

# Learning from Others: Introduction to the Special Review Series on Social Neuroscience

Chris Frith<sup>1,3,\*</sup> and Uta Frith<sup>2,3</sup>

<sup>1</sup>Wellcome Trust Centre for Neuroimaging at University College London

<sup>2</sup>Institute of Cognitive Neuroscience, University College London

<sup>3</sup>Interacting Minds Group, Center of Functionally Integrative Neuroscience, Aarhus University

\*Correspondence: [c.frith@ucl.ac.uk](mailto:c.frith@ucl.ac.uk)

DOI 10.1016/j.neuron.2010.03.015

The last decade has seen a dramatic rise of interest in the study of social neuroscience. Two observations have had a major role in driving this interest. First, there was the discovery that autism is associated with specific difficulties in social cognition, while nonsocial cognition, and in particular IQ, can remain intact (Frith, 1989; Hermelin and O'Connor, 1970). This discovery was made during the time when the information-processing revolution was transforming the behavioral sciences and when researchers were striving to find mechanisms underlying behavior, a significant departure from a preoccupation with surface appearances. This change of approach led to the proposal of a mechanism that could explain some of the characteristic social impairments of autism, a lack of Theory of Mind, or inability to mentalize (Baron-Cohen et al., 1985). The case of autism lent weight to the idea that there is a circumscribed brain system associated with social cognition: the social brain. The mentalizing deficit hypothesis encouraged the search for underlying neural mechanisms and posed the question of whether this was unique to the human brain.

A second impetus for the increase in research in social neuroscience came from the discovery of mirror neurons in the monkey. These neurons fire both when the monkey performs a specific goal-directed action and also when the monkey sees the experimenter performing the same goal-directed action (Rizzolatti et al., 1996). This observation reveals that there is a mechanism within the social brain with the potential to enable learning through imitation and to infer intentions from action observation. Researchers

were thus encouraged to try and specify such mechanisms (e.g., Kilner et al., 2007) in animals, including humans, where learning from conspecifics by imitation, emulation, or mimicry is pervasive.

The contributors to this special issue on social neuroscience review the research of the last decade and reveal how very much more there is to social cognition and that these earlier discoveries were only the beginnings of a vast enterprise. This enterprise, at least at first glance, focuses on learning from others. This kind of social behavior can be observed in animals from fruit flies to humans. The mechanisms underlying this behavior are beginning to be revealed at the molecular level. In addition to the wide range of animal species considered in this special review issue, a wide range of approaches and interpretations are applied to the observations. In this overview we will present our own ideas for drawing together this exciting work. There are three key issues to be discussed. First, there is the problem of how to bridge the gap between genes and neurons on one side and social behavior on the other, which in the case of humans includes a vast array of historically enduring accomplishments, including the existence of cultural institutions. Second, there is the problem of the distinction between social and nonsocial cognition. Third, there is the problem of determining what is special, if anything, about human social cognition.

Let us start with the gap between molecules and behavior. As is revealed in the exhaustive review by Ebstein et al. (2010), many unique aspects of human social behavior are, at least partially, under genetic control, and here remarkable work is being done at the molecular

level. However, this work is far removed from explaining, say, cultural learning. It is even far removed from explaining the processes by which genetic factors exert control on individual differences in social behavior. Twin studies show that there are complex interactions with nongenetic influences, and the study of epigenetic effects is thriving. One example of an epigenetic effect on social behavior is seen in honey bees: When worker bees feed larvae with royal jelly, the expression of genes involved in growth and metabolism is changed, and this leads to the development of new queens (Sokolowski, 2010).

Examples of behavior under partial genetic control mentioned by Ebstein et al. (2010) and Insel (2010) include economic decision making and political attitudes. Such behaviors were previously considered as typically human achievements, culturally prescribed and precariously taught with little if any connection to our biological nature. Now we can contemplate a genetic predisposition that biases you to vote for one political party rather than another and a predisposition for you to make more or less altruistic decisions. However, exciting as the idea is that proclivities in social behavior have a genetic basis, it is plainly not sufficient to explain social behavior. As Sokolowski (2010) points out, genes don't determine behavior; they encode molecules that build brain tissue. When we try to understand empathy or political attitudes, we need to know how these concepts are linked to basic mechanisms, what controls them and what doesn't, how to explain their origin in development, and how to account for their elaboration through culture.

### The Mediating Role of the Cognitive Level of Description

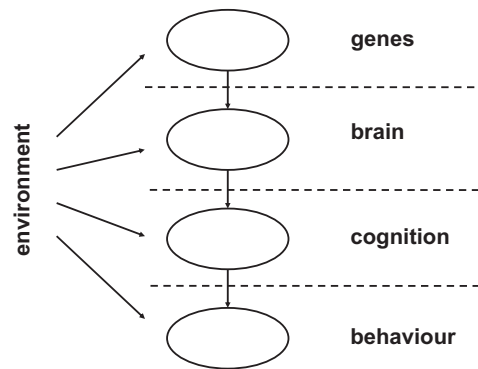
We were fascinated to learn from this special review issue of the extent to which the same social processes can be observed in so many different species. This tells us that, at some level, which we call the cognitive level, evolution has led to homologous solutions dealing with the problems and advantages that arise from living with conspecifics.

Figures 1 and 2 are simple illustrations of how to conceptualize a cognitive level of description and how it fits with the whole enterprise of social neuroscience (diagrams adapted from Morton and Frith, 1995).

We see in these figures that cognition is situated in between brain and behavior, and by virtue of this position forms a link between these two rather distinct levels of explanation. This is important because there is no one-to-one mapping when crossing levels. For example, as Figure 2 shows, at the biological level we can allow for a variety of genetic pathways and mechanisms. These pathways lead to the development and maintenance of distinct parts of the central nervous system. Different mechanisms can be modeled, as here in terms of multiple neural networks underlying the cognitive process termed mentalizing, which can be assessed by such diverse behaviors as joint attention, deception, and ostensive communication (Frith et al., 1991).

The critical question is what do the biological roots allow the mind to do? We imagine there is some parsimony, so that we allow for a many-to-one mapping from biology to cognition. On the other hand, we allow for a one-to-many mapping from cognition to behavior. We can assume that a single mental mechanism (often in interaction with other mechanisms) can be responsible for a large variety of behaviors. For example, the ability to learn language (Fitch et al., 2010) has different manifestations in different species and can be assessed with different tests at both the neural and behavioral level.

While vocalization appears to be crucial for the development of language and communication, we are still only guessing what other neurocognitive mechanisms are being enabled or changed by evolu-



**Figure 1. A Simple Conceptualization of Different Levels of Explanation in Comparative Social Neuroscience**

tionary pressures on social behavior. Mentalizing and the corepresentation of action and observation are two very recent examples of such mechanisms, which had hardly been envisaged earlier. The search for neural systems underlying these mechanisms has been remarkably successful, while the search for the genetic foundations for the origin of our ability to learn language has been nothing less than a triumph (Fitch et al., 2010). For now, however, we need to accept that there are huge gaps between brain and mind and behavior in almost any of the social behaviors and almost any of the biological mechanisms discussed by the present reviewers.

In the papers in this issue, there are a number of concepts that describe a cognitive mechanism, even if not explicitly classified as such by the author. Insel (2010) describes some of the links between genes and brain systems in his discussion of the role of oxytocin, but recognizes the problem of “the great dark matter of social neuroscience” that lies between perception and action. Adolphs (2010) also recognizes this problem and suggests that “analysis at the level of the brain could serve as a unifying base.” However, this aim will be difficult to fulfill in light of the idea that there are homologs of social capacities in species with very different brains. Animals, such as birds, cetaceans, and mammals, possessing very different brain structures, can nevertheless all be said to have some understanding of the point of view of others, including possibly their mental states. Furthermore, evidence of learning from the observation of conspecifics can be

found from fruit flies to humans. There are, however, considerable variations in the sophistication of this learning.

The cognitive level makes it simple to accommodate the possibility that a variety of neural mechanisms can all underpin critical processes that allow learning from others. At this level, mental processes, whether instantiated in the bird brain, the monkey brain, or the human brain, can be understood to serve the same aims. For example, all these creatures send out signals of communication and modulate their behavior in the presence of conspecifics. We believe that the cognitive level can be developed to fill the gap between basic molecular processes and intuitively perceived social abilities, since the vocabulary of cognition, and in particular the computational models associated with this level, can be applied equally to neural as to mental processes.

We note that we are using the term cognitive in its modern sense. We are not using cognition in the restricted sense of knowledge as opposed to emotion or will. We are certainly not using cognition in the sense of conscious processes. We are using it as in “cognitive neuroscience”; a mechanistic account of neural and psychological processes using terms derived from computational theory. Such terminology can be found in many of the contributions to this review issue. For example, Insel (2010) talks of the “brain employing specific receptors for the processing of social information.” Byrne and Bates (2010) talk of “representing unobservable causal factors.” Analysis at the cognitive level permits recognition that the same sensory signals can be processed in different ways. For example, if some species are not able to form the same mental representations, then what they do with the same information may be radically different (Byrne et al., 2004). Such recognition is critical when we start comparing different species.

### Learning by Observation

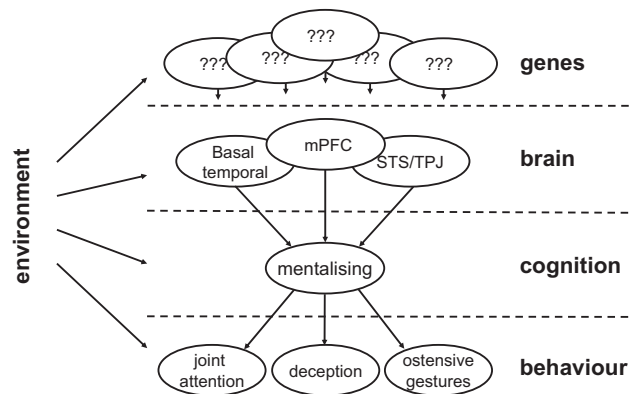
Learning from others is the most basic definition of social cognition that characterizes all social species. However, we can learn from others and about others in ways that do not qualify as implicating social processes at all. Very clear

indications of truly social learning come from examples where we can infer that an agent's reputation is at stake. For example, an agent may give a signal to another agent when this signal exposes him and might well endanger his life. This is often used to advertise prowess in mating rituals. Such a signal means a lot, as it tells the recipient that the signaler is an honest agent. If the signal was a fake, as in crying wolf, then the long-term reputation of the signaler will be damaged. In these cases, we can talk of a cognitive process that is

deeply engaged in the social cooperation and competition typical of group living. Fake signals and true but costly signals occur in many different species, and the response to these signals seems automatic (Maynard Smith and Harper, 2003).

As soon as we address long-term reputation, a central aspect of social cognition likely to depend on mentalizing ability, it is clear that other cognitive processes are required for this sophisticated social ability to flourish. One particularly critical prerequisite is the ability to distinguish between individuals. Memory for who did what and when is of central importance in social living. We must assume that the recognition of conspecifics, by whatever sense, is a prerequisite for the aim of influencing the opinion of others. This prerequisite need not be seen as a specifically social mechanism, but may equally serve as a prerequisite for episodic memory in general problem solving.

As noted by Insel (2010), some sensory information is primarily encoded as social, and there is multimodal sensitivity to the perception of others (Fitch et al., 2010). One of the key research questions is how do we know what to attend to and when? Social stimuli such as eye gaze and the face are highly compelling and have attracted much research interest. Studies of gaze following in different species allow us to see sharp divisions between geometric line of sight following and following gaze beyond the line of sight, even when there is an occluder. This type of gaze following relies on a special cognitive mechanism that allows



**Figure 2. A Simple Example of Conceptualizing the Putative Cognitive Mechanism “Mentalizing” or Theory of Mind as a Node that Accommodates Both Many-to-One and One-to-Many Mapping between Different Levels of Explanation**

the automatic inference of intention and desires (Fitch et al., 2010). Joint attention may go a step further by involving inference of knowledge and beliefs. If so, it can be seen as a basis for ostensive communication and natural pedagogy (Gergely et al., 2007). When speaker and listener interact truly reciprocally, as in intuitive teaching and learning, we can assume that there is a “closing of the loop” so that both participants in the interaction end up by adjusting their minds to each other (Frith, 2007). We will return later to the importance of this capacity as a primary vehicle for cultural evolution.

**Social and Nonsocial Cognition**

As we noted at the beginning, a division between social and nonsocial cognition fits with observations from autism. It also fits with observations from patients with brain lesions, with the proviso that the age at which a lesion is sustained may critically determine the extent to which social cognition is impaired (Blakemore, 2010). Adolphs (2010) argues that social cognition recruits processes for which there is no analog in nonsocial cognition, quoting examples that invoke the brain’s mirror system, such as empathy and contagion by others’ emotions, and reminds us of our ubiquitous tendency to anthropomorphize, which extends even to agents that are not biological entities.

Sokolowski (2010) concludes that all social species need social interaction for normal development. Blakemore (2010) reviews evidence that language learning in children requires interaction with real

people rather than videos. This phenomenon is also seen in some birds who will only learn their songs from a living tutor (Fitch et al., 2010). As Byrne and Bates (2010) point out, the set of cognitive skills shown by a population will depend upon opportunities for social learning.

The learning of songs by birds (Fitch et al., 2010) is a particularly interesting case because the molecular and cognitive mechanisms are beginning to be understood. Such learning depends upon auditory mirror neurons and

seems to be under the control of the FOXP2 gene. A critical requirement of this learning may be precise control of the vocal apparatus through direct connections from the avian equivalents of cortex to primary motor neurons in the brain stem. The parallels with the human speech system are striking (Jürgens, 2002). In this context, it is interesting to note a recent suggestion (Hamilton, 2008) that the possibly uniquely human ability to imitate non-goal-directed actions (mimicry) might also depend upon unique direct connections between relevant cortical regions.

However, is nonsocial cognition really distinct from social cognition? While it seems attractive to suppose that the requirement of living in social groups has shaped every mental function, Byrne and Bates (2010) point out that pressure from within social groups is not the only force driving the evolution of cognition. There is also the problem of predicting what happens in the physical environment as well as in the biological environment. Which lake is about to dry up? Which fruit is about to ripen? There is also pressure to understand the behavior of other species. What is the predator or prey going to do next? As these examples show, activities outside the social domain often revolve around obtaining and processing food, something in which great apes are especially sophisticated. However, even the food-processing skills of great apes have a social component, since these new skills are learned by observation of conspecifics.

Is the distinction between social and nonsocial cognition perhaps illusory? This difficulty of distinguishing social and nonsocial mechanisms certainly applies to insects. Natural variation in the foraging gene (*for*) in the common fruit fly results in flies with different food-related behavior called rovers or sitters (Sokolowski, 2010). When food is distributed in patches, rovers have a greater tendency than sitters to leave the food patch. This dimension of behavior bears a striking resemblance to the explore-exploit dimension, which has an important role in the habit learning of humans and other mammals and for which we now have computational models (Daw et al., 2006). In both humans and flies, the cognitive processes underlying this behavioral dimension would be considered not primarily social. In ants and bees, the *for* gene has the same role in manipulating sitter or rover behavior. However, this is now a social role, since the gene regulates the relative number of nurses or foragers in a colony.

We should, perhaps, not be surprised that cognitive processes that have evolved for nonsocial purposes can readily be co-opted for social purposes by natural selection. Evolution will always make use of what is already available. Traditionally, functions such as attention and memory were studied by cognitive psychologist outside the social domain, but they also have a critical role in social cognition. One of the cognitive functions that has been recognized in this way is regulation of behavior (Adolphs, 2010). Modulation or suppression of automatic behavior is often seen in the presence of conspecifics. One only needs to think of the child who resists taking a bite from a cake as long as an adult is present, or the cleaner fish who resists the temptation to bite a client fish when observed by other potential clients (Bshary and Grutter, 2006). The modulation of behavior through nonsocial rewards is well-studied in classic learning experiments, but, more recently, there has been a consensus that social and nonsocial rewards are a common currency and subject to the same principles of learning. Nevertheless, a study (Behrens et al., 2008) suggests that a division between social learning and object learning is valid. This study showed that individuals use different neural substrates when they learn to

associate an object with a reward as opposed to learning how trustworthy an individual is who tells them which object is the right one to choose. However, the basic computations instantiated in these different neural substrates were essentially the same.

### What Is Special about Human Social Cognition?

There are many ways in which human behavior and human society are special (Northoff, 2010). The most obvious special features are language, cumulative culture, and the tendency to ask difficult questions, such as what is special about human social cognition? But this last question, which concerns the processes that underlie human behavior, is indeed very difficult to answer. Many processes have been put forward as special. The ability to walk upright, to speak, or to make tools have been proposed for centuries. More recently, more sophisticated abilities have taken center stage, for instance, the ability to have episodic memory, the ability to represent things not actually present, and the ability to represent the mental states of others. But over the last decade, many of these processes have been observed in other primates and also in dogs and birds (Fitch et al., 2010). For example, the recognition that what agents know depends upon what they can see would seem to depend upon representing the mental state of another and is, at least, precursor of theory of mind. But there is now evidence that apes, monkeys, scrub jays, and ravens all have this ability. Even such treasured human faculties as empathy, fairness, and morality, all of which may to some extent require the ability to represent others' mental states, are present in rudimentary forms in other animals (e.g., Brosnan and De Waal, 2003; Langford et al., 2006).

Even more striking are demonstrations of the ability to convey information about objects that are not currently present. This can be achieved by ravens, who, having found a carcass to scavenge, will recruit conspecifics to join the feast and drive off competitors (Fitch et al., 2010). Bees show the same ability: a swarm makes a group decision about where to locate a new hive. This is done by forager bees indicating by their dance the location

and desirability of the site they have found. It is through competition between the different messengers that the swarm, after many hours, chooses one of these sites and travels to it (Sokolowski, 2010).

Perhaps, as Adolphs (2010) suggests, the difference is quantitative rather than qualitative: humans have more flexible top-down control and are more able to handle delayed rewards (temporal discounting in the language of neuroeconomics) and thus, for example, are able to develop reciprocal altruism in social interactions.

Nevertheless, humans have been such a successful species with a vital need for social interaction that we would still hope that it might be possible to identify a special form of human social cognition. Although other species may show precursors of processes like mentalizing, their abilities are so rudimentary compared to humans that some sort of qualitative leap seems likely to have occurred. Of course, one possibility is that the basic cognitive abilities of humans are not more advanced than other species, but that a small difference in mental capacity was sufficient for a gulf between humans and others to emerge very slowly as a result of the cumulative effects of culture (Tomasello, 1999).

We have two suggestions as to what the special feature of human social cognition might be. One idea is that humans have an automatic (unconscious) drive to constantly update the difference between their own knowledge and the knowledge of specific others. Such a tendency is critical to the human drive to share novel information with others (Fitch et al., 2010). Such sharing, and indeed any useful communication, depends on knowing what other people don't know.

The other idea is that much human knowledge is represented in the explicit (conscious) form that is needed for sharing experiences. In other words, there is a special form of human communication where we are aware that we are sending and receiving signals (Sperber and Wilson, 1995). This means that, when we receive a signal we make a distinction (among other distinctions) between unintentional and deliberate signaling. We know that unintentional signals may have more veracity than deliberate signals because deliberate

signals can be manipulated by the sender for the purposes of deception. On the other hand, we can use deliberate signals of communication to teach others. Both informal and formal teaching are the building materials of culture and serve to multiply learning from others (Gergely et al., 2007). This multiplication of experience over many generations may be the secret to the success of *Homo sapiens*.

Many would agree that it is the ability to reflect on what we, and others, are doing and why we are doing it that makes us unique. No doubt, this ability to reflect has in turn also led to the ability to predict the future better than any other species; whether for good or for ill remains to be seen.

#### ACKNOWLEDGMENTS

C.F. and U.F. are supported by the Danish National Research Foundation. C.F. is also supported by the AHRC CNCC scheme AH/E511112/1.

#### REFERENCES

Adolphs, R. (2010). *Neuron* 65, this issue, 752–767.

Baron-Cohen, S., Leslie, A.M., and Frith, U. (1985). *Cognition* 21, 37–46.

Behrens, T.E., Hunt, L.T., Woolrich, M.W., and Rushworth, M.F. (2008). *Nature* 456, 245–249.

Blakemore, S.-J. (2010). *Neuron* 65, this issue, 744–747.

Brosnan, S.F., and De Waal, F.B. (2003). *Nature* 425, 297–299.

Bshary, R., and Grutter, A.S. (2006). *Nature* 441, 975–978.

Byrne, R.W., and Bates, L.A. (2010). *Neuron* 65, this issue, 815–830.

Byrne, R.W., Barnard, P.J., Davidson, I., Janik, V.M., McGrew, W.C., Miklósi, A., and Wiessner, P. (2004). *Trends Cogn. Sci.* 8, 341–346.

Daw, N.D., O'Doherty, J.P., Dayan, P., Seymour, B., and Dolan, R.J. (2006). *Nature* 441, 876–879.

Ebstein, R.P., Israel, S., Chew, S.H., Zhong, S., and Knafo, A. (2010). *Neuron* 65, this issue, 831–844.

Fitch, T., Huber, L., and Bugnyar, T. (2010). *Neuron* 65, this issue, 795–814.

Frith, U. (1989). *Autism: Explaining the Enigma* (Oxford, UK: Blackwells).

Frith, C.D. (2007). *Making Up the Mind: How the Brain Creates Our Mental World* (Oxford: Blackwell).

Frith, U., Morton, J., and Leslie, A.M. (1991). *Trends Neurosci.* 14, 433–438.

Gergely, G., Egedy, K., and Király, I. (2007). *Dev. Sci.* 10, 139–146.

Hamilton, A.F. (2008). *Q. J. Exp. Psychol.* 61, 101–115.

Hermelin, B., and O'Connor, N. (1970). *Psychological Experiments with Autistic Children* (Oxford: Pergamon).

Insel, T.R. (2010). *Neuron* 65, this issue, 768–779.

Jürgens, U. (2002). *Neurosci. Biobehav. Rev.* 26, 235–258.

Kilner, J.M., Friston, K.J., and Frith, C.D. (2007). *Cogn. Process.* 8, 159–166.

Langford, D.J., Crager, S.E., Shehzad, Z., Smith, S.B., Sotocinal, S.G., Levenstadt, J.S., Chanda, M.L., Levitin, D.J., and Mogil, J.S. (2006). *Science* 312, 1967–1970.

Maynard Smith, J., and Harper, D. (2003). *Animal Signals* (Oxford: Oxford University Press).

Morton, J., and Frith, U. (1995). *Developmental Psychopathology*, D. Cicchetti and D.J. Cohen, eds. (New York: Wiley), pp. 357–390.

Northoff, G. (2010). *Neuron* 65, this issue, 748–751.

Rizzolatti, G., Fadiga, L., Gallese, V., and Fogassi, L. (1996). *Brain Res. Cogn. Brain Res.* 3, 131–141.

Sokolowski, M.B. (2010). *Neuron* 65, this issue, 780–794.

Sperber, D., and Wilson, D. (1995). *Relevance: Communication and Cognition*, second edition (Oxford: Blackwell).

Tomasello, M. (1999). *The Cultural Origins of Human Cognition* (Boston: Harvard University Press).