

Social cognitive neuroscience: where are we heading?

Sarah-Jayne Blakemore¹, Joel Winston² and Uta Frith¹

¹Institute of Cognitive Neuroscience, 17 Queen Square, London, WC1N 3AR, UK

²Wellcome Department of Imaging Neuroscience, 12 Queen Square, London, WC1N 3BG, UK

Humans crave the company of others and suffer profoundly if temporarily isolated from society. Much of the brain must have evolved to deal with social communication and we are increasingly learning more about the neurophysiological basis of social cognition. Here, we explore some of the reasons why social cognitive neuroscience is captivating the interest of many researchers. We focus on its future, and what we believe are priority areas for further research.

The field of social cognitive neuroscience is still relatively new but builds on a variety of well established disciplines including social, developmental and cognitive psychology, evolutionary biology, neuropsychology and computer science, each providing a solid basis of relevant research. In the past few years, interest in the neurological underpinnings of social cognition has burgeoned, as demonstrated by at least four special issues of major journals in this field [1–4]. What drives this interest in social cognitive neuroscience? And what is the future of this flourishing discipline? In this article, we pick out several areas of social cognitive neuroscience and focus on where we believe each area might head in terms of future research.

What is social cognitive neuroscience?

Most generally, social cognition encompasses any cognitive process that involves conspecifics, either at a group level or on a one-to-one basis. Social cognitive neuroscience encompasses the empirical study of the neural mechanisms underlying social cognitive processes. One key question is whether general cognitive processes involved in perception, language, memory and attention, are sufficient to explain social competence, or whether over and above these general processes there are specific processes that are special to social interaction. This possibility is exciting because it can explain social impairment in otherwise very able individuals, in particular in autism.

It may once have seemed foolhardy to work out connections between fundamental neurophysiological mechanisms and highly complex social behaviour, let alone to decide whether the mechanisms are specific to social processes. However, as we shall see, neuroimaging studies have provided some encouraging examples.

The next step of linking brain mechanisms to genes that contribute to social competence is already in sight (see Box 1).

However, we need to be cautious when interpreting the results of neuroimaging studies reporting brain activations during high level cognitive processes such as moral reasoning, deception and fairness. These kinds of processes are challenging to emulate and control within the scanning environment, and in some cases, what is labelled deception or morality in an experiment is far from those concepts in everyday life. Furthermore, in the context of social cognition there have as yet been relatively few attempts to replicate findings. On the other hand, it

Box 1. Social genes

It is unknown just how biological factors interact with environmental variables to produce individual differences and pathology. In the future, we anticipate that the genetic basis for different aspects of social cognition will be illuminated. This is feasible by studying individuals who are born without the ability to develop normal social communication, for example people with autism and people with psychopathy.

Congenital abnormalities in the neural substrates of social cognition can serve to identify endophenotypes that relate to disorders of social cognition. The term endophenotype refers to the 'inside phenotype' rather than overt behaviours, which are likely to be the product of many different endophenotypes. These then can lead the search for the genetic basis of specific social functions. Examples of allelic variation combining with environmental conditions contributing to social phenomena, such as the development of antisocial behaviour, are also being characterized [62]. The gene in this case (MOA-A) is implicated in central neurotransmitter pathways, which supports the contention that aspects of individual differences might be characterized by such pathways [63].

Social cognitive processes can be genetically selected. A prime example of this is in dogs, which are able to glean information about the location of an object from a human's eye gaze and pointing [64]. This appears to be specific to domesticated dogs; neither chimpanzees nor wolves are able to use a person's eye gaze to search for an object, demonstrating that this ability is neither specific to primates or canine species in general. By contrast, young puppies can use eye gaze information, implying that the ability is not learned from years of experience with people. Instead it is suggested that this ability has been bred into the dogs' gene pool over centuries of domestication. What do we know about social interaction in other species? A prime example of social species are insects. Ants are known to be able to change their social roles, say from worker to warrior, as the situation demands. Insect societies could serve as analogies to human societies, and in particular, insects could provide genetic models for human social adaptation.

is reassuring that in certain areas, for example in the study of mentalising (see section: Understanding others' minds), there are now at least ten studies using different stimuli and performed in different laboratories, which have yielded strikingly similar results.

Even when a neuroimaging study is highly controlled and the results have been replicated many times over, what does it mean to know that a brain region is activated by a certain task? Why does it matter and what does it add? In isolation, brain imaging data has been criticized as being of little importance for understanding the workings of the mind. But we would argue that brain imaging data complement and extend the results from behavioural, single cell and lesion studies. The next section provides an example of a field where all of these methods have been used to great effect. Scanning people's brains while they do nothing but observe another person do something has opened a new door to research on the neuroscience of social cognition.

Understanding others' actions

In the past decade, neurophysiological research has provided evidence of a brain system that decodes conspecifics' actions and may contribute to the understanding of other people's intentions, goals and desires. Mirror neurons, found in ventral premotor cortex of macaque monkeys, are activated both when the monkey executes grasping actions and when it observes someone else (or another monkey) making grasping actions [5]. Mirror neurons appear to distinguish between biological and non-biological actions, responding only to the observation of hand-object interactions and not to the same action if performed by a mechanical tool, such as a pair of pliers [6].

Following the discovery of mirror neurons in monkeys, there is increasing evidence that a large proportion of the human motor system is activated by the mere observation of action [7]. Brain imaging studies have revealed that the motor activation to observed action is functionally specific: premotor cortex and parietal cortex are activated in a somatotopic manner according to the modality of the action being observed [8]. In addition, observing an action affects the peripheral motor system in the specific muscles that are used in the action being observed [9].

The study of the mirror system provides an example of an attempt to identify the neurophysiological activity that underlies the ability to understand the meaning of one's own and another person's actions. This class of mechanism may be fundamental to several 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, and the ability to imitate as well as to teach others. Although it seems obvious that another person's actions can influence one's own actions, insight into the precise nature of this influence at the behavioural and physiological level was provided only recently in an experiment by Sebanz *et al.* [10]. When a subject performed a spatial compatibility task, the presence of a partner altered the timing of the subject's responses in the same way as when two simultaneous tasks were performed by a single subject.

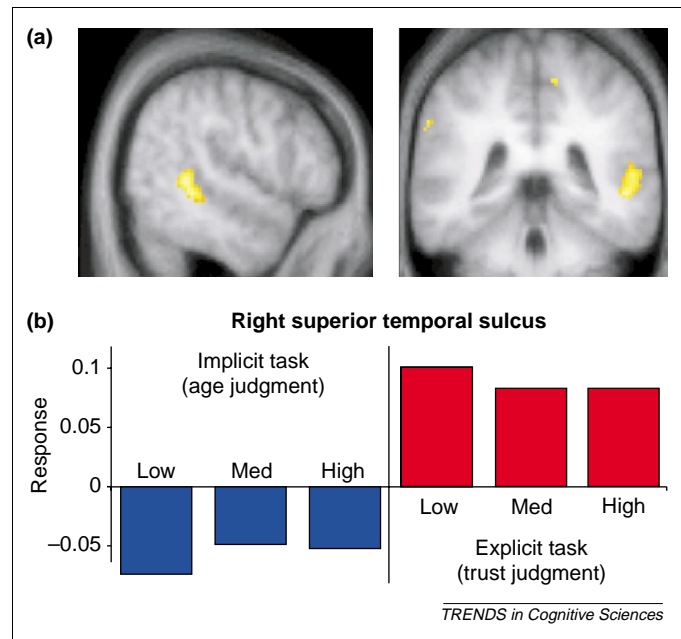


Figure 1. (a) Experimental design of a study of interference effects of observing biological movements on actions [13]. The subject (S) made sinusoidal movements with their right arm at the same time as observing movements that were either congruent or incongruent with their own movements. The observed movements were made either by another human (experimenter, E) or by a robotic arm (R). There was also a baseline condition in which the subject moved their arm without watching anything. Subject arm movements were recorded using an Optotrak system. (b) Interference effects. For each arm movement, the variance in the movement orthogonal to the dominant dimension of movement and in the dominant dimension of the incongruent movement was calculated. Mean variances (and standard error bars) are shown for the five conditions. The only condition in which movement variance differed significantly from the baseline movement condition was that in which subjects watched the human experimenter making incongruent arm movements. Thus, the interference effect seems to be specific for observed human actions. Reproduced with permission from [13].

Observing another person's actions also influences one's own ongoing movements. Recent evidence suggests that observing an action interferes with one's own actions when these are different from those being observed [11–13]. This interference effect seems to be specific for observed human actions; observing a robot making a movement does not interfere with ongoing actions [13] (Figure 1).

Understanding actions: future research

Why is it that mirror neurons require biological actions to be activated [6]? What is special about biological actions in this case? Why is it that the observation of biological movements performed by a human interferes with action, whereas robotic movements do not [13]? What is it about the presence of another person that is the influential factor? Does a human have to be present, or would a robot programmed to show the characteristic kinematics of biological motion have the same influence?

Does eye gaze, our own and that observed in people with whom we communicate, play a crucial role in these interactions [14,15]? Gaze bias can influence the perceived attractiveness of faces, not merely reflecting *a priori* preference [16]. Mere signals of an impending communication, either being looked at intently, or being called by one's name, activates significant portions of the brain regions known to be involved in understanding others [17].

Can the mirror system be trained? In a recent study monkeys were trained to rip paper [18]. When this was learned, specific mirror neurons started to fire in response to the action sound. Are mirror neurons sufficiently flexible and dynamic that they can start to represent any type of action in all modalities?

Does the mirror system enable us to understanding other people's minds? Is the mirror system functioning normally in people with autism whose understanding of other minds is impaired?

Understanding others' minds

Autism research has led to the hypothesis that social learning requires the detection of intentions and inner mental states of other agents [19]. Specifically, it is proposed that there is a brain mechanism that enables us automatically to attribute mental states to self and others, and this mechanism is faulty in autism. The search for the genetic basis of this ability has begun (see Box 1).

So automatic and pervasive is this mind-reading mechanism that ordinary adults feel compelled to attribute intentions and other psychological motives to animated abstract shapes, simply on the basis of their movement patterns [20]. This has been exploited in neuroimaging studies in which participants view animations of moving shapes [21,22] and has provided information on the underlying brain system. In the study by Castelli *et al.* [21], a comparison between animations that evoked mental state attributions (e.g. one triangle mocking another) and animations in which triangles moved randomly demonstrated activation of the medial frontal lobe, the superior temporal sulcus (STS) and the temporal poles. These regions have consistently been activated in

brain imaging studies using a wide variety of verbal and non-verbal stimuli to investigate mentalising (see [23]). The subcomponents of this mentalising process and the precise nature of the triggering stimuli still remain to be revealed.

Meanwhile, work on mentalising is rapidly evolving to the investigation of the neurophysiological basis of the complex behaviour shown by people when playing economic games [24], during deception and when showing empathy and moral sensitivity.

Cheating and bargaining

The ingenuity of people to outwit each other and to use bluff and double bluff is an instance of advanced social skills that rely on an intuitive mentalising ability. Several neuroimaging studies have attempted to investigate deception, but this is a challenging task because of the confined and artificial context of the brain scanner. Tasks have been devised in which subjects are instructed to withhold truthful responses and answer with their opposites to questions concerning recent autobiographical events [25], or to lie about a card's identity [26] or past events [27]. These studies have found activations in components of the mentalising system when subjects are lying. Whether this artificially engineered deception uses the same mechanisms as spontaneous deception remains to be seen.

It has been argued that being equipped with mechanisms for detection of cheaters would carry high evolutionary advantages [28]. An imaging study in which subjects viewed faces that varied on trustworthiness found automatic activation of the amygdala with magnitude proportional to the perceived untrustworthiness of the face

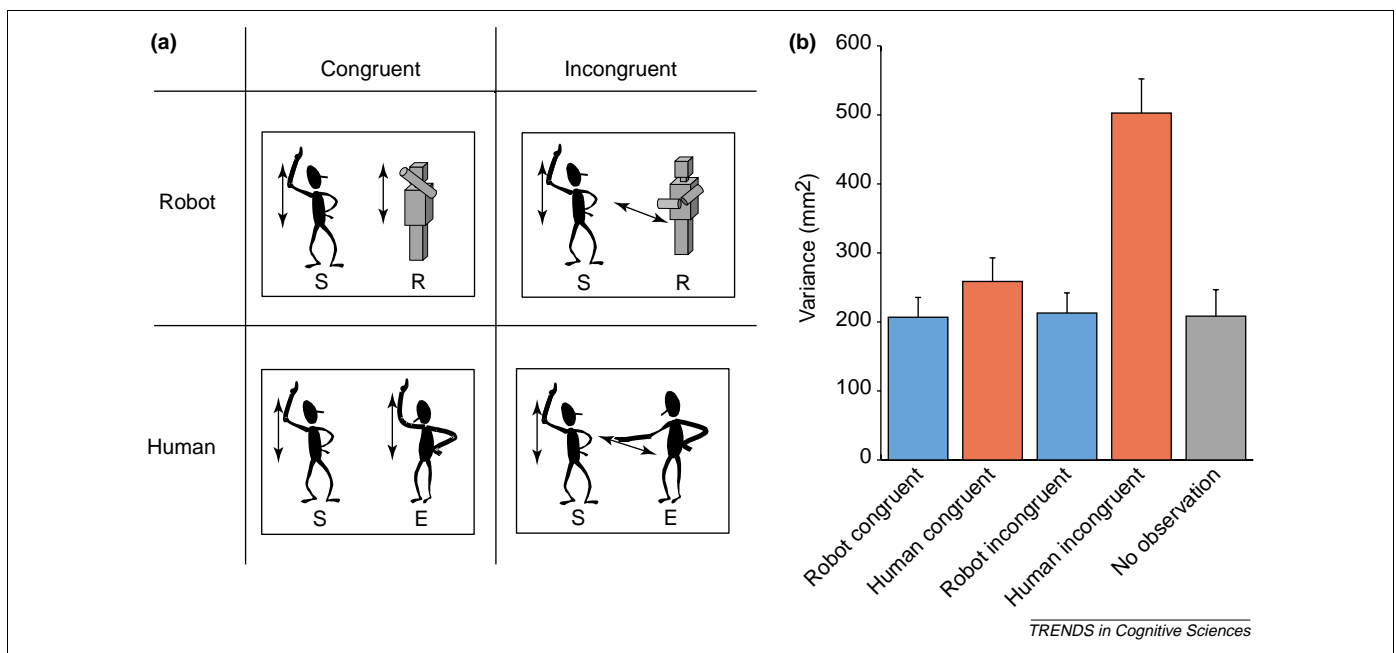


Figure 2. Superior temporal sulcus (STS) is activated when making explicit trustworthiness judgements. STS has been activated in many imaging studies of social cognition, for example mentalising, biological motion perception and even simple face perception. Here, greater STS activation was observed when subjects made explicit judgments of trustworthiness about faces compared with when they made age judgments (implicit task) about the same faces. (a) The STS activation in the explicit task. (b) The size of the response in the STS for the two tasks (age and trustworthiness judgment) and as a function of trustworthiness (low, medium or high) of the face. There is a clear difference between activation in the two tasks, the STS being activated for the explicit trustworthiness judgment task only, but no relationship with the perceived trustworthiness of the faces. Adapted from reference [29].

and activation of the STS during explicit trustworthiness judgements only [29]; (see Figure 2). What makes a face appear trustworthy, and whether these characteristics are universal or culturally specific, is still unknown. There is some evidence that untrustworthy people might have more memorable faces than trustworthy faces. This evidence comes from a study in which many different faces were presented to subjects whose memory for the faces was subsequently tested. The faces of people who had previously chosen to defect in prisoner's dilemma games were better remembered than those who cooperated, even though the subjects in the memory experiment saw only the faces and had no information about the performance in the prisoner's dilemma game [30].

Fairness and justice

Moral judgements activate brain regions that are involved in mentalising, including the medial frontal cortex, according to a recent study in which subjects were scanned while evaluating moral dilemmas [31]. Medial frontal cortex appears to be critical to moral development according to a study that compared patients who suffered lesions in this region at a young age and those whose cortex was damaged in adulthood [32]. Patients with childhood lesions showed defective social and moral reasoning, whereas this was not evident in those with later damage.

Mentalising: future research

Many aspects of social communication involve mentalising: understanding beliefs, intentions, desires of others; knowing that these can differ from one's own mental states; understanding that to see is to know; attributing intentions to actions, eye gaze and facial expressions, and so on. Does the brain's intuitive mentalising system play an equally important role in each of these? Can mentalising be reduced to subcomponents, such as a representation of intentional and contingent actions? What are the different roles of the brain regions involved in mentalising? What is the role of top-down control when reflecting on one's own and others' mental states?

How is mentalising related to competition and deception, cooperation and teaching, fairness and moral judgement? What can we learn about the brain basis of mentalising from individual differences in mentalising skills? What social skills do not involve mentalising?

Understanding others' emotions

The brain reads facial expressions extremely rapidly [33–35]. Several brain imaging studies have shown that the amygdala is activated by emotional expressions in faces (e.g. [36,37]), even independent of attention or awareness [38,39]. There is some suggestion that amygdala responses to other emotions might depend upon individual differences, such as extraversion [40]. More recently, there has been interest in the perception of dynamic displays of emotion in faces [41] and of emotion from bodily posture [42].

Complex emotions, such as jealousy, pride, embarrassment and guilt, are different from the simple emotions that

we might recognize in another person's face. They often imply awareness of another person's attitude to oneself, and an awareness of the self in relation to other people. If so, they are likely to involve the mentalising system. There is imaging evidence that this is the case for emotions such as embarrassment [43] and forgiveness [44].

The study of empathy has recently been advanced by scanning couples, where under highly controlled conditions, one partner suffered an electric shock, and the other's brain was scanned as they anticipated the partner's pain [45]. In this study, brain regions activated by the expectation of another's pain overlapped with those activated by the experience of one's own pain. The anterior cingulate and insula were the most critical regions activated in this study. These areas are not activated by mentalising tasks, and this raises the possibility that feeling another's pain is independent of seeing the world from another person's point of view.

Complex emotions: future research

Is there a difference in the brain between empathy for those we know and those we do not know? When does empathy develop? To what extent is it learned? To what extent is the brain equipped with an empathy system from birth? Which emotions show the most and the least cultural influence? The study of contagious emotions and motor acts, such as smiling and yawning, might enlighten these questions. Are the brain processes for empathy for positive and negative emotions different? What genetic basis underlies the brain abnormality that leads to disorders of empathy, such as psychopathy? How can we obtain information about how other people feel when we cannot see their faces or hear their voices?

Social learning and development

In the past two decades, infants have been increasingly recognized as seekers and providers of social interaction and communication. If there are innate predispositions for certain types of social abilities, and if lengthy periods of cultural learning are not necessary prerequisites for these abilities, it follows that infants should be socially competent right from birth. Indeed, much evidence has been amassed to show that infants have certain social capacities, for instance, recognizing faces, imitating (see Box 2) following eye gaze [46] and knowing the sounds of their language [47]. Our knowledge about neurophysiological processes that underpin these predispositions for social learning is as yet sparse.

Even though much of early learning appears to be automatic, it nevertheless seems to require a naturally rich and stimulating environment. The experience of social interaction with other people seems to be key. Kuhl *et al.* [48] demonstrated that infants older than nine months were able to learn new speech sounds to which they had never been exposed, after the previously established 'sensitive period' for sound categorisation. However, later learning occurred only if the new sounds came from a real person who interacted with the babies. No learning occurred at this age if the same sounds were presented on a tape recorder or video.

Box 2. Imitation

Although 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 [65], later forms of imitation suggest a more sophisticated mechanism. 18-month-old infants tend to imitate and complete actions made by a human but not similar movements made by a mechanical device [66]. This demonstrates that infants' 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 infants are capable of avoiding

slavish imitation [67]. Infants imitated an exact movement sequence when an adult pressed a button with her forehead when both her hands were free. However, they did not imitate the adult when she pressed the button with her forehead while holding a shawl around her using both hands (see Figure 1). In this case, the infants 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 facilitate, through development, the interpretation of the behaviours of others in terms of their underlying intentions and desires.

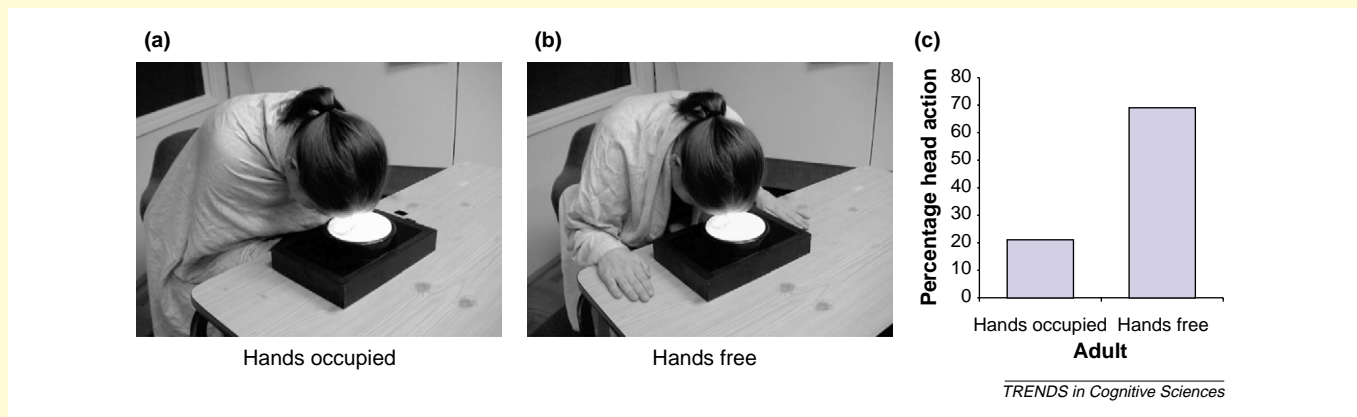


Figure 1. The behaviours shown to 14-month-old infants were: (a) an adult pressing a button with her forehead while holding a shawl around her using both hands, and (b) pressing the button with her forehead when both her hands were free. (c) Infants imitated the exact movement sequence when the adult's hands were free, but usually did not when her hands were occupied (they used their hands to press the button instead). This demonstrates that infants do not slavishly imitate anything they see, but are able to divide actions into means and goals. Reproduced with permission from [67].

The enigma of adolescence

Adolescence is a time of profound mental change, affecting social awareness, adaptation and character, as well as disposition to several forms of mental illness. In the teenage years, the incidence of antisocial behaviour increases ten-fold [49]. Understanding the cognitive and neural maturation during this period is vital, and yet, until recently (see Box 3), there has been surprisingly little empirical research on cognitive and neural development during adolescence.

Social learning and development: future research

How does social reward and punishment shape, nurture or eliminate behaviours that arise from innate social predispositions? Which type of learning requires the presence of others? How do others shape an individual's behaviour? Is this a form of imitation that is ultimately rooted in the mirror system of the brain? Is successful teaching facilitated by mentalising, e.g. evaluating the degree of knowledge or skill already available to the pupil and monitoring learning by adjusting the content of the communication?

How does exposure to films and computer games influence social learning and the social brain? Which artificial social rules (e.g. etiquette) are easy and which are hard to learn? How do individual differences in personality and temperament interact with social learning?

Computational modelling and robot communication

It feels very different communicating with a quick check-in machine at the airport than having the same 'conversation'

Box 3. The adolescent brain

In the past few years, several structural MRI studies have been performed to investigate the development of brain structure during childhood and adolescence in humans. A consistent finding from these studies is that the volume of grey matter decreases and the volume of white matter increases in the frontal cortex throughout adolescence. These data have been interpreted as reflecting a post-pubescent increase in axonal myelination and concomitant decrease in synaptic density [68–70]. Given these developmental changes in the frontal cortex, cognitive abilities that rely on the frontal lobes, including those involved in social communication, may change during adolescence. A small number of studies, which have mainly investigated executive function, have shown evidence of steady improvement in performance speed and accuracy on certain executive function tasks with age between childhood and late adolescence [71]. A recent study, using a match-to-sample task in which participants had to decide whether a facial expression matched a word, revealed a dip in performance at puberty: 11–12 year olds were ~15% slower than younger children [72]. After puberty, performance improved until it reached the pre-pubescent level by about 16 years. The researchers suggested that this pubertal dip in performance is due to the proliferation of synapses in the frontal cortex that is thought to occur at the onset of puberty [70].

Although a picture of a changing adolescent brain is beginning to emerge, we still know relatively little about changes in social cognition during this period of life. Whether brain development during adolescence is linear or non-linear requires further research. Very little is known about gender differences in cognitive or brain development, and yet there is evidence that such differences exist. In addition, future experiments could investigate the development of non-executive functions, including social cognitive processes such as self-awareness, awareness of others and interpretation of complex emotions.

face to face with an airline employee. Robots are already being developed that produce human-like emotional expressions – such as smiling and frowning – and that react to facial expressions of people. Robots already exist that imitate complex human actions (such as bouncing a ball on a tennis racquet; [50]). In the future, the development of robotic toys that respond to the eye gaze of the player, and change their behaviour according to the player's focus of attention, might become instrumental in intra-disciplinary social cognition research [51]

Several aspects of social cognition are beginning to be modelled computationally, and such endeavours have and undoubtedly will continue to inform empirical research. One example with a long history is the attempt to model face recognition processes computationally. Recent attempts have incorporated dissociable representations of identity and expression in face perception [52] based on empirical studies indicating different neural bases for coding these aspects of faces [e.g., 53,54].

By contrast, an example of a computational approach informing social cognitive neuroscientists comes from the game-theory literature. This literature, with its long history of computational simulation of interacting agents with competing behavioural strategies [55,56], has begun to enable predictions about the neural basis for cooperative behaviour, for example, the salience of mutual cooperation [24]. Why organisms will act altruistically in the absence of direct pay back (indirect reciprocity) is a debated problem, and recently 'image scoring' (reputation formation) has been proposed as a solution [57]. This has been shown to operate in experimental situations with humans [58,59]. Moreover, it likely relates to aspects of face perception that are beginning to be investigated in the social cognitive neuroscience literature, such as trustworthiness [29].

Conclusions and outlook

There are many reasons then why social cognitive neuroscience is currently exciting many researchers. The search is on for brain mechanisms that reflect some of the most complex aspects of human behaviour. However, mentalising, imitation, complex emotions, moral judgement, bargaining, and fairness, appear to depend at least partly on universal neurophysiological mechanisms, and precursors of these complex social capacities are likely to exist in many animal species.

Research on the neural correlates of social interactions will be facilitated by the possibility of dual scanning in which two brain scanners record the simultaneous neural responses of two interacting people. Some studies have duped subjects into believing that they are interacting with another person outside the scanner, using interactive games [60,61]. The natural reciprocity of human communication requires that we look at two brains and not just one. Important advances will be made when appropriate techniques are available for developmental scanning from birth to adulthood. This will allow us to understand better the respective roles of innate predisposition and cultural learning.

Acknowledgements

S.J.B. is supported by the Royal Society of London, J.W. by the Wellcome Trust, and U.F. by the Medical Research Council, UK.

References

- 1 *Neuropsychologia* (2003) 41, Issue 12
- 2 *Journal of Cognitive Neuroscience* (2004) Whole issue (in press)
- 3 *Journal of Personality and Social Psychology* (2003) 85, Issue 4
- 4 *Biological Psychiatry* (2002) 51, Issue 1
- 5 Gallese, V. *et al.* (1996) Action recognition in the premotor cortex. *Brain* 119, 593–609
- 6 Rizzolatti, G. *et al.* (2001) Neurophysiological mechanisms underlying the understanding and imitation of action. *Nat. Rev. Neurosci.* 2, 661–670
- 7 Rizzolatti, G. *et al.* (1996) Localization of grasp representations in humans by PET: 1. Observation versus execution. *Exp. Brain Res.* 111, 246–252
- 8 Buccino, G. *et al.* (2001) Action observation activates premotor and parietal areas in somatotopic manner: an fMRI study. *Eur. J. Neurosci.* 13, 400–404
- 9 Fadiga, L. *et al.* (1995) Motor facilitation during action observation: a magnetic stimulation study. *J. Neurophysiol.* 73, 2608–2611
- 10 Sebanz, N. *et al.* (2003) Representing others' actions: just like one's own? *Cognition* 88, B11–B21
- 11 Craighero, L. *et al.* (2002) Hand action preparation influences the responses to hand pictures. *Neuropsychologia* 40, 492–502
- 12 Brass, M. *et al.* (2001) Movement observation affects movement execution in a simple response task. *Acta Psychol. (Amst.)* 106, 3–22
- 13 Kilner, J.M. *et al.* (2003) An interference effect of observed biological movement on action. *Curr. Biol.* 13, 522–525
- 14 Baron-Cohen, S. (1995) *Mindblindness: Essay on Autism and the Theory of Mind, Learning, Development & Conceptual Change*, The MIT Press
- 15 Castiello, U. (2003) Understanding other people's actions: intention and attention. *J. Exp. Psychol. Hum. Percept. Perform.* 29, 416–430
- 16 Shimojo, S. *et al.* (2003) Gaze bias both reflects and influences preference. *Nat. Neurosci.* 6, 1317–1322
- 17 Kampe, K.K. *et al.* (2003) Hey John: signals conveying communicative intention toward the self activate brain regions associated with 'mentalizing', regardless of modality. *J. Neurosci.* 23, 5258–5263
- 18 Kohler, E. *et al.* (2002) Hearing sounds, understanding actions: action representation in mirror neurons. *Science* 297, 846–848
- 19 Baron-Cohen, S. *et al.* (1985) Does the autistic child have a theory of mind? *Cognition* 21, 37–46
- 20 Heider, F. and Simmel, M. (1944) An experimental study of apparent behavior. *Am. J. Psychol.* 57, 243–249
- 21 Castelli, F. *et al.* (2000) Movement and mind: a functional imaging study of perception and interpretation of complex intentional movement pattern. *Neuroimage* 12, 314–325
- 22 Martin, A. and Weisberg, J. (2003) Neural foundations for understanding social and mechanical concepts. *Cogn. Neuropsychol.* 20, 575–587
- 23 Frith, U. and Frith, C.D. (2003) Development and neurophysiology of mentalizing. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 358, 459–473
- 24 Rilling, J. *et al.* (2002) A neural basis for social cooperation. *Neuron* 35, 395–405
- 25 Spence, S.A. *et al.* (2001) Behavioural and functional anatomical correlates of deception in humans. *Neuroreport* 12, 2849–2853
- 26 Langleben, D.D. *et al.* (2002) Brain activity during simulated deception: an event-related functional magnetic resonance study. *Neuroimage* 15, 727–732
- 27 Lee, T.M. *et al.* (2002) Lie detection by functional magnetic resonance imaging. *Hum. Brain Mapp.* 15, 157–164
- 28 Cosmides, L. and Tooby, J. (1992) Cognitive adaptations for social exchange. In *The Adapted Mind: Evolutionary Psychology and the Generation of Culture* (Barkow, J.H. *et al.*, eds), pp. 163–228, Oxford University Press
- 29 Winston, J.S. *et al.* (2002) Automatic and intentional brain responses during evaluation of trustworthiness of faces. *Nat. Neurosci.* 5, 277–283
- 30 Yamagishi, T. *et al.* (2003) You can judge a book by its cover: evidence that cheaters may look different from cooperators. *Evol. Hum. Behav.* 24, 290–301

- 31 Greene, J.D. *et al.* (2001) An fMRI investigation of emotional engagement in moral judgment. *Science* 293, 2105–2108
- 32 Anderson, S.W. *et al.* (1999) Impairment of social and moral behavior related to early damage in human prefrontal cortex. *Nat. Neurosci.* 2, 1032–1037
- 33 Sugase, Y. *et al.* (1999) Global and fine information coded by single neurons in the temporal visual cortex. *Nature* 400, 869–873
- 34 Eimer, M. *et al.* (2003) The role of spatial attention in the processing of facial expression: an ERP study of rapid brain responses to six basic emotions. *Cogn. Affect. Behav. Neurosci.* 3, 97–110
- 35 Adolphs, R. (2003) Cognitive neuroscience of human social behavior. *Nat. Rev. Neurosci.* 4, 165–178
- 36 Morris, J.S. *et al.* (1996) A differential neural response in the human amygdala to fearful and happy facial expressions. *Nature* 383, 812–815
- 37 Breiter, H.C. *et al.* (1996) Response and habituation of the human amygdala during visual processing of facial expression. *Neuron* 17, 875–887
- 38 Vuilleumier, P. *et al.* (2001) Effects of attention and emotion on face processing in the human brain: an event-related fMRI study. *Neuron* 30, 829–841
- 39 Whalen, P.J. *et al.* (1998) Masked presentations of emotional facial expressions modulate amygdala activity without explicit knowledge. *J. Neurosci.* 18, 411–418
- 40 Canli, T. *et al.* (2002) Amygdala response to happy faces as a function of extraversion. *Science* 296, 2191
- 41 Kilts, C.D. *et al.* (2003) Dissociable neural pathways are involved in the recognition of emotion in static and dynamic facial expressions. *Neuroimage* 18, 156–168
- 42 Hadjikhani, N. and de Gelder, B. (2003) Seeing fearful body expressions activates the fusiform cortex and amygdala. *Curr. Biol.* 13, 2201–2205
- 43 Berthoz, S. *et al.* (2002) An fMRI study of intentional and unintentional violations of social norms. *Brain* 125, 1696–1708
- 44 Farrow, T.F. *et al.* (2001) Investigating the functional anatomy of empathy and forgiveness. *Neuroreport* 12, 2433–2438
- 45 Singer, T. *et al.* (2004) Empathy for pain involves the affective but not sensory components of pain. *Science* 303, 1157–1162
- 46 Farroni, T. *et al.* (2002) Eye contact detection in humans from birth. *Proc. Natl. Acad. Sci. U. S. A.* 99, 9602–9605
- 47 Dehaene-Lambertz, G. *et al.* (2002) Functional neuroimaging of speech perception in infants. *Science* 298, 2013–2015
- 48 Kuhl, P.K. *et al.* (2003) Foreign-language experience in infancy: effects of short-term exposure and social interaction on phonetic learning. *Proc. Natl. Acad. Sci. U. S. A.* 100, 9096–9101
- 49 Moffitt, T.E. (1993) Adolescence-limited and life-course-persistent antisocial behavior: a developmental taxonomy. *Psychol. Rev.* 100, 674–701
- 50 Miyamoto, H. and Kawato, M. (1998) A tennis serve and upswing learning robot based on bi-directional theory. *Neural Netw.* 11, 1331–1344
- 51 Steels, L. (2003) Evolving grounded communication for robots. *Trends Cogn. Sci.* 7, 308–312
- 52 Calder, A.J. *et al.* (2001) A principal component analysis of facial expressions. *Vision Res.* 41, 1179–1208
- 53 Tranel, D. *et al.* (1988) Intact recognition of facial expression, gender, and age in patients with impaired recognition of face identity. *Neurology* 38, 690–696
- 54 Hasselmo, M.E. *et al.* (1989) The role of expression and identity in the face-selective responses of neurons in the temporal visual cortex of the monkey. *Behav. Brain Res.* 32, 203–218
- 55 Maynard Smith, J. and Price, G.R. (1973) The logic of animal conflict. *Nature* 246, 15–18
- 56 Axelrod, R. and Hamilton, W.D. (1981) The evolution of cooperation. *Science* 211, 1390–1396
- 57 Nowak, M.A. and Sigmund, K. (1998) Evolution of indirect reciprocity by image scoring. *Nature* 393, 573–577
- 58 Wedekind, C. and Milinski, M. (2000) Cooperation through image scoring in humans. *Science* 288, 850–852
- 59 Milinski, M. *et al.* (2002) Donors to charity gain in both indirect reciprocity and political reputation. *Proc. R. Soc. Lond. B. Biol. Sci.* 269, 881–883
- 60 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
- 61 Gallagher, H.L. *et al.* (2002) Imagining the intentional stance. *Neuroimage* 16, 814–821
- 62 Caspi, A. (2002) Role of genotype in the cycle of violence in maltreated children. *Science* 297, 851–854
- 63 Depue, R.A. and Collins, P.F. (1999) Neurobiology of the structure of personality: dopamine, facilitation of incentive motivation, and extraversion. *Behav. Brain Sci.* 22, 491–517
- 64 Hare, B. *et al.* (2002) The domestication of social cognition in dogs. *Science* 298, 1634–1636
- 65 Meltzoff, A.N. and Moore, M.K. (1977) Imitation of facial and manual gestures by human neonates. *Science* 198, 74–78
- 66 Meltzoff, A.N. (1995) Understanding the intentions of others: re-enactment of intended acts by 18-month-old children. *Dev. Psychol.* 31, 838–850
- 67 Gergely, G. *et al.* (2002) Rational imitation in preverbal infants. *Nature* 415, 755
- 68 Huttenlocher, P.R. (1979) Synaptic density in human frontal cortex – developmental changes and effects of aging. *Brain Res.* 163, 195–205
- 69 Giedd, J.N. *et al.* (1999) Brain development during childhood and adolescence: a longitudinal MRI study. *Nat. Neurosci.* 2, 861–863
- 70 Sowell, E.R. *et al.* (2003) Mapping cortical change across the human life span. *Nat. Neurosci.* 6, 309–315
- 71 Anderson, V.A. *et al.* (2001) Development of executive functions through late childhood and adolescence in an Australian sample. *Dev. Neuropsychol.* 20, 385–406
- 72 McGivern, R.F. *et al.* (2002) Cognitive efficiency on a match to sample task decreases at the onset of puberty in children. *Brain Cogn.* 50, 73–89

Voice your Opinion in TICS

The pages of *Trends in Cognitive Sciences* provide a unique forum for debate for all cognitive scientists. Our Opinion section features articles that present a personal viewpoint on a research topic, and the Letters page welcomes responses to any of the articles in previous issues. If you would like to respond to the issues raised in this month's *Trends in Cognitive Sciences* or, alternatively, if you think there are topics that should be featured in the Opinion section, please write to:

The Editor, *Trends in Cognitive Sciences*, 84 Theobald's Road, London, UK WC1X 8RR,
or e-mail: tics@current-trends.com