Thinking about intentions

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In this fMRI study, we investigated the convergence of underlying neural networks in thinking about a scenario involving one's own intentional action and its consequences and setting up and holding in mind an intention to act. A factorial design was employed comprising two factors: i. Causality (intentional or physical events) and ii. Prospective Memory (present or absent). In each condition, subjects answered questions about various hypothetical scenarios, which related either to the link between the subject's own intentions and consequential actions (Intentional Causality) or to the link between a natural, physical event and its consequences (Physical Causality). A prospective memory task was embedded in half the blocks. In this task, subjects were required to keep in mind an intention (to press a key on seeing a red stimulus background) whilst carrying out the ongoing Causality task. Answering questions about intentional causality versus physical causality activated a network of regions that have traditionally been associated with Theory of Mind, including the medial prefrontal cortex (mPFC), the superior temporal sulcus and the temporal poles bilaterally. In addition, the precuneus bordering with posterior cingulate cortex, an area involved in self-awareness and self-related processing, was activated more when thinking about intentional causality. In the prospective memory task, activations were found in the right parietal cortex, frontopolar cortex (BA 10) and precuneus. Different subregions within the precuneus/posterior cingulate cortex were activated in both main effects of intentional causality and prospective memory. Therefore, the precuneus/posterior cingulate cortex subserves separately thinking about one's own intentions and consequent actions and bearing in mind an intention to make an action. Previous studies have shown that prospective memory, requiring the formation of an intention and the execution of a corresponding action, is associated with decreased activation in the dorsal mPFC, close to the region activated in Theory of Mind tasks. Here, we found that holding in mind an intention to act and at the same time thinking about an intentional action led to reduced activity in a dorsal section of the mPFC. This was a different region from a more anterior, inferior dorsal mPFC region that responded to intentional causality. This suggests that different regions of mPFC play different roles in thinking about intentions.
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Introduction

Understanding the causal relations between events is fundamental for understanding the world around us. Developmental studies have shown that an awareness of physical causality, such as gravity and collisions between moving objects, emerges early in life (Baillargeon et al., 1995; Kim and Spelke, 1992; Leslie, 1982; Leslie and Keeble, 1987; Oakes and Cohen, 1990; Spelke et al., 1992, 1994). Another type of causality is that between mental states and behaviour, in particular the link between intentions and actions. Understanding that intentions cause actions and inferring intentions from actions might be a precursor to understanding the minds of others (Theory of Mind or *mentalising*; Leslie, 1994; Premack and Woodruff, 1978). Theory of Mind (ToM) refers to the inferences that we naturally make about other people's intentions, beliefs and desires, which we then use to predict their behaviour. By 18 months, infants are able implicitly to ascribe agency to a system or entity (Johnson, 2003). This precedes more explicit mentalising, such as false belief understanding, which usually emerges by about 5 years of age (Barresi and Moore, 1996; Leslie, 1994; Rochat et al., 2004; Schlottmann et al., 2002).

A number of neuroimaging studies have explored the neural systems underlying mentalising. These studies have employed a variety of tasks, ranging from understanding the intentions and beliefs of characters in stories (Fletcher et al., 1995; Gallagher et al., 2000; Saxe and Kanwisher, 2003) and cartoons (Brunet et al., 2000; Gallagher et al., 2000; Vogeley et al., 2001) to attributing mental states to animated shapes (Castelli et al., 2000) and surmising another person's next move in a competitive game (Gallagher et al., 2000). These studies have consistently reported activation in what seems to be a highly circumscribed mentalising network, comprising the medial prefrontal cortex (mPFC),

the superior temporal sulcus (STS) especially around the temporo-parietal junction (TPJ) and the temporal poles adjacent to the amygdala. Lesion studies have also implicated the frontal cortex (Channon and Crawford, 2000; Gregory et al., 2002; Happé et al., 2001; Rowe et al., 2001; Stone et al., 1998; Stuss et al., 2001) and temporo-parietal junctions/STS (Samson et al., 2004) in mentalising.

The mPFC activations during mentalising tasks tend to be in the posterior and dorsal region of the PFC (cf. Frith and Frith, 2003; Ochsner et al., 2004 for meta-analysis, dorsal being defined as $Z > 0$ and ventral as $Z < 0$). A similar dorsal region is activated by knowledge about people relative to objects (Mitchell et al., 2002). Recently, in a meta-analysis of a large number of neuroimaging studies, Gusnard and Raichle have drawn attention to the fact that posterior, dorsal mPFC shows highest metabolic activity at 'rest', i.e. during low-level baseline conditions. Gusnard and Raichle's default mode hypothesis proposes that the mPFC activity reflects self-referential mental activity, which might be expected when task demands are low and subjects are free to think about what they like (Gusnard and Raichle, 2001; Gusnard et al., 2001). This implies that attributing thoughts to others involves the same network of brain regions as thinking about one's own mental states. Indeed, in a study comparing understanding mental states in stories involving oneself compared with stories involving another person, the Self condition activated the same mentalising network as when thinking about others (Vogeley et al., 2001). The results of several neuroimaging studies investigating self-processing also suggest that reflecting on one's own thoughts or personality trait adjectives that describe oneself, involves similar brain regions to those underlying the attribution of mental states to others, in particular dorsal mPFC (Happé, 2003; Johnson et al., 2002; Kelley et al., 2002; Kampe et al., 2003; Kjaer et al., 2002; Lou et al., 2004; Macrae et al., 2004). There is some evidence that self-referential tasks activate ventral mPFC (Ochsner et al., 2004). However, the precise localisation of self-related activations is inconsistent, with activity being reported widely throughout the frontal lobes (Gillihan and Farah, 2005). In addition to the dorsal mPFC, the posterior cingulate cortex (PCC) is activated when subjects reflect on themselves (Gusnard and Raichle, 2001; Gusnard et al., 2001; Johnson et al., 2002; Kelley et al., 2002; Kjaer et al., 2002; Lou et al., 2004).

An alternative hypothesis, entitled the gateway theory, suggests that the role of the PFC is to enable mental behaviour in situations where incoming stimuli are insufficient to trigger a behaviour, for example, when there is no established way of behaving or when the stimulus is entirely novel (Burgess et al., in press). Burgess et al. argue that baseline tasks fulfil these criteria. A second instance in which PFC would be recruited, according to this theory, is in very complex or ambiguous situations in which many behaviours are possible. Burgess et al. argue that "prospective memory" is such a situation. Prospective memory is a type of executive function defined as the ability to execute an intended action after a delay (Burgess et al., 2001). An example of prospective memory in everyday life is intending to post a letter on your way to work. You might encounter many distractions on the way to work, but passing a letterbox will usually trigger the intention to post the letter. Thus, you will act out an intention after a delay. Prospective memory is similar to the concept of implementation intentions (Gollwitzer and Schaal, 1998), in which an individual decides to initiate a goal-directed response when a certain situation arises. The initiation of the goal-directed response is more or less automatic. In contrast, in prospective memory, which depends to a greater degree on controlled processing, the intended action is not always triggered automatically (Chasteen et al., 2001).

Lesion studies suggest a role of the frontal lobes in prospective memory (Burgess, 2000; Cockburn, 1995). Neuroimaging studies suggest that prospective memory relies in particular on the lateral frontopolar cortex (Burgess et al., 2001, 2003; Okuda et al., 1998; West and Ross-Munroe, 2002). Burgess et al. (2001) found that holding an intention to act online during a delay activated the frontal poles, right lateral PFC, inferior parietal cortex and the precuneus. Whilst activity in lateral PFC is increased during prospective memory, it has been found that activity in mPFC is decreased during prospective memory tasks (Burgess et al., 2003). In a meta-analysis of a number of neuroimaging studies, this region was located anterior (mean $Y = 61$) to the mPFC activations in mentalising tasks (mean $Y = 55$; Gilbert et al., in preparation).

The first aim of this study was to investigate neural activity when subjects think about their own intentions and consequential actions ("intentional causality") in hypothetical scenarios. The scenarios focussed on the subject's own intentions and consequential actions in various hypothetical situations. In this respect, the task involved intentional causality related to the self.

The second aim of the current study was to investigate how thinking about intentional causality is modulated by having to bear in mind an intention to act after a delay, given that the posterior mPFC is activated by mentalising tasks and the anterior mPFC is deactivated in prospective memory tasks (Gilbert et al., in preparation). In prospective memory, the need to bear in mind an intention is implicit and internal, whereas the intentional causality task requires the subject to think explicitly about an externally presented question regarding their intentions. We employed a factorial design with the factors i. *Causality* (intentional causality vs. physical causality) and ii. *Prospective Memory* (having to bear in mind an intention to act at some later point in the trial, or not). This design enabled us to investigate the neural correlates underlying the processing of one's own intentions and those underlying bearing in mind an intention to act after a delay, as well as the interaction between these two processes.

In the intentional causality condition, the subject's task was to answer blocks of questions posing scenarios that involved themselves and the causal link between their intentions and actions. The physical causality condition involved answering questions about the causal link between physical events and their consequences. The background colour of the question stimuli changed randomly on each trial. In half the blocks of both intentional causality and physical causality questions, subjects were required to perform a prospective memory (PM) task in addition to the ongoing causality task. This involved having to respond to each question (the ongoing task) unless the background colour was red, in which case a different response had to be made. To achieve this, subjects must perform the ongoing task (answering questions) whilst bearing in mind the intention to respond to a red background. The other blocks were identical except there was no PM component and subjects were instructed to ignore the background colour of the question stimuli.

We predicted that thinking about intentional causality will activate regions associated with mentalising (posterior dorsal mPFC, STS and temporal poles) and self-reflection (posterior dorsal mPFC and PCC). We predicted activation in the frontopolar cortex during the PM tasks in which subjects had to bear in mind an intention to act at a future time (Burgess et al., 2001). Finally, we predicted that there would be an interaction between causality

and prospective memory in the mPFC. However, the direction of this predicted interaction, as well as the exact location within the mPFC, is not clear. According to the default mode hypothesis (Gusnard and Raichle, 2001) and the gateway hypothesis (Burgess et al., in press), dorsal mPFC activity might be expected to decrease when both thinking about intentions and holding in mind an intention to act. On the other hand, theories proposing that the dorsal mPFC is involved in mentalising (Frith, 2001) might predict that doing both tasks at once would cause an increase in mPFC activity.

Materials and methods

Subjects

Eleven female subjects (age range 21–37 years) with no history of psychiatric or neurological disorder took part in the study. Written informed consent was obtained from all subjects prior to participation in this study, which was approved by the National Hospital for Neurology and Neurosurgery Ethics Committee.

Experimental design

The experiment was split into two 11 min sessions during each of which the subject underwent 190 scans. A 2 × 2 factorial blocked design was employed in which i. *Causality* (Intentional versus Physical) and ii. *Prospective Memory* (present or absent) were manipulated.

Causality

Subjects were presented with a description of a scenario followed by a question relating to this scenario. Each block consisted of three scenario/question trials. In half the blocks, scenarios pertained to intentions and consequential actions (*intentional causality (IC)*, for example, *scenario stimulus*: "You are at the cinema and have trouble seeing the screen"; followed by *question stimulus*: "Do you move to another seat? Likely or Unlikely?"). In the other blocks, the scenarios pertained to natural occurrences and consequential events (*physical causality (PC)*, for example, *scenario stimulus*: "A huge tree suddenly comes crashing down in a forest"; followed by *question stimulus*: "Does it make a loud noise? Likely or Unlikely?"). In each block, the scenario stimulus was presented for 4.7 s and was immediately followed by the question stimulus. The question stimulus was presented for 4.7 s, during which time subjects were asked to respond by pressing one of two buttons on a keypad corresponding to "likely" and "unlikely". The scenarios and questions were matched between the two conditions in terms of number of characters, words and clauses. The text in the scenarios and questions was presented in black letters and positioned in the centre of the screen against a background colour. The background colour of each scenario and question stimulus varied randomly between red, blue, yellow, purple and green.

Prospective memory

In half of the blocks (the *Prospective Memory* blocks), subjects were instructed to answer the questions described above (the *ongoing task*), apart from the trials in which the background colour of the question screen was red (*PM task*). The background was red in 23% of the total number of trials over all 16 blocks. In trials in which the background was red, subjects were instructed to ignore the question and instead press a third key to indicate the presence of a red background. In the other blocks (noPM), subjects were instructed to pay attention only to the ongoing task and to ignore the changing background colour of the stimuli. An instruction screen, lasting 4.7 s and indicating whether the subject should look out for or ignore the red background, preceded each block. Each block lasted approximately 33 s.

In addition to the four conditions described above (ICPM, ICnoPM, PCPM, PCnoPM), a baseline condition was included in which subjects were asked to fixate on a black cross on a white background for a duration of 30 s. There were eight repetitions of each of the five conditions, resulting in a total of 40 blocks. Block order was counterbalanced within and between subjects. Each subject was trained on the task for approximately 4 min prior to scanning. Stimulus presentation was programmed in Cogent (http://www.vislab.ucl.ac.uk/Cogent) running in Matlab 6.5, which recorded subject responses.

Data acquisition

A 1.5 T Siemens Sonata MRI scanner was used to acquire both 3-D T_1-weighted fast-field echo structural images and multi-slice T_2*-weighted echo-planar volumes with blood oxygenation level dependent (BOLD) contrast (TR = 3.6 s). For each subject, functional data were acquired in two scanning sessions of approximately 11 min each in which 190 volumes were acquired. The first 5 volumes were discarded to allow for T1 equilibrium effects. Each functional brain volume was composed of 40 2 mm axial slices with a 1 mm gap and in-plane resolution of 3 × 3 × 2 mm positioned to cover the whole brain. The acquisition of a T1-weighted anatomical image occurred after the two sessions for each participant. The total duration of the experiment was approximately 35 min per subject.

Data analysis

Behavioural data analysis

Mean reaction times were calculated for the question task in both the PM and the noPM blocks. RTs corresponding to responses to the PM trials in which there was a red background were removed from the analysis. The main effects of causality (IC vs. PC) and prospective memory (PM vs. noPM), as well as the interaction between causality and prospective memory, were analysed using a repeated measures ANOVA.

Functional neuroimaging analysis

Functional imaging analysis used the technique of statistical parametric mapping, implemented in SPM2 [http://www.fil.ion.ucl.ac.uk/spm]. For each subject, a set of 380 fMRI scans was realigned to correct for interscan movement and stereotactically normalised using sinc interpolation (Friston et al., 1995), with a resolution of 3 × 3 × 3 mm³, into the standard space defined by the Montreal Neurological Institute (MNI) template. The scans were then smoothed with a Gaussian kernel of 6 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 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 for each condition. 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. Each component of the model served as a regressor in a multiple regression analysis. The resulting parameter estimates for each regressor at each voxel were then entered into a second level analysis where subject served as a random effect in a within-subjects ANOVA. The main effects and interactions between conditions were then specified by appropriately weighted linear contrasts and determined using the t statistic on a voxel-by-voxel basis.

Statistical analysis was performed to examine the main effect of the four experimental conditions compared with the baseline stimulus, the main effects of intentional causality [(ICPM + ICnoPM) − (PCPM + PCnoPM)], physical causality [(PCPM + PCnoPM) − (ICPM + ICnoPM)] and prospective memory [(ICPM + PCPM) − (ICnoPM + PCnoPM)] and the simple effect of intention causality [(ICnoPM) − (PCnoPM)]. The interaction between causality and prospective memory was modelled using the contrasts: [(ICPM − ICnoPM) − (PCPM − PCnoPM)] and (PCPM − PCnoPM) − (ICPM − ICnoPM)]. 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

Every subject made a response to every causality question. In the PM blocks, false positives, i.e. mistaking a non-PM stimulus for a PM stimulus, never occurred. Correct responses to the PM stimulus accounted for 86% of the PM trials. In the noPM blocks, the mean percentage of false positives (i.e. reacting to red background as if it were a PM stimulus) was 6.6%. Analysis of the mean reaction times to the questions revealed that subjects were significantly faster to answer IC questions than PC questions ($F(1,10) = 38.8$, $P < 0.001$). No significant differences were found in reaction times between responses in the PM blocks and noPM blocks ($F(1,10) = 2.62$, $P > 0.05$). There was no significant interaction between causality and PM ($F(1,10) = 0.13$, $P > 0.05$). Fig. 1 shows the mean reaction times in each condition.

Functional imaging results

Experimental conditions compared with baseline
Comparison of the four visual conditions with the fixation condition [(ICPM + IcnoPM + PCPM + PCnoPM) − baseline] resulted in significant activations in regions involved in visual, motor and language processing ($P < 0.05$ corrected), as would be expected.

Main effect of causality
Comparison between questions related to the causal link between one's own intentions and actions (IC), and questions related to the causal link between physical events and their consequences (PC) resulted in significant activation of the precuneus/PCC, posterior dorsal mPFC, temporal poles bilaterally and the superior temporal sulcus bilaterally. These activations are listed in Table 1 and shown in Fig. 2. These regions were also
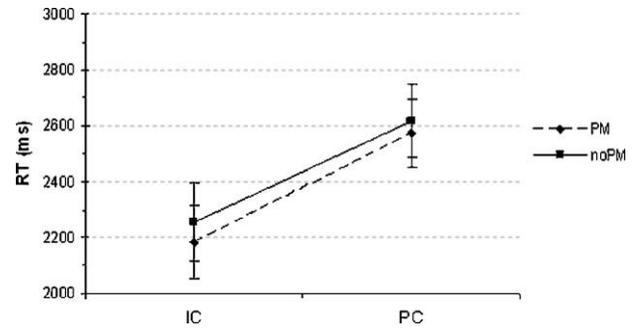

Fig. 1. Mean (±SD) reaction times in ms in the four conditions: IC = intentional causality, PC = physical causality, PM = Prospective Memory, noPM = no Prospective Memory.

activated in the simple effect of ICnoPM − PCnoPM (see Table 1), demonstrating that their activity was independent of the PM task.

Conversely, questions related to PC activated the intraparietal sulcus to a significantly greater extent than IC questions (see Table 1 and Fig. 3). In a study on mechanical (billiard ball) causality, the left intraparietal sulcus was more active in causal mechanical events (Blakemore et al., 2001). In addition, the right intraparietal sulcus was specifically active in the processing of mechanical causality as opposed to intentional causality (Blakemore et al., 2003).

Main effect of prospective memory
Comparison of the PM conditions, in which subjects were instructed to bear in mind an intention to act as well as performing the ongoing task and the noPM conditions in which subjects were instructed to perform only the ongoing task, resulted in activations in the precuneus, right parietal cortex and right frontopolar cortex (BA 10). These activations are listed in Table 1 and shown in Fig. 4.

Interaction between causality and prospective memory
There was a significant interaction between causality and prospective memory in the posterior dorsal mPFC. Activity in this region to the causality questions was significantly modulated by PM. The addition of the PM task to the PC task increased activity in posterior superior dorsal mPFC, whilst the addition of the PM task to the IC task reduced activity in this region (Fig. 5).

Discussion

The aim of the present study was to investigate the convergence of neural networks used when thinking about intentions and when bearing in mind an intention to act. Previous studies have suggested a role for the dorsal mPFC in both these types of task (Brunet et al., 2000; Gallagher et al., 2000; Happé, 2003; Johnson et al., 2002; Kampe et al., 2003; Kjaer et al., 2002; Lou et al., 2004; Vogeley et al., 2001). MPFC activations in tasks that involve thinking about intentions tend to be more posterior than mPFC activations in prospective memory tasks (Gilbert et al., in preparation). In the current study, subjects responded to questions related either to their own intentions and consequential actions (intentional causality) or to physical events and their consequences (physical causality). This task was combined with a second embedded prospective memory task in which subjects were instructed to bear in mind an intention to act whilst answering

Table 1
Coordinates and *Z* values for regions of significant activation in each contrast

Foci of activation	MNI coordinates			Z value
	x	*y*	*z*	
Main effects				
IC vs. PC				
Precuneus/posterior cingulate	0	−48	33	4.56
L superior temporal sulcus	−57	−57	18	3.85
R superior temporal sulcus	51	−48	24	3.59
L dorsal mPFC	−9	63	12	3.32
L temporal pole	−42	18	−39	3.41
R temporal pole	39	21	−33	3.48
L intraparietal cortex/TPJ	−42	−72	36	4.35
R intraparietal cortex/TPJ	48	−75	36	3.54
PC vs. IC				
L intraparietal sulcus	−57	−30	36	4.00
PM vs. noPM				
Precuneus/posterior cingulate	−3	−60	51	3.50
R parietal cortex	48	−45	45	3.59
R Frontal pole (BA 10)	27	63	6	2.92
Simple effect				
ICnoPM − PCnoPM				
Precuneus/posterior cingulate	3	−42	24	3.99
L superior temporal sulcus	−57	−57	21	2.75
R superior temporal sulcus	57	−66	27	4.24
L dorsal mPFC	−9	69	15	2.82
L temporal pole	−36	12	−30	3.42
R temporal pole	30	18	−27	3.52
L intraparietal cortex/TPJ	−45	−69	36	3.55
R intraparietal cortex/TPJ	48	−72	39	3.21
Interaction				
PC × PM				
Dorsal mPFC	−3	48	30	3.77

the ongoing causality questions. This design provided an opportunity to see what happens when task demands involve functions that rely on the same brain regions.

Subjects took significantly less time to respond to the intentional causality questions than to the physical causality questions. The difference in reaction times could not have been due to any difference in the structural features of the stimuli. Instead, this effect may be due to an inherent difference in cognitive processing demands for each type of question. This difference reflects a finding from a behavioural study in which normally developing children showed significantly better performance on tasks that involve intentional understanding than on similar tasks that involve mechanical understanding (Baron-Cohen et al., 1986). In this study, autistic children showed the opposite pattern, performing better on the mechanical task than the intentional task. It may be that the understanding of intentions is normally more automatic and instinctive, relies more on autobiographical memory and requires less explicit reasoning, semantic memory and 'working it out' than the understanding of physical causality.

Brain activations associated with intentional causality

Responding to questions that involved thinking about one's own intentions and consequential actions activated the dorsal mPFC, the STS especially around the temporo-parietal junction

(TPJ) and the temporal poles. These regions are all part of the highly circumscribed neural network that has consistently been activated by mentalising tasks in functional neuroimaging studies across a wide variety of tasks, ranging from attribution mental states to animated shapes (Castelli et al., 2000, 2002) to understanding beliefs and intentions in cartoons (Brunet et al., 2000; Gallagher et al., 2000; Vogeley et al., 2001) and in stories (Fletcher et al., 1995; Gallagher et al., 2000; Saxe and Kanwisher, 2003).

In a meta-analysis of 12 studies investigating the neural network subserving mentalising, Frith and Frith (2003) propose a functional division between the three regions that are consistently activated during mentalising tasks, and which were activated by intentional causality scenarios in the current study. The STS is activated during the perception of biological motion (Allison et al., 2000; Bonda et al., 1996; Grezes et al., 2001; Grossman et al., 2000; Puce and Perrett, 2003) and faces and body parts (Campbell et al., 2001; Chao et al., 1999; Grezes et al., 1998; Puce et al., 1998). Furthermore, the STS is activated by predicting complex patterns of non-animate objects (Maquet et al., 2003). Saxe and Kanwisher have recently shown that the STS (at the TPJ) is not only involved in processing biological motion but shows additional activation when an observed person is hidden but assumed to be engaged in some form of intentional action (Saxe et al., 2004). Frith and Frith hypothesise that in mentalising the STS plays a role in the prediction of observed patterns of behaviour in order to surmise the mental states underlying this behaviour; in essence, the STS may be involved in the detection of agency.

The temporal poles are activated by semantic decisions (Noppeney and Price, 2002a,b; Vandenberghe et al., 2002), retrieval from autobiographical memory (Fink et al., 1996; Maguire and Mummery, 1999; Maguire et al., 2000) and during recognition of familiar scenes and faces (Nakamura et al., 2000, 2001). Based on this, Frith and Frith propose that the temporal poles are involved in the retrieval of scripts, and in the case of mentalising, in the access to social knowledge in the form of scripts, which aid interpretation of social situations.

Finally, the dorsal mPFC is the region that is most robustly activated during mentalising tasks, whenever people attend to the mental states of oneself or others. These mental states must be decoupled from reality; the way we perceive the world is not the way the world is, but the way we believe the world to be. In order to understand another person's mental states, we must be able to decouple what the other person believes about the world from reality—these may be in agreement, but are not necessarily so. The dorsal mPFC has direct connections to the temporal pole and the STS (Bachevalier et al., 1997). Frith and Frith propose that the mPFC receives input about the content of mental states and their relation to people's actions from the STS and the temporal poles. Consequently, the mPFC may be the basis of the decoupling mechanism that distinguishes mental state representations from physical state representations (Frith and Frith, 2003). On the other hand, a recent study demonstrated that a patient with widespread mPFC damage showed no impairment on mentalising tasks, questioning the necessity of this region for mentalising (Bird et al., 2004).

All three of the described functional properties, prediction of behaviour, knowledge of social situations and decoupling of mental states and reality, also play a role when making decisions about one's own intentions, as in the current study. The activation of the dorsal mPFC, STS and temporal poles in the intentional causality conditions in the current study suggests that reasoning
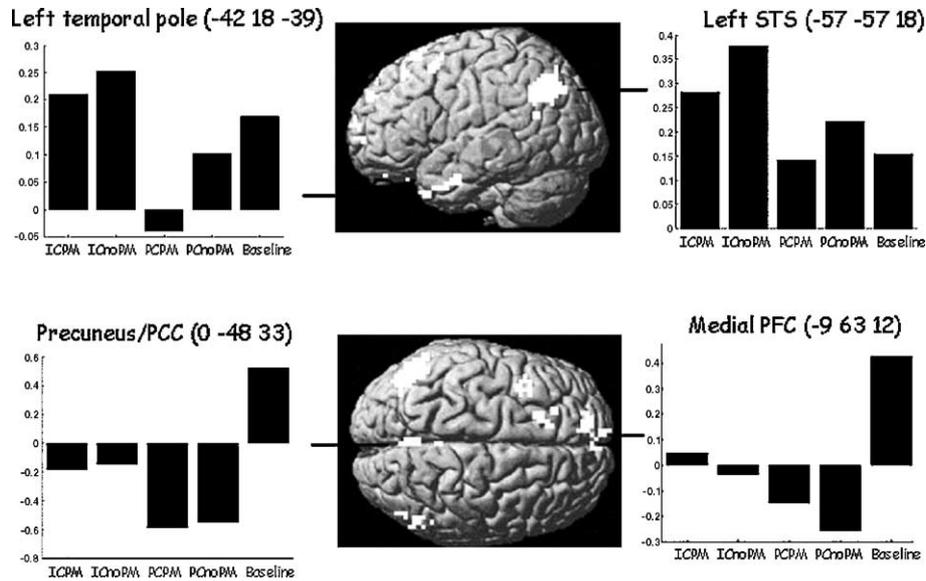
Fig. 2. The main effect of *IC − PC*. Top centre: group activation superimposed on a standard single subject T1-weighted sagittal view of the left hemisphere showing greater activations in the intraparietal/superior parietal cortex and temporal pole in the *intentional causality* condition versus the *physical causality* condition. Bottom centre: coronal view showing greater activations in the precuneus/PCC and the mPFC in the *intentional causality* condition relative to the *physical causality* condition. Plots show condition-specific parameter estimates, which reflect the adjusted BOLD signal in each condition relative to the fitted mean and expressed as a percentage of whole brain mean BOLD signal. Condition labels as in Fig. 1.

about intentional causality may be a precursor to, or a subcomponent of, mentalising. This is in agreement with developmental studies showing that intentional causality develops before fully fledged mentalising, such as false belief understanding, is in place (Barresi and Moore, 1996; Johnson, 2003; Leslie, 1994; Rochat et al., 2004; Schlottmann et al., 2002).

Additionally, we found significant activations in the precuneus/PCC in the intentional causality condition relative to the physical causality condition. In an fMRI study, Vogeley et al. (2001) investigated the neural correlates of attribution of mental states to others and to oneself by comparing verbal stories with ToM content in a third person and a first person perspective. Both tasks activated the mentalising network, but the Self condition also activated the precuneus/PCC. Results from several other neuro-imaging studies investigating the underlying neural networks in

self-awareness and self-processing report that thinking about adjectives that describe oneself, or considering one's own thoughts, activate similar brain regions to those underlying mentalising, as well as the PCC (Happé, 2003; Johnson et al., 2002; Kelley et al., 2002; Kampe et al., 2003; Kjaer et al., 2002; Lou et al., 2004).

From a different angle, Gusnard and Raichle (Gusnard and Raichle, 2001; Gusnard et al., 2001) have suggested that the mPFC, together with the precuneus/PCC, reflects a default mode in which, in the absence of more demanding task demands, subjects are free to reflect on themselves and their own thoughts. They have drawn attention to the higher activity in the these regions during low level baseline conditions than during more demanding task conditions. In the current study, this effect was present: activity in the dorsal mPFC and the precuneus/PCC was highest during the baseline condition (Fig. 2), even higher than in the intentional causality conditions. Alternatively, the PFC activity observed during baseline conditions, and during intentional causality in the current study, may reflect its purported role, the enabling of behaviour in situations where incoming stimuli are insufficient to trigger a behaviour (Burgess et al., in press). Burgess et al. suggest that the PFC plays a role in the co-ordination of stimulus-independent thought and stimulus-oriented thought. This would come into play in situations where the stimuli are not sufficient to capture full attention. That reaction times were faster to the IC questions than the PC questions suggests that the former are more automatic (and hence require less attention and calculation) than the latter.
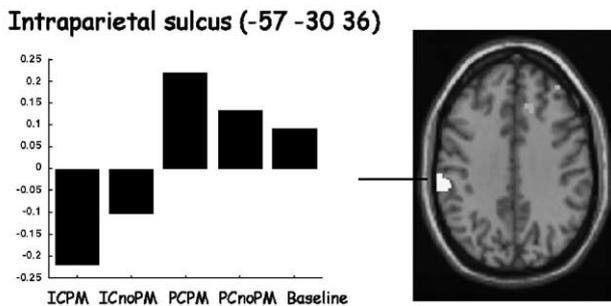
Prospective memory

We found expected activations for the PM task in the right parietal cortex, right frontopolar cortex (BA10) and precuneus/PCC. The lateral aspect of the frontopolar cortex (BA 10) activated by the PM task in the current study appears specifically to be involved in maintaining an intention whilst performing an ongoing
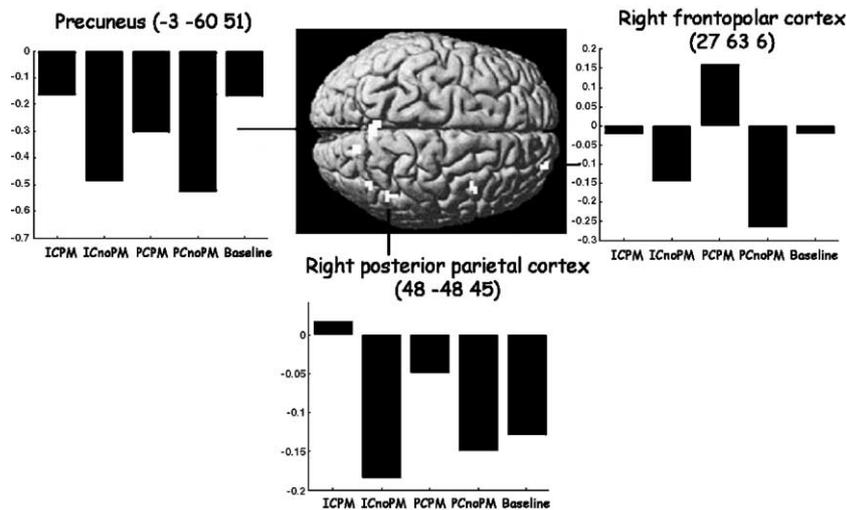

Fig. 3. The main effect of *PC − IC*. Centre: group activation superimposed on a standard single subject T1-weighted sagittal view of the left hemisphere showing greater activations in the intraparietal sulcus in the *physical causality* condition versus the *intentional causality* condition. The plot shows condition-specific parameter estimates, which reflect the adjusted BOLD signal in each condition relative to the fitted mean and expressed as a percentage of whole brain mean BOLD signal. Condition labels as in Fig. 1.

Fig. 4. The main effect of *PM−noPM*. Centre: top view of group activation superimposed on a standard single subject T1-weighted image showing greater activations in the frontal pole (BA10), the precuneus/PCC and the right parietal cortex in the prospective memory condition compared with blocks in which subject did not execute the prospective memory task. Plots show condition-specific parameter estimates, which reflect the adjusted BOLD signal in each condition relative to the fitted mean and expressed as a percentage of whole brain mean BOLD signal. Condition labels as in Fig. 1.

task (Burgess et al., 2001, 2003). The right parietal lobe has been suggested to play a role in sustained attention or vigilance, i.e. looking out for the target stimulus (Burgess et al., 2001). In contrast to the increased activity in lateral frontopolar cortex during PM, activity in anterior, dorsal mPFC is decreased during PM tasks relative to noPM tasks (Burgess et al., 2003).

Convergent neural networks: precuneus/posterior cingulate cortex

The precuneus/PCC showed higher activations in both the intentional causality (Fig. 2) and the PM conditions (Fig. 4). In addition, this region appears to be most active in the baseline condition in the current experiment (Figs. 2 and 3; cf. Gusnard and Raichle, 2001; Gusnard et al., 2001). Slightly different regions within this large area were activated by intentional causality and prospective memory. The precuneus activation in the PM condition was superior and posterior to the activation in the IC condition.
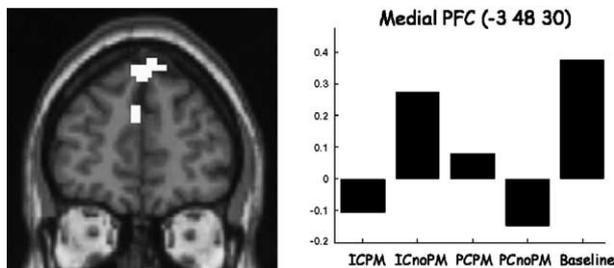

Fig. 5. Interaction (PCPM − PCnoPM) − (ICPM − ICnoPM). Left: group activation superimposed on a standard single subject T1-weighted coronal view showing that, in the PC condition, the dorsal mPFC is activated more in PM blocks than in noPM blocks. Note that this region is posterior and superior to the region of dorsal mPFC activated by the main effect of IC− PC (Fig. 2). Right: the plot shows condition-specific parameter estimates, which reflect the adjusted BOLD signal in each condition relative to the fitted mean and expressed as a percentage of whole brain mean BOLD signal. Condition labels as in Fig. 1.

One possibility is that the precuneus/PCC is specifically involved in processing intentions related to the self. The precuneus has been activated in neuroimaging studies across a wide variety of tasks related to intentions to act and thinking about one's own intentions (Gusnard and Raichle, 2001; Gusnard et al., 2001; Johnson et al., 2002; Kjaer et al., 2002; Kelley et al., 2002; Lou et al., 2004). The precuneus is commonly activated in prospective memory experiments (Burgess et al., 2001; Burgess et al., 2003; Okuda et al., 1998; West and Ross-Munroe, 2002). In a study on anticipation, preparation and execution of movements, greater activation was found in the precuneus and mPFC during the preparation of movement, i.e. the intention to move versus the actual execution of the movement (Sahyoun et al., 2004). The localisation of the precuneus activation in the PM condition in the current study is very similar to that in previous PM studies (Burgess et al., 2001), being superior and posterior to the activation in the IC condition. The precuneus/PCC activation in the IC condition was widespread (see Fig. 2) and was in a similar location to precuneus/PCC activations found in previous mentalising studies (Gallagher et al., 2000) and in studies that involved self-reflection (Johnson et al., 2002; Lou et al., 2004). Kircher et al. (2002) compared 'intentional' self-processing, in which subjects judged traits on self-descriptiveness, and 'incidental' self-process-ing, in which subjects categorised words on physical versus psychological attributes, unaware that these words had been arranged in blocks of self-descriptiveness. When contrasted, the sole area more active in the intentional (aware) versus incidental (unaware) conditions was the left precuneus, its location being close to that in the IC condition in the current study.

Interaction between causality and prospective memory

The causality task was significantly modulated by the presence of the embedded prospective memory task. When subjects answered questions related to intentional causality at the same time as executing a prospective memory task (ICPM condition), the dorsal mPFC was less active than when subjects answered questions related to intentional causality in the absence

of the PM task (ICnoPM; Fig. 5). Previously, it has been found that a slightly anterior region of mPFC (−2 62 22 in the study by Burgess et al., 2003; −3 48 30 in this study) shows decreased activity during PM relative to non-PM tasks (Burgess et al., 2003). Whilst previous studies have convincingly demonstrated that activations during PM are independent of the nature of the ongoing task (Burgess et al., 2001, 2003), our data suggest that PM-related activity in the dorsal mPFC is modified by the nature of the ongoing task. Burgess et al. (2003) propose that the role of PFC in PM is in maintaining an intention whilst performing an ongoing task, which requires some attentional withdrawal from the external (i.e. ongoing) stimuli, and a corresponding increase of attentional focus upon internally generated intentions. In their account, mPFC plays a role in maintaining attention to external stimuli whereas lateral, polar PFC is involved in the maintenance of attention to internal cognitions.

The posterior superior region of dorsal mPFC that showed an interaction between causality and PM is distinct from the slightly more anterior inferior region activated in the main effect of intentional versus physical causality. The posterior superior region of dorsal mPFC showed decreased activity when the intentional causality task was carried out at the same time as the PM task. In contrast, the more anterior inferior region of the dorsal mPFC showed no such modulation: its activation during intentional causality was not significantly modulated by having to carry out the PM task (see Fig. 2). Posterior superior dorsal mPFC seems to be unnecessary for intentional causality in that its activity can be low whilst subjects are performing such a task. In contrast, activity in the more anterior inferior region in the dorsal mPFC was always high when subjects were performing the intentional causality task, irrespective of the PM task. This suggests that different regions of mPFC may play different roles in thinking about intentions. The nature of these roles requires further investigation.

Acknowledgments

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