



Interacting Minds—A Biological Basis

Chris D. Frith^{1*} and Uta Frith²

The ability to “mentalize,” that is to understand and manipulate other people’s behavior in terms of their mental states, is a major ingredient in successful social interactions. A rudimentary form of this ability may be seen in great apes, but in humans it is developed to a high level. Specific impairments of mentalizing in both developmental and acquired disorders suggest that this ability depends on a dedicated and circumscribed brain system. Functional imaging studies implicate medial prefrontal cortex and posterior superior temporal sulcus (STS) as components of this system. Clues to the specific function of these components in mentalizing come from single cell recording studies: STS is concerned with representing the actions of others through the detection of biological motion; medial prefrontal regions are concerned with explicit representation of states of the self. These observations suggest that the ability to mentalize has evolved from a system for representing actions.

The success of human social interactions depends on the development of a “social intelligence,” which has a number of different components. These include the ability to recognize conspecifics, to know one’s place in society, to learn from others, and to teach novel skills to others. In this review, we explore the physiological basis of one particular aspect of this social intelligence: the capacity to understand and manipulate the mental states of other people and thereby to alter their behavior. This capacity reaches beyond the ability to manipulate the behavior of others by direct instrumental action. The awareness that other people have beliefs and desires different from our own and that their behavior can be explained by these beliefs and desires has been referred to as “theory of mind” (1) or “intentional stance” (2). For the ability that underlies these accomplishments, the term “mentalizing” has been coined (3). The acid test of mentalizing is the ability to compute what another person will do on the basis of a false belief (4, see Fig. 1). To predict what a person will do on the basis of a true belief is not a sufficiently stringent test, since here the belief coincides with reality, and it is hard to tell whether the action is governed by physical reality or mental state. In everyday life, beliefs rather than reality determine what people do, and false beliefs play an important role. False beliefs can be removed by education and implanted by deception.

Many aspects of social intelligence are

already found in highly developed form in monkeys and apes (5). Unlike most mammals, monkeys rely on the support of other individuals rather than on their own individual power (6). Monkeys are also sensitive to the characteristics of individuals and the relationships between individuals. In conflict

situations, they can redirect their aggression to the kin of their persecutor (7). As might be expected from the pressures of living in social groups, monkeys and apes have been observed to use deception to manipulate the behavior of their companions. However, such actions are not necessarily based on insight into mental states. Byrne and Whiten (8) concluded that the majority of reports of deception could be explained on the basis of rapid learning from a series of coincident reinforcements rather than from a mentalizing insight. The few incidents that could not be explained in this way were observed only in great apes and never in monkeys. Furthermore, there is as yet no unequivocal evidence from laboratory-based tasks that chimpanzees or other great apes can make use of intentional deception (9). These observations suggest that monkeys are not capable of attributing mental states to others and that apes, which may be able to make such attributions, have a

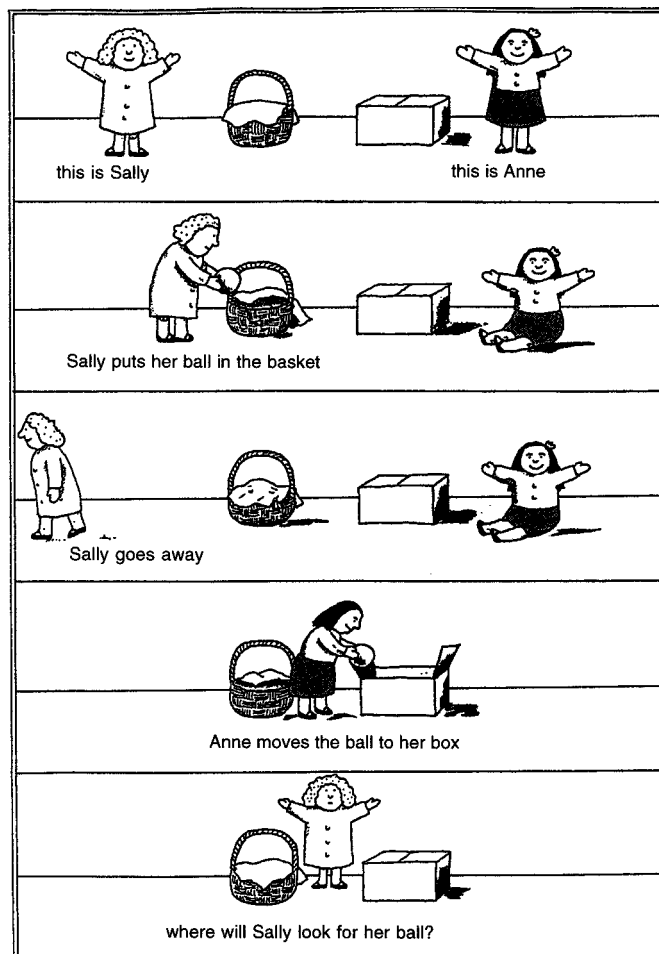


Fig. 1. The Sally-Anne task. The child is shown the scenario illustrated, which can be enacted by puppets or real people. At the end the child is asked, “Where will Sally look for her ball?” To answer this question the child must realize that Sally has not seen the ball being moved and, therefore, that Sally falsely believes that the ball is still in the basket (17). [Reproduced by kind permission of the artist, Axel Scheffler.]

¹Wellcome Department of Cognitive Neurology, Institute of Neurology, University College London, 12 Queen Square, London WC1N 3BG, UK. ²Institute of Cognitive Neuroscience and Department of Psychology, University College London, 17 Queen Square, London, WC1N 3AR, UK.

*To whom correspondence should be addressed. E-mail: cfrith@fil.ion.ucl.ac.uk

primitive form of the ability at the very limits of their cognitive skills.

In contrast, for humans, mental state attribution plays a major role in all social interactions and forms the basis of daily gossip, as well as novels and plays. The development of the ability to attribute mental states in increasingly explicit form has been studied in many paradigms (10). By age four, deliberate deception is commonplace and can easily be demonstrated in laboratory-based tasks (11). By 18 months, infants show clear evidence of understanding pretence, an ability that requires not just the representation of an event, but of an agent's informational relation to the event (12). At the same age, children can imitate and complete an action that they have seen an adult attempt, but fail to finish (13). During the first year of life infants can orient toward another person's focus of attention and can point out objects of interest. However, whether such behavior requires mentalizing remains controversial (14).

In certain cases the development of mentalizing is severely compromised. This is the case for children diagnosed with autism (15). In infancy, these children are remarkable by not appearing to orient toward other people's focus of attention, by not showing or pointing out things, and by not engaging in pretend play (16). As they get older, many individuals with the diagnosis of autism remain unable to understand the concept of a false

belief. In a simple experiment (see Fig. 1), a child watches two actors and observes the transfer of a ball from one hiding place to another. Most normal 4-year-olds recognize that Sally, who has not seen Anne transfer the ball, must think that the ball is still in its original place. She has a false belief that causes her to look for the ball in the original place. Most children with autism even up to their teens say that Sally will look for the ball where it really is, failing to take into account her false belief (17). The developmental consequences of mentalizing failure are severe and manifest themselves in a lack of social insight and impaired communication.

The empirical studies of mentalizing in normal development and in autism suggest that the ability to attribute mental states is largely independent of other abilities. Cases have been described where individuals with autism have achieved tertiary levels of education but still make errors on tasks requiring mentalizing (18). More important, dissociations can be seen even within the domain of social intelligence. Thus autistic children can use sabotage to prevent another person from attaining a goal, demonstrating their understanding of simple social situations, but they cannot use deception for this purpose (19; see Fig. 2). They can use instrumental communicative gestures ("come here") to affect another's behavior, but not expressive gestures ("well done") to affect another's mental state (20). They can feel the basic pleasure in mastering a task, but not pride, an emotion that requires taking into account other people's expectations (21).

In schizophrenia, a disease of adult onset, mentalizing failures can also be observed (22). Patients with delusions of persecution and with delusions of reference make false inferences about the intentions of others. In these cases, the attribution of mental states is overproductive and goes beyond the normal inferences about other people's behavior. Patients with schizophrenia, like those with autism, often perform badly on tests of executive function that are sensitive to frontal lobe damage (23). This observation suggests a possible role for prefrontal cortex in mentalizing. However, poor performance on mentalizing tasks is not simply a consequence of general executive problems. For example, autistic children who failed a task involving attribution of mental states were able to pass a formally identical task that did not involve the mental domain (24). Patients with damage to prefrontal cortex, especially the orbital and medial regions, are known to show severe problems in social behavior, consistent with a lack of social insight (25). However, there are, as yet, few studies directly examining the effects of brain damage on mentalizing abilities (26).

If there is a brain system dedicated to the

representation of mental states, analogous to those systems already identified for spatial navigation (27) or face recognition (28), then it should be possible to localize components of this system using functional brain imaging. There are already a number of studies in the literature in which volunteers have been asked to monitor and report their own mental states (in circumstances in which these states are not simply a reflection of external reality). The reported states have included pain (29), emotions aroused by pictures (30), spontaneous thoughts (31), actions (32), and tickling (33). However, in spite of the wide variation in the nature of the states reported on, activity was observed in all these studies in medial frontal cortex, or, more precisely, along the border between rostral anterior cingulate cortex and medial prefrontal cortex (the paracingulate sulcus, see Fig. 3A).

To date there are very few brain imaging studies in which volunteers have been asked to report on the mental states of others. In the two earliest positron emission tomography (PET) studies (34), activity was observed in medial prefrontal cortex. This observation was confirmed in a recent functional magnetic resonance imaging (fMRI) study in which volunteers had to make inferences about the mental states of characters in stories or non-verbal cartoons (35). Activity associated with mentalizing was again observed in medial prefrontal cortex. Both forms of presentation also elicited activity in the region of the temporo-parietal junction, and in lateral inferior frontal cortex.

Although preliminary, these results suggest that a brain system dedicated to mentalizing can be localized. Simple localization, however, is not enough. We also need to know something about the functions of the different areas comprising the system. The interpretation of results from human brain imaging studies has depended critically on information gained from single-cell studies in nonhuman primates. Of necessity, such information is not available for studies of mentalizing. We do not believe, however, that mentalizing abilities arose in humans *de novo*. Nature is a tinkerer and not an inventor (36). New abilities are adapted from preexisting abilities. Likely preexisting abilities that are relevant to mentalizing include (i) the ability to distinguish between animate and inanimate entities, (ii) the ability to share attention by following the gaze of another agent (14), (iii) the ability to represent goal-directed actions (37), and (iv) the ability to distinguish between actions of the self and of others (38).

Cells with properties relevant to these abilities have already been found in a number of brain regions. Cells in the superior temporal sulcus (STS, upper bank) of the monkey respond to moving hands and faces, but not the movement of inanimate objects (39).

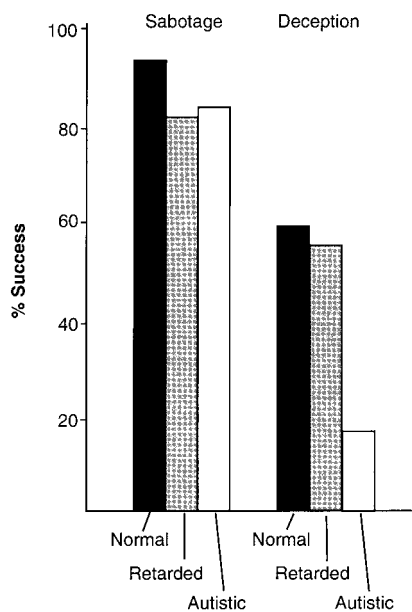


Fig. 2. Deception and sabotage. Children participated in a game where he or she had to prevent a rival (enacted by the experimenter with the aid of puppets) from obtaining a reward, which was kept in a box. In the sabotage condition this could be achieved by locking the box. In the deception condition this could be achieved by claiming (untruthfully) that the box was locked (19).

Similar results have been obtained in brain imaging studies with humans (40). The location of regions in STS that are activated by "biological motion" are adjacent to the regions activated in studies of mentalizing (see Fig. 3B). Cells have been found in adjacent areas that respond to particular directions of gaze (41). In addition, there is behavioral evidence that monkeys can use gaze direction to guide their own attention (42). Activity in cells in STS (lower bank) relates to the observation of movements as goal-directed actions. These cells respond to a hand reaching for an object but not to the hand movement alone. By contrast, activity in cells in lateral inferior frontal regions (F5) reflects an additional motor component so that these cells respond when the monkey performs a specific action, such as a precision grip, and also when the monkey observes another agent performing the same action (43). Such "mirror" neurons could provide the basis for the abstract representation of goals (44). Since they do not specify whether the goal was of the self or another agent, additional information is required to make this distinction (45). Cells have been found, once again in STS (upper bank), which are activated by sights and sounds generated by others, but not by the same stimuli when these are self-generated

(46). Thus, there are neurons that provide information about the actions of others. Which neurons provide information about the actions of the self?

Evidence from the brain imaging studies already discussed suggests a role for medial frontal regions, since activity in these regions increases when volunteers are asked to report on their own mental states. Very little is known about cells in anterior cingulate and adjacent medial prefrontal areas. However, in the posterior part of this region (but anterior to the so-called motor cingulate area) are cells where activity is observed before the production of self-initiated movements (47). Such cells might be involved in the explicit representations of the goals of the self.

If we take seriously the homologs between these studies of single-cell activity in monkeys and areas implicated in mentalizing from brain imaging studies, then the components of the mentalizing system include (i) STS, for detection of the behavior of agents and analysis of the goals and outcomes of this behavior; (ii) inferior frontal regions, for representations of actions and goals; and (iii) anterior cingulate cortex (ACC)/medial prefrontal regions, for representations of mental states of the self. An implication of this proposal is that the analysis of another agent's

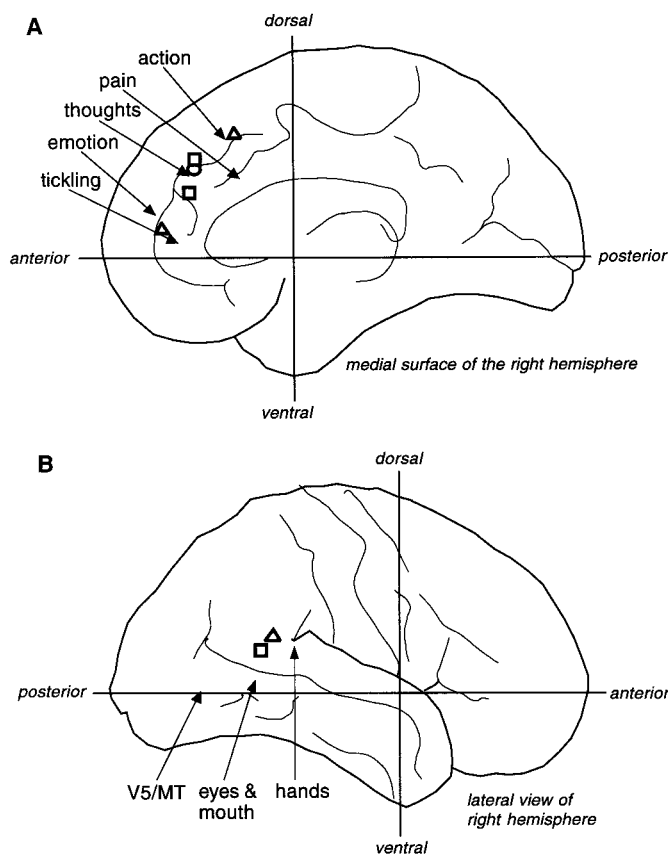
behavior in conjunction with the representation of our own mental states allows us to make inferences about the intentions of that agent.

Another striking implication of the data presented in this review is that our ability to mentalize seems to have evolved largely from the dorsal action system, rather than the ventral object identification system (48). The components of social intelligence that developed in the monkey before the emergence of mentalizing abilities include recognition of subtle differences in emotional expression, recognition of other individuals, and recognition of their status and relationships. These all depend on complex and sophisticated object recognition of the kind supported by the ventral system. In contrast, the emergence of mentalizing required the development of capabilities relating to the representation of actions, the goals implicit in actions, and the intentions behind them.

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Fig. 3. (A) Medial frontal regions associated with mentalizing. An outline of the medial surface of the human brain is shown in Talairach space with location of activity in three experiments of mentalizing [square (31), circle (32), triangle (32)]. Arrows indicate the location of peak activity from the studies mentioned in the text in which subjects reported on their mental states [pain (26), emotion (27), thoughts (28), action (29), and tickling (30)]. (B) Regions in superior temporal sulcus associated with mentalizing. An outline of the lateral surface of the right hemisphere of the human brain is shown in Talairach space with location of activity in two studies of mentalizing [square (31), triangle (32)]. Arrows indicate the location of peak activity from two studies of biological motion (37).



Similar activations in the left hemisphere were also observed in the majority of these studies. The location V5/MT responds to motion in general, both biological and nonbiological (37).

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