Current Biology 17, H724-H732, August 21, 2007 ©2007 Elsevier Ltd All rights reserved DOI 10.1016/j.cub.2007.05.068

Social Cognition in Humans



Chris D. Frith^{1,3} and Uta Frith^{2,3}

We review a diversity of studies of human social interaction and highlight the importance of social signals. We also discuss recent findings from social cognitive neuroscience that explore the brain basis of the capacity for processing social signals. These signals enable us to learn about the world from others, to learn about other people, and to create a shared social world. Social signals can be processed automatically by the receiver and may be unconsciously emitted by the sender. These signals are non-verbal and are responsible for social learning in the first year of life. Social signals can also be processed consciously and this allows automatic processing to be modulated and overruled. Evidence for this higher-level social processing is abundant from about 18 months of age in humans, while evidence is sparse for non-human animals. We suggest that deliberate social signalling requires reflective awareness of ourselves and awareness of the effect of the signals on others. Similarly, the appropriate reception of such signals depends on the ability to take another person's point of view. This ability is critical to reputation management, as this depends on monitoring how our own actions are perceived by others. We speculate that the development of these high level social signalling systems goes hand in hand with the development of consciousness.

Introduction

Social cognition [1] is the sum of those processes that allow individuals of the same species (conspecifics) to interact with one another. Such interaction is a matter of survival, for individuals as well as for the species as a whole. Essentially it depends upon the exchange of signals. While speech is the most obvious signal that typifies social communication in humans, there are many other more basic signals, which humans share with other social animals. For example, facial expression and body posture tell us what someone may be feeling [2]. By monitoring eye gaze we can learn where someone is focussing their attention, and likewise, by watching their body movements we can infer what they are intending to do [3]. Many animals make use of such signals emanating from both conspecifics and members of other species [4,5]. We assume that human social cognition includes all the processes that are used by other social animals, many of which are discussed elsewhere in this special issue, but also includes special processes that are unique to humans. Presumably, it is these processes that have allowed the development of language, institutionalised teaching and what we generally consider under the label of culture. A novel question that we will consider in the last section of this review is whether these processes also determine the nature of human conscious experience.

In this review we make a distinction between signals that are processed automatically and those that are processed deliberately. We assume that most social signals are processed automatically and without awareness. They provide information about the person from whom the signal emanates (the sender). Neither sender nor receiver need be aware that they are exchanging signals. Whether or not this information is valid, is another matter. We treat people as dangerous or trustworthy on the basis of their appearance, without knowing anything else about them. We automatically read peoples' emotions from their faces regardless of whether these are acted or true. Automatic signals also tell us about the things or the people the sender is interacting with. An expression of disgust tells us that we should avoid whatever the sender is eating. Another person's eye gaze direction tells us where we may find something interesting in the environment. Signals can also tell us about the interaction in which we are engaged. When we interact with someone we often mirror each other's movements and mannerisms. We are unaware of this mirroring, but when it occurs it creates the feeling that we have good rapport with each other - the chameleon effect [6]. Interestingly, the rapport associated with the chameleon effect may be destroyed if we become aware that we are being imitated [7]. Instead we may feel we are being mocked.

So what is the benefit of higher-level processing of social signals? Social interactions enable a dramatic increase in the possibilities for group actions when signalling is conscious. The critical feature of deliberate and conscious signalling is that we recognise that the signals are signals and therefore imbued with meaning. We suggest that, when both sender and receiver are aware that they are exchanging signals, then uniquely human communication can emerge. In this essay we shall present some of the evidence for these two different levels of signalling and review studies on the brain basis underlying the capacity to exchange social signals.

Learning about the World from Other People

The story of little Albert, who was conditioned by Watson and Rayner [8] to be afraid of a white rat, is much quoted to show the powerful effects, the generalisation and the persistence of classical conditioning. But one of the critical advantages of being a social, rather than a solitary, animal is that we can learn about the world thorough the experience of other people without needing to have first hand experience. Social learning enables us to avoid sickness from eating a

¹Welcome Trust Centre for Neuroimaging at University College London, UK. ²Institute of Cognitive Neuroscience, University College London, 12 Queen Square, London WC1N 3BG, UK. ³Center for Functionally Integrative Neuroscience, Aarhus University, Denmark.

poisonous mushroom. We do not have to try out everything ourselves and receive punishment for incorrect responses; we can avoid punishment by observing another's fate, hearing about another's past experience and even from reading about the accumulated experiences of many generations of people.

One of the most basic means we use for social learning is to follow eye gaze. In all likelihood, the direction of someone's gaze will point to something of interest and importance for us. This effect is indeed automatic and obligatory. For example, in the experiment of Bayliss and Tipper [9], discussed below, the participants still attended in the direction indicated by the gaze of another person, even when this person consistently looked away from the target the participant was trying to detect.

As well as following peoples' eye movements, we also covertly mirror many of the facial expressions that we see and, as a result, experience the same emotions in ourselves [10]. This is the case for pain [11], fear [12] and disgust [13]. When we see such expressions in others we can learn something about the world and, by mirroring these expressions, we can adopt the appropriate response. If we see a fearful face looking at a particular location in space, it is likely that, at that location, there is something that we too should be afraid of. Thus, we can get ready to run away even before we have verified the target.

The use of another person's emotional reactions to guide our response to novel situations is called social referencing. Human infants tend to reference the mother's expression, when faced with a novel object. Thus, generally speaking, if the mother shows fear, infants will tend to avoid touching the toy, but if she shows pleasure, they will explore it [14]. This learning is not confined to children. Adults too can learn to associate a fear response to a stimulus by watching someone else receiving a mild shock every time they see that stimulus [15].

This kind of social signal does not require higher level conscious processing. In seminal studies on observational learning with rhesus monkeys, Mineka and colleagues [16,17] showed that infant monkeys who had never met a snake, having been born into a safe laboratory colony, rapidly acquired fear of snakes when observing a model in a video being afraid of a snake. In contrast, they did not acquire fear of a flower even after 12 trials of observation. By its evolutionary history the brain is pre-prepared to learn archaically threatening stimuli [16,17]. Thus, little Albert probably would have learned on one trial to be afraid of a snake simply by watching another person being afraid.

Do we learn more easily from another person whom we trust and to whom we ascribe knowledge? It is likely that we do, but experimental and neurophysiological evidence on this point is still sparse. The experiments on social referencing nearly always use the mother as the sender of the signal. Normally, the mother will be the most trustworthy and knowledgeable person that a very young and inexperienced individual interacts with. However, in the course of development, the models used for social learning change. While 14-month-old infants do not learn from a complete stranger in a social referencing situation [18], they will learn from a familiarized stranger [19]. By the age of 24 months, strangers are used as a source for social learning [20]. Peers as social models become particularly important in later childhood and adolescence, and we all use public figures and icons as role models for social learning and emulate their style.

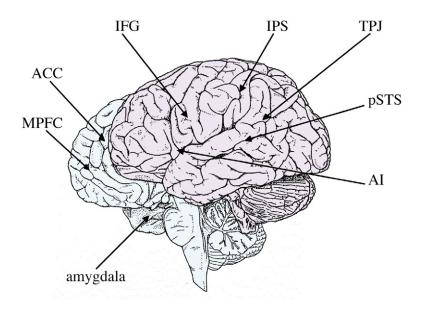
How does our brain assess the quality and validity of a social signal? There is an inherent ambiguity about a person's attitude to an object. When we observe a person gazing at an object, this may correctly indicate that the object is highly desirable and should be approached, but the response could also indicate something about that person's idiosyncratic likes and dislikes, rather than something about the object. For example, some people consider rhubarb to be vile, while others consider it a delicacy. Gergely and colleagues [21] have shown that 14-month-old infants use social referencing to learn about the value of objects, but do not seem to recognise that different people may have different attitudes to the same object. It is only by about 18 months that infants use social referencing to learn about people's dispositions. At this point they can recognise that a nice object may be disliked by some people. Once this stage is reached social signals can be treated by both sender and receiver as deliberately communicative. We will discuss this in more detail later.

Learning about Other People

Many cues are available for learning about peoples' dispositions, both stable personality traits as well as ever changing intentions and emotions. A host of social psychological experiments have shown that we are quick judges of other peoples' competence and warmth [22]. For instance, after looking at a person's face for 100 milliseconds, we decide whether they are trustworthy or not and this judgement does not change when given longer time to study the face [23]. The sight of a person with an untrustworthy face elicits activity in the amygdala (see Figure 1) even when we have not been explicitly asked to judge whether the person is trustworthy or not [24]. A major role of the amygdala is to attach value (either positive or negative) to stimuli as in fear conditioning [25,26]. Such stimuli do not need to be social, but through such conditioning we can learn to approach people with trustworthy faces and avoid people with untrustworthy faces.

Prejudice

Although there is widespread agreement among groups of people about what an untrustworthy face looks like, there is no evidence that this characterisation has any validity. This is an example of unjustified prejudice, presumably derived from cultural norms and innate preferences for one's own family and for privileged groups of people rather than from direct experience. Thus, in-groups and out-groups can be identified in every society. Some groups are acknowledged as more privileged than others and attract the positive stereotypes, whereas others attract negative stereotypes. For instance, children showed consistent



preferences for lucky groups compared to unlucky ones defined as victims of uncontrollable natural disasters [27]. The evolutionary benefit of making alliances with fortunate, rather than unfortunate, groups of people explains the apparent ease with which we harbour negative feelings towards the disadvantaged. Prejudice, while increasing inequality and offending our rational mind as well as our sense of fairness, is based on an automatic mechanism, which may have evolved for coping with situations where we have no prior knowledge of the person we are confronting [28].

Our irrational feelings reveal their strength in autonomic and brain imaging measures. When white Americans were shown the faces of unknown black Americans, activity was elicited in the amygdala [29]. The magnitude of the activity in the amygdala correlated with an implicit measure of race prejudice (the Implicit Association Test), an important tool for investigating the presence of unconscious prejudices [30,31]. In this example, black faces have become conditioned stimuli for fear responses largely through cultural transmission rather than direct experience. The amygdala response is not elicited by the faces of familiar and positively regarded black Americans [29]. In this case, the prejudice applied to the group has been overcome through learning about specific individuals.

Experience

We can learn to trust or distrust specific individuals through direct interaction. Singer and colleagues [32] invited participants to play trust and reciprocity games with people they had not met before. In fact, only photographs of their faces were shown. The game was designed so that some people reliably reciprocated trust (co-operators), while others usually defected. Participants rapidly came to like the faces of co-operators and to dislike the faces of the defectors. Indeed, they Figure 1. Location of key brain areas involved in social cognition on the lateral (pink) and medial (blue) surface of the brain.

The amygdala, a complex structure buried in the anterior temporal lobe is involved in attaching value, for example, trustworthiness, to objects, for example, faces [24]. The medial prefrontal cortex (MPFC) is consistently activated when thinking about the mental states of self and others [98,99]. Activity in the anterior cingulate cortex (ACC) and the anterior insula (AI, buried between frontal and temporal lobes) is associated with experience of emotions such as pain and disgust in self and others [13,45]. Activity in the inferior frontal gyrus (IFG) and interparietal sulcus (IPS) occurs in response to action execution and action observation [35,36]. Activity in the temporo-parietal junction (TPJ) seems to be associated with perspective taking [101,102], both spatial and mental, and hence with understanding false beliefs [86,103]. Activity in the posterior superior temporal sulcus (pSTS) is elicited by action observation [38] and when reading intentions from actions [40,41].

actually rated the faces of the co-operators as more attractive, even though the same face was assigned to be cooperators for some participants and defectors for others. Faces that had acquired value (co-operators and defectors *versus* neutral) elicited more activity in the amygdala. Thus, participants rated the same faces as either attractive or unattractive depending entirely on their behaviour in the game.

It is important to rule out that these effects did not arise simply because of negative feelings about monetary losses associated with some faces, and positive feelings about gains associated with other faces. Participants 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 particpants. The subsequent responses to the faces confirmed that the attribution of intention was crucial. Liking and disliking only emerged for the faces of those who played as free agents and could therefore be held responsible for their actions. Participants in the game were not simply learning which faces were associated with reward. They were learning who to trust.

Cues about trustworthiness can be more indirect. Bayliss and Tipper [9] used eye gaze direction as a cue in a spatial attention task. Some faces reliably looked toward the target location, while others more often looked in the wrong direction. Subsequently, participants rated the people who had looked in the wrong direction as less trustworthy.

Intentions

Mental states such as desires and intentions are invisible, but we can learn about them by watching other people's movements and the direction of their gaze. Gaze is a telltale sign of what someone is interested in. This use of gaze appears early in life: Lee and colleagues [33] showed children pictures of a boy (Larry) surrounded by four different objects. Two-year old children could use Larry's eye gaze direction to decide which toy he wanted.

We are finely attuned to inferring goals from movements, not only from movement of the eyes and face, but of the whole body, and particularly arms and hands. Even 6-month-old babies respond with interested looks when they see an adult reach to a novel goal but habituate when an adult reaches to the same goal repeatedly [34]. Hamilton and Grafton [35] used a similar approach where they showed adults a series of movies depicting an actor repeatedly reaching to the same goal, and using the same movement unexpectedly reaching to a different goal. Repeated presentation of the same goal caused a suppression of brain activation in two regions of the left anterior intraparietal sulcus (Figure 1). This finding suggests that the anterior intraparietal sulcus is critical for representing the goal of an observed action.

Our ability to perceive the goals and intentions of others from watching their movements is often ascribed to mirror neurons. These neurons become active when animals observe an action as well as when they execute the same action [36]. In humans, a more extensive mirror system has been identified [37]. In addition to regions in inferior frontal cortex and inferior parietal cortex that are activated by action observation and action execution, there are regions in anterior cingulate and anterior insula cortex that are activated by the experience and by the observation of emotions such as disgust [13], and pain [11]. By linking action observation to action execution, the brain's mirror system provides a mechanism for inferring the intention or goal of the person whose action is being observed.

Watching eye movements and other kinds of biological motion reliably elicits activity in the posterior end of the superior temporal sulcus (pSTS, see Figure 1), especially on the right [38]. The STS is therefore often treated as part of the mirror system, although execution of action is not associated with activity in this region. However, the magnitude of this activation depends upon context in which the movement occurs. Here we wish to highlight the importance of prior predictions that we make about another person's actions. Pelphrey and colleagues [39] created a visual display in which an avatar looked either towards or away from a visual stimulus that suddenly appeared to the left or the right. Activity in pSTS of observers was greater when the avatar looked away from the stimulus. A similar result was obtained when observers watched reaching and grasping movements [40]. More activity was seen in pSTS when the avatar did not reach for the salient stimulus. Clearly, observers expect the avatar to attend to, or reach for, the salient stimulus. When this prediction is violated the observer has to think again about what the intentions and goals of the avatar might be. This elicits greater activity in STS.

More direct evidence that activity can be elicited in pSTS by a failure to predict intentions comes from a study by Saxe and colleagues [41]. Observers watched an actor disappear behind a bookcase and then emerge from the other side. Greater activity was elicited in pSTS when there was an unexpected delay in the actor's reemergence. Evidence such as this for

the importance of prediction and prediction errors in action observation suggests possible mechanisms, analogous to predictive coding in vision [42], by which the brain's mirror system might be used to perceive goals and intentions [43].

Creating a Shared World

A major function of social cognition in humans is to allow us to create a shared world in which we can interact. The mirror system enables a simple form of sharing [44]. Areas in the brain associated with pain or touch are activated when we observe others in pain [45] or being touched [46]. Through these forms of empathy, the feelings of two people who are interacting become aligned. We have already mentioned the chameleon effect [6]: this refers to the observation that, when two people are interacting, they start imitating each other's actions leading to synchronised leg-crossing, nodding, and so on. When this alignment occurs the protagonists feel that they have greater rapport. Communication can be further enhanced by adopting a shared vocabulary, which enables us to share goals so that we can engage in joint activities common ground [47].

For successful interactions it is not enough to share feelings. We also need to share representations of the world. Ideally, we should share each other's perception of the world. The starting point for sharing our perception about the world is to align the focus of our attention. This process is called joint attention and is typically achieved by pointing at an object. This leads to the triadic relationship in which two people focus their attention on the same object. Background and foreground in their two perceptual worlds are now aligned. The ability to share attention in this way can be observed in infants as young as 12 months (Figure 2) [48,49].

Recent studies have shown that people share the representation of a task as a whole, even when each performs only part of it. In one paradigm [50], a pair of participants performed a 'go-nogo' task, sitting alongside each other. Even though no interpersonal coordination was required, each actor integrated the co-actor's alternative action into their own action planning. This resulted in an action selection conflict when a stimulus required different action from each actor, such as a 'nogo' response from one actor and a 'go' response from the other (see also [51]). In spite of this interference, the task was still performed faster when shared between two people than when performed by a single person as a two-choice reaction time task.

In a shared world, many tasks demand complementary rather than imitative actions. For example, when two people are carrying a heavy object, one may walk facing backwards, while the other walks forwards. In these circumstances the shared representation of the task should be in terms of goals rather than specific motor movements [52]. When interpersonal coordination is required to perform a simple reaction time task, complex strategies for sharing control of the movement spontaneously arise. In one study [53], when having to make a single rapid movement, one actor controlled the acceleration phase of the movement, while the other controlled the



Figure 2. An infant points to 'Grover' and the experimenter reacts with joint attention. Twelve-month-olds point to share attention and interest. (Reproduced with permission from [49].)

deceleration phase. This complementary form of control enables the two-person action to be more efficient than the same action performed by a single person.

Processes for creating a shared world have been studied most extensively in the context of spoken dialogue (for example [54]). For example, speakers give largely unconscious eye gaze signals to control turn taking in discourse [55]. Likewise, they use interjections like 'ah' and 'um' to signal respectively forthcoming smaller or larger delays in speaking so as to avoid premature interruption [56]. There is substantial evidence that speakers co-ordinate their contributions in dialogue through having common ground. This common ground is partly created in the long-term by learning and culture, but needs also to be rapidly established at the beginning of any cooperative endeavour [57].

Not only do we need a common goal in order to achieve the joint action, we also need to have a common view of the nature of the task we are carrying out [58]. This applies both at a concrete level - it is better to be able to see what the other person is doing [59], but also at a conceptual level. We need, for example, to have an agreed vocabulary for describing the objects we are manipulating [60]. Two speakers also become more similar in their use of syntax. In one study [61], pairs of speakers had to take turns in describing pictures to each other. One speaker was a confederate of the experimenter and produced descriptions that systematically varied in syntactic structure. This primed a similar syntactic structure in the other speaker's subsequent description. As with the reading of intentions, the alignments that develop during discourse may depend upon prediction and emulation [62].

All these signals, which so strongly affect our verbal interactions, are largely unconscious and often come as a surprise when revealed by clever experiments. In the following section we will turn to conscious signals and the deliberate rather than automatic creation of a shared world.

Extracting Meaning from Social Signals

In the first part of this review we gave examples of how we learn about the world by observing other people when the signals in question are mostly unintentional. In human society, however, there is a much larger class of signals that are sent deliberately, rather than unintentionally, and this is complemented by a class of signals that we withhold or disguise. This means that we can control to some extent when others can acquire knowledge from us. The ability to attribute and manipulate mental states, such as knowledge and ignorance, in others is part and parcel of the capacity to mentalize.

Mentalizing is a prerequisite for the ability to participate in a deliberately and consciously shared social world. The development of mentalizing is a long drawn-out process. We already mentioned the work by Gergely and colleagues [21] suggesting that only above the age of 18 months do infants recognise that different people have different attitudes to objects, so that their response to the object may be telling us something about the person rather than the object. At this stage the infant is representing the mental state of the person: for example, that they fear an object that most people like. Infants can also recognise that an adult may have a desire to communicate. Once this stage is reached, both sender and receiver can treat social signals as deliberately communicative. Infants can now interpret signals as 'ostensive' [63], indicating the sender's overt communicative intention to reveal new and relevant information about an object that is identified by non-verbal cues (such as gaze direction or pointing) [21].

It is possible that there are even earlier forms or precursors of mentalizing, as seen in the ability to tease and understand teasing at the end of the first year of life [64]. Similarly, we find indications in a number of other species that they exhibit behaviour that we can readily interpret as teasing, pretense and joint attention (for example [65]). The ability to engage in joint attention behaviour and its development in pre-linguistic infants between 9 and 15 months has been studied extensively [66] and has given rise to a theory of shared intentionality. Tomasello and colleagues [67.68] suggest that there is a drive towards social cooperation, which unites the earliest social attempts at communication with advanced attempts at culturally defined social learning. Infants respond to the gaze of adults towards an object of interest with evident signs of pleasure and engagement from about 10 months,

and are capable of drawing an adult's attention towards objects by pointing, facial expressions or vocalisations (see Figure 2). From about 12 months, infants will move to follow an adult's gaze over barriers to find a target that is out of their view, thus showing that they implicitly grasp the notion that seeing is knowing [69]. Further, at 12 months of age infants can understand what is old news and new news for other people [70]. From here, it is but a small step towards social cooperation, as shown in remarkable videos of prelinguistic toddlers who spontaneously open a door for an adult who is carrying a load with both hands [71].

The fact that the ability to take into account the mental states of others is available so early in life means that it can have downstream effects on other aspects of cognitive development. In particular it is critical for learning words [72,73]. First, the infant can recognise those signals where the mother is naming an object for the infant to learn and distinguish them from those signals in which spoken words and objects come together incidentally [74]. Second, the infant can pick out the person who knows something from the person who does not, and pay special attention to the signals coming from the one who knows [75,76]. It is this ability to pick out the signals that are reliable and have communicative intent that enables infants to learn at the amazing rate of ten new words a day [77]. Furthermore, children learn abstract words relating to mental states, such as wishes, thoughts, intentions and beliefs very early [78] and most readily when cues from meaning and syntax converge [79].

The literature on Theory of Mind — the ability to predict and explain other people's behaviour in terms of mental states - highlights a step change in development. Children younger than about 5 years are not explicitly aware of mental states and their role in communication [80]. Yet, there are abundant signs of an implicit awareness of other's intentions and desires from at least about 18 months. A famous example is pretend play. Young children from about 18 months are able to understand and preferentially attend to signals of pretense, such as exaggerated voices and expressive features. Indeed the hallmark of this behaviour is that children do not mistake the signals of pretense for information about the state of affairs in the real world [81]. However, this understanding is implicit and thus differs from the explicit justification of a false belief and the assured prediction of the behavioural consequences at age 5.

We believe that the same step change applies to the implicit and explicit understanding of communicative signals. Indeed the gap is intimately connected with the cultural leap that has led to institutionalized teaching and trading. Thus it is no coincidence that the age of school entry in most cultures is round about the landmark age of 5. Most people would agree that, leaving aside exceptionally precocious children, it is difficult to engage children younger than 5 in explicit teaching and learning. Clearly this learning depends on full awareness of communicative signals. Understanding the meaning of these signals allows us also to manipulate other people's mental states. Thus, we can engage in reputation management by using social signals to manipulate what other people think about us.

Through being aware that socials signals are communicative, we can use them to transmit ideas efficiently from one mind to another [82]. Such signals have meaning and can be true or false. For example, when we tell a lie we use signals to create a false belief in another person's mind. The ability to deliberately deceive is well developed in humans with explicit knowledge of false beliefs and their use in deception is manifest from the age of about 5 years [83]. This ability is not found in monkeys, but may be seen in a rudimentary form in great apes [84,85]. The ability to represent the mental states of self and others, upon which deception depends, is supported by a network of brain regions, including medial prefrontal cortex and temporo-parietal junction [86,87] (see Figure 1).

Consciousness and Social Cognition

In earlier sections of this essay we have seen that much of the processing of social signals occurs automatically and without the need for awareness. We respond emotionally to a fearful face even when we are unaware of seeing that face [88]. Likewise we can be conditioned to show a fearful response to a previously neutral stimulus - the conditioned stimulus, CS+ — when this is repeatedly followed by a shock – the unconditioned stimulus, US — without awareness of that stimulus [89]. Phelps and colleagues [90] have shown that learning fear from observing others being conditioned can also occur without awareness of the conditioned stimulus. However, this does not happen with instructed fear. In instructed fear, the experimenter tells the subject that the presentation of a previously neutral stimulus (a blue square for example) will be followed by a shock. After such an instruction, the presentation of the stimulus is followed by autonomic arousal and other signs of fear. But, in contrast to learning fear by conditioning or by observation, this effect of instructed fear does not occur if the stimulus is masked and does not reach awareness [15].

This result hints at the idea that consciousness is required for the kinds of representations that are created by deliberately communicative signals. Evidence in favour of this idea is as yet sparse. There is still no agreed procedure for determining unequivocally whether events have been registered without consciousness (for example [91]). Nevertheless it is generally agreed that information processing in the brain largely occurs without awareness [92]. This leaves open the question as to how processing associated with consciousness should be characterised. It also leaves open the question of what the function of consciousness might be. In the previous section we have suggested that conscious representations have a special role in the shared social world that is created by deliberate communicative signals. Rather than being private, conscious experiences are represented in a form that can be shared with others, thereby creating the common around for culture [93].

Another hint of the relevance of consciousness for social cognition comes from a study of race prejudice. Amodio and colleagues [94] recorded electro-encephalograms (EEGs) while participants performed a cognitive task purporting to measure their level of race bias

either confidentially (in private) or while being observed by an ostensibly non-prejudiced experimenter (in public). Control of responses in private was associated with the amplitude of error-related negativity. This component of the EEG occurs within milliseconds of a response and reflects an early, preconscious stage of conflict monitoring. By contrast, when responding in public, better control of responding was associated with the amplitude of the errorrelated positivity component of the EEG. This occurs later, ~200 milliseconds after responding and is associated with awareness of error commission [95,96]. Error correcting in public in this task is concerned with reputation building: trying to influence how we are seen by others. The sources of these two error related components of the EEG have been located in the anterior cingulate cortex, with the source of the component associated with awareness being more anterior [96,97]. This more anterior region of anterior cingulate cortex and adjacent paracingulate cortex (anterior rostral medial frontal cortex) has been associated with meta-cognition (thinking about thinking) [98] and the uniquely human representation of triadic relations between two minds and an object [99] (see Figure 1).

In a clinical setting, a lack of awareness of our own failings is referred to as a lack of insight. This is a feature of many disorders of social interaction and communication, including autism, schizophrenia and various forms of dementia. Patients with dementia and accompanying loss of insight into their own failings also show reduced empathy and impaired recognition of emotional expressions [100]. This highlights the link between awareness of self and awareness of others. Our suggestion is that this link arises because awareness of self might be more accurately described as awareness of self as others see us.

Conclusions

In this review we have drawn together studies that highlight the importance of social signals. These signals act as gatekeepers for learning about the world from other people, making it possible to enhance our own learning through the experience of others. They also are critical in learning about other people and in particular whether or not we should trust them and value the social signals they send. In learning about the world as well as in learning about other people, we can distinguish purely automatic signals and conscious signals. The evidence we have discussed suggests that it is the deliberate and conscious signals that are crucial to creating a shared social world of which we are in control. This shared world is particularly refined in verbal communication, where meanings of words and concepts can be measured by the degree of shared understanding. At the same time to share meanings and to negotiate the social world we need to be aware of our own and other's beliefs, knowledge and feelings.

Thus the emergence of consciousness goes hand in hand with the development of advanced social signalling. This may explain why the most pervasive task in our social life is the management of our own reputation, both in our own eyes and in the eyes of others. A shared culture allows both these viewpoints to be aligned. The evolutionary benefits of such coordination may be seen in enhanced cooperation and the continuous intergenerational creation of what we call culture. Conversely, the absence of such alignment can be seen to result in disturbed and pathological social interactions.

Acknowledgments

Our work is supported by the Welcome Trust, the Medical Research Council of Great Britain and the Danish National Research Foundation.

References

- Adolphs, R. (1999). Social cognition and the human brain. Trends Cogn. Sci. 3, 469–479.
- Vuilleumier, P., and Pourtois, G. (2007). Distributed and interactive brain mechanisms during emotion face perception: evidence from functional neuroimaging. Neuropsychologia 45, 174–194.
- Frith, C.D., and Frith, U. (2006). How we predict what other people are going to do. Brain Res. 1079, 36–46.
- Maynard Smith, J., and Harper, D. (2003). Animal Signals (Oxford: Oxford University Press).
- Danchin, E., Giraldeau, L.A., Valone, T.J., and Wagner, R.H. (2004). Public information: from nosy neighbors to cultural evolution. Science 305, 487–491.
- Chartrand, T.L., and Bargh, J.A. (1999). The chameleon effect: the perception-behavior link and social interaction. J. Pers. Soc. Psychol. 76, 893–910.
- Lakin, J.L., and Chartrand, T.L. (2003). Using nonconscious behavioral mimicry to create affiliation and rapport. Psychol. Sci. 14, 334– 339.
- Watson, J.B., and Rayner, R. (1920). Conditioned emotional reactions. J. Exp. Psychol. 3, 1–14.
- Bayliss, A.P., and Tipper, S.P. (2006). Predictive gaze cues and personality judgments: Should eye trust you? Psychol. Sci. 17, 514–520.
- Gallese, V., Keysers, C., and Rizzolatti, G. (2004). A unifying view of the basis of social cognition. Trends Cogn. Sci. 8, 396–403.
- Botvinick, M., Jha, A.P., Bylsma, L.M., Fabian, S.A., Solomon, P.E., and Prkachin, K.M. (2005). Viewing facial expressions of pain engages cortical areas involved in the direct experience of pain. Neuroimage 25, 312–319.
- Adolphs, R. (2002). Neural systems for recognizing emotion. Curr. Opin. Neurobiol. 12, 169–177.
- Wicker, B., Keysers, C., Plailly, J., Royet, J.P., Gallese, V., and Rizzolatti, G. (2003). Both of us disgusted in My insula: the common neural basis of seeing and feeling disgust. Neuron 40, 655–664.
- Feinman, S., Roberts, D., Hsieh, K.F., Sawyer, D., and Swanson, K. (1992). A critical review of social referencing in infancy. In Social Referencing and the Social Construction of Reality in Infancy, S. Feinman, ed. (New York: Plenum Press).
- Olsson, A., and Phelps, E.A. (2004). Learned fear of "unseen" faces after Pavlovian, observational, and instructed fear. Psychol. Sci. 15, 822–828.
- Mineka, S., and Cook, M. (1993). Mechanisms involved in the observational conditioning of fear. J. Exp. Psychol. Gen. 122, 23–38.
- Cook, M., and Mineka, S. (1989). Observational conditioning of fear to fear-relevant versus fear-irrelevant stimuli in rhesus monkeys. J. Abnorm Psychol. 98, 448–459.
- Zarbatany, L., and Lamb, M.E. (1985). Social referencing as a function of information source – mothers versus strangers. Infant Behav. Dev. 8, 25–33.
- Klinnert, M.D., Emde, R.N., Butterfield, P., and Campos, J.J. (1986). Social referencing - the infants use of emotional signals from a friendly adult with mother present. Dev. Psychol. 22, 427– 432.
- Walden, T.A., and Kim, G. (2005). Infants' social looking toward mothers and strangers. Int. J. Behav. Dev. 29, 356–360.
- 21. Gergely, G., Egyed, K., and Kiraly, I. (2007). On pedagogy. Dev. Sci. 10, 139–146.
- Fiske, S.T., Cuddy, A.J., and Glick, P. (2007). Universal dimensions of social cognition: warmth and competence. Trends Cogn. Sci. 11, 77–83.

- Willis, J., and Todorov, A. (2006). First impressions: making up your mind after a 100-ms exposure to a face. Psychol. Sci. 17, 592–598.
- Winston, J.S., Strange, B.A., O'Doherty, J., and Dolan, R.J. (2002). Automatic and intentional brain responses during evaluation of trustworthiness of faces. Nat. Neurosci. 5, 277–283.
- 25. Dolan, R.J. (2002). Emotion, cognition, and behavior. Science 298, 1191–1194.
- LeDoux, J.E. (2000). Emotion circuits in the brain. Annu. Rev. Neurosci. 23, 155–184.
- Olson, K.R., Banaji, M.R., Dweck, C.S., and Spelke, E.S. (2006). Children's biased evaluations of lucky versus unlucky people and their social groups. Psychol. Sci. 17, 845–846.
- Hirschfeld, L. (1996). Race in the Making (Cambridge, Mass: MIT Press).
- Phelps, E.A., O'Connor, K.J., Cunningham, W.A., Funayama, E.S., Gatenby, J.C., Gore, J.C., and Banaji, M.R. (2000). Performance on indirect measures of race evaluation predicts amygdala activation. J. Cogn. Neurosci. 12, 729–738.
- Banaji, M.R. (2001). Implicit attitudes can be measured. In The Nature of Remembering: Essays in Honor of Robert G. Crowder, H.L. Roediger, J.S. Nairne, I. Neath, and A. Surprenant, eds. (Washington, DC: American Psychological Association), pp. 117–150.
- Greenwald, A.G., McGhee, D.E., and Schwartz, J.L. (1998). Measuring individual differences in implicit cognition: the implicit association test. J. Pers. Soc. Psychol. 74, 1464–1480.
- Singer, T., Kiebel, S.J., Winston, J.S., Dolan, R.J., and Frith, C.D. (2004). Brain responses to the acquired moral status of faces. Neuron 41, 653–662.
- Lee, K., Eskritt, M., Symons, L.A., and Muir, D. (1998). Children's use of triadic eye gaze information for "mind reading". Dev. Psychol. 34, 525–539.
- 34. Woodward, A.L. (1998). Infants selectively encode the goal object of an actor's reach. Cogn. 69, 1–34.
- Hamilton, A.F., and Grafton, S.T. (2006). Goal representation in human anterior intraparietal sulcus. J. Neurosci. 26, 1133–1137.
- Rizzolatti, G., and Craighero, L. (2004). The mirror-neuron system. Annu. Rev. Neurosci. 27, 169–192.
- Keysers, C., and Gazzola, V. (2006). Towards a unifying neural theory of social cognition. Prog. Brain Res. 156, 379–401.
- Puce, A., and Perrett, D. (2003). Electrophysiology and brain imaging of biological motion. Philos. Trans. R. Soc. Lond. B. Biol. Sci. 358, 435–445.
- Pelphrey, K.A., Singerman, J.D., Allison, T., and McCarthy, G. (2003). Brain activation evoked by perception of gaze shifts: the influence of context. Neuropsychologia *41*, 156–170.
- Pelphrey, K.A., Morris, J.P., and McCarthy, G. (2004). Grasping the intentions of others: the perceived intentionality of an action influences activity in the superior temporal sulcus during social perception. J. Cogn. Neurosci. 16, 1706–1716.
- Saxe, R., Xiao, D.K., Kovacs, G., Perrett, D.I., and Kanwisher, N. (2004). A region of right posterior superior temporal sulcus responds to observed intentional actions. Neuropsychologia 42, 1435–1446.
- 42. Kersten, D., Mamassian, P., and Yuille, A. (2004). Object perception as Bayesian inference. Annu. Rev. Psychol. 55, 271–304.
- 43. Kilner, J.M., Friston, K.J., and Frith, C.D. (2007). The mirror system: a Bayesian perspective. NeuroReport, in press.
- Gallese, V. (2003). The manifold nature of interpersonal relations: the quest for a common mechanism. Philos. Trans. R. Soc. Lond. B. Biol. Sci. 358, 517–528.
- Singer, T., Seymour, B., O'Doherty, J., Kaube, H., Dolan, R.J., and Frith, C.D. (2004). Empathy for pain involves the affective but not sensory components of pain. Science 303, 1157–1162.
- Blakemore, S.J., Bristow, D., Bird, G., Frith, C., and Ward, J. (2005). Somatosensory activations during the observation of touch and a case of vision-touch synaesthesia. Brain *128*, 1571–1583.
- Clark, H.H. (1996). Using Language (Cambridge: Cambridge University Press).
- Tomasello, M., Carpenter, M., Call, J., Behne, T., and Moll, H. (2005). Understanding and sharing intentions: the origins of cultural cognition. Behav. Brain Sci. 28, 675–691, discussion 691–735.
- Liszkowski, U., Carpenter, M., Henning, A., Striano, T., and Tomasello, M. (2004). Twelve-month-olds point to share attention and interest. Dev. Sci. 7, 297–307.
- Sebanz, N., Knoblich, G., and Prinz, W. (2003). Representing others' actions: just like one's own? Cogn. 88, B11–B21.
- Tsai, C.C., Kuo, W.J., Jing, J.T., Hung, D.L., and Tzeng, O.J. (2006). A common coding framework in self-other interaction: evidence from joint action task. Exp. Brain Res. 175, 353–362.

- Sebanz, N., Bekkering, H., and Knoblich, G. (2006). Joint action: bodies and minds moving together. Trends Cogn. Sci. 10, 70–76.
- Reed, K., Peshkin, M., Hartmann, M.J., Grabowecky, M., Patton, J., and Vishton, P.M. (2006). Haptically linked dyads: are two motorcontrol systems better than one? Psychol. Sci. 17, 365–366.
- Pickering, M.J., and Garrod, S. (2004). Toward a mechanistic psychology of dialogue. Behav. Brain Sci. 27, 169–190, discussion 190–226.
- 55. Hedge, B.J., Everitt, B.S., and Frith, C.D. (1978). The role of gaze in dialogue. Acta. Psychol. (Amst) *42*, 453–475.
- Clark, H.H., and Fox Tree, J.E. (2002). Using uh and um in spontaneous speaking. Cogn. 84, 73–111.
- Barr, D.J. (2004). Establishing conventional communication systems: Is common knowledge necessary? Cogn. Sci. 28, 937–962.
- Roepstorff, A., and Frith, C. (2004). What's at the top in the topdown control of action? Script-sharing and 'top-top' control of action in cognitive experiments. Psychol. Res. 68, 189–198.
- Clark, H.H., and Krych, M.A. (2004). Speaking while monitoring addressees for understanding. J. Mem. Lang. 50, 62–81.
- Markman, A.B., and Makin, V.S. (1998). Referential communication and category acquisition. J. Exp. Psychol.-Gen. 127, 331–354.
- Branigan, H.P., Pickering, M.J., and Cleland, A.A. (2000). Syntactic co-ordination in dialogue. Cognition 75, B13–B25.
- Pickering, M.J., and Garrod, S. (2007). Do people use language production to make predictions during comprehension? Trends Cogn. Sci. 11, 105–110.
- 63. Sperber, D., and Wilson, D. (1995). Relevance: Communication and Cognition, second edition (Oxford: Blackwell).
- 64. Reddy, V. (2007). Getting back to the rough ground: deception and 'social living'. Philos. Trans. R. Soc. Lond. B. Biol. Sci. 362, 621–637.
- Call, J., Brauer, J., Kaminski, J., and Tomasello, M. (2003). Domestic dogs (Canis familiaris) are sensitive to the attentional state of humans. J. Comp. Psychol. 117, 257–263.
- Carpenter, M., Nagell, K., and Tomasello, M. (1998). Social cognition, joint attention, and communicative competence from 9 to 15 months of age. Monogr. Soc. Res. Child Dev. 63, i-vi, 1–143.
- 67. Tomasello, M., and Carpenter, M. (2007). Shared intentionality. Dev. Sci. 10, 121-125.
- Moll, H., and Tomasello, M. (2007). Cooperation and human cognition: the Vygotskian intelligence hypothesis. Philos. Trans. R. Soc. Lond. B. Biol. Sci. 362, 639–648.
- Moll, H., and Tomasello, M. (2007). How 14- and 18-month-olds know what others have experienced. Dev. Psychol. 43, 309–317.
- Liszkowski, U., Carpenter, M., and Tomasello, M. (2007). Pointing out new news, old news, and absent referents at 12 months of age. Dev. Sci. 10, F1–F7.
- Warneken, F., Chen, F., and Tomasello, M. (2006). Cooperative activities in young children and chimpanzees. Child Dev. 77, 640–663.
- 72. Bloom, P. (2002). Mindreading, communication and the learning of names for things. Mind Language 17, 37–54.
- Kuhl, P.K. (2007). Is speech learning 'gated' by the social brain? Dev. Sci. 10, 110–120.
- Baldwin, D.A., Markman, E.M., Bill, B., Desjardins, R.N., Irwin, J.M., and Tidball, G. (1996). Infants' reliance on a social criterion for establishing word-object relations. Child Dev. 67, 3135–3153.
- Povinelli, D.J., and deBlois, S. (1992). Young children's (Homo sapiens) understanding of knowledge formation in themselves and others. J. Comp. Psychol. 106, 228–238.
- Sabbagh, M.A., and Baldwin, D.A. (2001). Learning words from knowledgeable versus ignorant speakers: links between preschoolers' theory of mind and semantic development. Child Dev. 72, 1054–1070.
- 77. Bloom, P. (2000). How Children Learn the Meaning of Words (Cambridge, MA: MIT Press).
- Shatz, M., Wellman, H.M., and Silber, S. (1983). The acquisition of mental verbs: a systematic investigation of the first reference to mental state. Cogn. 14, 301–321.
- Papafragou, A., Cassidy, K., and Gleitman, L. (2006). When we think about thinking: The acquisition of belief verbs. Cognition epub. ahead of print.
- Wimmer, H., and Perner, J. (1983). Beliefs about beliefs: representation and constraining function of wrong beliefs in young children's understanding of deception. Cognition. 13, 103–128.
- Leslie, A.M. (1987). Pretense and representation: The origins of 'theory of mind'. Psychol. Rev. 94, 412–426.
- 82. Frith, C.D. (2007). Making up the Mind; How the Brain Creates our Mental World (Oxford: Blackwell).
- Astington, J.W., Harris, P.L., and Olson, D.R. (1988). Developing Theories of Mind (Cambridge: Cambridge University Press).

- Tomasello, M., Call, J., and Hare, B. (2003). Chimpanzees understand psychological states – the question is which ones and to what extent. Trends Cogn. Sci. 7, 153–156.
- Povinelli, D.J., and Vonk, J. (2003). Chimpanzee minds: suspiciously human? Trends Cogn. Sci. 7, 157–160.
- Apperly, I.A., Samson, D., Chiavarino, C., and Humphreys, G.W. (2004). Frontal and temporo-parietal lobe contributions to theory of mind: neuropsychological evidence from a false-belief task with reduced language and executive demands. J. Cogn. Neurosci. 16, 1773–1784.
- Frith, U., and Frith, C.D. (2003). Development and neurophysiology of mentalizing. Philos. Trans. R. Soc. Lond. B. Biol. Sci. 358, 459– 473.
- Whalen, P.J., Rauch, S.L., Etcoff, N.L., McInerney, S.C., Lee, M.B., and Jenike, M.A. (1998). Masked presentations of emotional facial expressions modulate amygdala activity without explicit knowledge. J. Neurosci. 18, 411–418.
- Morris, J.S., Ohman, A., and Dolan, R.J. (1999). A subcortical pathway to the right amygdala mediating "unseen" fear. Proc. Natl. Acad. Sci. USA 96, 1680–1685.
- Phelps, E.A., O'Connor, K.J., Gatenby, J.C., Gore, J.C., Grillon, C., and Davis, M. (2001). Activation of the left amygdala to a cognitive representation of fear. Nat. Neurosci. 4, 437–441.
- Holender, D., and Duscherer, K. (2004). Unconscious perception: the need for a paradigm shift. Percept Psychophy. 66, 872–881, discussion 888–895.
- 92. Kihlstrom, J.F. (1987). The cognitive unconscious. Science 237, 1445–1452.
- Frith, C.D. (in press). The social function of consciousness. In Frontiers of Consciousness, L. Weiskrantz, J. Davies and A. Parker, eds. (Oxford: Oxford University Press).
- Amodio, D.M., Kubota, J.T., Harmon-Jones, E., and Devine, P.G. (2006). Alternative mechanisms for regulating racial responses according to internal vs. external cues. in submission 1, 26–36.
- Nieuwenhuis, S., Ridderinkhof, K.R., Blom, J., Band, G.P., and Kok, A. (2001). Error-related brain potentials are differentially related to awareness of response errors: evidence from an antisaccade task. Psychophysiology 38, 752–760.
- O'Connell, R.G., Dockree, P.M., Bellgrove, M.A., Kelly, S.P., Hester, R., Garavan, H., Robertson, I.H., and Foxe, J.J. (2007). The role of Cingulate Cortex in the detection of errors with and without awareness. Eur. J. Neurosci., in press.
- Van Veen, V., and Carter, C.S. (2002). The timing of action-monitoring processes in the anterior cingulate cortex. J. Cogn. Neurosci. 14, 593–602.
- Amodio, D.M., and Frith, C.D. (2006). Meeting of minds: the medial frontal cortex and social cognition. Nat. Rev. Neurosci. 7, 268–277.
- 99. Saxe, R. (2006). Uniquely human social cognition. Curr. Opin. Neurobiol. 16, 235–239.
- O'Keeffe, F.M., Murray, B., Coen, R.F., Dockree, P.M., Bellgrove, M.A., Garavan, H., Lynch, T., and Robertson, I.H. (2007). Loss of insight in frontotemporal dementia, corticobasal degeneration and progressive supranuclear palsy. Brain *130*, 753–764.
- Blanke, O., Mohr, C., Michel, C.M., Pascual-Leone, A., Brugger, P., Seeck, M., Landis, T., and Thut, G. (2005). Linking out-of-body experience and self processing to mental own-body imagery at the temporoparietal junction. J. Neurosci. 25, 550–557.
- Aichhorn, M., Perner, J., Kronbichler, M., Staffen, W., and Ladurner, G. (2005). Do visual perspective tasks need theory of mind? Neuroimage 30, 1059–1068.
- Saxe, R., and Kanwisher, N. (2003). People thinking about thinking people. The role of the temporo-parietal junction in "theory of mind". Neuroimage 19, 1835–1842.