How does the brain deal with the social world?

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It is only relatively recently that the search for the biological basis of social cognition has started. It is still unknown just how biological factors, from genes to brain processes, interact with environmental variables to produce individual differences in social competence and in pathology of social communication. It may seem over-ambitious to work out how connections can be made between sophisticated social behaviour and basic neurophysiological mechanisms. However, examples already exist. The neural basis of social processes such as deception and morality are now being studied by cognitive neuroscientists. In this review, we summarize recent work that has illuminated the neuro-cognitive basis of complex social interaction and communication in humans. *NeuroReport* 14:000–000 © 2003 Lippincott Williams & Wilkins.

Key words: ■■■

MECHANISMS OF SOCIAL COGNITION

Most animals' survival depends upon their ability to detect the movements, eye gaze, and social signals of other creatures, to distinguish whether they are prey, predators or mates and to anticipate their future actions. As social animals, humans behave largely on the basis of their interpretations of the actions of others. We are continually, and implicitly, reading, analysing and decoding multiple social signals from people around us. This enables us to recognise a friend on the one hand, and a treacherous enemy on the other. How do you know an enemy is treacherous? How do you know you can trust someone? And how do you convince others to trust you? These abilities are intuitive. They are activated by certain stimuli of which we are not necessarily aware. Often perception is turned into action so fast that deliberation and rational thought have no time to intervene. However, one ability that may well be unique to humans is the ability to reflect consciously on our negotiations with the social world, and for this ability too, the foundation in neural processes is being investigated.

In this review, we discuss mechanisms that are candidates for explaining our social and communicative competence (see also [1]). Some mechanisms develop early in infancy and are relatively low level, such as reading faces, detecting eye gaze and recognising emotional expressions. Other higher level mechanisms develop later in childhood, such as imitating the intentional actions of others, attending to the same object when directed by another person, attributing mental states, such as desires and beliefs, to oneself and to other people.

It is not always appreciated that the latter group of abilities is just as automatic as the former, and just as pervasive in everyday social understanding and interaction. One hypothesis about the evolutionary origin of the higher level mechanisms is that they build upon the lower level mechanisms that are shared with other animals, i.e. those concerned with the perception of basic emotions, eye gaze, biological motion, goal directed action and agency. However, over and above these low level mechanisms, a qualitatively different type of mechanism may have evolved in humans. To speculate wildly, this might coincide with the spectacular success of *Homo sapiens*, which eclipsed that of other humanoids, such as Neanderthal man. Social, rather than physical, prowess might have helped *H. sapiens* to dominate others.

Reading faces: Babies are born with a basic, but impressive, capacity to respond to faces. At birth, the brain has some information about what a face should look like. Newborn babies prefer to look at drawings of whole faces than drawings of faces whose features have been scrambled. Within a few days of birth babies learn to respond preferentially to the face they have been exposed to most, usually their mother's: they will look at a picture of their mother's face longer than at a picture of a stranger's face.

This early ability to respond to the human face in general, and to respond preferentially to a specific face, relies on subcortical pathways, for example in the superior colliculus. The early recognition of faces might have evolved because it produces an automatic attachment of new-born babies onto the people they see most [2]. These structures are part of a pathway in the brain that allows us to make movements quickly and automatically on the basis of what we see.

Research on monkeys has shown that a region in the fusiform gyrus contains cells that respond to particular faces [3]. Brain imaging research has demonstrated that an equivalent region in the human brain, called the fusiform face area (FFA), responds to faces more than to other visual objects such as buildings, scenes or objects [4]. Only from about 2–3 months of age do these cortical brain regions start to take over a baby's face recognition ability.

Recent research has demonstrated that human babies are born with the inherent ability to recognise a large number of faces, including faces from other species (monkeys). Only after about 10 months of age do we lose this ability, a process that depends on the types of face to which we are naturally exposed [5]. This is analogous to the well known finding that after about 10 months of age we lose the ability to identify large number of different sounds, and again this process depends on what sounds we are exposed to during the first 10 months of life [6]. These findings are important because they highlight the fact that development is, in part, an experience dependent process that depends on the species-specific environment. Fine-tuning rather than indiscriminate adding of information seems to be the rule.

Recognising emotional expressions: Within social psychology, research has demonstrated the ubiquity of facial expression, the same expressions being used for basic emotions such as anger, happiness and sadness in all different cultures [7]. The brain reads facial expressions extremely rapidly. PET and fMRI studies, in which subjects observed expressions in different faces, have shown that the amygdala is particularly important for analysing fearful and sad faces, and this processing often occurs without awareness of the face [8]. Impairments in emotion recognition are clearly detrimental to social interaction. Imagine not realising when someone is angry. Normally the effect of seeing an angry face even for a split second is to stop in your tracks or to run away.

Eye gaze: The ability to respond to the direction of eye gaze has high evolutionary significance. Human babies are automatically drawn to look where another person is looking and prefer direct eye contact [9]. The involuntary tendency to look in the same direction as another individual has obvious benefits: the target that another attends to is also likely to be of interest to you. In conjunction with the ability to read emotional expressions, it can allow instant response selection, e.g. approach or avoidance.

A critical neural system implicated in the detection of eye gaze is located in the superior temporal sulcus. Cells in this region in the monkey brain respond to eye gaze direction information from other monkeys or humans [3]. In humans, a number of recent studies have found that simply viewing eye gaze stimuli or stimuli that display animate motion cues, activates a homologous region of the superior temporal sulcus amongst other regions [10]. In animals, direct eye gaze usually indicates threat. This is clearly not the case in humans, who use eye gaze to indicate a wide variety of emotions and intentions, positive as well as negative. Support for this notion comes from a recent fMRI study demonstrating that the brain's reward networks are activated by direct eye gaze when the eyes belong to someone the subject finds attractive [11] (see Fig. 1).

Joint attention: Babies' attention can be directed to an object by another person simply by looking at them directly and drawing their attention to the object using gaze direction. Attention can also be drawn to an object or event by pointing. In the first year of life babies respond to pointing only when the object is already in the field of vision. From the middle of the second year of life the attention can be drawn to an object that initially is out of view. This form of triadic attention (that is, interaction between two people about a third object) is thought to be one of the earliest signs of an implicit theory of mind (see later).

Joint attention may not be unique to humans. There is evidence, both anecdotal and empirical, that dogs are able to glean information from joint attention cues (such as pointing and gaze direction) given by humans. This is intriguing because there is no evidence that non-human primates can use this kind of cue from humans. Recently a rigorous study investigated this evolutionary anomaly. Hare and colleagues [12] compared the ability of chimpanzees, wolves, dogs and puppies to glean information about where an object was hidden by human pointing. The chimps were no good at this, and nor were the wolves, demonstrating that the ability is not inherently canine. However, puppies, which had not had much experience with humans, and therefore unlikely

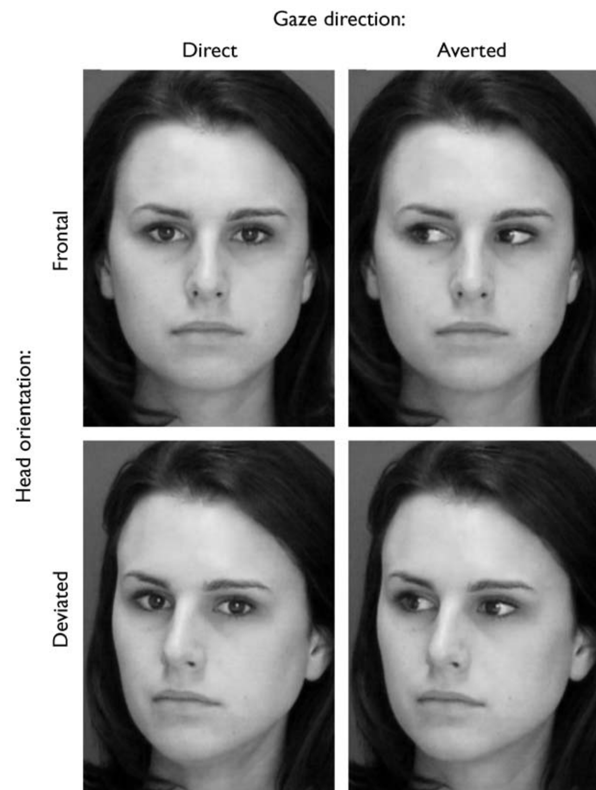

Fig. 1. Examples of the stimuli used in [11], in which eye gaze was varied. Only when a face was found to be attractive and gazing directly at the viewer were parts of the brain's reward networks activated. (Reprinted with permission from [11]).

to have learned the significance of pointing, were nevertheless able to use human pointing information to find objects. This suggests that the ability of dogs to use joint attention information has been bred over years of domestication. Possibly, the importance of selective mating on social skills also needs to be considered in human societies.

Sensitivity to biological motion: Among all sensory inputs, one crucial source of information about another creature is their pattern of movement. There are various types of motion in the natural environment, of which motion of biological forms is essential to detect in order to predict the actions of other individuals. Here we refer to biological motion as distinct from mechanical, Newtonian motion: biological motion is self-propelled and non-linear in that it may undergo sudden changes in acceleration, velocity and trajectory.

The Swedish psychologist Johansson [13] devised an ingenious method for studying biological motion without interference from shape. He attached light sources to actors' main joints and recorded their movements in a dark environment. He then showed the moving dot configurations to naive perceivers who, rapidly and without any effort, recognised the moving dots as a person walking. Using the same technique, several researchers have demonstrated that observers are capable of recognising not only locomotion, but also the gender of the person, even their personality traits and emotions, and complex actions such as dancing represented by moving dots [14]. The ability to distinguish between biological and non-biological movement develops early: 3-month-old babies can discriminate between displays of moving dots that have biological motion and displays in which the same dots move randomly [15]. This suggests that the detection of biological motion becomes hardwired in the human brain at an early age.

Single cell studies in the macaque monkey have revealed that superior temporal sulcus cells selectively respond to depictions of the face and the body in action [3]. Superior temporal sulcus neurons continue to respond to biological movements even when part of the action is occluded [16], which has been interpreted as demonstrating the contribution of the superior temporal sulcus to the representation and understanding of others' actions. This area receives information from both dorsal and ventral visual streams (involved in vision for action and vision for identification, respectively), rendering it an interface between perception for identification and perception for action. This combination of visual information would be useful for recognising the movements of other animate beings and categorising them as threatening or enticing. Furthermore, the emotional value of this information is likely to be stored in memory and will enter into predictions about future actions of the agent in question.

Several brain imaging studies have investigated the neural processing of biological motion in humans. Most of these have compared brain activity while subjects observe Johansson point-light walkers with brain activity while subjects observe visual stimuli made of the same dots but moving in non-biological ways, such as showing coherent motion [17] and rigid object motion [18]. These studies demonstrated activation of the ventral bank of the superior temporal sulcus, often more pronounced in the right hemisphere than in the left (see Fig. 2). Other neuroimaging studies have detected activation in this region in response to seeing hand, eye, and mouth movements [19].

Perception into action: mirror neurons: Although it has long been proposed that actions are intrinsically linked to perception, this idea has only recently received direct evidence. This evidence came from the discovery of mirror neurons, which are located in an area known as ventral premotor cortex (F5) in monkeys [20]. These neurons respond to an action being carried out by the animal itself (execution), and by the mere observation of the same action being carried out by an experimenter or another monkey. Mirror neurons appear to distinguish between biological and non-biological motion, responding only to the observation of hand-object interactions and not to the same action performed by a mechanical tool, such as a pair of pliers [21] (see Fig. 3).

Mirror neurons provide a perfect example of what we mean by a social cognitive mechanism where neurophysiological activity is shown in response to one's own and another person's action. Some of the other mechanisms we discussed earlier are conceivable in machines that passively view other animals and categorise their appearance, eye gaze and movements. Mirror neurons open up another class of mechanism altogether. This class of mechanism may be

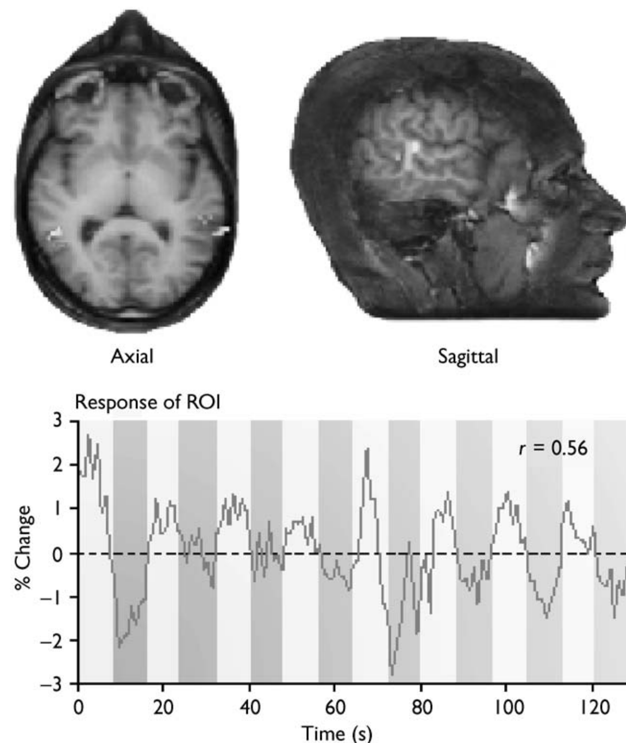

Fig. 2. Brain images showing activity in the superior temporal sulcus when subjects observe biological motion. The graph shows the percentage signal change in superior temporal sulcus a higher level of activity is detected when subjects observe biological motion (light bars) than when they view scrambled motion (darker bars). Reprinted from Grossman *et al.* (2001), with permission.

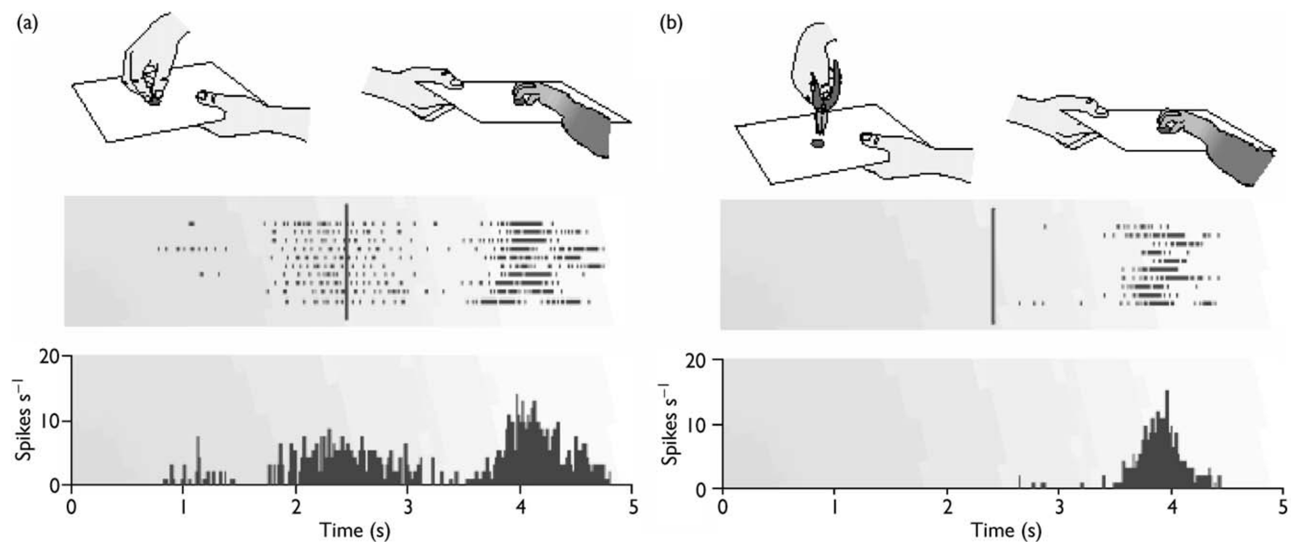

Fig. 3. (**a**) Visual and motor responses of a mirror neuron in ventral premotor cortex of the macaque monkey. A piece of food is placed on a tray and presented to the monkey; the experimenter grasps the food, and then moves the tray with the food towards the monkey. The raster plot and histogram below show the activation of the premotor neuron when the monkey observes the experimenter's grasping movements, and when the same action is performed by the monkey. (**b**) This figure depicts a similar experiment in which the experimenter grasps the food with a pair of pliers. The raster plot and histogram below show the absense of response from the same premotor neuron when the observed action is performed with a tool. Reprinted from Rizzolatti *et al.* (2001), with permission.

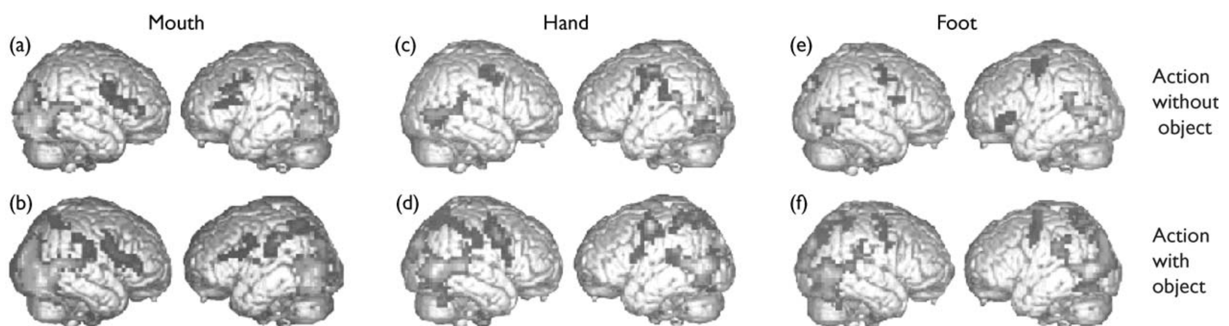

Fig. 4. Brain activation in frontal and parietal areas during the observation of mouth, hand and foot actions. Observed actions were performed with the mouth (**a,b**), hand (**c,d**) or foot (**e,f**), and with (b,d,f) or without objects (a,c,e). During the observation of both object-related actions and actions performed without objects, premotor cortex was activated in a somatotopic manner according to the body part performing the observed action. During the observation of object-related actions, there was an additional activation of the posterior parietal lobe. Reprinted from Rizzolatti *et al.* (2001), with permission.

fundamental to a number of higher level social processes, where the actions of other agents are interpreted in such a way that they directly influence one's own actions. This is the case in the attribution of intentions to others and oneself (mentalising), and the ability to imitate others as well as to teach others.

There is a large body of evidence that in humans several brain regions are activated both during action generation and during observation of others' actions [22]. In some brain regions the overlap between action observation and action execution is highly specific. Action observation activates premotor cortex according to the body schema that is represented in this region. In an fMRI experiment, subjects observed actions performed by the mouth, hand, and foot that were either performed in isolation or with an object (chewing food, grasping a cup and kicking a ball). The results demonstrated that watching mouth, hand, and foot movements alone (without objects) activates the same functionally specific regions of premotor cortex as making those respective movements. Furthermore, when actions were directed to objects, the parietal cortex became activated. Again, functionally specific regions of the parietal cortex were activated according to the object-directed action being performed [22] (see Fig. 4).

Observing a movement has measurable consequences on the peripheral motor system [23]. Fadiga and colleagues stimulated left primary motor cortex of human subjects using TMS while the subjects observed meaningless actions and grasping movements (and other control tasks). Motor evoked potentials (MEPs) were recorded from the subjects' hand muscles. It was found that during observation of hand movements there was a selective increase of MEPs from the hand muscles that would be used to make the observed movements.

Rizzolatti and colleagues argue that the mirror system facilitates action understanding, suggesting that we under-

stand other people's actions by mapping observed action onto our own motor representations of the same action. It has been proposed that the mirror system might have evolved to facilitate communication, empathy and the understanding of other people's minds [24]. Simulating other people's actions would trigger an action representation from which the underlying goals and intentions could be inferred on the basis of what our own goals and intentions would be for the same action. Recently it has been found that observing another human making arm movements interferes with the execution of different arm movements [25] (see Fig. 5). This might be due to interference within the mirror system, which processes both movement observation and execution.

Detecting agency: distinguishing the self and other agents: Given the overlapping brain network that processes action execution and observation, one key question concerns how we are able easily to distinguish the actions we produce from those generated by other people. How do we know who the agent of an action is? Because humans are constantly interacting with others, it is crucial to know who did what. The perception of the self as agent is simply 'the sense that I am the one who is causing or generating an action' [26]. According to Gallagher, a low-level sense of agency, the minimal self, is present from birth.

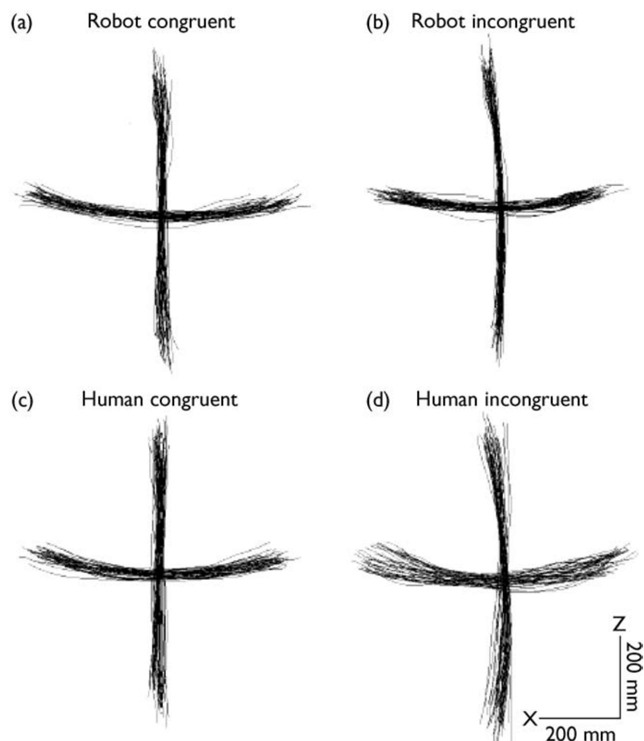

Fig. 5. The plots show horizontal and vertical arm movements made by a single subject during four action observation conditions: while the subject observed a robot making similar (congruent) movements (**a**); the robot making orthogonal (incongruent) movements (**b**), the experimenter making similar (congruent) movements (**c**) and the experimenter making orthogonal (incongruent) movements (**d**). Note the small but significant increase in the variance of the movement in (d), when the subject observes an incongruent biological movement. No such increase in variance was found in (b). Reprinted from Kilner *et al.* (2003), with permission.

One mechanism that has been proposed to contribute to the recognition of self-produced action involves the use of internal models [27]. It has been proposed that a forward model (an internal representation of the world and the body's kinematics) is used to predict the consequences of self-generated movements using a copy of the motor command (called efference copy) [28]. This prediction is then used to determine whether a movement or sensation is self-produced or externally generated by cancelling the results of self-generated sensations. There is evidence that the perceptual attenuation of the sensory consequences of movement is accompanied by, and might be due to, a reduction in activity in regions of the brain that process the particular sensory stimulation being experienced [29]. This predictive system is one mechanism that facilitates the distinction between self and other.

There is accumulating evidence that the parietal cortex plays a role in the distinction between self-produced actions and observed actions generated by others. The right inferior parietal cortex is activated when subjects mentally simulate actions from someone else's perspective but not from their own [30]. This region is also activated when subjects lead rather than follow someone's actions [31] and when subjects attend to someone else's actions rather than their own [32]. Patients with parietal lesions have problems in distinguishing their own and others' actions [33].

Imitation: Motor imitation involves observing the action of another individual and matching one's own movements to those body transformations. The finding that very young babies are capable of imitating certain facial gestures suggests an innate, or early developed, system for coupling the perception and production of movements [34]. This research emphasises another aspect of the early social responsiveness of the infant but it is not clear how the mechanisms involved relate to later intentional imitation of action. Preverbal infants of 18 months were exposed either to a human or to a mechanical device attempting to perform various actions (such as pulling apart a dumb-bell), but failing to achieve them [35]. The children tended to imitate and complete the action when it was made by the human but not when it was made by the mechanical device. This demonstrates that their understanding of people, but not inanimate objects, is within a framework that includes goals and intentions, which can be gleaned from surface behaviour alone.

Another experiment showed that children of this age are capable of using what we might call common sense to avoid slavish imitation [36]. They imitated an exact movement sequence when the adult pressed a button with the forehead when both her hands were free. However, they did not imitate when the adult pressed the button with her forehead while holding a shawl around her using both hands. In this case the children generally used their hands to press the button, presumably inferring that the woman would have done so too, had her hands been free. These experiments suggest that imitation might serve, through development, as an automatic way of interpreting the behaviour of others in terms of their underlying intentions and desires.

Several recent functional imaging studies have attempted to explore the neural correlates of imitation in the human

brain. The simple observation of another person's actions activates brain regions involved in motor execution to a greater extent if subjects are told that they later have to imitate the observed actions than if they are told merely to recognise them [37]. Other brain imaging studies have implicated several different neural structures in imitation, depending on which aspect of an action is imitated [38] and who imitates whom [31].

Theory of mind: Humans have an inherent ability to understand other people's minds which comes in both implicit and explicit forms. An experimental paradigm to study this ability was first introduced in the early 1980s [39] and since then has generated much research in developmental psychology. At around 4 years of age children start to develop an explicit understanding of the content of other people's minds and use this understanding in the manner of a theory to predict others' behaviour. Hence the term theory of mind. At this age children are aware that people can have different beliefs about states of affairs in the real world, and for good reasons. For instance, they may be told a lie by someone else or they may not be present when vital information about a change in the state of affairs is provided.

However, the implicit attribution of mental states to others is available to children at a much younger age. Evidence for the implicit awareness of intentions and desires in others is plentiful from around 18 months. For instance, they understand pretend play and they engage in joint attention. In adults too, there is evidence of both implicit and explicit mentalising abilities. To investigate neural systems involved in mentalising, several brain imaging studies have used a wide variety of tasks and stimuli, both verbal (stories) and non-verbal (cartoons), which do or do not require an understanding of other people's desires and beliefs. The comparison of mentalising and non-mentalising tasks consistently activates at least three brain regions. These are the medial frontal lobe (Brodmann areas 8/9/32), the superior temporal sulcus and the temporal poles (adjacent to the amygdala) [40].

One very implicit mentalising task involves showing participants animations of moving shapes. As long ago as 1944, Heider and Simmel established that ordinary adults feel compelled to attribute intentions and other psychological motives to animated abstract shapes, simply on the basis of their movement patterns [41]. Castelli *et al.* [42] showed such animations to volunteers in a PET study, contrasting sequences where the movements of two triangles were scripted to evoke mental state attributions (e.g. one triangle surprising the other or mocking the other), and sequences where the triangles moved randomly and did not evoke such attributions. This comparison showed activation in the same system as in other studies with more explicit mentalising tasks (see Fig. 6).

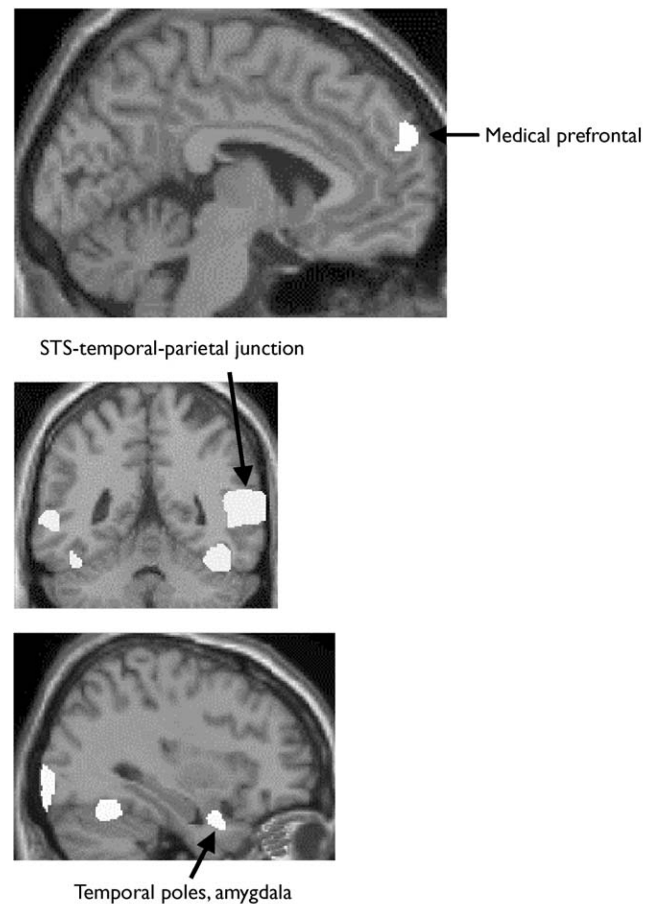

Fig. 6. Brain images depicting activation in the medial prefrontal cortex, the STS and temporal pole when subjects observed animated shapes to which they attributed mental states [42]. These regions have been consistently activated in a variety of theory of mind tasks, and are underactive in high functioning individuals with autism [77]. Reprinted from Castelli *et al.* (2001), with permission.

Predicting an opponent's next move: Interactive games that involve mentalising have also been used in imaging experiments. In one such study, volunteers were scanned while they played a prisoner's dilemma type game with another person [43]. In this game, mutual cooperation between players increased the amount of money that could be won. In the comparison task, the volunteers believed they were playing with a computer that used fixed rules. A comparison of brain activation during the game task and the comparison task revealed activity within the medial prefrontal cortex. The same region was also activated when subjects played stone–paper–scissors, a competitive game in which success depends upon predicting what the other player will do next [44]. Again, the comparison condition was created by telling the volunteers that they were playing against a computer. In fact, the sequence of the opponent's moves was the same in both conditions. Participants described guessing and second guessing their opponent's responses and felt that they could understand and go along with what their opponent, but not the computer, was doing. The medial prefrontal cortex was activated only when the volunteers believed that they were interacting with another person.

What is the involvement of the brain regions that are reliably activated during mentalising? At present we still have conjectures only. It is tempting to conclude that the superior temporal sulcus plays a role in mentalising because it is sensitive to biological motion. The medial prefrontal region activated by mentalising studies is connected to the temporal pole and to the superior temporal sulcus [45], and is situated in the most anterior part of the paracingulate

cortex, where it lies anterior to the genu of the corpus callosum and the anterior cingulate cortex proper. It is thought to be activated by self-monitoring, e.g. attending to one's feelings. Although this region is an ancient structure that belongs to the limbic lobe, the existence of an unusual type of projection neuron (spindle cell) found in sub-areas of the anterior cingulate cortex in humans and some other higher primates, but not monkeys, suggests that the anterior cingulate cortex has undergone changes in recent evolution. It remains to be seen whether the recent evolutionary changes observed in anterior cingulate cortex are relevant to other regions where activations associated with mentalising are observed (see [40] for detailed discussion).

Deception: Understanding someone else's beliefs and how these beliefs can be manipulated and maintained is what having a theory of mind means, and underlies the ability to deceive people. The fully-fledged ability does not develop until about 5 years, from which time children can tell lies to hide things from other people rather than just physically manipulate situations. Recently a number of functional neuroimaging studies have attempted to investigate deception. This is a difficult task because of the confined and artificial context of the brain scanner. So tasks have been devised in which subjects are instructed to withhold truthful responses [46]. These studies have found activations in components of the mentalising system when subjects are lying.

Interpretation of complex emotions: Complex emotions, such as jealousy, envy, pride, embarrassment, resentment, self-esteem, disdain, empathy, guilt, are the stuff of novels, and indeed of everyday life. They have been explored for centuries in many art forms, and in particular the theatre. In contrast, mechanisms in the brain underlying complex emotions have hardly been studied.

Complex emotions are different from simple emotions that we might recognise in another person's face. Even split second exposure to faces expressing fear, sadness, anger and disgust seems to instantly activate amygdala function [8], which may be part of a hard-wired response to threat. Complex emotions are different and involve more than an amygdala response. They often imply awareness of another person's attitude to oneself, and an awareness of self in relation to other people. If so, they are likely to involve the mentalising system of the brain. These emotions are truly social emotions and probably unique to humans. Research attempting to understand the cognitive and neural processes underlying these emotions and their decoding is only just beginning.

A recent study used fMRI to scan the brains of subjects while they were thinking about embarrassing scenarios [47]. Subjects read short vignettes in which social transgressions occurred. In comparison to matched stories in which no transgression occurred, these vignettes elicited activity in the same three regions that were activated in mentalising tasks: the medial prefrontal cortex, temporal poles and superior temporal sulcus. Activity was also seen in the orbitofrontal cortex, a region involved in emotional processing.

When subjects were asked to make explicit judgements about the trustworthiness of someone based on their eyes, the right superior temporal sulcus was activated [48]. This region bilaterally was activated by faces that subjects found trustworthy compared with faces they did not find trustworthy.

Empathy: We need to distinguish between basic instinctive empathy and more complex intentional empathy. Instinctive empathy, accompanied by autonomic responses, is a basic emotional response that is contagious, and is not complex in the sense that the person feeling it has to be aware of their feelings. When somebody is sad and crying, you become sad. Empathy as a complex emotion is different. It requires awareness of the other person's feelings and of one's own reactions. The appropriate reaction may not be to cry when another person cries, but to reassure them, or even to leave them alone. Children start showing more complex empathy responses when perceiving that another person is upset or in pain at around the age of two. Research on empathy has recently become topical, but, so far, has mainly been conducted in the context of lack of empathy (callousness, an inability to respond to a victim's distress). Because we are interested in highlighting potential mechanisms of social cognition we will pick out a few recent brain imaging studies which at least attempt to arrive at such mechanisms.

In a recent fMRI study subjects were asked to make empathic and forgiving judgements based on hypothetical scenarios [49]. Several regions in the superior medial frontal cortex were activated by empathic judgements (subjects had to give an explanation as to why somebody might be acting in a certain way) and forgiving judgements (subjects had to think about which crimes seem most forgivable given a certain situation) compared with the baseline social reasoning judgements.

Morality: Not so long ago, the search for a brain mechanism underlying morality would have been considered absurd. Of course, the development of morality does involve cultural input and explicit teaching. The existence of a code of laws has been a major leap in the cultural evolution of social interactions. However, neuroscience has started to tackle the question of a universal sense of morality without which this cultural achievement might not have occurred. Paradigms for studying this question include the ability to make intuitive moral judgements regardless of any existing code of law. Even young children seem to be able to distinguish what is right or wrong in simple stories where conventional rules are broken and those where moral rules are broken [50]. These two kinds of rules are not usually distinguished explicitly. Yet, 4-year-old children can indicate that if permission is given it is all right to break a conventional social rule (talking in class), but not all right to break a rule that prevents harm being done to others (hitting another child). Even those children who had poor role models around them and had themselves been maltreated were unerring in this judgement. This paradigm has not yet been used in scanning studies.

In adults, moral judgements have been found to activate brain regions that are involved in mentalising, including the medial frontal cortex and the right posterior superior temporal sulcus. These regions were activated by morally upsetting stimuli compared with unpleasant pictures that

had no moral connotations (a picture of a man assaulting a woman compared with a picture of an injured body, for instance) [51]. In another study, fMRI was used to scan subjects while they were evaluating moral dilemmas [52]. An example of a moral dilemma is the train dilemma: a runaway train is heading towards five people who will be killed if the train proceeds on its current course. The only way to save them is to hit a switch that will turn the train onto an alternate set of tracks where it will kill one person. Should you turn the train in order to save five people at the expense of one? Evaluating these problems involves emotional processing, resolving conflict, accommodating cultural beliefs and putting oneself in someone else's shoes. In the study by Greene *et al.*, subjects responded to various different types of dilemma, some that were moral, some not; some involved people; others did not. The results showed that the medial frontal cortex was activated by dilemmas that were moral and personal more than by dilemmas that were neither.

This work, though still preliminary, demonstrates that mechanisms of social cognition can be studied even in those complex and culturally influenced human interactions that involve the ability to tell right from wrong.

WHEN SOCIAL COMMUNICATION FAILS

Biologically caused abnormalities that lead to mild or severe developmental disorders are surprisingly common. They occur in a sizeable proportion of children, estimated at between 5 and 10%. Developmental disorders do not just affect children, but more often than not persist lifelong and very often they involve a degree of social impairment. These disorders tend to have a genetic origin but other causes exist as well, for instance, viral illness can attack the brain at a young age.

Autism: Autism is characterised by difficulties in communication, social interaction and play [53]. Autism comes in many degrees and is often associated with mental retardation. However, it can also occur together with high intelligence and good language (then usually labelled Asperger's syndrome). The signs and symptoms only appear gradually and can often only be fully recognised from the second and third year.

Some features of autism, such as stereotyped movements and obsession with routines, are not in the social domain at all. The social communication failure is the core feature of autism, the feature that unites all the many varieties of the autistic spectrum, as it is now called.

One striking feature about individuals with autism is that they tend to be more interested in objects than in people. A deficit in the recognition of faces has been recently identified and related to abnormal brain activation in the FFA [54]. Other social mechanisms, such as a deficit in imitation and the inability to recognise emotional expressions are also hypothesised, but still lack systematic investigation. One mechanism that has been studied systematically is theory of mind or mentalising. This seems to be impaired or at least delayed in all individuals with autistic disorder.

The normally developing child shows implicit mentalising from about 18 months, and failure to mentalise can only be observed reliably from that age. Early signs of mentalising failure in autism is an absence of triadic joint attention, while dyadic attention may be present. Another sign is a lack of understanding pretence. Imaginative social play (pretend play) is an activity that is normally pervasive in early childhood and implies the ability to tell the difference between a real state of affairs and a pretended one. Its absence in autism was one of the key observations that led to the hypothesis of a mentalising deficit [55]. The mind blindness hypothesis explains the ability of autistic people to form friendships and understand jokes. Social competence is not globally absent in people with autistic disorder. An example is the poor understanding of deception which co-exists with good understanding of sabotage, the latter requiring the ability to distinguish between goodies and baddies and the motivation to win in a competitive game [56].

Tasks of explicit mentalising, i.e. predicting someone's behaviour on the basis of that person's belief, even if it clashes with the real state of affairs, are an important tool in the study of mentalising failure in autism. Children with autism who have sufficient verbal ability to follow the scenarios show a delay of about 5 years before they can pass these tasks. However, it is likely that this slow acquisition of an explicit theory of mind does not replace the missing intuitive mentalising ability. Even very able adults with Asperger's syndrome show slow and error prone responses in mentalising tasks. The brain activation normally shown during mentalising is reduced in individuals with autistic disorder and the connectivity between the components of the mentalising network of the brain is weak [57].

Antisocial behaviour: Antisocial behaviour is salient and perceived in all societies as intolerable. Deviant behaviour comes under various labels such as oppositional defiant disorder, conduct disorder, attention deficit disorder and, in adults, antisocial behaviour disorder. These labels at present confound cases with a primarily biological and those of a purely environmental origin.

Of course, biology and environment always interact. Thus, children who grow up in an abusive environment are likely to attribute hostile causes to actions in others. This mechanism may be responsible for the so-called cycle of violence over generations. However, predisposing genes seem to be a necessary prerequisite. A longitudinal study in New Zealand showed that only those maltreated people who also had a certain predisposing gene later became severely antisocial [58].

Antisocial behaviour is not only a developmental phenomenon, it can also occur out of the blue, as a result of brain damage. Phineas Gage was a railroad construction supervisor in Vermont, USA, when in 1848, an explosion occurred, which resulted in a steel rod destroying a large part of the frontal lobes of his brain. As a result of this accident, Gage started to undergo changes in his personality and mood. In particular, he became extremely anti-social, impulsive, rude and extravagant. The part of the frontal lobes which had been damaged, including the orbito-frontal cortex, is associated with inhibition of inappropriate behaviour, rational decision making and the processing of emotion. Since Phineas Gage, several patients with orbito-frontal cortex lesions have been studied extensively, and the same kinds of social impairments have been found [59]. These patients generally have

specific deficits in emotional expression detection and in making decisions that involve emotional evaluation. This demonstrates the importance of relatively low level emotional cues for understanding other people.

Psychopathy: The most serious form of antisocial behaviour disorder in childhood leads to psychopathy or antisocial personality disorder in adulthood and this disorder may well have a genetic basis.

What kind of neurodevelopmental disorder is psychopathy? Blair [60] has proposed that psychopathy results if there is a fault in the brain system that normally enables instinctive empathy and uses a violence inhibition mechanism. This idea built on evidence that certain emotional expressions trigger innate brain mechanisms located in circuits involving the amygdala. These circuits can become active in quite subtle situations, causing instinctive reactions to fearful events without any need for awareness of the event (see above). We do not like to see other creatures suffer or be afraid. When we see fear or hurt in someone's eyes and we are the cause of it, we tend to stop what we are doing. This is like a reflex that Konrad Lorenz described in fighting dogs and other animals: certain signals, so-called submission cues tend to make the winning animal stop and shrink back from doing further damage. Blair argued that the same reflex exists in humans, and that this reflex is vital for intuitive moral knowledge.

What would be the consequence for development in the case of a fault in the instinctive empathy circuit? Blair *et al.* [60] predicted and confirmed that such children find it difficult to recognise expressions of fear and sadness. They also have problems in learning moral imperatives, such as not to hurt others, and are unable to distinguish between rules that govern social conventions, and rules that are motivated by a deeper moral sense.

Although psychopaths lack instinctive sympathy and feel no guilt at having caused harm to another person, they may nevertheless have excellent mentalising skills. Not all people with an inability to feel instinctive empathy are excessively violent. If they have no motive to offend, then no harm may come to others. However, individuals who perpetrate violence without pity or remorse are dangerous. From this point of view, and contrary to popular opinion, psychopathy is not the same as being a violent type. A violent person (like a fighting dog) may still respond to the distress cues of a victim and stop his or her action and feel guilt.

Social impairments in schizophrenia: People with schizophrenia and other mental illnesses have significant social problems. One symptom that carries severe social penalties is a delusion of persecution, in which a person holds a bizarre and paranoid belief with extraordinary conviction, despite experiences to the contrary and counter-arguments. Persecutory delusions are symptoms commonly associated with schizophrenia, but they also occur in other psychiatric disorders including depression, bipolar disorder and schizoaffective disorder.

Within the cognitive approach to psychopathology it has been argued that processes involved in social inference, that is the processes by which we interpret the actions of other people and events involving others, play an important role in the development of paranoid delusions. One such social inference process that may be associated with paranoid delusions involves inferring the causes of social interactions. Individuals readily attribute causes to external events. Bentall and his colleagues have argued that paranoid beliefs may be a product of abnormal causal attributions. Overall, research findings support this proposal. Paranoid patients tend excessively to believe that the course of life is influenced by powerful others. Furthermore, patients with persecutory delusions over-attribute negative events to external causes and to the actions of other people [61].

A second type of social inference process that has been proposed to underlie delusions of persecution involves over-attributing intentions to other people. Frith [62] has argued that dysfunctional mentalising may be implicated in psychotic symptoms including persecutory delusions [63]. It is possible, that, just as in autism, this later maturing high level mechanism is particularly vulnerable to the brain anomalies that lead to this disorder.

FUTURE DIRECTIONS

We have sketched out the current state of research on social cognition as far as it has been influenced and, to some extent, revolutionized by the methods of neuroscience. There are many areas of social cognition which are still unexplored. What is prejudice, and how is it processed in the brain? How can we manage our emotions in interpersonal situations? How is the brain influenced by the action of role models, whether real or fictional? What are the causes of individual differences in social competence? When should we be responsible for our actions? When the genetic and neural basis of psychopathy is uncovered, what shall we do with those people who have the genetic potential to become a psychopath? If you can decipher someone's future actions based on their intentions (as determined by some objective measure) could you stop them from executing that action if it were harmful? Could transgenic mice be useful in the study of social cognition? These are just a few possible areas of future research. Clearly, such investigations, and more, will need to be done to clarify the neural basis of social mechanisms before a fully coherent picture emerges.

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