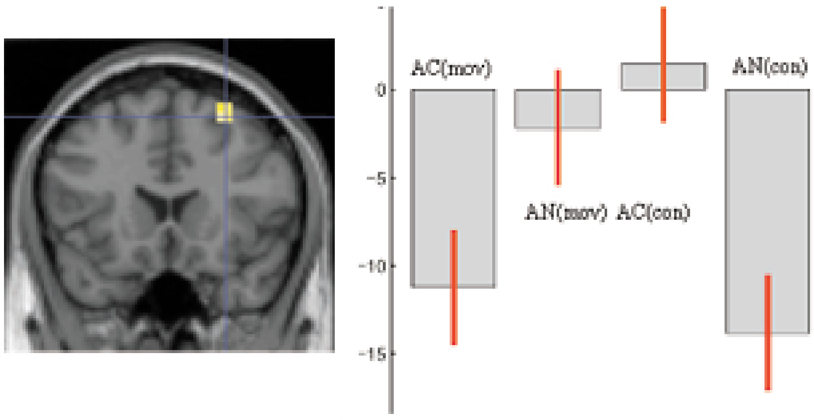


Figure 6