

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/10902889>

Functional imaging of ‘Theory of Mind’

Article *in* Trends in Cognitive Sciences · March 2003

DOI: 10.1016/S1364-6613(02)00025-6 · Source: PubMed

CITATIONS

1,749

READS

1,528

2 authors:



Helen L Gallagher

Glasgow Caledonian University

21 PUBLICATIONS 4,236 CITATIONS

[SEE PROFILE](#)



Chris D Frith

University College London

890 PUBLICATIONS 155,645 CITATIONS

[SEE PROFILE](#)

Some of the authors of this publication are also working on these related projects:



MRC-CRC Psychiatry [View project](#)



Gingerella (RockaFela) [View project](#)

Functional imaging of 'theory of mind'

Helen L. Gallagher and Christopher D. Frith

School of Health and Social Care, Glasgow Caledonian University, 70 Cowcaddens Road, Glasgow G4 0BA, UK

Our ability to explain and predict other people's behaviour by attributing to them independent mental states, such as beliefs and desires, is known as having a 'theory of mind'. Interest in this very human ability has engendered a growing body of evidence concerning its evolution and development and the biological basis of the mechanisms underpinning it. Functional imaging has played a key role in seeking to isolate brain regions specific to this ability. Three areas are consistently activated in association with theory of mind. These are the anterior paracingulate cortex, the superior temporal sulci and the temporal poles bilaterally. This review discusses the functional significance of each of these areas within a social cognitive network.

One aspect of social cognition sets us apart from other primates. It underpins our ability to deceive, cooperate and empathize, and to read others' body language. It also enables us to accurately anticipate other people's behaviour, almost as if we had read their minds. This exceptional capacity is known as having a 'theory of mind', or mentalizing. It underlies our ability to explain and predict the behaviour of ourselves and others by attributing to them independent mental states, such as beliefs, desires, emotions or intentions. Theory of mind is an automatic, high-level and – almost without exception – human function. In these circumstances we can have no data from animal studies directly relevant to the brain systems underlying this ability. Furthermore, neuropsychology data, although identifying involvement of brain regions such as the frontal lobes and amygdala, are limited by their ability to pinpoint functions to specific structures. Thus, in recent years, functional imaging has become one of the more powerful methods for studying the neural correlates of this important human ability.

Theory of mind mechanisms

There is, as yet, no computational account of the mechanisms that underlie theory of mind or mentalizing ability. However, it is thought to depend on an innate cognitive mechanism [1], possibly dedicated and domain specific [2,3]. Evidence from studies of autism support this theory. Autism is a biologically based disorder that seems to be characterized by a selective impairment in theory of mind [4,5] (for example, see Box 1) that is able to account for many of the deficits in communication, socialization and imagination that are manifest in individuals with this disorder [6]. Leslie's model of mentalizing [1,7] proposes that the theory-of-mind mechanism (ToMM) depends on a

representation of imaginary circumstances 'decoupled' from reality. When explaining a person's behaviour in terms of a belief, we have to recognize that this belief might not correspond to reality. Even when it conflicts with reality, it is the belief, not the reality, that determines behaviour. To have a theory of mind, we must recognize that other people are agents whose behaviour is determined by their goals. In addition, we have to recognize that other people have a different perspective on the world from ours. To understand their behaviour we have to take account of their perspective as well as the state of the world from our own perspective. We have to be able to separate and compare the two perspectives.

The importance of this distinction is most clear-cut in situations involving false beliefs. Chris knows that Helen wants a chocolate. He also knows that the chocolates are in the cupboard. So does he expect Helen to go to the cupboard? No. Because he also knows that Helen believes that the chocolates are still in the drawer. Chris's knowledge of Helen's desire enables him to predict that she will go to the chocolate, but his recognition of her false belief enables him to predict that she will go to the drawer and not to the cupboard where the chocolates really are.

Our ability to understand the behaviour of others in terms of their goals and beliefs requires that we have some expectations as to what these goals and beliefs are likely to be. These expectations derive from our general knowledge of the world, from our specific knowledge of this person and from our observations of what he or she is doing. Of particular relevance is the kind of knowledge of the world that is referred to as a script [8]. Scripts record the particular goals and activities that take place in a particular setting at a particular time. For example, the goals associated with the 'restaurant script' would include reading the menu, ordering a drink and getting the bill. If I catch the waiter's eye and make the gesture of writing on my left palm with my right forefinger he will usually bring me the bill. He correctly interprets my action on the basis of his knowledge of my likely goals. He will not bring me pencil and paper (although this did happen to one of us, C.D.F., on one occasion).

The primary aim of functional imaging is to isolate the neural basis of the theory-of-mind mechanism. This mechanism is likely to have evolved from several pre-existing processes that contributed to its development and are probably still involved during mentalizing. It has been suggested that such functions might include the ability to distinguish between animate and inanimate entities, the ability to share attention by following the gaze of another agent, the ability to represent goal-directed actions and the ability to distinguish between actions of the self and

Corresponding author: Helen L. Gallagher (h.l.gallagher@gcal.ac.uk).

Box 1. Theory-of-mind tasks

A good illustration of what is meant by 'theory of mind', or mentalizing, and how it differs from other non-mentalizing social predicaments is the 'sabotage/deception task' [a] (Fig. 1). This test makes a distinction between two behaviours differing only in the demands they make upon the ability to mentalize. Several other tests have been devised that make similar 'fine-cut' comparisons between intact and impaired abilities by using cognitively similar tasks: false photograph/false belief test [b,c], understanding see/understanding know [d], and understanding literal/metaphorical expression [e], recognition and spontaneous use of instrumental gestures (gestures that are intended to regulate or change the behaviour of others by communicating commands, e.g. go away) but not expressive gestures (gestures deliberately expressing inner feeling states, or responses to feeling states in others, e.g. embarrassment) [e,f]. These types of tasks lend themselves well to functional imaging paradigms and cognitive subtraction analyses.

References

- a Sodian, B. and Frith, U. (1992) Deception and sabotage in autistic, retarded and normal children. *J. Child Psychol. Psychiatry* 33, 591–605
- b Leslie, A.M. and Thaiss, L. (1992) Domain specificity in conceptual development: neuropsychological evidence from autism. *Cognition* 43, 225–251
- c Leekam, S. and Perner, J. (1991) Does the autistic child have a metarepresentational deficit? *Cognition* 40, 203–218
- d Leslie, A.M. and Frith, U. (1988) Autistic children's understanding of seeing, knowing and believing. *Br. J. Dev. Psychol.* 6, 315–324
- e Happé, F.G.E. (1993) Communicative competence and theory of mind in autism: a test of relevance theory. *Cognition* 48, 101–119
- f Attwood, A.H. et al. (1988) The understanding and use of interpersonal gestures by autistic and Down's syndrome children. *J. Autism Dev. Disord.* 18, 241–257

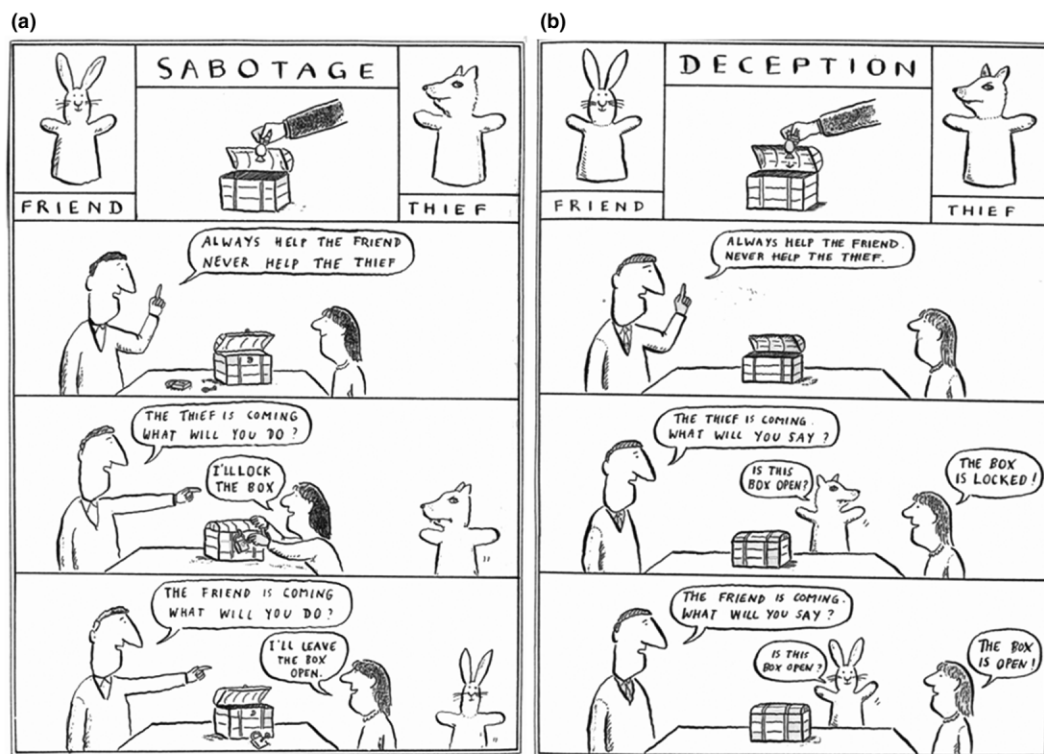


Fig. 1. The sabotage and deception task. In this task, a child is shown two puppets: one is the 'friend' and the other the 'thief'. A sweet is placed in a box and the child is given the instruction: "always help the friend; never help the thief". In the sabotage task (a) this would require the child to sabotage the thief's attempts to steal the sweet by locking the box. If the child sees the friend puppet coming, however, he should leave the box open. In the deception task (b) the box is unlocked and the child is asked what he will say when the puppet asks if the box is open. The child should lie to the thief but tell the truth to the friend. It was found that when autistic children were required to lie, they performed worse than control and mentally retarded children matched for mental age. However, they performed as well when required to sabotage using physical manipulation (locking the box), demonstrating that their failure on the deception task was not due to an inability to understand the task but an inability to 'understand the mind' of their opponent. (Reproduced with kind permission of the artist Axel Scheffler).

others [9]. Thus we would expect that the mentalizing mechanism is a component of a network of functionally related regions. We would also predict that such a uniquely human mechanism might involve regions of the brain that have undergone recent evolutionary changes.

Neuroimaging studies of theory of mind

Several functional imaging studies have been undertaken to isolate the neural substrates of mentalizing ability [10–18]. These have demonstrated remarkably consistent

results despite using multimodal and diverse cognitive paradigms, such as verbal and non-verbal or on- and off-line tasks. In accordance with Leslie's theory [1], the findings of these studies indicate that this ability is mediated by a highly circumscribed region of the brain, the anterior paracingulate cortex (approximately corresponding to Brodmann area (BA) 9/32). Two other regions of the brain, the superior temporal sulcus (STS) and the temporal poles bilaterally, also consistently activate in these studies but are not uniquely associated

with mentalizing. These two regions provide clues to the origins of this mechanism as they both support pre-existing functions and are involved in processing explicit behavioural information such as the perception of intentional behaviour (the STS) and the retrieval from memory of personal experiences (the temporal poles), which are believed to be essential prerequisites for the development of such an ability. In this review we argue that the anterior paracingulate cortex is the location of the cognitive mechanism underpinning the ability to represent mental states 'decoupled' from reality. We also speculate on the roles of other key brain regions believed to comprise the 'social brain' [12,19] and their role in the development of this ability.

Anterior paracingulate cortex: the decoupling mechanism

To date, functional imaging studies have activated networks of regions in association with theory of mind [10–16] that involve both common areas (the anterior paracingulate, the STS and the temporal poles) and unique task-related areas. However, two recent studies suggest that the anterior paracingulate cortex is the key region for mentalizing [17,18]. In contrast to the earlier studies that have all used 'off-line' paradigms requiring the volunteer to consider a scenario and retrospectively explain the behaviour of the person or persons involved, both of these studies have used paradigms that require their volunteers to mentalize in real time or, in other words, 'on-line' [7].

Using positron emission tomography (PET), Gallagher *et al.* [18] asked volunteers to play a competitive game that was a computerized version of the children's game 'stone, paper, scissors'. The game was played under three different experimental conditions that allowed tight control of other cognitive demands. In the mentalizing condition volunteers believed they were playing against the experimenter and thus adopted what Dennett [20] describes as an 'intentional stance', which is to treat a system as an agent, attributing to it beliefs and goals. In the comparison condition, volunteers believed they were playing against a computer using a predetermined, rule-based strategy, and thus treated their opponent not as an agent but as a machine. In fact, in both instances during the critical scanning window they played against a random sequence. The only difference between the conditions was the attitude, or 'stance', adopted by the volunteer. In a third condition the volunteers were told they were playing against a random sequence that acted as a low-level control. The main comparison of the mentalizing condition versus rule solving showed only one region of significant activation – the anterior paracingulate cortex bilaterally ($x = 8, y = 54, z = 1$; Fig. 1). No further regions appeared even when the statistical threshold was lowered to $p = 0.1$.

McCabe *et al.* [17] also found activation in the anterior paracingulate cortex in association with cooperation, which the authors suggest 'requires the ability to infer each other's mental states to form shared expectations over mutual gains and make cooperative choices that realize these gains'. In this functional magnetic resonance imaging (fMRI) study, volunteers played standard two-person 'trust

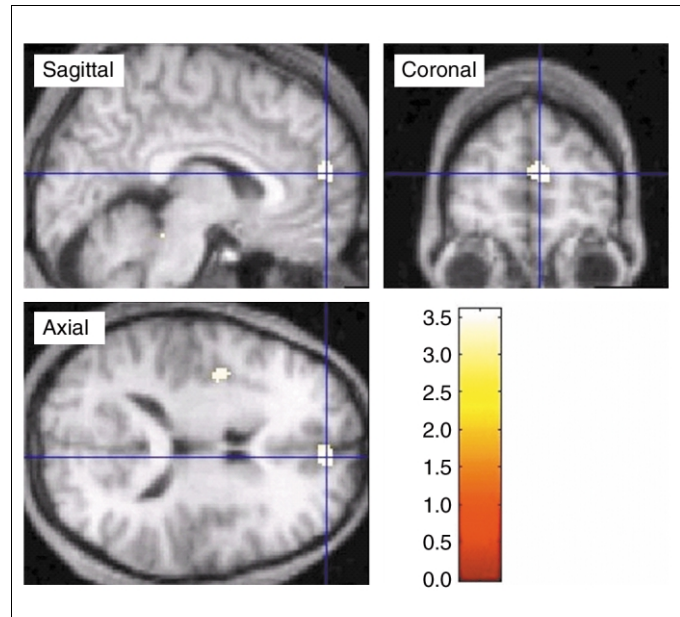


Fig. 1. Region of maximum activity in the region of the anterior paracingulate cortex elicited when subjects adopted an 'intentional stance'. This image displays group data mapped onto a template brain.

and reciprocity' games with both human and computer counterparts for cash rewards. Activity in the anterior paracingulate cortex was seen in a group of volunteers who consistently cooperated with the person they were playing against. This activity was not seen when they played the same game against a computer. These two studies differ from the earlier functional imaging studies of mentalizing ability in two important characteristics. As mentioned earlier, both studies examined 'on-line' mentalizing ability. In addition, the only difference between the mentalizing condition and the control conditions in both of these studies lay in the 'stance' adopted by the volunteers. Because the interactions occurred via a computer, no explicit behavioural cues such as eye gaze or expressive body language were available. Furthermore, the cues that were available were identical in the various conditions. This lack of differential cues to aid mentalizing might explain why these studies failed to activate any other regions in association with mentalizing. Had the volunteers been able to view their opponents it is probable that some of the other regions seen in previous studies of mentalizing, such as the STS or the temporal poles, might also have activated. We propose that activity in the medial prefrontal cortex occurs when cues are used in a particular way; that is, to determine an agent's mental state, such as a belief, that is decoupled from reality, and to handle simultaneously these two perspectives on the world.

Anterior paracingulate cortex: anatomical features

The medial prefrontal region activated by these studies and all of the previous studies of mentalizing ability [10–16] can be described as the most anterior part of the paracingulate cortex, where it lies anterior to the genu of the corpus callosum and the anterior cingulate cortex (ACC) proper. The paracingulate cortex (approximately corresponding to BA 32) is often considered to be part of the

ACC that incorporates the cytoarchitecturally defined Brodmann areas 24, 25 and 33. The ACC is an ancient structure that has been broadly defined by Broca as belonging to the limbic lobe [21]. However, the existence of an unusual type of projection neuron (spindle cell) found in the human, and in some other higher primates (pongids and hominids) but not in monkeys, is evidence that the ACC has undergone changes in recent evolution [22]. Furthermore, in humans these cells are not present at birth, but first appear at around 4 months of age [23]. In the human brain BA32 often extends anteriorly into the paracingulate gyrus [24]. This is dependent on the presence or absence of a paracingulate sulcus, the incidence of which is approximately 50% [24]. The presence of a paracingulate sulcus indicates that this frontal region is likely to be located on a gyral crown and this increased cortical folding might be indicative of a progressive evolution of this region in humans [25]. However, BA32 has been described cytoarchitecturally as a cingulofrontal transition area [26] and therefore anatomically (and speculatively functionally) distinct from the ACC proper. It remains to be seen whether the recent evolutionary changes observed in the ACC are relevant to the more anterior region of the medial frontal lobe, where activations associated with mentalizing are observed.

Theory-of-mind: lesion studies

As yet, we have no information about the effects of lesions in circumscribed regions of the paracingulate cortex. However, there is evidence from studies of neurological patients that intact frontal cortex, in particular the medial frontal region, is necessary for good performance of mentalizing tasks. Rowe *et al.* [27] found that patients with frontal lesions had difficulties with mentalizing tasks and these difficulties were independent of problems they had with traditional executive tasks. Stuss *et al.* [28] also found that patients with frontal lesions had difficulties with mentalizing tasks. In particular, patients with medial frontal lesions (especially on the right) were unable to detect the deception of a protagonist, a classic task requiring mental state attribution.

Alternative accounts of paracingulate activity

Could the activation of the anterior paracingulate cortex in studies of theory of mind simply reflect autonomic arousal? This idea is based on evidence from neuroimaging studies that have attributed activation in regions of the ACC to autonomic arousal, in particular cognitive uncertainty and anticipatory arousal [29,30]. However, the region activated in those studies was significantly more posterior to the anterior paracingulate cortex seen in the mentalizing studies (see Fig. 2).

Is it possible that mentalizing tasks activate the medial prefrontal cortex because they are intrinsically difficult and involve components typical of executive tasks? This also seems unlikely. In a meta-analysis of functional imaging studies in which cognitive demand was manipulated, Duncan and Owen [31] found a dorsal part of the ACC to be associated with increasing task difficulty. However, the coordinates of the anterior paracingulate activations seen in the imaging studies of mentalizing

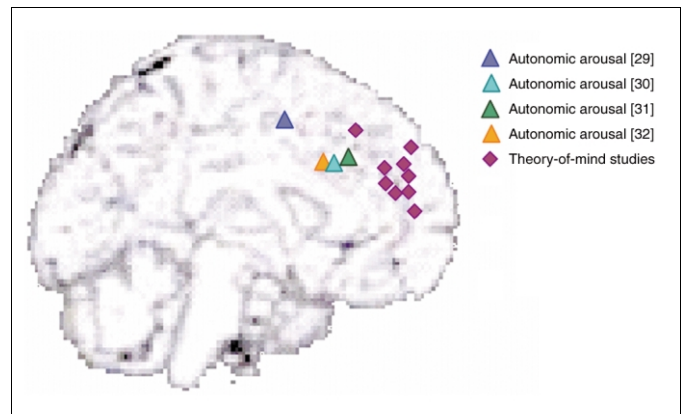


Fig. 2. The points of maximum activity in the anterior cingulate cortex found to be associated with autonomic arousal, cognitive demand and response conflict displayed with the same data from theory-of-mind studies in the anterior paracingulate cortex.

are more anterior to this region. Similarly, in the meta-analysis of ACC activations associated with Stroop-like tasks reported by Barch *et al.* [32], the focus of activity was posterior to that observed in studies of mentalizing (see Fig. 2).

There are, however, several studies in which this region of the medial prefrontal cortex has been activated by tasks that did not involve thinking about the mental states of other people. For example, activation of this area is seen in studies of emotion [33], especially when volunteers are asked to reflect upon the emotions they are currently experiencing [34,35]. These tasks also involve mentalizing, except that it is our own mental states rather than those of other people that have to be represented. The paracingulate cortex has been activated in imaging studies involving many forms of this kind of self-monitoring: visual self-recognition [36], autobiographical memory [37,38], verbal self-monitoring [39], self-generated thoughts [40], externally produced tickling [41], and perception of pain [42]. Gusnard *et al.* [35] have noted that the paracingulate cortex is active during the 'rest' condition in many studies of cognitive processes. They speculate that this might reflect a 'default' mode of functioning in which we think about ourselves when there is nothing external to attend to. It is well established that the ACC has a role in directed attention. Perhaps its most anterior section is specialized for directing attention to mental states.

The role of the STS

In addition to the anterior paracingulate cortex, two regions, the STS and the temporal poles bilaterally, consistently activate in studies of theory-of-mind ability. This activity is probably not related to the decoupling that is necessary for mentalizing. The functions of these regions might relate to abilities that aid mentalizing. It is from these pre-existing abilities that mentalizing has evolved. The precise role of the STS is still unclear. Gallagher *et al.* [13] found predominantly right STS to be associated with understanding the meaning of stories and cartoons involving people, with or without the requirement to mentalize. Other functional neuroimaging studies of theory-of-mind tasks

have associated STS activity with the involvement of people when understanding causality and intentionality [14], the attribution of intentions to the movements of geometric shapes [15] and taking the self-perspective [16]. It is likely that all of these tasks share one common function that is able to account for this consistent activation.

Biological motion

Functional imaging studies that examine the perception of biological motion activate the same region of the STS in association with hand actions [43,44], body movements [45–47], mouth movements and lip reading [48,49], implied biological motion [46,50] and eye movements and gaze direction [48,51–53]. In addition, Narumoto *et al.* [54] found that the right STS was part of a network of face-responsive brain regions. Selective attention to facial emotion specifically enhanced the activity of the right STS compared with attention to the face *per se*. They attribute this activation to facial emotion recognition within a distributed face-processing system.

Consideration of these findings has led researchers to speculate on the role of this region within a social cognitive network. Allison *et al.* [55] suggest that the STS is sensitive to stimuli that signal the actions and intentions of another individual. The results of neuroimaging, electrophysiological and single-cell recording studies converge to suggest that initial analysis of social cues occurs in the STS region, which is anatomically well sited to integrate information derived from both the ventral and dorsal visual pathways. In accordance with this notion, Frith and Frith [9] suggest that the STS is involved in the detection of the behaviour of agents and analysis of the goals and outcomes of this behaviour. The results of the Gallagher *et al.* [13] study, in particular, indicate that the right STS is involved in explaining the behaviour of others as a result of recognizing a physical cause or their mental state. This idea gains support from a recent fMRI study of social judgement. Winston *et al.* [56] asked volunteers to view faces and make judgements on either trustworthiness or age. They found right STS activity when volunteers made explicit judgements about trustworthiness. The authors attribute this activity to intention detection from visual cues, a critical component in determining whether or not to trust an individual.

The role of the temporal poles

The temporal poles are generally associated with object and face recognition in primates [57]. However, functional imaging studies of humans have activated the temporal poles in association with the broader context of episodic memory retrieval in visual and auditory domains. Thus the temporal poles are active during the recollection of familiar faces and scenes [58], the recognition of familiar voices [59], emotional memory retrieval [60] and autobiographical memory retrieval [61]. Taken together, these results suggest that the temporal poles are a store for personal semantic and episodic memories.

There are several reasons why episodic memory might

be useful for mentalizing. If we are engaged in deception we need to remember what we said to someone the last time we met them. We might remember past episodes in which the behaviour we are observing now was associated with a particular mental state. We might draw on our past experience to imagine ourselves in the situation of another person and thereby ‘simulate’ their experience [62]. We have already mentioned the importance of semantic memory for generating the scripts that enable us to anticipate the likely goals of particular people in particular situations. Patients with semantic dementia show atrophy in the anterior temporal lobes, especially on the left [63]. As this atrophy progresses, these patients lose knowledge of all but the simplest and most concrete scripts [64]. This should lead to specific difficulties with theory-of-mind tasks.

The amygdala and orbitofrontal cortex

It is clear that mentalizing recruits regions of the brain involved in the general interpretation of behaviour that contribute to a neural network of social cognition, the extent of which remains to be identified and the specific functions to be determined. Other brain regions have been implicated in social cognition, which might also contribute to this network, in particular the amygdala and the orbitofrontal cortex [19]. There have been suggestions that the amygdala might play a part in either the development or functioning of theory of mind [12,65]. However, among all the functional imaging studies of theory of mind [10–18,66], only Baron-Cohen *et al.* [12] found amygdala activation. In this study volunteers were required to read a mental or emotional state from another individual’s eye expression. It is feasible that this finding might reflect the amygdala’s responsiveness to eye gaze information [67] or the recognition of emotional behaviour.

It has been suggested that the amygdala responds automatically to socially salient stimuli. A functional imaging study of social cognition [56] found automatic amygdala activation in response to untrustworthy faces, independent of whether the volunteer was making judgements about gender or explicitly judging trustworthiness. This is in contrast to the STS, which was only active during explicit judgements of trustworthiness. The rapid and automatic response of the amygdala to socially salient stimuli might have an important role in the development of theory of mind. Recognizing that the mother is afraid is the cue for the child to find out what the mother is afraid of. This idea would explain the theory-of-mind impairments seen in a patient who suffered a congenital lesion of the left amygdala [65]. Taken together, these findings suggest that although the amygdala might have a role in the appropriate development of theory of mind, it might not be involved in mentalizing *per se*.

Baron-Cohen and Ring [68] have proposed that the orbitofrontal cortex is also part of a theory-of-mind circuit and suggested that damage to this region would produce subtle impairments in theory of mind, rather than the complete loss of mentalizing ability. However, as in the case of the amygdala, only one neuroimaging

study of theory of mind, to date, has found increased activity in the orbitofrontal cortex [66] and this was relative to the left frontopolar region. No other regions were analysed in this study and so interpretation of the results is limited. Clinical observations in humans and experimental reports in primates have consistently indicated that the orbitofrontal cortex is engaged in the regulation of social behaviour [69,70]. A study by Stone *et al.* [71] found that patients with bilateral damage to the orbitofrontal cortex were found to be impaired on a sophisticated test of theory of mind – the *faux pas* test, leading to suggestions that this area of the brain is important to theory of mind. However, these patients, who did not suffer any damage to the paracingulate region of the brain, performed well on standard first- and second-order false belief tasks. This indicates that their theory-of-mind abilities remained intact. Recognizing a *faux pas* requires both an understanding of false or mistaken belief and an empathic inference of the effect it has on someone. In a recent neuroimaging study examining the neural basis of social norm violations (Berthoz *et al.*, unpublished), the orbitofrontal cortex was activated in association with both intentional and unintentional (embarrassing) violations of social norms. The authors suggest that the orbitofrontal cortex is a component of a system that responds to the aversive reactions of others, in particular others' anger. Therefore, although the orbitofrontal cortex seems to form part of the social brain with respect to processing aversive or more generally affective social stimuli, it is unlikely to be directly responsible for theory of mind.

Conclusions

Neuroimaging data have provided compelling evidence to suggest that our ability to mentalize is mediated by a circumscribed region of the anterior paracingulate cortex. Nonetheless, this region seems to be strongly associated with a more widespread network of brain regions involved in social cognition. Neuroimaging is set to play a significant role in determining the precise functions of the neural substrates comprising this network and the mechanisms underlying theory of mind. In particular, the specific involvement of the amygdala and the orbital frontal cortex in mentalizing needs to be examined. Do these areas support functions that are essential prerequisites for acquiring a theory of mind? Or is their role to provide additional information for processing more heterogeneous social tasks such as *faux pas*. Imaging normal children, with fMRI, at different stages of social development might answer some of the enduring questions about the brain systems involved in the acquisition of this highly specialized ability – which could help to elucidate the brain basis of autism.

References

- 1 Leslie, A.M. (1987) Pretense and representation in infancy: the origins of 'theory of mind'. *Psychol. Rev.* 94, 412–426
- 2 Leslie, A.M. and Thaiss, L. (1992) Domain specificity in conceptual development: neuropsychological evidence from autism. *Cognition* 43, 225–251
- 3 Fodor, J.A. (1992) A theory of the child's theory of mind. *Cognition* 44, 283–296
- 4 Baron-Cohen, S. *et al.* (1985) Does the autistic child have a 'theory of mind'? *Cognition* 21, 37–46
- 5 Frith, U. (2001) Review mind blindness and the brain in autism. *Neuron* 32, 969–979
- 6 Wing, L. and Gould, J. (1979) Severe impairments of social interaction and associated abnormalities in children: epidemiology and classification. *J. Autism Dev. Disord.* 9, 11–29
- 7 Leslie, A.M. (1994) Pretending and believing: issues in the theory of mind TOMM. *Cognition* 50, 211–238
- 8 Schank, R.C. (1982) *Dynamic Memory*, Cambridge University Press
- 9 Frith, C.D. and Frith, U. (1999) Interacting minds – a biological basis. *Science* 286, 1692–1695
- 10 Fletcher, P.C. *et al.* (1995) Other minds in the brain: a functional imaging study of 'theory of mind' in story comprehension. *Cognition* 57, 109–128
- 11 Goel, V. *et al.* (1995) Modelling other minds. *NeuroReport* 6, 1741–1746
- 12 Baron-Cohen, S. *et al.* (1999) Social intelligence in the normal and autistic brain: an fMRI study. *Eur. J. Neurosci.* 11, 1891–1898
- 13 Gallagher, H.L. *et al.* (2000) Reading the mind in cartoons and stories: an fMRI study of 'theory of mind' in verbal and nonverbal tasks. *Neuropsychologia* 38, 11–21
- 14 Brunet, E. *et al.* (2000) A PET investigation of the attribution of intentions with a nonverbal task. *NeuroImage* 11, 157–166
- 15 Castelli, F. *et al.* (2000) Movement and mind: a functional imaging study of perception and interpretation of complex intentional movement patterns. *NeuroImage* 12, 314–325
- 16 Vogeley, K. *et al.* (2001) Mind reading: neural mechanisms of theory of mind and self-perspective. *NeuroImage* 14, 170–181
- 17 McCabe, K. *et al.* (2001) A functional imaging study of cooperation in two-person reciprocal exchange. *Proc. Natl. Acad. Sci. U. S. A.* 98, 11832–11835
- 18 Gallagher, H.L. *et al.* (2002) Imaging the intentional stance. *NeuroImage* 16, 814–821
- 19 Brothers, L. (1990) The social brain: a project for integrating primate behaviour and neurophysiology in a new domain. *Concepts Neurosci.* 1, 27–51
- 20 Dennett, D.C. (1996) *Kinds of Minds*, Basic Books
- 21 Bush, G. *et al.* (2000) Cognitive and emotional influences in anterior cingulate cortex. *Trends Cogn. Sci.* 4, 215–222
- 22 Nimchinsky, E.A. *et al.* (1999) A neuronal morphologic type unique to humans and great apes. *Proc. Natl. Acad. Sci. U. S. A.* 96, 5268–5273
- 23 Allman, J.M. *et al.* (2001) The anterior cingulate cortex, the evolution of an interface between emotion and cognition. *Ann. New York Acad. Sci.* 935, 107–117
- 24 Paus, T. (2001) Primate anterior cingulate cortex: where motor control, drive and cognition interface. *Neuroscience* 2, 417–424
- 25 Zilles, K. *et al.* (1988) The human pattern of gyrification in the cerebral cortex. *Anat. Embryol.* 179, 173–179
- 26 Devinsky, O. *et al.* (1995) Contributions of anterior cingulate cortex to behaviour. *Brain* 118, 279–306
- 27 Rowe, A.D. *et al.* (2001) 'Theory of mind' impairments and their relationship to executive functioning following frontal lobe excisions. *Brain* 124, 600–616
- 28 Stuss, D.T. *et al.* (2001) The frontal lobes are necessary for 'theory of mind'. *Brain* 124, 279–286
- 29 Critchley, H.D. *et al.* (2000) Cerebral correlates of autonomic cardiovascular arousal: a functional neuroimaging investigation in humans. *J. Physiol. London* 523, 259–270
- 30 Critchley, H.D. *et al.* (2001) Neural activity in the human brain relating to uncertainty and arousal during anticipation. *Neuron* 29, 537–545
- 31 Duncan, J. and Owen, A.M. (2000) Common regions of the human frontal lobe recruited by diverse cognitive demands. *Trends Neurosci.* 23, 475–483
- 32 Barch, D.M. *et al.* (2001) Anterior cingulate cortex and response conflict: effects of response modality and processing domain. *Cereb. Cortex* 11, 837–848
- 33 Phan, K.L. *et al.* (2002) Functional neuroanatomy of emotion: a

- meta-analysis of emotion activation studies in PET and fMRI. *NeuroImage* 16, 331–348
- 34 Lane, R.D. *et al.* (1997) Neural activation during selective attention to subjective emotional responses. *NeuroReport* 8, 3969–3972
 - 35 Gusnard, D.A. *et al.* (2001) Medial prefrontal cortex and self-referential mental activity: relation to a default mode of brain function. *Proc. Natl. Acad. Sci. U. S. A.* 98, 4259–4264
 - 36 Kircher, T.T. *et al.* (2000) Recognizing one's own face. *Cognition* 78, B1–B15
 - 37 Maguire, E.A. and Mummery, C.J. (1999) Differential modulation of a common memory retrieval network revealed by positron emission tomography. *Hippocampus* 9, 54–61
 - 38 Maguire, E.A. *et al.* (2000) Patterns of hippocampal-cortical interaction dissociate temporal lobe memory subsystems. *Hippocampus* 10, 475–482
 - 39 McGuire, P.K. *et al.* (1996) Functional neuroanatomy of verbal self-monitoring. *Brain* 119, 907–917
 - 40 McGuire, P.K. *et al.* (1996) Brain activity during stimulus independent thought. *NeuroReport* 7, 2095–2099
 - 41 Blakemore, J.S. *et al.* (1998) Central cancellation of self-produced tickle sensation. *Nat. Neurosci.* 1, 635–639
 - 42 Rainville, P. *et al.* (1997) Pain affect encoded in human anterior cingulate but not somatosensory cortex. *Science* 277, 968–971
 - 43 Grezes, J. *et al.* (1998) Top-down effect of strategy on the perception of human biological motion: a PET investigation. *Cogn. Neuropsychol.* 15, 553–582
 - 44 Grezes, J. *et al.* (1999) The effects of learning and intention on the neural network involved in the perception of meaningless actions. *Brain* 122, 1875–1887
 - 45 Bonda, E. *et al.* (1996) Specific involvement of human parietal systems and the amygdala in the perception of biological motion. *J. Neurosci.* 16, 3737–3744
 - 46 Senior, C. *et al.* (2000) The functional neuroanatomy of implicit-motion perception or representational momentum. *Curr. Biol.* 10, 16–22
 - 47 Grossman, E.D. and Blake, R. (2001) Brain activity evoked by inverted and imagined biological motion. *Vis. Res.* 41, 1475–1482
 - 48 Puce, A. *et al.* (1998) Temporal cortex activation in humans viewing eye and mouth movements. *J. Neurosci.* 18, 2188–2199
 - 49 Calvert, G.A. *et al.* (1997) Activation of auditory cortex during silent lipreading. *Science* 276, 593–596
 - 50 Kourtzi, Z. and Kanwisher, N. (2000) Activation in humans MT/MST by static images with implied motion. *J. Cogn. Neurosci.* 12, 48–55
 - 51 Wicker, B. *et al.* (1998) Brain regions involved in the perception of gaze: a PET study. *NeuroImage* 8, 221–227
 - 52 Hoffman, E.A. and Haxby, J.V. (2000) Distinct representations of eye gaze and identity in the distributed human neural system for face perception. *Nat. Neurosci.* 3, 80–84
 - 53 Calder, A.J. *et al.* (2002) Reading the mind from eye gaze. *Neuropsychologia* 40, 1129–1138
 - 54 Narumoto, J. *et al.* (2001) Attention to emotion modulates fMRI activity in human right superior temporal sulcus. *Cogn. Brain Res.* 12, 225–231
 - 55 Allison, T. *et al.* (2000) Social perception from visual cues: role of the STS region. *Trends Cogn. Sci.* 4, 267–278
 - 56 Winston, J.S. *et al.* (2002) Automatic and intentional brain responses during evaluation of trustworthiness of faces. *Nat. Neurosci.* 5, 277–283
 - 57 Nakamura, K. and Kubota, K. (1996) The primate temporal pole: its putative role in object recognition and memory. *Behav. Brain Res.* 77, 53–77
 - 58 Nakamura, K. *et al.* (2000) Functional delineation of the human occipito-temporal areas related to face and scene processing: a PET study. *Brain* 123, 1903–1912
 - 59 Nakamura, K. *et al.* (2001) Neural substrates of familiar voices: a PET study. *Neuropsychologia* 39, 1047–1054
 - 60 Dolan, R.J. *et al.* (2000) Dissociable temporal lobe activations during emotional episodic memory retrieval. *NeuroImage* 11, 203–209
 - 61 Fink, G.R. *et al.* (1996) Cerebral representation of one's own past: neural networks involved in autobiographical memory. *J. Neurosci.* 16, 4275–4282
 - 62 Harris, P.L. (1992) From simulation to folk psychology: the case for development. *Mind Lang.* 7, 120–144
 - 63 Chan, D. *et al.* (2001) Patterns of temporal lobe atrophy in semantic dementia and Alzheimer's disease. *Ann. Neurol.* 49, 433–442
 - 64 Funnell, E. (2001) Evidence for scripts in semantic dementia: implications for theories of semantic memory. *Cogn. Neuropsychol.* 18, 323–341
 - 65 Fine, C. *et al.* (2001) Dissociation between 'theory of mind' and executive functions in a patient with early left amygdala damage. *Brain* 124, 287–298
 - 66 Baron-Cohen, S. *et al.* (1994) The brain basis of theory of mind: the role of the orbito-frontal region. *Br. J. Psychiatry* 165, 640–649
 - 67 Kawashima, R. *et al.* (1999) The human amygdala plays an important role in gaze monitoring. *Brain* 122, 779–783
 - 68 Baron-Cohen, S. and Ring, H. (1994) A model of the mindreading system: neuropsychological and neurobiological perspectives. *Origins of an Understanding Mind* (Mitchell, P., Lewis, C. eds), pp. 183–207, Erlbaum
 - 69 Damasio, A.R. and VanHoesen, G.W. (1983) Emotional disorders associated with focal lesions of the limbic frontal lobe. *Neuropsychology of Human Emotion* (Heilman, K.M., Satz, P. eds), pp. 85–110, Guilford Press
 - 70 Stone, V.E. (2000) In *The Role of the Frontal Lobes and Amygdala in Theory of Mind* (Baron-Cohen, S. *et al.*, eds), Oxford University Press
 - 71 Stone, V.E. *et al.* (1998) Frontal lobe contributions to theory of mind. *J. Cogn. Neurosci.* 10, 640–656

Managing your references and BioMedNet Reviews

Did you know that you can now download selected search results from *BioMedNet Reviews* directly into your chosen reference-managing software? After performing a search, simply click to select the articles you are interested in, choose the format required (e.g. EndNote 3.1) and the bibliographic details, abstract and link to the full-text will download into your desktop reference manager database.

BioMedNet Reviews is available on institute-wide subscription. If you do not have access to the full-text articles in *BioMedNet Reviews*, ask your librarian to contact reviews.subscribe@biomednet.com