available at www.sciencedirect.com
SCIENCE DIRECT®
www.elsevier.com/locate/brainres
ELSEVIER
BRAIN RESEARCH

Research Report

How we predict what other people are going to do

Chris D. Frith[a,*], Uta Frith[b]

[a]Wellcome Department of Imaging Neuroscience, UCL Institute of Neurology, 12 Queen Square, London WC1N 3BG, UK
[b]UCL Institute of Cognitive Neuroscience, 17 Queen Square London WC1N 3AR, UK

ARTICLE INFO

Article history:
Accepted 30 December 2005
Available online 28 February 2006

Keywords:
Social
Prejudice
Contagion
Mentalizing
Prediction

ABSTRACT

We present a framework for discussing two major aspects of social cognition: the ability to predict what another person is like and what another person is likely to do next. In the first part of this review, we discuss studies that concern knowledge of others as members of a group and as individuals with habitual dispositions. These include studies of group stereotypes and of individual reputation, derived either from experience in reciprocal social interactions such as economic games or from indirect observation and cultural information. In the second part of the review, we focus on processes that underlie our knowledge about actions, intentions, feelings and beliefs. We discuss studies on the ability to predict the course of motor actions and of the intentions behind actions. We also consider studies of contagion and sharing of feelings. Lastly, we discuss studies of spatial and mental perspective taking and the importance of the perception of communicative intent. In the final section of this review, we suggest that the distinction between top–down and bottom–up processes, originally applied to non-social cognitive functions, is highly relevant to social processes. While social stimuli automatically elicit responses via bottom–up processes, responses to the same stimuli can be modulated by explicit instructions via top–down processes. In this way, they provide an escape from the tyranny of strong emotions that are readily aroused in social interactions.

1. Introduction

A principal function of the various processes that are involved in social cognition is to enable us to predict what other people are going to do. In this essay, we will present a framework for discussing the different components of this aspect of social cognition and explore their neural underpinnings. The neural substrates we will mainly focus on are well-accepted components of the social brain, such as the medial prefrontal cortex (MPFC), the superior temporal sulcus (STS), orbitofrontal cortex (OFC), the amygdala and the anterior insula (Adolphs, 1999; Brothers, 1990). All these regions are activated when we try to understand other people.

Because we have not been impressed by the consistency of the pattern of activations obtained in different studies, we will not attempt to delineate in detail the anatomy of social cognition. However, when reviewing neuroimaging studies, which indicate differential activations, we will refer to brain regions in terms of Tailarach coordinates. We believe that the coordinates can prevent confusion that is often introduced by using different labels to refer to similar brain regions.

The simple framework that we will use distinguishes two kinds of knowledge on which our predictions of other people's behaviour are based: knowing who people are and knowing what people do. Each of these categories spans many different

* Corresponding author.
E-mail address: cfrith@fil.ion.ucl.ac.uk (C.D. Frith).

0006-8993/$ – see front matter © 2006 Elsevier B.V. All rights reserved.
doi:10.1016/j.brainres.2005.12.126

domains that rely on a range of neural mechanisms and brain regions.

Cutting across these categories is the distinction between top–down and bottom–up processes, which can be loosely mapped onto explicit and implicit knowledge. This distinction emerged from the study of processes that evolved for making predictions about the physical world. We believe that it is also useful for making predictions about the social world.

1.1. The structure of this review

Our review is divided into three parts. The first part deals with knowledge about people; within the broad category of knowledge of people, we will discuss two subcategories, one to do with group stereotypes, the other with individual dispositions. Here, we focus on one major aspect of this knowledge, namely, reputation. Knowledge about people is relatively enduring.

The second part deals with knowledge about what people do, feel or believe. This section is accordingly divided into a number of subheadings: prediction of actions and intentions, contagion and sharing feelings and, lastly, prediction from belief and knowledge. This last section reviews studies on spatial perspective taking, mental perspective taking and communicative intent. Knowledge of what people do, feel and believe can be computed on the fly and is constantly updated.

In the third part of the review, we will consider the effects of top–down and bottom–up processes on our predictions of what people are going to do. In our conclusions, we comment on the interplay and sometimes conflict between the different types of knowledge and on the success and failure of our ability to predict the behaviour of other people.

2. Knowledge of other people

2.1. Knowledge of other people as members of groups

Individuals may be experienced as members of a group, and this enables prediction of their behaviour in terms of stereotypes when we know nothing about them as individuals. The two major types of stereotypes studied to date are race and gender. Group stereotypes can be remarkably effective predictors of behaviour, even though they are very rough and often incorrect. For instance, to boost sales, retailers offer different lists of presents to choose for men and for women. This is despite the fact that some women like to have toolkits for presents and some men would like to have baking trays. Here, we are simply categorising the person as a member of a group.

Race prejudice has been studied in a number of imaging paradigms, and amygdala activation has been consistently shown as a sign of fear that is elicited unconsciously by viewing a face from another race. When white Americans were shown the faces of unknown black Americans, activity was elicited in the amygdala (Phelps et al., 2000). The magnitude of the activity in the amygdala correlated with implicit measures of race prejudice. In this experiment, the amygdala is responding to black faces in the same way as it responds to any object that has acquired a conditioned fear response (Buchel et al., 1998).

Extensive research with animals has shown that the amygdala is part of a system that learns to associate value with stimuli (Dolan, 2002) whether or not these stimuli are social (LeDoux, 2000). This system operates on both positive and negative values. For example, the amygdala responds to objects that elicit fear because of their association with punishment (negative value), but the amygdala also responds to objects associated with food and sex (positive value). The involvement of this system in social cognition arises because social prejudices are fundamentally about how much we value other groups of people, but there is nothing specifically social about this system.

Amygdala damage does not remove race prejudice (Phelps et al., 2003), and amygdala response magnitude does not correlate with explicit measures of race prejudice. Our consciously held attitudes about race are often at variance with our implicit prejudices, and there is evidence that we try to suppress these rapid automatic responses. The amygdala response to black faces was reduced when the faces were presented for 525 ms rather than 30 ms, and, associated with this reduction, there was increased activity in areas of frontal cortex concerned with control and regulation (Cunningham et al., 2004). Amodio et al. (2004a) had subjects perform a task, which purported to measure their race bias while measuring EEG. ‘Errors’ in performance (i.e. race-biased responses) elicited larger error-related negativity waves (ERNs). In both these studies, the brain system implicated in the control of race bias is one generally concerned with the top–down regulation and control of action. Likewise, Wheeler and Fiske (2005) discuss attention to particular social goals as a means to modify prejudice.

Of course, there is more to prejudice than fear. Fiske et al. (2002) demonstrated that the perception of out-group could evoke distinctly different feelings of envy, pity, admiration and contempt. Trust is another emotion that plays a vital role in interaction with people even when we do not know them individuals. There is quite good agreement about what untrustworthy people look like, even though this has nothing to do with reality. Amygdala damage impairs the ability to rate trustworthiness (Adolphs et al., 1998). In healthy volunteers, presentation of the faces of unknown people rated as untrustworthy elicits activity in the amygdala and the insula. Activity in these areas is seen even when subjects are not required to rate the trustworthiness of the faces explicitly. Activity in posterior STS, in contrast, is only observed when subjects make explicit trustworthiness judgements (Winston et al., 2002).

The neural systems that support gender stereotypes have been studied less frequently. However, a study by Milne and Grafman (2001) showed that patients with ventromedial lesions did not show the typical effect that is obtained in the well-known implicit association task (Greenwald et al., 1998), here involving female and male names and adjectives denoting strength and weakness. These patients therefore seemed to lack access to the implicit knowledge of gender stereotypes, which appears to be dependent on intact ventromedial cortex functioning. However, they still showed explicit knowledge of gender stereotype.

The studies reviewed in this section give evidence of the huge importance of emotions and value judgements that are often implicit when predicting the behaviour of people not as individuals, but as members of a group. The studies also remind us of the important distinction between implicit and explicit knowledge. Prejudice may be counteracted by explicit knowledge in top–down control over automatically elicited knowledge.

2.2. *Knowledge of other people as individuals*

Other people are not only experienced as members of a group, but also as individuals, especially when we know them over a period of time. This knowledge is manifest in attribution of traits and dispositions to other people. Just like group stereotypes, this individual knowledge may have little to do with reality but can nevertheless be useful in the absence of more specific knowledge. Knowledge about an individual's reputation allows us to make risky emotional decisions. For example, if we know someone is trustworthy, we can predict that they will return our lost wallet and we are happy to trade with them, to confide in them and even to adopt their friends and enemies. How do we acquire enduring knowledge of individuals? We propose that we learn it in just the same way as we typically learn to associate value with objects. This learning can be acquired from different sources: directly interacting with people, observing people interacting with others and being told about people.

2.2.1. *Learning about other people through direct experience*

Direct experience is perhaps the most basic way of learning. If we repeatedly experience an electric shock shortly after seeing a red square, then mere presentation of the red square will eventually elicit a response in the amygdala (e.g. Buchel et al., 1998). The red square has acquired a conditioned fear response. This response can be extinguished when we learn that the red square is no longer followed by a shock (e.g. Phelps et al., 2004).

Once we have interacted with people, they gain individual reputations based on how they have treated us. Singer et al. (2004a) had subjects play trust and reciprocity games with previously unknown people. In fact, the 'people' in these games were just faces randomly associated with particular playing modes. Some faces reliably reciprocated trust (co-operators), while others reliably defected. In addition, there were neutral faces that were associated with neither trust nor defection. Subjects rapidly came to like the faces of co-operators and to dislike the faces of the defectors. In the next stage of the experiment, subjects were scanned while observing the faces and making gender judgements. Faces that had acquired value (co-operators and defectors vs. neutral) elicited activity in OFC, amygdala and anterior insula.

It is important to note that these effects did not arise simply because the faces had become associated with monetary gain or loss. Subjects had been told that some of the 'players' were simply obeying the instructions of a computer rather than deciding for themselves how much money to return to the subject. The subsequent responses to the faces were modified by this factor of intentionality. Faces of intentional co-operators elicited more activity in anterior insula, OFC and posterior STS than faces of non-intentional co-operators. Subjects were not simply learning which faces were associated with reward. They were learning whom to trust. If someone is simply obeying the instructions of a computer, then we can learn nothing about how trustworthy they are. An important question for social neuroscience is to discover how the brain modifies its value learning system in order to take account of the intentionality and hence responsibility of agents. Our feelings are strongly engaged when we blame others for betrayal of trust, and we feel satisfaction when they are punished (see below).

In learning about the reputation of other individuals, their familiarity is an important factor. Schmitz et al. (2004) looked at processes associated with the task of reporting trait attributions to a close friend or relative (is she *daring*, *shy*, *intelligent*, etc.) contrasted with the task of judging whether these same adjectives were of positive or negative valence. Anterior medial prefrontal cortex (aMPFC) was activated when subjects thought about the reputation of a friend (or of themselves). Ochsner et al. (2005) went a step further and compared metacognitive processes involved in self and other appraisal. Direct appraisal of the self recruited MPFC and right rostrolateral PFC. Reflected appraisal (how we think we might be seen through the eyes of others) recruited regions associated with emotion and memory (insula, orbitofrontal and temporal cortex).

2.2.2. *Learning about other people through observation*

We can learn through observation as well as experience. If we watch the emotional expression of someone else being conditioned to associate a shock with a red square, we will also acquire a fear response to the red square (Olsson and Phelps, 2004). We can also learn about the reputation of people by watching them interact with others. Extensive work with economic games such as the public good game has demonstrated the existence of altruistic third party punishment. A third party observing an economic transaction will punish an unfair player, even at some cost to themselves (Fehr and Fischbacher, 2004). Preliminary data suggest that the willingness to punish unfair people, even though this comes with a cost, arises because such punishment is associated with activation in the reward system of the dorsal striatum (de Quervain et al., 2004). However, in this experiment, the subjects had direct experience of the unfairness of the person that they were punishing. It seems very likely that the same system would be engaged after third person observation of unfair behaviour.

2.2.3. *Learning about other people through cultural information*

A special feature of human culture is that we can learn from the experiences of others. We do not ourselves have to experience the electric shock that always comes after a red square to acquire a conditioned response to that square. It is not even necessary to observe; it is sufficient to be told by someone that the red square will be followed by a shock for the red square to elicit activity in the amygdala (Phelps et al., 2001). In the same way, we do not need to interact with others to acquire knowledge about them. We can learn about their reputation from other people who have interacted with them. Delgado et al. (2005) had subjects play a trust game with 'trading partners' about whom they had just read vivid vignettes concerning their moral character. As in previous experiments, activity in the caudate nucleus distinguished whether the outcome of trials was positive or negative. However, this effect was much reduced for trials involving partners with a prior reputation. Again, it seems that the brain modifies its value learning system in circumstances where an agent has already acquired some status.

The different ways of learning about the enduring qualities of other people are likely to be as often implicit as explicit. The studies reviewed here demonstrate profound effects on emotional valuation, which arise automatically according to the value we give to individuals. An escape from these automatic processes is provided by top–down control via explicit knowledge. For example, we can forgive a wrong in an economic game despite the anger this has aroused and can re-establish trust after it was lost.

2.2.4. *Knowledge in conflict*

Group stereotypes can be brought into conflict with individual reputation. How would we predict behaviour in this case? The amygdala response elicited by the faces of unknown black Americans is not elicited by the faces of familiar and positively regarded black Americans (Phelps et al., 2000). These people have been individuated. What we have learned about them as individuals overrides crude information based on categories. Similarly, Richeson and Trawalter (2005a) showed that responses to famous individuals from different racial groups differed from responses to ordinary members of the groups.

How do we predict what someone will do when a gender and race stereotypes are brought into conflict with individual predispositions? Hirschfeld et al. (submitted for publication) presented children with pictorial vignettes of the following type: "Here are two people (points to picture containing a male and a female). This is James and this is Susan. Susan doesn't like to cook for people. One of these people has baked biscuits. Which person baked biscuits?" Children aged 6, but not children aged 3, avoided a response in line with group stereotype (women typically bake) and predicted behaviour in line with disposition (this particular woman doesn't like to bake).

This study included also 8-year-old children with autism. These children, whose social behaviour was impaired, were nevertheless able to predict other people's behaviour in terms of stereotypes. This was also true for normally developing 3-year-olds, whose social experience was very limited. This result suggests that race and gender stereotypes can be acquired very early and in the presence of other social deficits.

Social knowledge is learned fast perhaps because there are so many ways to acquire it: directly from experience and indirectly from observation or cultural transmission. It is also likely that innate predispositions play a role. For example, learning fear through observation occurs much faster for objects that have had survival threat in evolutionary history (Mineka and Ohman, 2002). This effect may also operate in the development of race prejudice (Olsson et al., 2005).

3. Knowledge of actions, intentions, feelings and beliefs

In this section, we review studies that reveal neural processes underlying our ability to predict 'what happens next' in a social interaction. Social interactions involve predicting a person's movements, intentions, bodily states and mental states. If we observe where someone is going to throw a ball, we can anticipate the trajectory with more or less accuracy and can catch the ball. The motor system works by prediction. The prediction of where and how people are going to move has obvious relevance for social interactions. We can also infer the intentions behind movements and can judge whether movements are intended or not (e.g. Wolpert et al., 2003). In contrast to the previous section, here, it is not important what sort of a person the actor is. This type of prediction applies to any person.

3.1. *Predicting the course of actions*

We can learn about other peoples' intentions and goals by watching their movements. At the most basic level, from seeing the start of a movement, we can predict how it will finish. However, your own expertise matters. Romani et al. (2003) showed expert and novice basketball players 10-frame film clips of free throw shots. By frame 3, experts were already much better than novices at predicting whether the ball would enter the basket. Sebanz and Shiffrar (2006) showed film clips of basketball players about to make a pass or a fake. While both experts and novices could predict better than chance how the movement would finish, experts outperformed novices.

There are many studies showing that watching human movements elicits activity in posterior STS (e.g. Puce and Perrett, 2003). However, activity in this region is also associated with learning to predict complex movements of a target with no biological features (Maquet et al., 2003 Talairach coordinates 40, −50, 12). Schultz et al. (2004) showed subjects an animation in which one circle followed and sometimes caught another. The catching circle either followed exactly in the track of the target circle or, through prediction, moved directly to the endpoint of the target's movement. In pSTS (−8, −44, 12), watching the prediction condition elicited more activity than watching the simple following condition. This effect was enhanced when the subject's task was to report the strategy being used by the chasing circle. The movement of the circles in this experiment was not biological in the way the movements of a cat or a human arm are biological. It therefore seems likely that the brain system involved is concerned with analysing all kinds of complex predictable movements rather than being specialised for biological movements.

3.2. *Predicting intentions from movements*

Wolpert et al. (2003) have suggested that, when we observe the movements of other people, we make implicit inferences about the intentions and goals associated with these movements. These inferences are made at the start of the movements and tested by predicting how the movement will continue. The experiments described below all involve conditions in which such predictions are violated. These violations elicit increased activity in pSTS consistent with the idea that this region has a special role in reading intentions from movements.

Pelphrey et al. (2003) have demonstrated an important effect of context on the activity elicited in pSTS when observing eye movements. On congruent trials, subjects saw a virtual actor move her eyes towards a target that has just appeared at the side of the screen. On incongruent trials, the actor moved her eyes towards empty space rather than the target. Both trials elicited activity in pSTS, but the activity was significantly greater for the incongruent trials (41, −51, 11 from Pelphrey et al., 2005). The authors suggest that the subjects expected the actor to look at the target. When this did not occur, they had to think again about the intention behind the movement, thus eliciting more processing in pSTS.

Similarly, Saxe et al. (2004b) showed subjects a video in which an actor walked across a room but was unseen for a time because he passed behind a bookcase. On some trials, the actor remained hidden by the bookcase for a longer period, indicating that he had stopped moving for a time. This unexpected delay elicited more activity in pSTS (54, −42, 9).

Grezes et al. (2004b) also studied what happened when subjects observed unexpected behaviour. They showed subjects a video in which an actor picked up a box that varied in weight. On some trials, the actor had been misinformed about the weight of the box. This produced a just detectable change in the kinematics of her movement as a result of postural adjustments. Watching lifting associated with false expectations elicited more activity in pSTS (−48, −46, 14). This effect seems to be a bottom–up effect, driven largely by the kinematics of the movement since it is observed even when subjects incorrectly classified a trial as one involving true expectations. Activity that reflected the subject's top–down classification rather than the kinematics of the movement was observed in a number of areas including medial prefrontal cortex (−2, 26, 52; BA 8).

This study also gives a hint as to how we might be able to recognise whether an action is intended or unintended. When the actors in the experiment picked up boxes with a different weight from what they expected, they automatically made postural adjustments. These movements were not planned by the actor and, in that sense, were unintended. The observers in this experiment were able to recognise that these movements were unintended. As mentioned in Section 2.2.1, the ability to distinguish intended from unintended actions has implications for our ability to assign responsibility and blame to another person.

3.3. *Contagion and sharing feelings*

In recent years, one of the most influential suggestions of a neural mechanism underlying prediction of actions is the mirror neuron system (e.g. Rizzolatti and Craighero, 2004). This system may be responsible for the fact that observing physiological states and emotional expressions in others affects our own bodily state. If we see someone yawn, we are likely to yawn ourselves.

There is now abundant evidence that we have an automatic tendency to share another person's experiences. Similarly, observing someone making a specific movement activates the representation of that same movement in the observer, to the extent that there will be interference if the observer is required to perform a different movement from the one he is observing (e.g. Kilner et al., 2003).

Facial expressions and body postures are also contagious. This helps us to share what other people are currently feeling and hence to experience empathy. Seeing a facial expression of disgust activates the same brain regions as the direct experience of a disgusting smell (Wicker et al., 2003 AI −38, 25, −6: ACC 4, 24, 30). Seeing a facial expression of pain activates the same areas as the direct experience of pain (Botvinick et al., 2005). We can share the pain of others from cues other than facial expression. Seeing a painful stimulus being applied to someone's body activates the same areas (AI and ACC) as having the same pain applied to oneself (Jackson et al., 2005; Morrison et al., 2004), and even a symbolic cue indicating that a loved one is receiving a painful stimulus will activate these areas (Singer et al., 2004b). The stimulus does not have to be painful for us to share the experience of the person we are observing. Seeing someone being touched will elicit activity in somatosensory brain regions in the observer (Keysers et al., 2004). The location of this activity can show precise correspondence between what is seen and what is felt. Seeing someone else being touched on the face will elicit activity in the same area of primary somatosensory cortex as being touched on the face of oneself (Blakemore et al., 2005).

This automatic tendency to imitate the actions and share the feelings of others at the neural level provides a possible basis for the 'chameleon effect' (Chartrand and Bargh, 1999). Interacting partners show a non-conscious mimicry of each other's movements and facial expressions, which improves the quality of the interaction and increases the liking between partners.

However, there is preliminary evidence that this social contagion is modified by the reputation of the person we are observing. Singer et al. (2006) used a trust and reciprocity game to create good and bad reputations for two previously unknown partners. Subjects showed empathy (i.e. neural activity in AI and ACC) for the pain of partners who had played cooperatively. In contrast, far less empathy was shown for partners who had acquired a bad reputation through defecting. Indeed, for male subjects at least, knowledge that a defector was receiving pain activated the ventral striatum, a brain region associated with reward.

Most of the studies discussed in this section have concerned automatic, bottom–up effects of signals about the feelings of others. These signals elicit activity in the brain regions in the observer associated with the same feelings. However, there is also some evidence about top–down signals relevant to such tasks. Ochsner et al. (2004) showed subjects slides and asked them either to say what the people in the slides were feeling (pleasant, neutral or unpleasant) or whether the slides were of indoor or outdoor scenes. The task of attributing feelings to the people in the slides was associated with activity in medial prefrontal cortex (−2, 56, 10; −6, 52, 32), precuneus (−10, −58, 32) and STS (44, −42, 6).

3.4. *Perspective taking: predicting from belief and knowledge*

A third and hugely important factor for our ability to predict behaviour from moment to moment is how well we can appreciate another person's point of view. This is subtly different from mirroring another person's states and actions and relies on the ability to put ourselves into someone else's shoes, regardless of whether we share their feelings.

We can take another person's spatial perspective and predict what they can see, which may be different from what we can see. Likewise, we can take another person's mental perspective and predict what they can know. This is referred to as mentalising (Frith and Frith, 2003). For example, if we know that someone does not know that their chocolate has been moved, we can predict that they are likely to look for it in the wrong place. Mental states other than knowledge or ignorance, for instance, pretence, desire and belief, and even more complex mental states, such as deception and double bluff, are also computed when we mentalise. Like social knowledge of actions and feelings, mentalising relies on processes that act over the short term and need constant updating. Mentalising applies to any agent we are observing, reading about or interacting with, friend or foe, member of our own group or an out-group. Thus, it allows very powerful prediction. It may well be that through mentalising we come to understand ourselves in exactly the same way as we understand other people.

The bottom line of the idea of mentalising is that we predict what other individuals will do in a given situation from their desires, their knowledge and their beliefs, and *not* from the actual state of the world. In the classic false belief task (Wimmer and Perner, 1983), little Max looks for his chocolate in the blue cupboard because he does not know that his mother has moved the chocolate into the red cupboard. It is his *belief* that the chocolate is in the blue cupboard that determines his behaviour, not the *presence* of the chocolate in the red cupboard. It is this type of social prediction that is impaired in autism (Baron-Cohen et al., 1985).

3.4.1. *Spatial perspective taking*

In the simplest case, we do not know about things we cannot see. Things that are visible from one spatial perspective may not be visible from another spatial perspective. Thus, by adopting the spatial perspective of another person, we can predict what they can see and therefore what they know.

Zacks et al. (2003) asked subjects what a scene would look like from another point of view (a perspective transformation), contrasting this task with an object-based rotation. The perspective transformation elicited activity in the left temporo-parietal junction (−59, −50, −2). It is interesting to note that abnormal activity (or electrical stimulation) of this region (on the left or the right) is associated with 'out of the body experiences' in which patients experience their own bodies from a third person perspective (Blanke et al., 2004). Vogeley et al. (2004) obtained rather different results when they explicitly asked subjects to indicate what someone else would see from a different position in a simple scene. The greatest activity when taking a third person perspective (reporting what someone else would see), rather than a first person perspective (reporting what I see), was seen in the precuneus (2, −60, 56). There may well be an important effect on spatial perspective taking when we are asked to think about what another person would see in contrast to thinking about what the scene would look like from another position.

3.4.2. *Mental perspective taking*

Studies on the topic of mental perspective identify themselves with terms such as 'theory of mind' or mentalising and have been concerned more generally with thinking about the contents of other people's minds. Most of these studies have used off-line tasks. Rather than interacting directly with another person, subjects are given verbal or pictorial narratives and are asked to explain the behaviour of the protagonists or infer what they are thinking. Studies using a variety of such task have consistently reported activation in the medial prefrontal cortex and the pSTS (Frith and Frith, 2003; Saxe et al., 2004a).

These tasks engage many cognitive processes including both bottom–up and top down effects. One kind of stimulus that seems automatically to engage mental perspective taking is the animated cartoon. Even abstract shapes such as triangles can be made to move about in such a way that viewers will readily attribute emotions, desires and false beliefs to them (Heider and Simmel, 1944). Imaging studies have shown that viewing such animations (in contrast to animations showing random movements or mechanical movements) elicits robust increases in activity in pSTS along with lesser increases in a number of brain areas including MPFC (Castelli et al., 2000; Martin and Weisberg, 2003). In the study of Castelli et al., subjects were given advance information on half the trials as to whether the movements would be intentional or random, but this information had no effect on the activations elicited.

Pure top–down effects in mental perspective taking can be studied by presenting the same stimuli, but giving subjects different instructions. Gallagher et al. (2002) told subjects that they were playing the competitive game rock–paper–scissors either against a person or against a computer. During the PET scanning window, the sequence of moves made by the competitor were identical in these two conditions. However, activity was elicited in MPFC when playing against a person in contrast to playing against computer, but not in pSTS or any other region. Similar results were obtained by McCabe et al. (2001) when subjects played a cooperative trust game with a person or a computer. Rilling et al. (2004) also observed greater activity in MPFC when subjects believed that they were playing an economic game against a person rather than a computer, but found similar effects in other areas too, including pSTS.

The 'theory of mind' tasks used in the above studies have not typically been designed to isolate our ability to predict people's behaviour on the basis of what they know. While this is often an important component, subjects may also need to make inferences about feelings and intentions. Most studies so far have made little attempt to isolate these aspects of mental perspective taking. Likewise, when subjects interact directly while playing economic games, a number different processes are involved, depending upon the precise nature of the game. In some games, such as the dictator game and the ultimatum game, subjects must decide whether offers are fair or unfair, and there is little demand for predicting the behaviour of the other player. In other games, such as the prisoners' dilemma, subjects do need to predict whether or not the other player will reciprocate trust, but this is as much to do with attributing a habitual disposition rather than transitory intentions or knowledge.

The study by Brunet et al. (2000) is exceptional since subjects were specifically required to attribute intentions rather than any other mental state to characters in comic strips. Activity was observed in mPFC (among other areas) in comparison with a physical logic condition. Future research could benefit from taking this strategy a stage further and making direct comparisons between tasks involving the attribution of intentions, desires, emotions or knowledge.

One recent study to adopt this strategy is that of Walter et al. (2004). Subjects were shown comic strips, like those used by Brunet et al. (2000). In one condition, the intention to be attributed was directed toward the physical world (private intention), e.g. changing a light bulb in order to be able to read a book. In another condition, the intention was directed towards another person (communicative intention), e.g. showing a map to request directions. Consistent differences were observed between these conditions. In comparison with control conditions, attributing communicative intent activated anterior mPFC (para-cingulate cortex; 0, 60, 18), while attributing private intent activated a more posterior and superior region of ACC proper (−6, 18, 45) (see Amodio and Frith, in press for a more detailed discussion of the distinct roles of these two regions of mPFC). Activity in pSTS seems to be similar in both conditions, although no direct comparison is reported.

3.5. *Communicative intent*

The study by Walter et al. (2004) reminds us that social interactions are not normally a one-way process. We do not simply observe other people, make inferences about their mental states and predict what they are going to do. We use our inferences to help us communicate with others so that they, in their turn, can make inferences about our mental states. There are relative few imaging studies investigating such communicative intent.

To initiate a communication, an 'ostensive signal' is required such as calling someone's name or making eye contact. Kampe et al. (2003) presented these signals to subjects and observed that both modalities elicited activity in anterior mPFC (6, 60, 20), but not pSTS.

Grezes et al. (2004a,b) reported a highly relevant pair of experiments, one of which we have referred to already. In both studies, subjects observed the movements of a person picking up a box. However, only in the second experiment did this movement have a communicative intent since the actor was asked to pretend that the box had a different weight from what was actually the case. In other words, the actor had to try to move in such a way as to make the observer think the box had a different weight. On the basis of the movement kinematics, the observers could detect better than chance the trials on which the actor was trying to deceive them. As in the previous experiment (see Section 3.1), activity in pSTS (66, −44, 22) reflected the kinematics of the movements rather than the subjects' judgement, with deceptive movements eliciting greater activity. Observation of unintentional movements with no communicative intent also elicited activity in this area. In contrast, activity in mPFC (−8, 42, 20) was determined by the subjects' judgement rather than kinematics of the movement, with greater activity when the movement was judged to be deceptive. Activity in this location was significantly greater when subjects were trying to detect deception than when they were observing *unintentional* movements with no communicative intent.

Communicative intent can also be a component of economic games. For example, in sequential trust and reciprocity games (Berg et al., 1995), players are concerned not only to find out how trustworthy the other player is, but also to signal that they themselves are trustworthy. King-Casas et al. (2005) attempted to study this communicative loop directly by scanning both players of a trust game at the same time. Activity associated with both signalling and expecting trustworthy behaviour was observed in caudal and rostral regions of anterior cingulate cortex (0, 12, 40, 8, 40, −8).

4. Bottom–up and top–down processes in social cognition

In this essay, we have frequently referred to the distinction between bottom–up and top–down processes. However, in many of the experiments we have discussed, it is not made explicit which of these processes is predominant. Bottom–up processes relate to the stimuli being presented, while top–down processes relate to the task being performed. Thus, a social task like assessing the character traits of faces will engage different brain regions from a physical task like rating the symmetry of the faces, even though the same stimuli are being presented in both tasks.

The distinction is best developed in studies of selective attention (Desimone and Duncan, 1995). The problem is to pick out from among all the sensory stimuli that deluge us those that are most important for our current activity. A bottom–up winner-take-all mechanism allows the most salient stimulus to take control, with salience determined intrinsically (e.g. the loudest) or through conditioning. However, this competition can be biased by top–down signals so that a stimulus can be made temporarily salient to suit the task in hand. Bottom–up effects occur in sensory processing areas specific to the signal being processed, while top–down signals are thought to arise in frontal cortex. For example, in conflict situations, such as the Stroop task, frontal areas are involved in detecting conflict and engage appropriate cognitive control systems. One aspect of this cognitive control is the transient amplification of cortical activity in posterior brain regions processing task-relevant stimuli (Egner and Hirsch, 2005).

However, top–down signals do more than increase the activity elicited by task-relevant stimuli. They also alter the way the signals are processed. Sugase et al. (1999) showed that single neurons in visual temporal cortex of the monkey at first make global distinctions between stimuli, distinguishing between faces and shapes. Only at a later stage of processing the signal do they make fine distinctions about the identity or the emotional expression of the face. The authors speculate that the neurons' ability to make fine social distinctions depends upon feedback from more anterior brain regions such as the prefrontal cortex and the amygdala.

More direct evidence for this speculation comes from a study by Vuilleumier et al. (2004). In the normal case, presentation of emotional faces elicits greater activity in inferior temporal cortex than neutral faces. This effect is no longer found in patients with amygdala damage. The implication is that, in the normal case, feedback signals from the amygdala, which indicate that a face has emotional significance, enhance processing of the signal in inferior temporal cortex.

However, activity in the amygdala is modulated in turn by top–down signals. For example, Ochsner et al. (2004) showed that amygdala responses to emotional stimuli were modified when subjects attempted to exert voluntary control over their emotional responses. The source of this modulation was located in prefrontal cortex.

As we have already seen, studies of race prejudice reveal a very similar system. Increased amygdala activity is a largely automatic response to people of other races. However, this activity too can be modulated by conscious, controlled processes associated with frontal activity (Amodio et al., 2004b; Cunningham et al., 2004; Richeson and Trawalter, 2005b).

A similar story is beginning to emerge for the mechanisms underlying mentalising with mPFC exerting top–down modulation of pSTS. Activity in pSTS seems to be more related to the precise nature of the stimulus. This is most obviously the case in the studies of Grezes et al. (2004a,b) in which activity in pSTS (66, −44, 22) relates to the kinematics of the movement rather than the judgement of the subject. In contrast, activity in mPFC relates more to the task reflecting the judgements of the subjects rather than the kinematics of the movement.

Further evidence favouring this interpretation comes from the study of Saxe and Wexler (2005). In this study, subjects were given sequential information about a person, starting with descriptions of their social background and continuing with statements about their desires. Activity in right temporoparietal junction (rTPJ; 54, −54, 24) did not respond to background information but was tightly linked to the time of presentation of information about mental states. Activity in mPFC (0, 60, 12), in contrast, increased with the presentation of background and showed much less temporal linkage with the presentation of the mental state information.

These results would be consistent with the idea that activity in mPFC is concerned with the 'set' appropriate to social tasks and is the source of top–down signals that modify signal processing in more posterior brain areas, such as pSTS, concerned with the analysis of social signals.

It is possible that different regions of mPFC are concerned with different kinds of social task, but, at this stage, this is very speculative (see Amodio and Frith, in press). In particular, we suggest that the most anterior part of mPFC (approximately in the vicinity of 0, 60, 20) might be the source of top–down signals in tasks involving communicative intent. A signal initiating communication, such as eye contact, activates this region. As a result, the processing of any stimulus occurring thereafter is modified in order to maximise the extraction of socially relevant information.

This control mechanism linked to communicative intent operates on all aspects of social cognition. For example, we have seen how automatic amygdala responses reflecting race prejudice can be modified by top–down control processes originating in prefrontal cortex. Such modification is particularly likely to occur in public situations where we wish to demonstrate to others that we are not prejudiced. We have already mentioned the study by Amodio et al. (submitted for publication) of just such a situation in which the monitoring of prejudiced responses was associated with signals originating in anterior mPFC.

There is even behavioural evidence that empathy for pain, that most contagious and automatic of responses, can be modified by communicative intent. A subject sat in a waiting room, unaware that his or her behaviour was being recorded. The experimenter entered the room carrying a television set which he dropped on his hand in a manner that looked very painful. The subject responded with facial gestures indicating some degree of empathy with the pain. However, this response was dramatically larger if the experimenter was looking at the subject when the accident occurred (Bavelas et al., 1986).

Emotions are the joker in the pack of our social knowledge, but not the trump card. Emotions aroused by social interactions tend to capture our tendencies to reward and punish others. Emotions also dominate our predictions of actions, feelings and beliefs. We get angry when we observe an incident of cheating and feel elated when we watch a player score a goal. But, we are not entirely at the mercy of our automatic reactions to social stimuli. Top–down processes allow us an escape route. Thus, inhibition of impulses generated by negative emotions allows us to stop retaliation and to reinstate normal interpersonal relations.

5. Conclusions

One of the many exciting features of social cognitive neuroscience is that data from a wide range of disciplines must be considered. In this review, we have developed a framework for discussing two aspects of social cognition: the ability to predict what other people are like, a more enduring type of knowledge, and the ability to predict what other people are going to do, a more transient type of knowledge that has to be updated constantly. On the basis of a wide range of studies, we have categorised the various components of these two different types of knowledge and related them to other psychological processes. We have shown how some basic psychological mechanisms, such as conditioning, reward evaluation and top–down control, are essentially the same as those that enable us to deal with the physical world. These processes seem to govern the type of knowledge that we have classified as being about people rather than actions.

As regards the type of knowledge that we have classified as being about actions, feelings and beliefs, at least some of this may be supported by dedicated neural processes, such as inferring intention from action, mirroring feelings and body states and perspective taking. We have speculated at a very basic level on how some of these processes are supported by specialised brain systems.

The effect of top–down processes on all our predictions of social behaviour is an example of a general cognitive process that applies to all the information that we process, either from the physical or from the social world. Thus, top–down processes allow us to become aware of what we are doing and in this way allow us to repair and redirect inappropriate but powerful automatic responses.

It is often stated that human social interactions are far less predictable than interactions between physical agents. This is why the brain has evolved special purpose mechanisms for dealing with the social domain. Thus, we conclude that if anything the human brain is particularly well equipped to predict social behaviour. Of course, predictions are not always correct. More often than not, knowledge of group membership or knowledge of an individual's disposition and reputation may not lead to accurate predictions. More often than not, predicting actions, intentions, communications and feelings of others from moment to moment are mere working models, and not necessarily a true reflection of the other person's bodily and mental states.

Does this matter? We believe that prediction in social interactions is so vital for our social life that occasional errors do not detract from the usefulness. Errors usually can be sorted out through mutual feedback. Indeed, the nature of the errors allows us to improve our predictions in future. Perspective taking makes us aware that our interacting partners also may view our actions erroneously, and this makes clear to us that uncertainty will remain in all our social interpretations. This uncertainty is often exploited to advantage, for instance, in diplomatic negotiations where deception and double bluff are routinely employed and the content of agreements may be deliberately left ambiguous.

In this review, we have focussed entirely on the prediction of *other people's* behaviour. Yet, a number of studies have shown that, when introspecting on one's own feelings, intentions and motives for actions, very similar brain regions are activated. This is especially true for the medial prefrontal cortex. This overlap in neural substrates when thinking about one's own and other's behaviour is clearly not a coincidence. However, there is not space in this review to speculate about the nature of this overlap and the close relationship between explaining our own actions and the actions of others.

It is likely that almost all our speculations will turn out to be wrong, but we believe our framework provides a useful starting point for developing new experiments in social cognitive neuroscience.

Acknowledgments

CDF is supported by a Wellcome Trust Principal Research Fellowship. UF is supported by programme grant 65013 of the Medical Research Council UK.

REFERENCES

Adolphs, R., 1999. Social cognition and the human brain. Trends Cogn. Sci. 3 (12), 469–479.

Adolphs, R., Tranel, D., Damasio, A.R., 1998. The human amygdala in social judgment. Nature 393 (6684), 470–474.

Amodio, D., Frith, C.D., in press. Meeting of minds: the role of the medial frontal cortex in social cognition, Nat. Rev., Neurosci.

Amodio, D., Shah, J., Sigelman, J., Brazy, P., Harmon-Jones, E., 2004a. Implicit regulatory focus associated with asymmetrical frontal cortical activity. J. Exp. Soc. Psychol. 40 (2), 225–232.

Amodio, D.M., Harmon-Jones, E., Devine, P.G., Curtin, J.J., Hartley, S.L., Covert, A.E., 2004b. Neural signals for the detection of unintentional race bias. Psychol. Sci. 15 (2), 88–93.

Amodio, D.M., Kubota, J.T., Harmon-Jones, E., Devine, P.G., submitted for publication. Alternative mechanisms for regulating racial responses according to internal vs. external cues.

Baron-Cohen, S., Leslie, A.M., Frith, U., 1985. Does the autistic child have a "theory of mind"? Cognition 21 (1), 37–46.

Bavelas, J.B., Black, A., Lemery, C.R., Mullett, J., 1986. I show how you feel—Motor mimicry as a communicative act. J. Pers. Soc. Psychol. 50 (2), 322–329.

Berg, J., Dickhaut, J., McCabe, K., 1995. Trust, reciprocity, and social history. Games Econ. Behav. 10 (1), 122–142.

Blakemore, S.J., Bristow, D., Bird, G., Frith, C., Ward, J., 2005. Somatosensory activations during the observation of touch and a case of vision–touch synaesthesia. Brain 128 (Pt. 7), 1571–1583.

Blanke, O., Landis, T., Spinelli, L., Seeck, M., 2004. Out-of-body experience and autoscopy of neurological origin. Brain 127 (Pt. 2), 243–258.

Botvinick, M., Jha, A.P., Bylsma, L.M., Fabian, S.A., Solomon, P.E., Prkachin, K.M., 2005. Viewing facial expressions of pain engages cortical areas involved in the direct experience of pain. NeuroImage 25 (1), 312–319.

Brothers, L., 1990. The social brain: a project for integrating primate behavior and neurophysiology in a new domain. Concepts Neurosci. 1, 27–51.

Brunet, E., Sarfati, Y., Hardy-Bayle, M.C., Decety, J., 2000. A PET investigation of the attribution of intentions with a nonverbal task. NeuroImage 11 (2), 157–166.

Buchel, C., Morris, J., Dolan, R.J., Friston, K.J., 1998. Brain systems mediating aversive conditioning: an event-related fMRI study. Neuron 20 (5), 947–957.

Castelli, F., Happe, F., Frith, U., Frith, C., 2000. Movement and mind: a functional imaging study of perception and interpretation of complex intentional movement patterns. NeuroImage 12 (3), 314–325.

Chartrand, T.L., Bargh, J.A., 1999. The chameleon effect: the perception–behavior link and social interaction. J. Pers. Soc. Psychol. 76 (6), 893–910.

Cunningham, W.A., Johnson, M.K., Raye, C.L., Chris Gatenby, J., Gore, J.C., Banaji, M.R., 2004. Separable neural components in the processing of black and white faces. Psychol. Sci. 15 (12), 806–813.

de Quervain, D.J., Fischbacher, U., Treyer, V., Schellhammer, M., Schnyder, U., Buck, A., Fehr, E., 2004. The neural basis of altruistic punishment. Science 305 (5688), 1254–1258.

Delgado, M.R., Frank, R.H., Phelps, E.A., 2005. Perceptions of moral character modulate the neural systems of reward during the trust game. Nat. Neurosci. 8 (11), 1611–1618.

Desimone, R., Duncan, J., 1995. Neural mechanisms of selective visual attention. Annu. Rev. Neurosci. 18, 193–222.

Dolan, R.J., 2002. Emotion, cognition, and behavior. Science 298 (5596), 1191–1194.

Egner, T., Hirsch, J., 2005. The neural correlates and functional

integration of cognitive control in a Stroop task. NeuroImage 24 (2), 539–547.
Fehr, E., Fischbacher, U., 2004. Social norms and human cooperation. Trends Cogn. Sci. 8 (4), 185–190.
Fiske, S.T., Cuddy, A.J., Glick, P., Xu, J., 2002. A model of (often mixed) stereotype content: competence and warmth respectively follow from perceived status and competition. J. Pers. Soc. Psychol. 82 (6), 878–902.
Frith, U., Frith, C.D., 2003. Development and neurophysiology of mentalizing. Philos. Trans. R. Soc. London, Ser. B Biol. Sci. 358 (1431), 459–473.
Gallagher, H.L., Jack, A.I., Roepstorff, A., Frith, C.D., 2002. Imaging the intentional stance in a competitive game. NeuroImage 16 (3 Pt. 1), 814–821.
Greenwald, A.G., McGhee, D.E., Schwartz, J.L., 1998. Measuring individual differences in implicit cognition: the implicit association test. J. Pers. Soc. Psychol. 74 (6), 1464–1480.
Grezes, J., Frith, C., Passingham, R.E., 2004a. Brain mechanisms for inferring deceit in the actions of others. J. Neurosci. 24 (24), 5500–5505.
Grezes, J., Frith, C.D., Passingham, R.E., 2004b. Inferring false beliefs from the actions of oneself and others: an fMRI study. NeuroImage 21 (2), 744–750.
Heider, F., Simmel, M., 1944. An experimental study of apparent behavior. Am. J. Psychol. 57, 243–249.
Hirschfeld, L., Bartmess, E., White, S., Frith, U., submitted for publication. Does the autistic child have a “theory of society”?
Jackson, P.L., Meltzoff, A.N., Decety, J., 2005. How do we perceive the pain of others? A window into the neural processes involved in empathy. NeuroImage 24 (3), 771–779.
Kampe, K.K., Frith, C.D., Frith, U., 2003. “Hey John”: signals conveying communicative intention toward the self activate brain regions associated with “mentalizing,” regardless of modality. J. Neurosci. 23 (12), 5258–5263.
Keysers, C., Wicker, B., Gazzola, V., Anton, J.L., Fogassi, L., Gallese, V., 2004. A touching sight: SII/PV activation during the observation and experience of touch. Neuron 42 (2), 335–346.
Kilner, J.M., Paulignan, Y., Blakemore, S.J., 2003. An interference effect of observed biological movement on action. Curr. Biol. 13 (6), 522–525.
King-Casas, B., Tomlin, D., Anen, C., Camerer, C.F., Quartz, S.R., Montague, P.R., 2005. Getting to know you: reputation and trust in a two-person economic exchange. Science 308 (5718), 78–83.
LeDoux, J.E., 2000. Emotion circuits in the brain. Annu. Rev. Neurosci. 23, 155–184.
Maquet, P., Schwartz, S., Passingham, R., Frith, C., 2003. Sleep-related consolidation of a visuomotor skill: brain mechanisms as assessed by functional magnetic resonance imaging. J. Neurosci. 23 (4), 1432–1440.
Martin, A., Weisberg, J., 2003. Neural foundations for understanding social and mechanical concepts. Cogn. Neuropsychol. 20, 575–587.
McCabe, K., Houser, D., Ryan, L., Smith, V., Trouard, T., 2001. A functional imaging study of cooperation in two-person reciprocal exchange. Proc. Natl. Acad. Sci. U. S. A. 98 (20), 11832–11835.
Milne, E., Grafman, J., 2001. Ventromedial prefrontal cortex lesions in humans eliminate implicit gender stereotyping. J. Neurosci. 21 (12), RC150.
Mineka, S., Ohman, A., 2002. Phobias and preparedness: the selective, automatic, and encapsulated nature of fear. Biol. Psychiatry 52 (10), 927–937.
Morrison, I., Lloyd, D., di Pellegrino, G., Roberts, N., 2004. Vicarious responses to pain in anterior cingulate cortex: is empathy a multisensory issue? Cogn. Affect. Behav. Neurosci. 4 (2), 270–278.
Ochsner, K.N., Knierim, K., Ludlow, D.H., Hanelin, J., Ramachandran, T., Glover, G., Mackey, S.C., 2004. Reflecting upon feelings: an fMRI study of neural systems supporting the attribution of emotion to self and other. J. Cogn. Neurosci. 16 (10), 1746–1772.
Ochsner, K.N., Beer, J.S., Robertson, E.R., Cooper, J.C., Gabrieli, J.D., Kihsltrom, J.F., D'Esposito, M., 2005. The neural correlates of direct and reflected self-knowledge. NeuroImage 28 (4), 797–814.
Olsson, A., Phelps, E.A., 2004. Learned fear of “unseen” faces after Pavlovian, observational, and instructed fear. Psychol. Sci. 15 (12), 822–828.
Olsson, A., Ebert, J.P., Banaji, M.R., Phelps, E.A., 2005. The role of social groups in the persistence of learned fear. Science 309 (5735), 785–787.
Pelphrey, K.A., Singerman, J.D., Allison, T., McCarthy, G., 2003. Brain activation evoked by perception of gaze shifts: the influence of context. Neuropsychologia 41 (2), 156–170.
Pelphrey, K.A., Morris, J.P., McCarthy, G., 2005. Neural basis of eye gaze processing deficits in autism. Brain 128 (Pt. 5), 1038–1048.
Phelps, E.A., O'Connor, K.J., Cunningham, W.A., Funayama, E.S., Gatenby, J.C., Gore, J.C., Banaji, M.R., 2000. Performance on indirect measures of race evaluation predicts amygdala activation. J. Cogn. Neurosci. 12 (5), 729–738.
Phelps, E.A., O'Connor, K.J., Gatenby, J.C., Gore, J.C., Grillon, C., Davis, M., 2001. Activation of the left amygdala to a cognitive representation of fear. Nat. Neurosci. 4 (4), 437–441.
Phelps, E.A., Cannistraci, C.J., Cunningham, W.A., 2003. Intact performance on an indirect measure of race bias following amygdala damage. Neuropsychologia 41 (2), 203–208.
Phelps, E.A., Delgado, M.R., Nearing, K.I., LeDoux, J.E., 2004. Extinction learning in humans: role of the amygdala and vmPFC. Neuron 43 (6), 897–905.
Puce, A., Perrett, D., 2003. Electrophysiology and brain imaging of biological motion. Philos. Trans. R. Soc. London, Ser. B Biol. Sci. 358 (1431), 435–445.
Richeson, J.A., Trawalter, S., 2005a. On the categorization of admired and disliked exemplars of admired and disliked racial groups. J. Pers. Soc. Psychol. 89 (4), 517–530.
Richeson, J.A., Trawalter, S., 2005b. Why do interracial interactions impair executive function? A resource depletion account. J. Pers. Soc. Psychol. 88 (6), 934–947.
Rilling, J.K., Sanfey, A.G., Aronson, J.A., Nystrom, L.E., Cohen, J.D., 2004. The neural correlates of theory of mind within interpersonal interactions. NeuroImage 22 (4), 1694–1703.
Rizzolatti, G., Craighero, L., 2004. The mirror-neuron system. Annu. Rev. Neurosci. 27, 169–192.
Romani, M., Cesari, P., Aglioti, S., 2003. Riconoscere ed eseguire un movimento: sapere e saper fare in giocatori professionisti di pallacanestro, studi psicofisici e di stimolazione magnetica transcranica (Movement recognition and movement execution in basketball players: knowing and knowing by doing). Movimento 19 (2), 58–61.
Saxe, R., Wexler, A., 2005. Making sense of another mind: the role of the right temporo-parietal junction. Neuropsychologia 43 (10), 1391–1399.
Saxe, R., Carey, S., Kanwisher, N., 2004a. Understanding other minds: linking developmental psychology and functional neuroimaging. Annu. Rev. Psychol. 55, 87–124.
Saxe, R., Xiao, D.K., Kovacs, G., Perrett, D.I., Kanwisher, N., 2004b. A region of right posterior superior temporal sulcus responds to observed intentional actions. Neuropsychologia 42 (11), 1435–1446.
Schmitz, T.W., Kawahara-Baccus, T.N., Johnson, S.C., 2004. Metacognitive evaluation, self-relevance, and the right prefrontal cortex. NeuroImage 22 (2), 941–947.
Schultz, J., Imamizu, H., Kawato, M., Frith, C.D., 2004. Activation of the human superior temporal gyrus during observation of goal attribution by intentional objects. J. Cogn. Neurosci. 16 (10), 1695–1705.
Sebanz, N., Shiffrar, M., 2006. Bluffing bodies: inferring intentions from actions. EPS Conference Proceedings.

Singer, T., Kiebel, S.J., Winston, J.S., Dolan, R.J., Frith, C.D., 2004a. Brain responses to the acquired moral status of faces. Neuron 41 (4), 653–662.

Singer, T., Seymour, B., O'Doherty, J., Kaube, H., Dolan, R.J., Frith, C.D., 2004b. Empathy for pain involves the affective but not sensory components of pain. Science 303 (5661), 1157–1162.

Singer, T., Seymour, B., O'Doherty, J.P., Stephan, K.E., Dolan, R.J., Frith, C.D., 2006. Empathic neural responses are modulated by the perceived fairness of others. Nature 439 (7075), 466–469.

Sugase, Y., Yamane, S., Ueno, S., Kawano, K., 1999. Global and fine information coded by single neurons in the temporal visual cortex. Nature 400 (6747), 869–873.

Vogeley, K., May, M., Ritzl, A., Falkai, P., Zilles, K., Fink, G.R., 2004. Neural correlates of first-person perspective as one constituent of human self-consciousness. J. Cogn. Neurosci. 16 (5), 817–827.

Vuilleumier, P., Richardson, M.P., Armony, J.L., Driver, J., Dolan, R.J., 2004. Distant influences of amygdala lesion on visual cortical activation during emotional face processing. Nat. Neurosci. 7 (11), 1271–1278.

Walter, H., Adenzato, M., Ciaramidaro, A., Enrici, I., Pia, L., Bara, B.G., 2004. Understanding intentions in social interaction: the role of the anterior paracingulate cortex. J. Cogn. Neurosci. 16 (10), 1854–1863.

Wheeler, M.E., Fiske, S.T., 2005. Controlling racial prejudice: social–cognitive goals affect amygdala and stereotype activation. Psychol. Sci. 16 (1), 56–63.

Wicker, B., Keysers, C., Plailly, J., Royet, J.P., Gallese, V., Rizzolatti, G., 2003. Both of us disgusted in my insula: the common neural basis of seeing and feeling disgust. Neuron 40 (3), 655–664.

Wimmer, H., Perner, J., 1983. Beliefs about beliefs: representation and constraining function of wrong beliefs in young children's understanding of deception. Cognition 13 (1), 103–128.

Winston, J.S., Strange, B.A., O'Doherty, J., Dolan, R.J., 2002. Automatic and intentional brain responses during evaluation of trustworthiness of faces. Nat. Neurosci. 5 (3), 277–283.

Wolpert, D.M., Doya, K., Kawato, M., 2003. A unifying computational framework for motor control and social interaction. Philos. Trans. R. Soc. London, Ser. B Biol. Sci. 358 (1431), 593–602.

Zacks, J.M., Vettel, J.M., Michelon, P., 2003. Imagined viewer and object rotations dissociated with event-related FMRI. J. Cogn. Neurosci. 15 (7), 1002–1018.