Movement and Mind: A Functional Imaging Study of Perception and Interpretation of Complex Intentional Movement Patterns

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We report a functional neuroimaging study with positron emission tomography (PET) in which six healthy adult volunteers were scanned while watching silent computer-presented animations. The characters in the animations were simple geometrical shapes whose movement patterns selectively evoked mental state attribution or simple action description. Results showed increased activation in association with mental state attribution in four main regions: medial prefrontal cortex, temporoparietal junction (superior temporal sulcus), basal temporal regions (fusiform gyrus and temporal poles adjacent to the amygdala), and extrastriate cortex (occipital gyrus). Previous imaging studies have implicated these regions in self-monitoring, in the perception of biological motion, and in the attribution of mental states using verbal stimuli or visual depictions of the human form. We suggest that these regions form a network for processing information about intentions, and speculate that the ability to make inferences about other people's mental states evolved from the ability to make inferences about other creatures' actions. © 2000 Academic Press

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INTRODUCTION

Recent interest in the evolution, development, and breakdown of social cognition has focused on Theory of Mind, the ability to attribute independent mental states to self and others in order to explain and predict behaviour (Carruthers and Smith, 1996; Baron-Cohen *et al.,* 2000). Fodor (1992), Leslie and Thaiss (1992), Scholl and Leslie (1999), and others have suggested that our ability to attribute mental states, or "mentalize," results from a dedicated, domain-specific, and possibly modular cognitive mechanism. This proposal gains particular support from studies of autism, a biologically based developmental disorder, which appears to be characterized by a selective impairment in Theory of Mind (Baron-Cohen *et al.,* 1985; Frith *et al.,* 1991; Happé and Frith, 1996). Interest in the brain basis of normal Theory of Mind is fired by the hope of a better understanding of the neural systems affected in people with autism, who are (in the main) unable to "mind-read" (Baron-Cohen, 1995).

There is a growing number of published reports of functional brain imaging studies of Theory of Mind (ToM). Most of these studies implicate activation in medial frontal and temporoparietal regions. For example, Fletcher *et al.* (1995), in a PET study, scanned volunteers reading and answering questions about stories involving complex mental states (ToM stories) and those involving inferences of physical cause and effect ("physical" stories). Comparison of activation during ToM versus "physical" stories revealed increased activation in the medial frontal gyrus on the left (BA 8/9), as well as in the posterior cingulate cortex and the right inferior parietal cortex (BA 40) at the temporoparietal junction. Gallagher *et al.* (2000) used the same set of stories in an fMRI study with normal volunteers. In addition to the written stories, subjects were shown figurative drawings (humorous cartoons) which also prompted attribution of mental states. With the greater resolution of fMRI it was possible to distinguish a number of peaks in Brodmann areas 8/9 and the border of 10 and 32, associated with both ToM cartoons and stories. The location of these areas of activity was close to those previously reported by Fletcher *et al.* (1995) and by Goel *et al.* (1998), and relates to the paracingulate sulcus. Activity was also observed in the temporoparietal junction bilaterally.

Previous brain imaging studies of mental state attribution have tended to use high-level verbal stimuli (Baron-Cohen *et al.,* 1994; Fletcher *et al.,* 1995; Happé *et al.,* 1996; Goel *et al.,* 1998) or visual depictions of humans (Gallagher *et al.,* 2000; Baron-Cohen *et al.,* 1999). Mentalizing, however, involves processes at a number of levels, from perceptual to conceptual. If mentalizing relies on a dedicated cognitive mechanism,

or module, then one interesting question concerns the nature of its obligatory triggering inputs. The aim of the present study was to examine brain activation during exposure to simple, nonverbal stimuli designed to evoke mental state attribution by their kinetic properties alone. Inspiration for appropriate stimuli came from the classic work of Heider and Simmel (1944), who demonstrated that even simple geometric shapes could elicit by their pattern of contingent movement the attribution of complex internal states, such as intentions and beliefs. Subsequent work by Berry and colleagues (Berry *et al.,* 1992; Berry and Springer, 1993) has shown that properties of the movement, rather than of the stimuli/characters, are fundamental to the complex attributions made by adults and children from the late preschool years onwards.

To explore brain activation during such movement-provoked mental state attribution we used silent animations of three types. In our Theory of Mind (ToM) condition, interaction between two shapes (big and small triangle) was scripted to imply complex mental states, such as intention to deceive. Thus, in these animations one character's actions were readily seen as determined by what the other character "thought." In the second animation type, "Goal-directed" (GD), the characters interacted on a simple, purposeful level. That is, in these animations, one character's actions were seen as determined by what the other character "did." In the third animation type, "Random action" (R), the two characters did not interact, and their behavior was not contingent—in effect they were merely floating or bouncing around. Stimuli in all three animation types moved in a self-propelled fashion. Our stimuli could therefore be graded in terms of complexity of predominantly evoked descriptions, from random movements, to goal-directed actions, and finally to complex intentional states. Conversely, people's descriptions could be graded in terms of their degree of mentalizing regardless of the animation sequences they were describing.

The present animations were first used in a behavioral study that collected descriptions from children with autism, children with developmental delay, normally developing children, and adults (Abell *et al.,* 2000). Results from this study supported the validity of the three types of animations. Children with autism proved to be less accurate in their descriptions of ToM animations than children without autism. The 14 adults taking part in this study attributed precise mental states, matching the underlying script in 89% of their responses to the ToM animations, with descriptions of purposeful movements for the remaining responses. They attributed precise purposeful interactions in 93% of their responses to the Goal-directed animations with the remaining responses all involving mental state attribution. Descriptions of simple movement without a purposeful component were given in

64% of responses to the Random sequences while purposeful movement was described for the remainder. Even though the vast majority of descriptions of the three types of animations fell into an orderly pattern, the animations were ambiguous enough for interpretations to occur that were either simpler or richer than intended by the designers. Our prediction for the present study was that the ToM animations, but not the Random animations, would evoke mental state attributions and show activation patterns similar to those found in previous functional imaging studies of Theory of Mind (Goel *et al.,* 1995; Fletcher *et al.,* 1995; Baron-Cohen *et al.,* 1999; Gallagher *et al.,* 2000). We expected the GD animations to have an intermediate status. Going one step further, we predicted activation in ToM related areas for all sequences that provoked mental state interpretations, regardless of the animation condition.

METHOD

Subjects. Six right-handed male volunteers (aged 20 to 31, mean 24.5 years) took part in this study. All subjects were healthy, with no history of significant medical, psychiatric, or neurological illness. All gave written, informed consent to take part in the study, which was approved by the ethics committee of the National Hospital for Neurology and Neurosurgery and the Administration of Radioactive Substances Advisory Committee (ARSAC), UK.

Data acquisition. All subjects underwent both PET and MRI scanning on the same day. A Siemens VISION (Siemens, Erlangen) operating at 2.0T was used to acquire axial T1 weighted structural MRI images for anatomical coregistration. PET scans were performed with an ECAT EXACT HR+ scanning system (CTI Siemens, Knoxville, TN) in high sensitivity 3-D mode with septa retracted (Townsend *et al.,* 1991). A venous cannula to administer the tracer was inserted in the antecubital fossa vein. Approximately 350 Mbq of $H_2{}^{15}O$ in 3 ml of normal saline were loaded into intravenous tubing and flushed into subjects over 20 s at a rate of 10 ml/min by an automatic pump. After a delay of approximately 35 s, a rise in counts could be detected in the head that peaked 30–40 s later (depending on individual circulation time). The interval between successive administrations was 8 min. The data were acquired in one 90 s frame, beginning 5 s before the rising phase of the head curve. After correcting for background activity, the true counts accumulated during this period were taken as an index of cerebral blood flow (Fox and Minton, 1989). Images were reconstructed by filtered back projection (Hanning filter, cut off frequency 0.5 cycles per pixel) into 63 image planes (separation 2.4 mm) and into a 128×128 pixel image matrix (pixel size 2.1 mm). Twelve scans were acquired per subject.

Statistical analysis. Functional imaging analysis used the technique of Statistical Parametric Mapping implemented in SPM97 (Wellcome Department of Cognitive Neurology, London, UK) (http://www.fil.ion.ucl.ac.uk/spm). For each subject, a set of 12 PET scans was automatically realigned and then stereotactically normalized (Friston *et al.,* 1995b) into the space of Talairach and Tournoux (1988). The scans were then smoothed using a Gaussian kernel of 12 mm full-width half maximum.

The analysis of functional imaging data entails the creation of statistical parametric maps that represent a statistical assessment of condition-specific effects hypothesised by the experimenter (Friston *et al.,* 1995a). The effects of global changes in blood flow were modelled as a confound using a subject-specific ANCOVA (Friston *et al.,* 1990). 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 by voxel basis. We created the relevant SPM [*t*] for each comparison of conditions, which was then transformed into an SPM [*Z*] and thresholded at a *Z* score of 3.09 ($P <$ 0.001 uncorrected). Clusters of activated voxels were characterized in terms of their peak height and spatial extent conjointly.

Design. A 3×2 repeated measures within subjects design was used. Four different examples of each of three types of animation, ToM, Goal-directed, and Random were displayed over the course of 12 scans, divided into two consecutive counterbalanced blocks: cued animation and uncued animation. In a previous study (Fletcher *et al.,* 1995) subjects were cued before the scan. They were told in advance which kind of stimuli they were going to see (see Appendix 1). In the present study we counterbalanced cued with uncued animations in order to control for the effect of prior knowledge.

Animation materials. Twelve animations were used during the scanning, and an additional three were shown for practice. All the animations featured two characters, a big red triangle and a small blue triangle, moving about on a framed white background. Each sequence lasted between 34 and 45 s, and the three types of animations were matched for length. The "scripts" for the ToM sequences involved the two triangles persuading, bluffing, mocking, and surprising one another. The Goal-directed "scripts" involved the two triangles dancing together, one chasing, one imitating, and one leading the other. The Random movement showed the two triangles bouncing off the walls resembling the movement of billiard balls, or merely drifting about. While the type of movement was by definition different between the three conditions, the basic visual characteristics in terms of shape, overall speed, and orientation changes were as similar as possible.

Procedure. Subjects were instructed before scanning (see Appendix 1) and were given practice examples of the three types of animations. The animations were presented on the screen of a Power Macintosh computer suspended on a adjustable cradle at a suitable distance for each subject. Prior to scanning, it was ascertained that the subject could watch the animations comfortably.

There was a cued and an uncued condition. Before the cued condition subjects were told either that they were going to see an animation showing "an interaction with feelings and thoughts" (ToM), or "a random movement" (R), or "a simple interaction" (GD). Before the uncued condition, subjects were simply told that they were about to see the next animation. Order of cued and uncued blocks was counterbalanced across subjects, so that half the subjects obtained cued animations first, and half uncued animations first.

After each scan subjects were asked to tell the experimenter what they thought the triangles were doing. The experimenter always asked the same neutral question: "What was happening in this animation?" Answers were recorded for later scoring. On no occasion was feedback given, but subjects were generally praised for their descriptions.

Scoring. The verbal descriptions given after each presentation (in between scans) were coded along four different dimensions. The aim of the scores was to distinguish in each answer (1) the implied "intentionality," that is, the degree of appreciation of mental states, (2) their appropriateness, that is, how well the underlying script was captured, (3) the certainty of the explanation, and (4) the length of each answer. The Intentionality score reflected the use of mental state terms, with scores ranging from 0 (nondeliberate action), to 5 (deliberate action aimed at affecting another's mental state; see Appendix 2 for examples). Two raters gave the identical score 65% of the time, and had an average discrepancy of only 1.4 points in the remaining 35% of the cases. The Appropriateness score measured the understanding of the event depicted in the animations, as intended by the designers (0 to 3). The Certainty score graded the degree of hesitation present in the verbal description (0 to 3). The Length score classified the number of clauses in each answer (0 to 4). Details of scoring are given in Appendix 2.

RESULTS

Behavioral data. Table 1 shows the ratings of the descriptions of each type of animation. As can be seen, the three animation types differed significantly in the degree of mental state attribution they evoked ($F(2,10) = 154.75$, $P < 0.001$). As expected on the basis of Abell *et al.*'s results (2000) subjects attributed more intentionality to the characters' behavior during ToM animations than during GD (t value $= 5.89$, $P = 0.002$)

TABLE 1

Verbal Descriptions Given by the Six Subjects for ToM, Goal-Directed,
and Random Animations Rated on Four Dimensions

	Total score maximum	ToM mean (s.d.)	Goal-Directed mean (s.d.)	Random mean (s.d.)
Intentionality	20	15.8 (1.5)	9.7 (1.5)	0.7 (1.2)
Appropriateness	12	11.2 (1.6)	10.5 (1.4)	11.2 (1.2)
Certainty	12	10.7 (0.8)	10 (1.9)	11.3 (1.2)
Length	16	12.5 (3)	8.5 (3)	7.7 (3.6)

Note. Differences between the three conditions were significant at $P < 0.01$ for Intentionality. Differences between ToM animations vs GD and R animations were significant at $P < 0.01$ for Length. All other differences were not significant.

and R animations (t value = 16.04, $P < 0.001$). Random animations evoked significantly fewer mental state attributions than Goal-directed animations (t value = 17.43, $P < 0.001$).

The length of the descriptions differed significantly ($F(2,10) = 19.49$, $P < 0.001$), with the ToM animations eliciting longer explanations than Goal-directed ($t = 5.48$, $P = 0.003$) or Random animations ($t = 5.11$, $P = 0.004$), which did not differ from each other ($t = 1.05$, $P = 0.341$). There was no difference, however, in the "appropriateness" or "certainty" of the explanations given to the three animation types ($F(2,10) = 0.49$, $P = 0.628$ and $F(2,10) = 3.33$, $P = 0.078$, respectively). Absence or presence of cueing revealed neither a main effect nor interaction with the animation type in any of the four scores.

Regional cerebral blood flow: Subtraction analysis. There were no significant differences between cued and uncued presentations, nor were there any order effects, or any significant interactions. Data for cued and uncued sequences were therefore combined. There were significant differences between the three types of animation. ToM animations elicited more activity than Random animations in four regions: temporalparietal junction (at the end of the superior temporal sulcus), basal temporal region (fusiform gyrus and temporal poles, immediately adjacent to the amygdala), extrastriate cortex (occipital gyrus), and medial prefrontal cortex (see Table 2). All these differences were observed in both hemispheres, but were more significant in the right hemisphere, except for the medial prefrontal cortex. For all these regions differences occurred between the ToM and the Random condition, with the Goal-directed condition showing intermediate activity (see Fig. 1). Direct comparison of ToM with GD confirmed that the differences apparent in Fig. 1 were significant in the case of temporoparietal regions and the temporal pole at a level of $P < 0.0001$ uncorrected and for occipital gyrus and fusiform gyrus at $P < 0.01$. Random movement when compared to ToM movement, elicited more activity in one region of medial occipital cortex ($-2x$, $-94y$, $14z$). The locations of the activa-

TABLE 2

Subtraction Analysis: Regions Where ToM Animations Elicited More Activity Than Random Animations

Foci of activation	BA	Coordinates					
		Left (x, y, z)	Z score	$P <$	Right (x, y, z)	Z score	$P <$
Temporal-parietal junction							
STS	22/39	**−58, −48, 4**	**4.3**	**0.06**	**60, −56, 12**	**6.2**	**0.001**
Basal temporal							
FuG	37	−38, −44, −22	3.8		**36, −56, −20**	**5.1**	**0.01**
TmP/Am	38	−38, −4, −32	3.2		**34, 6, −26**	**4.0**	**0.05**
Occipital lobe							
OcG	19/18	**−30, −94, −12**	**4.6**	**0.02**	**38, −96, −10**	**5.0**	**0.01**
OcG	19/18	−32, −82, −24	4.1				
Medial prefrontal							
SFG	9	−4, 60, 32	4.1				

Note. The coordinates are given in the stereotactic space of Talairach and Tournoux (1988). Numbers in bold type indicate regions where differences in activity were significant when corrected for multiple comparisons. Numbers in plain type indicate regions where differences in activity were significant at $P < 0.0001$, uncorrected. Brain regions are identified by name and by putative Brodmann Area (BA) on the basis of the atlas of H. M. Duvernoy (1999) *The Human Brain: Surface, Three-Dimensional Sectional Anatomy with MRL and Blood Supply.* Springer, Wien, New York. STS, superior temporal sulcus; TmP/Am, temporal pole adjacent to amygdala; FuG, fusiform gyrus; OcG, occipital gyrus; SFG, superior frontal gyrus.
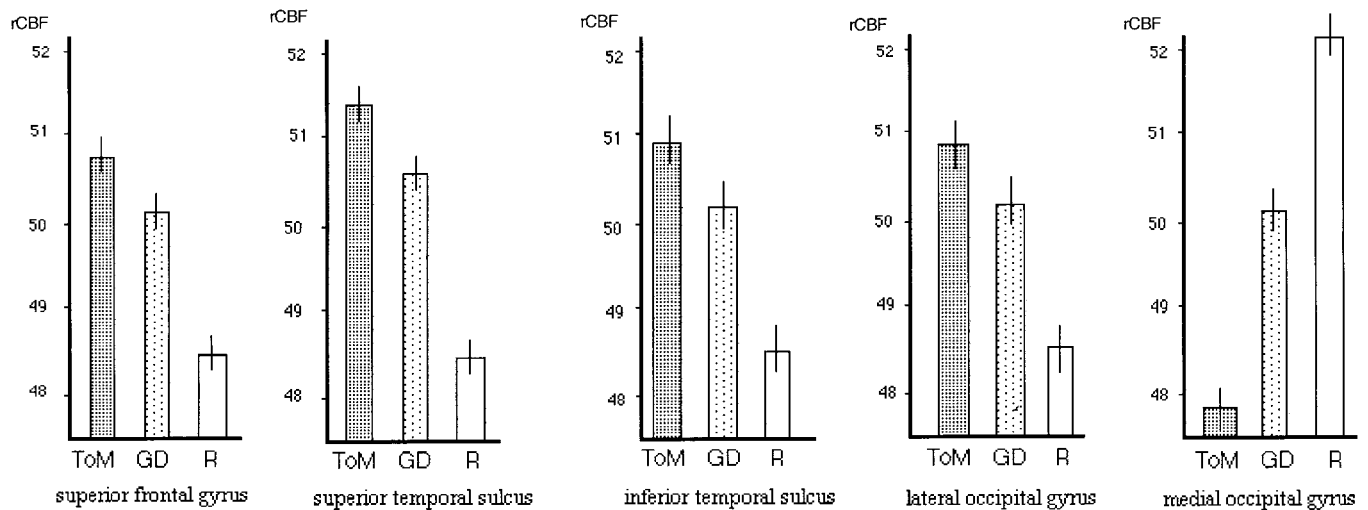
FIG. 1. Blood flow as a function of condition (ToM, Goal-directed, and Random) in key regions.

tions are shown superimposed on a standard brain in Fig. 2.

Regional cerebral blood flow: Correlational analysis. A further analysis was performed in which Intentionality scores, regardless of condition, were correlated with blood flow response. This analysis was carried out within subjects, thus avoiding the assumption that different individuals use the same range of descriptions. An assumption inherent in this analysis is a linear relationship between intentionality scores and blood flow response. However, further analysis which allowed for a nonlinear relationship did not produce a significant increase in variance accounted for.

The results of the correlational analysis were clearcut. The same four areas were identified as more active as in the comparison of the three conditions (see Table 3). These results were not affected when the length of the descriptions given by the subjects was entered as a confounding covariate.

DISCUSSION

The present experiment took as its starting point the pervasive tendency to perceive intentions in complex movement patterns even when no human forms are depicted. We showed that different types of silent animations selectively evoked descriptions of what the characters were thinking or descriptions of what the characters were doing. The different types of descriptions occurred spontaneously, since alerting subjects in advance to the nature of a particular sequence had no effect.

The main aim of this study was to locate a brain system associated with the attribution of mental states evoked by kinetic stimulus properties. At the same time we wished to relate the findings to earlier studies of mentalizing with different kinds of stimuli. Subtrac-
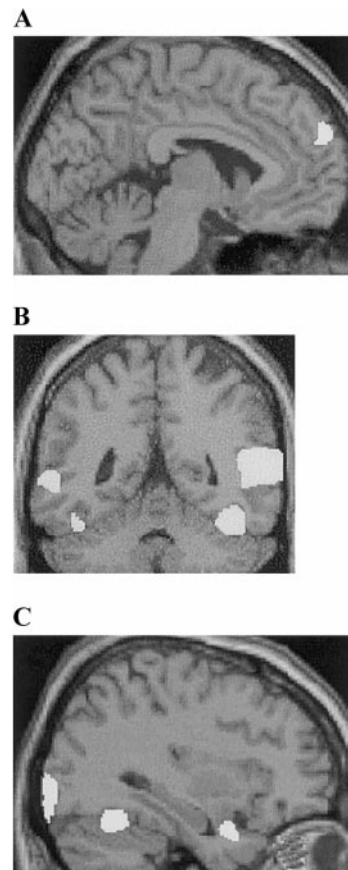

FIG. 2. Regions of significant cerebral blood flow (rCBF) change associated with the perception of ToM animations vs Random animations. (A) Saggital view of activation in superior frontal gyrus. (B) Coronal view of activation in superior temporal sulcus and fusiform gyrus. (C) Saggital view of activation in temporal pole adjacent to the amygdala, fusiform gyrus, and occipital gyrus.

TABLE 3

Correlation Analysis: Regions with Significant Correlations
between Blood Flow Response and Intentionality Score

Foci of activation	BA	Coordinates						
		Left (x, y, z)	Z score	P <	Right (x, y, z)	Z score	P <
Temporal-parietal junction							
MTG	21/37	−60, −48, 4	4.6	0.02			
STS	39				62, −58, 12	6.6	0.001
Basal temporal							
FuG	37	−36, −42, −22	3.7		38, −54, −22	4.9	0.01
TmP/Am	34/38				30, 4, −24	2.9	
					22, 0, −16	3.05	0.08
Occipital lobe							
OcG	18				40, −96, −10	4.8	0.01
OcG	17	−16, −100, −8	4.2	0.05			
Medial prefrontal							
SFG	8/9	−6, 58, 32	3.0				

Note. Conventions as in Table 2. MTG, middle temporal gyrus; STS, superior temporal sulcus; FuG, inferior temporal gyrus; TmP/Am, temporal pole adjacent to amygdala; OcG, occipital gyrus; SFG, superior frontal gyrus.

tion analysis (contrasting the ToM sequences with Random or Goal-directed sequences) gave the same picture as correlational analysis (correlating blood flow with degree of mental state description across all animations). The results showed increased activation in four main areas bilaterally. These areas include medial prefrontal cortex, temporoparietal junction (superior temporal sulcus), basal temporal region (fusiform gyrus and temporal poles adjacent to the amygdala), and occipital cortex. All of these areas have been implicated in prior studies of mentalizing. This suggests that a system can be delineated which is to some extent independent of the mode of stimulus input, visual or verbal.

The results of this study do not enable us to identify the functions of these four regions, but clues to their significance can be gained by considering previous studies involving different paradigms.

The medial prefrontal region. An as yet unpublished fMRI study using Heider and Simmel type silent animations has recently been summarized by Klin *et al.* (2000). The results appear to be highly consistent with our findings. In particular, these authors mention strong activation in medial prefrontal cortex. The medial prefrontal region activated during the attribution of mental states to animated triangles has also been shown to be activated by other stimuli evoking attribution of beliefs and intentions. These studies are summarized in Table 4.

For example, Goel *et al.* (1995) found left medial prefrontal gyrus activation associated with reasoning about other people's thoughts regarding a novel object. Fletcher *et al.*'s (1995) story comprehension task, requiring inferences about a character's intentions, showed peak activation in a dorsal region of medial

frontal cortex. This region was not activated in individuals with Asperger Syndrome, who show delays and deficits in Theory of Mind (Happé *et al.,* 1996). Gallagher *et al.* (2000) have compared the same story task with a nonverbal comprehension task, using static single frame cartoons. They found a convergence between activations in response to verbal and visual stimuli that prompt mental state attribution (reading a text and viewing a cartoon, respectively), with bilateral activation in a ventral area of the medial prefrontal cortex.

In addition, medial prefrontal areas have been shown to be activated during a rather different task that may, nonetheless, require attribution of mental states. In a task of metaphor comprehension, which, according to some theorists (Sperber and Wilson, 1986; Happé, 1993), requires recognition of the speaker's intentions, Bottini *et al.* (1994) found activation in several loci, including left rostral anterior cingulate cortex, very close to the area implicated in the studies of mentalizing mentioned above. It appears, therefore, that a number of very different mentalizing tasks across several modalities (e.g., verbal, nonverbal) and with differing stimulus qualities (e.g., static, moving), activate regions of medial frontal cortex (see Table 4 for coordinates). Prefrontal cortex is implicated in a number of cognitive processes that might have a role in mentalizing tasks such as working memory and retrieval from episodic memory. However, these processes usually engage lateral regions of prefrontal cortex rather than medial regions as observed in the present experiment (Grady, 1999).

Studies of *self-monitoring* have also shown increased activity in areas including medial prefrontal and cingulate cortex. This suggests that when subjects have to

TABLE 4

Coordinates for Activation of Medial Frontal Regions in Present and Related Studies

Task	Cognitive process	Study	Coordinates	
			Left (x, y, z)	Right (x, y, z)
Observing complex intentional movement (vs random movement)	Mental state attribution	Present study	−4, 60, 32	
Judge others' knowledge	Mental state attribution	Goel *et al.* (1995)	−12, 38, 32	
Story comprehension	Mental state attribution	Fletcher *et al.* (1995)	−12, 42, 40	
Story comprehension (Asperger Syndromes)	Mental state attribution	Happé *et al.* (1996)	−12, 36, 36	
Story and cartoon comprehension	Mental state attribution	Gallagher *et al.* (2000)	−10, 48, 12	8, 22, 46
Metaphor comprehension	Attribution of speaker's communicative intention	Bottini *et al.* (1994)	−2, 42, 8	
Intended speech monitoring	Monitoring own mental states	McGuire *et al.* (1996a)	−2, 36, 36 −10, 32, 24	2, 52, −4
Self generated thoughts	Monitoring own mental states	McGuire *et al.* (1996b)	−8, 38, 24 0, 38, 36	
Perceiving pain	Monitoring own mental states	Rainville *et al.* (1997)		3, 20, 30
Perceiving tickle	Monitoring own mental states	Blakemore *et al.* (1998)		2, 42, 6
Reporting emotions	Monitoring own mental states	Lane *et al.* (1997)		0, 50, 16
Intended response monitoring	Monitoring own mental states	Carter *et al.* (1998)		4, 25, 43
Observing human body movement	Perception of biological motion	Bonda *et al.* (1996)	−7, 58, 26	

reflect on their *own* mental states, they may use neural pathways similar to those underlying attribution of mental states to others. For example, subjects required to monitor their intended speech, in order to judge whether distorted feedback was their own or another person's voice (McGuire *et al.,* 1996a), showed activation of bilateral medial frontal cortex and anterior cingulate gyrus/medial prefrontal cortex as well as temporoparietal junction bilaterally. The prefrontal region was also activated in a study where subjects reported self-generated thoughts independent from stimuli in the immediate environment (McGuire *et al.,* 1996b). A quite different type of self-monitoring task investigated the neural substrates of perceived pain (Rainville *et al.,* 1997). The anterior cingulate cortex showed increased activity when subjects perceived (under hypnosis) the increasing unpleasantness of hot water on their hand. Blakemore *et al.* (1998) found anterior cingulate activity associated with reporting a tickling sensation from self-produced tactile stimulation. Activity in anterior cingulate, extending into the medial prefrontal region, was also observed when subjects reported their own emotional responses to pleasant, unpleasant and neutral pictures (Lane *et al.,* 1997). A more complex self-monitoring task elicited activity in anterior cingulate cortex when subjects were required to choose between competing responses (Carter *et al.,* 1998). Taken together, these results seem to indicate

that online monitoring of inner states—own or others'—may engage the anterior cingulate cortex and neighbouring medial frontal regions, regardless of the specific source of information.

The medial frontal region activated by our ToM animations also overlaps with regions activated by point-light displays of biological motion. Bonda *et al.* (1996) used two biological movement conditions, a dancing figure (human body movement) and a grasping hand simulating the act of reaching out for a glass and bringing it to the mouth (goal-directed action). The comparison of activation during the two conditions showed that perception of a dancing figure versus a grasping hand elicited a network of activation, including left medial prefrontal cortex, close to that activated by our ToM animations.

Grady (1999) provides an exhaustive list of activations observed in prefrontal cortex classified in terms of putative Brodmann areas. The vast majority of these are lateral. However, some medial activations have been observed in the vicinity of the area reported in the present study. The only study observing a relevant activation in Brodmann area 10 was that of Bottini *et al.* (1994) on metaphor comprehension. Activation in relevant regions of Brodmann area 9 have been observed in motor learning tasks and working memory tasks, but the majority of the activations observed during such tasks are more lateral and more posterior.

Activations are also reported in medial Brodmann area 8 for some language tasks and for some object processing tasks, but here again all the activations are more posterior than the one observed in the present study.

In previous studies of mentalizing the activity in medial frontal cortex lies at the border of anterior cingulate cortex and medial frontal cortex in the paracingulate sulcus (Gallagher *et al.,* 2000). In an exhaustive examination of studies that have activated anterior cingulate cortex, Paus *et al.* (1998) conclude that this region has distinct functions. The posterior part of ACC is primarily engaged by motor tasks while the more anterior portions are particularly engaged when emotions are involved. The areas associated with mentalizing are clearly anterior to the motor region of anterior cingulate cortex.

Temporo-parietal region. Increased activation in the junction between parietal and temporal lobes has been observed using a story comprehension task and static cartoons (Gallagher *et al.,* 2000). Again this area was highly active in response to stimuli that share properties of biological motion. Bonda *et al.* (1996), for example, reported activity in the left caudal–most part of the superior temporal sulcus when viewing grasping hand movement compared to random movement. Puce *et al.* (1998) found increased superior temporal sulcus activation when viewing faces in which eye gaze repeatedly changed direction, and faces in which the mouth opened and closed. Similarly Calvert *et al.* (1997) observed increased activation in a region of the superior temporal gyrus during silent lip-reading of numbers versus still lips, and Grezes *et al.* (1999) reported activation of the superior/middle temporal region during viewing of meaningful hand gestures with tools and objects compared to stationary hands. Taken together these studies implicate the superior temporal sulcus and adjacent cortex in the perception of a variety of human body movements. This region is anterior and superior to the visual motion area MT/V5 (Puce *et al.,* 1998), indicating that these activations are not attributable to movement *per se.* It is notable, too, that all our animations (including Random) displayed self-propelled movement as might be expected of animate agents. Our triangles, when described as moving purposefully and intentionally, activated the key brain regions that have been activated by viewing biological motion. Human-like face or body characteristics thus do not appear to be necessary to trigger the attribution of mental states. Future investigations are needed to clarify what particular properties of biological motion are functionally associated with temporoparietal activation, and whether distinct regions respond preferentially to specific visual attributes of biological stimuli.

Basal temporal cortex. The ToM animations also elicited bilateral activation in the basal temporal region, with peak components in the caudal part of the fusiform gyrus and in the temporal poles adjacent to the amygdala. Baron-Cohen *et al.* (1999) reported increased activation in the amygdala region during a mentalizing task involving judgement of a person's eyes, as well as activation in medial prefrontal cortex and the temporoparietal region. Connections between these areas are known to be strong (Amaral *et al.,* 1992). Temporal pole activation has previously been associated with narratives (Mazoyer *et al.,* 1993; Fletcher *et al.,* 1995) and this fits with the idea that subjects inferred the scripts underlying ToM animations. These animations had certainly more narrative content compared to the other sequences.

The studies of biological movement perception discussed above, also reported peak activations in left fusiform gyrus and left temporal pole in response to observing meaningful hand gestures compared to stationary hands (Grezes *et al.,* 1999). Left fusiform gyrus activation was found during observation of a dancing human figure compared to random movement (Bonda *et al.,* 1996). The ventral temporal area has also been implicated in visual processing of static stimuli: while reading words and naming pictures (e.g., Vandenberge *et al.,* 1996) and while reading Braille words, versus letter-strings (Buchel *et al.,* 1998). Several imaging studies have reported specific regions of the fusiform gyrus to be more active during face viewing compared to assorted pictures, hands, scrambled faces, and houses (e.g., Kanwisher *et al.,* 1997), and more active during face than letter-string and texture perception (e.g., Puce *et al.,* 1996). Gorno-Tempini *et al.* (1998) reported increased activity in bilateral temporal poles associated with famous and non-famous face and proper name processing. Activity in bilateral fusiform gyri was increased while processing faces relative to names and scrambled faces. Thus different areas of the fusiform gyrus appear to be specialised for recognition of different kinds of objects, including animate agents.

Occipital cortex. In the present study, the ToM animations (relative to Random) elicited increased bilateral occipital activation in a lateral area, as was also found in Gallagher *et al.*'s (2000) study using a mentalizing task involving static cartoons. In contrast, the reverse comparison (Random versus ToM) activated a medial region of occipital cortex. This result indicates a task specific effect, not found in other studies of mentalizing, that deserves further exploration. These areas were implicated in recent studies of global and local processing of complex visual stimuli (Fink *et al.,* 1997a,b). In the Fink *et al.* study (1997a) subjects were presented with large letters made out of small letters, and required to switch attention between global and local perceptual levels. Attentional modulation between local and global processing was associated with differential activity in prestriate cortex along the mediolateral axis. Local processing elicited increased left

lateral activation, whereas global processing elicited increased right medial activation. This distinction between lateral and medial occipital regions was replicated in a second study using objects rather than letters (Fink *et al.,* 1997b): local processing elicited increased lateral activation, while global processing elicited increased medial activation. It is notable that the comparisons between our ToM and Random animations showed similar differential activations: lateral during ToM stimuli, and medial during Random stimuli. An important difference between the method used in the present study and in Fink *et al.*'s studies is that the latter reported activations associated with global and local processing resulting from a "top-down" (endogenous) process. Subjects were specifically instructed to attend to the stimuli at either the global or the local level, whereas in our study subjects were not instructed how to view the stimuli. It makes some intuitive sense, however, that participants may have attended to global patterns of movement in the, effectively meaningless, Random condition (floating, bouncing), and paid more attention to the specifics of movement, interaction, and character details (e.g., which way a triangle is pointing) in the ToM scenarios. Taken together, these studies suggest that occipital sites may be implicated in the perception of movement patterns that engage attention at different (local-global) levels relevant to the attribution of animacy and intention. Although this speculation is unsupported with regard to the present animations, it is amenable to empirical testing.

Of necessity, the movements in the ToM animations were more complex in terms of greater variation of speed and direction of movement. It may be this greater complexity that results in increased activity in extrastriate regions. Thus, it remains possible that the pattern of activation we attribute to mentalising reflects in part extraneous tasks differences in, for example, psychophysical properties of the stimuli or resulting eye-movement differences. Future tests in which psychophysical properties are systematically varied, are clearly needed.

In conclusion, the present study has shown that abstract movement patterns activate regions previously associated with mentalising in stories and static pictures. Our ToM animations revealed increased activation in a network of brain regions, including the medial prefrontal cortex, the temporal pole adjacent to the amygdala region and the temporoparietal junction. All these regions have been repeatedly implicated in previous studies of mental state attribution and might reflect different components of this process. Two particularly important components, paracingulate sulcus and temporoparietal junction, show overlap with previous mentalizing studies as well as studies of self-

monitoring and perception of biological motion. We tentatively suggest that the ability to make inferences about other people's mental states evolved from the ability to make inferences about other creatures' actions and movements. This fits with the observation that we commonly infer intentions on the basis of observed action outcomes. The activity of the prefrontal cortex and temporoparietal junction in our study is combined with activity in a ventral visual pathway, from the extrastriate cortex to the inferior and middle temporal gyri. Thus the regions activated by viewing artfully animated triangles appear to reveal a network for processing visual-kinetic information about intention in action.

APPENDIX 1

Instructions Given to Participants

The aim of this experiment is to understand which parts of your brain are active while watching a short animated film sequence.

All you have to do is relax, and watch the animations shown on the monitor in front of you. Each animation lasts approximately 40 seconds. The sequences are similar to one another (two triangular shapes moving about) but different in their content. The triangles act as characters performing different movements, for example, dancing, drifting or courting each other.

There are different types of content: In some animations the behaviour of both triangles will appear disconnected from each other. They just move about, with random movement.

By contrast, other animations will show the two triangles moving about doing something together, interacting. Their actions are somehow connected to each other, for example, they are imitating each other, or one is feeding the other.

Still other animations show the two triangles doing something more complex together, as if they are taking into account their reciprocal feelings and thoughts. By just watching them you will probably imagine they are interacting, for example, courting each other.

In this experiment there is no "right" or "wrong" answer. Sometimes I will tell you in advance what kind of animation you are going to see, for example, a random movement, a simple interaction or an interaction involving thoughts and feelings. While you are watching the animations, be relaxed, and . . . enjoy them! After each cartoon is over, I will ask you what you think the triangles were doing, whether they were randomly moving about, or whether they were doing something more specific.

APPENDIX 2

Scoring Criteria and Examples for Verbal Descriptions of Animations

Score (0–5) for Intentionality:

0 = action, nondeliberate

   (e.g., "Bouncing," "Moving around," "Rotating")

1 = deliberate action with no other

   (e.g., "Ice-skating")

2 = deliberate action with another

   (e.g., "Blue and red are fighting," "Parent is followed by child")

3 = deliberate action in response to other's action

   (e.g., "Big is chasing little," "Red is allowing the Blue to get close to him," "Big is guarding little who was trying to escape")

4 = deliberate action in response to other's mental state

   (e.g., "The little one is mocking the big one," "Two people are arguing," "A parent is encouraging a child to go outside")

5 = deliberate action with goal of affecting other's mental state

   (e.g., "The blue triangle wanted to surprise the red one," "Child pretending not to be doing anything")

Score (0–3) for Appropriateness:

0 = no answer, "I don't know"

1 = inappropriate answer: reference to the wrong type of interaction between triangles

2 = partially correct answer: reference to correct type of interaction but confused overall description

3 = appropriate, clear answer
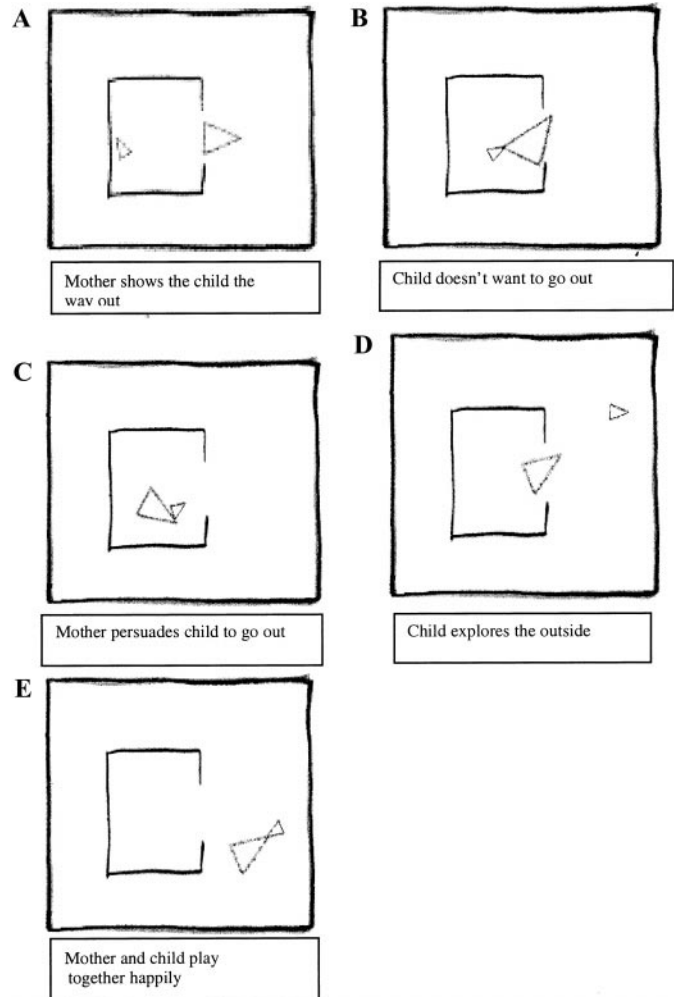
Score (0–3) for Certainty (based on voice tone):

0 = long hesitation or silence

1 = hesitation, few words, sentences unfinished, need to be prompted to say more

2 = hesitation between words, alternative answers

3 = no hesitation at all, quick answer, description correctly reflects the script underlying the animation

Score (0–4) for Length:

0 = no response

1 = one clause

2 = two clauses

3 = four clauses

4 = more than four clauses

APPENDIX 3

The stills below illustrate a "Theory of Mind" animation. The animation was designed following a script in which Big Triangle is coaxing the reluctant Little Triangle to come out of an enclosure. Subjects were presented with the animations without any suggestion relative to a story or characters' roles. The captions have been added here for clarification.

A — Mother shows the child the way out

B — Child doesn't want to go out

C — Mother persuades child to go out

D — Child explores the outside

E — Mother and child play together happily

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