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The left temporo-parietal junction is necessary for representing someone else´s belief

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A standard view in the neuroscience literature is that the frontal lobes sustain our ability to process mental states such as beliefs, intentions, desires (often referred to as "theory of mind"). We report the case of three brain-damaged patients with a deficit in reasoning about the belief of another person following sustained lesions involving the left temporo-parietal junction. We conclude that, in addition to any role played by the frontal lobes in reasoning about the beliefs of others, the left temporo-parietal junction is necessary for this function.

Tasks commonly used to examine mental state reasoning require, for example, the inference that someone has a false belief, or the inference that someone is lying or is making a joke. Recent findings highlight the contribution of the frontal lobes to this form of reasoning by showing that mental state reasoning is both accompanied by frontal brain activation in neurologically intact adults[1,2] and is impaired following lesions to the frontal lobes[3]. Additionally, imaging studies show activation in more posterior regions, especially the temporo-parietal junction, when participants perform mental state reasoning tasks[4,5]. To date, however, no study has shown whether these more posterior regions are *necessary* for social reasoning. Furthermore, since the temporo-parietal junction also appears to be involved in the processing of socially meaningful cues such as gaze direction and goal-directed action[6,7] and since mental state reasoning tasks typically also involve the processing of such socially meaningful cues, the precise cause of temporo-parietal activation is unclear. Studies of brain-damaged patients can help resolve these issues. Firstly, finding that damage to the temporo-parietal junction may cause specific impairment of mental state reasoning would suggest that this region was *necessary* for such social-cognitive activity. Secondly, finding that such an impairment could not be explained by a deficit in processing social cues would suggest that this region was not only involved in low-level social perception but also in higher-level social reasoning. Here we present the first such evidence from a case series of three patients with damage to the left temporo-parietal junction (see **Table 1** for a description of the case studies). Informed consent was obtained from all participants (written consent from the patients and oral consent from the control participants). The patients were asked to perform a story-based and a video-based non-linguistic false belief reasoning task (see **Supplementary Methods**).

The three patients failed to perform above chance level on the false belief trials in either of the two tasks (see **Fig 1**). Potentially, the patients' false belief reasoning errors could have occurred because of difficulties in handling the incidental task demands such as understanding, integrating and remembering the sequence of events within the stories or videos. Both tasks included control trials that were closely matched to the false belief trials in terms of incidental task demands but did not require the inference that someone has a false belief. Impaired performance on both the control and the false belief trials would thus indicate difficulties in handling the incidental task demands. PF had no difficulties with any of the control trials in either of the two tasks. DB and RH, two aphasic patients, only had difficulties with the control trials in the more language-laden task. In contrast, once the language demands were reduced (in the video-based task), neither of these patients made mistakes on control trials.

Difficulties in inhibiting one's own knowledge of the correct answer is often held as another reason why participants may fail to correctly infer someone else's belief[13]. This explanation could have accounted for our patients' false belief errors in the story-based task. However, the video-based false belief task was designed in such a way that participants do not know the correct answer when inferring that one of the characters has a false belief. Thus, false belief errors could not be due to a failure to inhibit such knowledge of the objectively correct response. Despite this, no patient performed significantly above chance level on the false belief items from the video-based task.

A general reasoning deficit is another alternative explanation for the patients' false belief reasoning errors. If this were the case, we would expect the patients to make errors when performing formally similar types of reasoning. Counterfactual reasoning (e.g. If the object had not moved, where would it be?) has important formal similarities to false belief reasoning[14,15]. This was assessed by one of the control conditions in the story-based task. DB and RH made some errors for this type of reasoning (although DB still performed above chance), but their difficulties in passing memory and reality control questions in the story-based task obscure the interpretation of their reasoning errors. In contrast, PF's errorless performance in the counterfactual condition provides clear evidence that her problem with belief reasoning does not extend to all formally similar types of reasoning.

Finally, we assessed if the false belief reasoning errors in our patients were due to a low-level social perception deficit. Social meaningful visual cues such as gaze, pointing or head movement were absent in the story-based task. Moreover, in the video-based false belief task, the sole socially meaningful cue (i.e. where the woman pointed) had to be processed for memory control trials as well as for false belief trials. Yet the three patients made no errors on the memory control trials. Spared discrimination of pointing is further supported by all three patients' good performance in independent pointing processing tasks. Importantly, we do not claim that the patients had no difficulties in low-level social processing. On the contrary, all three patients showed some difficulties in gaze direction processing. But we do claim that the patients' deficit in high-level social reasoning was not the result of incorrect processing of low-level social cues.

To conclude, our data suggest that lesions to the left temporo-parietal junction can impair the cognitive processes specifically involved in the inference of someone else's belief. This is consistent with previous neuroimaging studies that have shown the activation of the temporo-parietal junction when healthy adults reason about mental states such as beliefs[4,5]. It provides the first evidence from brain-damaged patients showing that the left temporo-parietal junction is not only involved but *necessarily* mediates mental state processing, in addition to any further role of the frontal lobes. Importantly, our data further suggest that the left temporo-parietal junction sustains not only low-level social perception but also higher-level social reasoning, such as false belief reasoning.

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Table 1 Patients' characteristics and patients' and control participants' performance on language, executive function and low-level social perception tasks. Scores reflect the percentage of correct responses unless otherwise stated. Scores falling outside the range of controls' performance are presented in bold. All 16 subjects (aged 46 to 68) were given the executive function tasks (except for the Brixton, for which we considered the published norms). Three of the subjects were presented with gaze and pointing tasks. For the inhibition and shifting tasks the cost was calculated by subtracting the score (reaction time divided by number of correct responses) in the "baseline" condition from the score in the "executive" condition. Three gaze direction tasks used photograph stimuli. Participants judged the gaze direction of an actor who looked upwards at one of 5 or 9 positions on an arc (angle judgement), either left or right (left/right), or directly towards *versus* away from the viewer (at you/not at you). The pointing direction tasks were similar, with the actor pointing in the same directions as in the eye gaze tasks.

	PF	**DB**	**RH**	**Controls Mean (range)**
Gender	F	M	M	
Age	55	62	70	
Handedness	R	R	L	
Main lesion site	Left angular and supramarginal gyri, superior temporal gyrus	Left angular gyrus, superior and middle temporal gyri	Left angular and supramarginal gyri, superior temporal gyrus	
Aetiology	Stroke	Stroke	Stroke	
Years post-onset	8	6	8	
Major clinical symptoms	Right extinction, dysgraphia	Aphasia	Right neglect, deep dysphasia, dyslexia and dysgraphia	
Language				
Written synonym matching	84%	**50%**	**39%**	-
Sentence/picture matching – PALPA55[8]	78%	77%	**58%**	-
Executive function				
Working memory – manipulation	94%	**73%**	-*	99% (88-100)
Working memory – resistance to interference	39%	**23**%	-*	71% (31-100)
Working memory – updating	**33%**	**50%**	-*	86% (67-100)
Inhibition – stimulus selection (cost)	0.25	0.48	0.33	0.18 (0.02-0.53)
Inhibition – response selection (cost)	**3.93**	0.40	0.20	0.30 (0.09-0.63)
Shifting – alternation of focus of attention (cost)	1.72	1.56	**2.46**	0.97 (0.44-1.75)
Shifting – alternation of arithmetical operation (cost)	**3.59**	1.53	1.23	0.87 (0.05-2.20)
Brixton[9]	50%	67%	**39%**	Impaired if <42%
Gaze and pointing				
Gaze direction detection – angle judgement	85%	75%	77%	75% (69-81)
Gaze direction – left/right	**69%**	**90%**	**90%**	99% (98-100)
Gaze direction – at you/not at you	**88%**	**75%**	**60%**	97% (94-100)
Pointing direction – angle judgement	**96%**	100%	100%	100%
Pointing direction – left/right	100%	100%	98%	97% (90-100)
Pointing direction – at you/not at you	77%	92%	90%	87% (65-100)
Faces Test[10]	95%	95%	**80%**	97% (95-100)
Revised Child Eyes Test[11]	79%	**64%**	**57%**	76% (71-79)
Revised Adult Eyes Test[12]	**56%**	**47%**	-**	69% (64-72)

* Performance at floor due to language impairment.
** Not tested due to language impairment.

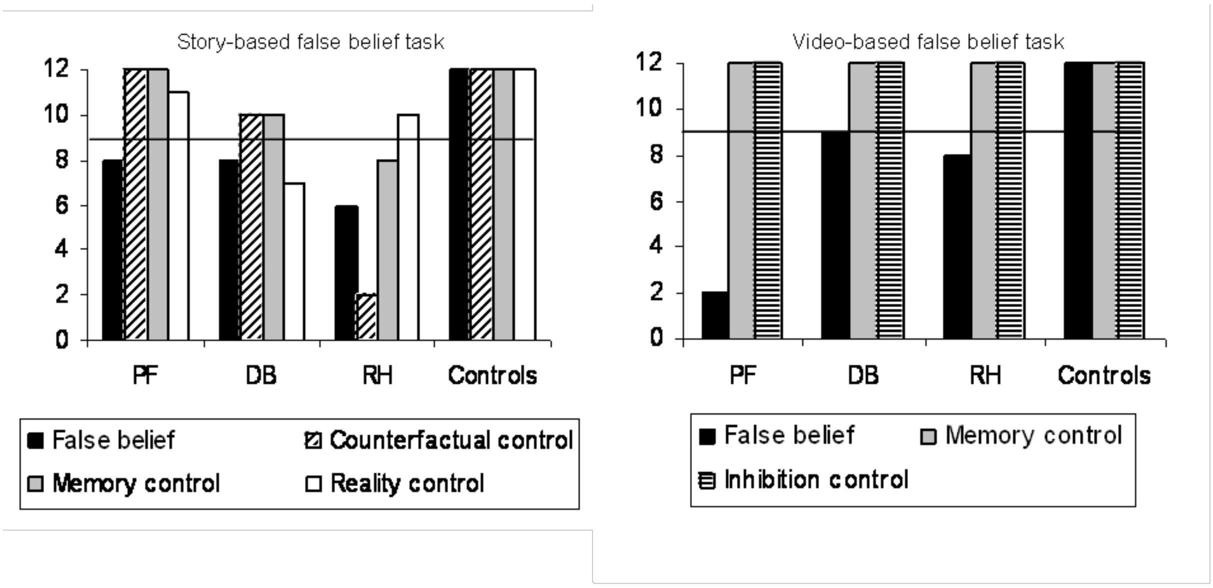

Figure 1 Patients' and controls' (n=3) performance on the false belief tasks as a function of the type of trial (false belief *versus* control trials). A score of more than 9 correct answers is significantly above chance level (one-tailed probability of 10/12 correct= 0.019 by binomial test).

Supplementary Methods

The story-based task consisted of 12 verbal stories. The stories first related a character's awareness of one reality (e.g. Zack puts the milk in fridge), then the character' unawareness of a change in reality (e.g. Zack leaves the room and Kim finishes the milk with her cereal and throws the milk carton in the bin). For each story, four questions were asked (each with a binary choice): (1) a false belief question (e.g. Where does Zack think the milk carton is?), (2) a counterfactual question that does not call upon false belief reasoning but assesses the participant's ability to simultaneously hold two representations of the world (e.g. What if Kim had not had cereal, where would the milk carton be?), (3) a memory question (e.g. Where was the milk carton at the beginning?) and (4) a reality question (e.g. Where is the milk carton now?). Questions (3) to (4) controlled for the incidental processing demands of the false belief reasoning task (i.e. understanding, integrating and remembering the sequence of events).

The video-based and non-verbal false belief task was adapted from a previous study[1]. The task consisted of 12 false belief, 12 memory and 12 inhibition control videos. The false belief videos showed a woman watching as a man placed a green object in one of two boxes. The participant could not see which box contained the green object. The woman then left the room and while she was away, the man swapped the two boxes. The woman then returned and pointed to one of the boxes. In order to locate the green object, the participant had to infer that the woman had a false belief and that the green object was therefore located in the box other than the one indicated. Importantly, the participant does not know the true location of the object until they make this belief inference. Thus, unlike most false belief tasks, participants' attribution of a false belief cannot be disrupted by interference from their own knowledge of the correct answer.

The memory control videos were exactly the same, except that the sequence of two events had been inverted, i.e. the woman pointed to one of the boxes before leaving the room. The participant could then infer where the green object was without inferring that the woman had a false belief, but participants needed update their memory of the object's location after the boxes had been swapped. The inhibition control video showed the same sequence of events as the false belief video but instead of swapping the boxes, the man performed a visible transfer of the green object from one box to the other. In order to locate the green object, participants did not need to infer that the woman has a false belief (they saw where the green object was transferred) but they needed to inhibit pointing to the (wrong) box indicated by the woman. Twenty-four filler-trials were added to minimise the possibility that participants solved the false belief trials by superficial means (e.g. always responding to the box opposite from where the woman pointed).

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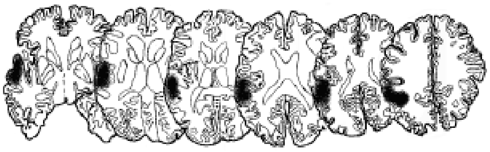
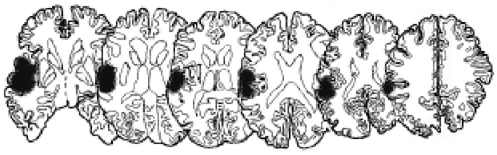
PF



DB



RH