

# Mechanisms of Social Cognition

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Annu. Rev. Psychol. 2012.63:287-313

First published online as a Review in Advance on August 11, 2011

The *Annual Review of Psychology* is online at [psych.annualreviews.org](http://psych.annualreviews.org)

This article's doi:  
10.1146/annurev-psych-120710-100449

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0066-4308/12/0110-0287\$20.00

## Keywords

observational learning, imitation, reputation, teaching, mentalizing, meta-cognition

## Abstract

Social animals including humans share a range of social mechanisms that are automatic and implicit and enable learning by observation. Learning from others includes imitation of actions and mirroring of emotions. Learning about others, such as their group membership and reputation, is crucial for social interactions that depend on trust. For accurate prediction of others' changeable dispositions, mentalizing is required, i.e., tracking of intentions, desires, and beliefs. Implicit mentalizing is present in infants less than one year old as well as in some nonhuman species. Explicit mentalizing is a meta-cognitive process and enhances the ability to learn about the world through self-monitoring and reflection, and may be uniquely human. Meta-cognitive processes can also exert control over automatic behavior, for instance, when short-term gains oppose long-term aims or when selfish and prosocial interests collide. We suggest that they also underlie the ability to explicitly share experiences with other agents, as in reflective discussion and teaching. These are key in increasing the accuracy of the models of the world that we construct.

## Contents

INTRODUCTION.....	288	Reputation and Audience Effect.....	297
What Is Social About Social Cognition?.....	288	Tracking Mental States.....	298
The Importance of Comparative Studies.....	289	Tracking Other Points of View.....	299
The Importance of Implicit Processes.....	289	Tracking False Beliefs.....	299
LEARNING THROUGH OBSERVING OTHERS.....	291	COSTS AND BENEFITS OF LEARNING ABOUT OTHER MINDS.....	300
Learning About Places.....	291	The Dark Side of Mentalizing.....	300
Learning About Objects.....	292	Helping Behavior.....	300
Learning About Actions.....	292	Mutual Trust.....	300
Learning About Agents.....	292	EXPLICIT PROCESSES IN SOCIAL COGNITION AND THEIR MECHANISMS.....	301
NEURAL MECHANISMS OF LEARNING THROUGH OBSERVATION.....	293	Top-Down Modulation of Competing Implicit Processes.....	301
Association Learning.....	293	Executive Control of Social Cognition.....	301
Reward Learning.....	293	Verbal Instruction.....	302
Gaze Following.....	294	Teaching.....	302
Mirroring.....	294	SHARING EXPERIENCES: THE IMPORTANCE OF META-COGNITION.....	303
COSTS AND BENEFITS OF OBSERVATIONAL LEARNING.....	294	Reflective Discussion.....	303
Self-Interest and Copying.....	294	Reflective Discussion of Action Changes Behavior.....	304
Prosocial Effects of Copying...	295	Reflective Discussion of Sensations Creates a More Accurate Model of the World.....	304
Alignment.....	295	The Neural Basis of Meta-Cognition.....	304
Group Decisions.....	295	CONCLUSIONS.....	305
Group Identity.....	296		
LEARNING ABOUT OTHER MINDS.....	296		
Taking Account of Other Individuals.....	296		
Tracking Past Behavior to Predict Future Actions.....	297		

## INTRODUCTION

### What Is Social About Social Cognition?

Consider the red-footed tortoise. These are not social animals. They live lives of almost

complete isolation, apart from the brief interactions necessary for reproduction. And yet they can learn to perform a difficult detour task simply by observing an experienced conspecific (Wilkinson et al. 2010). Imagine a hive of bees. Bees are undeniably social animals.

Remarkably, their social behavior is governed by rules that allow them to share knowledge and make group decisions (Visscher 2007). Like the tortoise, human beings can learn a lot from simply observing others even when this behavior has no deliberate communicative intent and when social information is being used just like any other publicly available information in the environment (Danchin et al. 2004). But also, like bees, human beings cooperate and can make group decisions that are better than those made by individuals (Couzin 2009).

Gaining benefit by watching and interacting with conspecifics—and even other species—is widespread among animals, including humans (Galef & Laland 2005, Leadbeater & Chittka 2007). We review work that shows that by following others and by observing their choices it is possible to learn not only about places, but also about actions, objects, and other agents. This is very useful because by observing what happens to others, we can learn without experiencing potentially disastrous errors. We also discuss cognitive processes that enable deliberate communication, teaching, and cooperation but are beyond the capacities of tortoises and bees. These are processes that enable individuals to understand one another with a high degree of precision. They are often referred to as mentalizing or having a theory of mind. A largely implicit form of mentalizing is likely to be involved in perspective taking and tracking the intentional states of others, and this has been claimed for a variety of social animals as well as humans (e.g., Clayton et al. 2007). It is only the explicit form of mentalizing that appears to be unique to humans (see Apperly & Butterfill 2009 for a discussion of the two forms of mentalizing). We point out that explicit mentalizing is closely linked to meta-cognition: the ability to reflect on one's action and to think about one's own thoughts. This ability, we argue, confers significant benefits to human social cognition over and above the contribution from the many powerful implicit processes that we share with other social species. However, these abilities also have

emerged as the end result of a long evolutionary process.

## The Importance of Comparative Studies

Neural mechanisms, which have evolved to allow social interaction, need to be studied systematically across species, and most of this work still remains to be done. In this review we do not go into details of such mechanisms when pertinent reviews already exist. This is the case in particular for general learning mechanisms, which are also fundamental to social learning. These involve conditioning and associative and instrumental learning (see, e.g., Schultz 2008). This comparative approach to social cognition can identify processes in common across species. It can also help identify the nature of those processes that are dramatically more highly developed in humans.

We passionately believe that social cognitive neuroscience needs to break away from a restrictive phrenology that links circumscribed brain regions to underspecified social processes. Although we build on such links, as shown in **Table 1**, we are committed to the idea that it is necessary to develop a mechanistic account of these processes. In this review we provide some pointers toward such accounts.

## The Importance of Implicit Processes

One of the proudest achievements of human beings is the ability to reflect on themselves and their past, present, and future. This tends to obscure the fact that most of our cognition occurs automatically and without awareness. It comes as a surprise that even such sophisticated social processes as group decision and mentalizing can occur automatically and can happen without a deliberate attempt to achieve that decision, individually or collectively. Here we follow the tradition of cognitive psychologists who make a fundamental distinction between implicit (automatic, unconscious) processes and processes that generate explicit, conscious products (e.g.,

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**Mentalizing:** implicit or explicit attribution of mental states to others and self (desires, beliefs) in order to explain and predict what they will do

**Meta-cognition:** reflection on mental states, including own mental states (introspection); others' mental states (popular psychologizing); mental states in general (philosophy of mind)

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**Table 1 Neural mechanisms underpinning processes relevant to social cognition\***

	Mechanism	Relevant brain regions	Social processes
1. Reward learning	Updating estimated value of reward through prediction error signals, whether about primary reinforcers or money (e.g., Peters & Buchel 2010)	Ventral striatum	<i>Social rewards</i>
		Ventromedial PFC/ medial OFC	Smiling face (Lin et al. 2011)
			Gaining status (Zink et al. 2008)
			Gaining reputation (Izuma et al. 2010a)
			Agreement of others (Campbell-Meiklejohn et al. 2010)
			Being imitated (Schilbach et al. 2010)
			Observing mimicry (Kühn et al. 2010)
			Experiencing fairness & cooperation (Tabibnia & Lieberman 2007)
			Sight of cooperative person (Singer et al. 2004a)
			Reward for similar other (Mobbs et al. 2009)
			<i>Social modulation of reward value</i>
Object value affected by others (Campbell-Meiklejohn et al. 2010)			
Value of cooperation modified by knowledge of intentions (Cooper et al. 2010)			
2. Imitation			
Who to imitate	Orienting to agents and faces (Klein et al. 2009)	Posterior STS FFA and posterior STS	Perception of biological motion (Puce & Perrett 2003) Facial identity & eye gaze (Hoffman & Haxby 2000)
How to imitate	Linking observed to executed behavior via associative learning (e.g., Heyes 2011)	IFG and IPL ACC and anterior insula Lateral interparietal area	Mirroring action (Rizzolatti & Craighero 2004)
			Mirroring emotion (Singer et al. 2004b) Gaze following (Shepherd et al. 2009)
When to imitate	Representing the value of social information	LIP	Signaling value of gaze following (Klein et al. 2008)
3. Tracking intentions	Predictive coding: updating estimated intention through prediction, error signals relating expected to observed behavior (e.g., Kilner et al. 2007)	pSTS/TPJ (and mPFC)	<i>Implicit mentalizing</i>
			Monitoring own actions (Miele et al. 2011)
			Monitoring others' actions (Pelphrey et al. 2004, Saxe et al. 2004)
			Monitoring others' trustworthiness (Behrens et al. 2008)
			Monitoring others' generosity (Cooper et al. 2010) Monitoring influence on others (Hampton et al. 2008)
4. Supervisory system	Top-down biasing of competition between low-level processes (Beck & Kastner 2009)	dlPFC	Overcoming race prejudice (Cunningham et al. 2004)
			Overcoming response to unfairness (Kirk et al. 2011)
			Overriding trial-and-error learning of reputation by instructed knowledge (Li et al. 2011)
		dlPFC and ACC	Managing conflicting information about emotional states (Zaki et al. 2010)

(Continued)

**Table 1 (Continued)**

	Mechanism	Relevant brain regions	Social processes
5. Meta-cognition	Reflection on our knowledge about the mental states of self and others (Perner & Lang 1999)	mPFC	Explicit mentalizing or theory of mind (Van Overwalle 2009)
			Intentional stance (Gallagher et al. 2002)
			Mentalizing stance (Hampton et al. 2008)
			Impression formation (Mitchell et al. 2006)
	Reflection on communication		Monitoring own reputation (what others think of us) (Bengtsson et al. 2009, Izuma et al. 2010b)
			Communicative signaling (Kampe et al. 2003)
Estimation of the reliability of our knowledge (Lau 2007)	Anterior PFC (BA10)	Judgment of perception (Fleming et al. 2010)	
		Judgment of agency (Miele et al. 2011)	
	mPFC	Judgment of strategy of others (Coricelli & Nagel 2009)	
		Uncertainty about partner's strategy (Yoshida et al. 2010)	

\*This table is organized in terms of mechanisms and processes rather than brain regions. We have restricted our list to five mechanisms for which there is some evidence of the specific neural processes involved. We attempt to specify the mechanisms through connected brain systems rather than circumscribed brain regions. However, at this stage our knowledge is so limited that we still end up with list of brain regions. Note that since we are emphasizing mechanisms rather than localized functions, the same brain region is sometimes linked with more than one mechanism. The social processes that are enabled by the five selected mechanisms are listed in the right hand column.

Abbreviations: ACC, anterior cingulate cortex; dlPFC, dorsolateral prefrontal cortex; FFA, fusiform face area; IPL, inferior parietal lobe; mPFC, medial prefrontal cortex; OFC, orbital frontal cortex; pSTS, posterior part of the superior temporal sulcus; TPJ, temporo-parietal junction; vmPFC, ventromedial prefrontal cortex; vSTR, ventral striatum.

Kahneman & Frederick 2002). Many recent reviews of social cognition have emphasized the same distinction (Adolphs 2009), although it is by no means straightforward to categorize behavior in this way (Heyes 2011).

Explicit processes can be recognized through their interference with currently ongoing activity. Implicit processes can be recognized when people cannot report the stimulus that elicits their behavior or are unaware of the behavior that is elicited. However, many cognitive abilities that seem so evidently “explicit” actually work just as well without awareness, as shown, for instance, in Dijksterhuis’s (2006) study of complex decision making. Furthermore, the study of explicit processes in nonhumans is extremely difficult (see the thoughtful discussion of this problem in relation to the study of declarative memory by Murray & Wise (2010). We certainly cannot

assume that explicit cognition is unique to humans.

## LEARNING THROUGH OBSERVING OTHERS

### Learning About Places

Fish are among the many animals that learn about the location of food by observing the behavior of others. Here is an example. An individual, isolated nine-spined stickleback learns that food can be found on the left side of a tank (private information) and will therefore swim to the left when given the choice. But, after a delay of seven days, if he can observe other fish feeding on the right side of the tank (public information), he will swim to the right (van Bergen et al. 2004). This is presumably because the private information the fish has about food

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**pSTS:** the posterior part of the superior temporal sulcus

**FFA:** fusiform face area

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being on the left is now too old and unreliable. Examples of social influence on foraging behavior can be observed in many other animals (Galef & Giraldeau 2001), including humans.

A related process is gaze following, through which we automatically look at the place toward which someone else is looking. This example of social influence has been demonstrated in ravens, goats, dogs, and primates (reviewed in Zuberbühler 2008). **Gaze following is reliably used by human infants to learn about objects and events from around one year of age** (Flom & Johnson 2011). In adult humans, gaze following seems to be automatic, in the sense that people follow the gaze of another person even when this behavior runs counter to their intentions. Bayliss & Tipper (2006) used a target-detection task to show that individuals would follow the gaze of another person even when that person persistently looked in the wrong direction. Intriguingly, although participants were unable to stop themselves in their gaze following and were unaware of the contingency, they did register a socially relevant fact: They rated the person who looked in the wrong direction as less trustworthy.

### Learning About Objects

Animals need to distinguish between nice objects that should be approached and dangerous objects that should be avoided. Here again, learning commonly occurs through observation. For example, in a series of experiments, Mineka and colleagues have demonstrated that rhesus monkeys acquire a fear of snakes very quickly by observing another monkey showing fear toward a snake (see, e.g., Mineka & Ohman 2002). Fear conditioning through observation has also been demonstrated in humans (Olsson et al. 2007). But learning about objects is not just restricted to fear conditioning. For example, objects looked at by other people are preferred more than objects that do not receive attention (Bayliss et al. 2006).

### Learning About Actions

Many animals learn which actions to perform by observing others (Huber et al. 2009). For

example, chimpanzees will imitate a demonstrated sequence of actions to gain access to food in a puzzle box (see Whiten et al. 2009). Wild mongoose pups learned, by observing an adult, to open plastic containers of food (modified Kinder eggs) by either smashing them on the ground or biting them (Müller & Cant 2010). Both actions are equally effective at getting access to the food inside the container. However, the action chosen by the pups was determined by what they saw the adult do. Such **imitative learning** can also be seen in human infants from around the age of one year (e.g., Carpenter et al. 1998). By this age infants will imitate both instrumental and arbitrary actions when they see an adult interacting with a novel object. For example, they quickly learn that they can press buttons on remote controls and phones with remarkable ease.

### Learning About Agents

How do animals distinguish agents from objects? Agents move of their own intention and have motion patterns that are different from moving physical objects. Specific brain structures in the temporal lobe are involved in detecting this difference. Thus, in humans, perception of biological motion is subserved by a circumscribed brain region, the posterior part of the superior temporal sulcus (pSTS; Puce & Perrett 2003; see **Table 1**), and the ability to distinguish this motion from other kinds of motion is exquisitely tuned.

Over and above detecting animacy, animals need the ability to detect agents who might be friend or foe. This is critical for survival even immediately after birth. One would therefore expect to see specially adapted neural mechanisms that require little if any learning. Indeed, newly hatched chicks exhibit a spontaneous preference for biological motion patterns, and this mechanism facilitates imprinting (Vallortigara et al. 2005).

Agents also typically have faces, and their eyes give cues to what they are interested in. A posterior region of STS is specialized for analysis of facial movements, while invariant



aspects of faces are analyzed in the fusiform gyrus [fusiform face area (FFA)] (Haxby et al. 2000; see **Table 1**).

Another important cue to agency is contingent responding. Human infants and adults alike are likely to treat a shapeless object as being animate if the object moves or makes noises that are contingent on their own actions (Johnson 2003). Learning about other individuals and how to interact with them is vital for all social animals. This is most particularly relevant for mate choice. Naïve female fruit flies will choose as partners male flies they have seen mating with experienced females (Mery et al. 2009). Effects of observation on mate choice are also seen in guppies and quail (White 2004).

Well-disposed agents need to be distinguished from those who are not. Pre-verbal human infants (aged 6 to 10 months), after observing agents interacting with each other, prefer those who help others to those who hinder others (e.g., Jacob & Dupoux 2008). Learning about the status of conspecifics is also important for knowing whom to approach and whom to avoid. Many animals can infer social rank by observation alone. For instance, fish learn whom not to pick a fight with through observation (Grosenick et al. 2007).

## NEURAL MECHANISMS OF LEARNING THROUGH OBSERVATION

### Association Learning

It seems plausible that learning through observation (see **Table 1**) could be built from the basic mechanisms of association learning (Catmur et al. 2010). Mineka & Cook (1993) report that the model monkey's behavior on seeing a snake elicits fear in the observer monkey. For the observer monkey, the fear response of the model monkey acts as an unconditioned stimulus (through emotional contagion) and elicits the fear response. Through classical conditioning the snake becomes associated with the fear response in the observer monkey. Note, however, that classical conditioning has strict limitations

forged by evolution (Breland & Breland 1961). Thus, a potentially dangerous thing like a snake readily triggers conditioning of the fear response in the observer monkey but an innocuous flower does not (Cook & Mineka 1989).

Fear conditioning through observation in humans presumably uses the same mechanism (Olsson & Phelps 2004). It can occur even when the conditioned stimulus is presented subliminally, which suggests that the learning depends on an implicit process. Indeed, we suspect that most, if not all, of the learning processes we have discussed so far are examples of implicit processes.

### Reward Learning

Conditioning mechanisms can be applied to other kinds of social learning through observation. We know that places and objects acquire value through being associated with reward. We go to the places and approach the objects with the highest value. A simple extension of this mechanism would entail that places and objects should gain value if they are approached by others and lose value if they are avoided by others. Evidence for such a simple model comes from the finding that in many species including fish and rodents, the probability that an observer will adopt a particular behavior increases monotonically with the proportion of potential models exhibiting that behavior (Pike & Laland 2010).

Social learning seems to involve the same neural systems as nonsocial reward-based learning. Lin and colleagues (2011) have shown that learning for social rewards involves the same neural system as learning for money, with values being represented in ventromedial prefrontal cortex (vmPFC) and reward prediction errors being represented in the ventral striatum (vSTR). Furthermore, this same reward-learning system is activated when we see others choosing the objects we like. Neural signals in this system that reflect how much we value an object increase when we know that others also value this object (Campbell-Meiklejohn et al. 2010; see **Table 1**).

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**vmPFC:**  
ventromedial  
prefrontal cortex

**vSTR:** ventral  
striatum

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**Imitation:** used in automatic learning by observation, including repeating the actions (mimicry) and aiming for the goals of another agent (emulation)

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## Gaze Following

Investigations of the neural basis of gaze following indicate something of the complexity of the mechanisms involved when we imitate actions (Klein et al. 2009). At least three highly automatic components are necessary. The observer must first recognize an agent and orient toward the face and eyes. This is probably mediated by a long-established subcortical route. The observer must then work out the target of the gaze from the position of the agent's eyes. It is not sufficient simply to imitate the eye movement since the observer and the agent have different viewpoints. The lateral intraparietal area (LIP), a brain region previously linked to attention and saccade planning, is likely to have a role in this computation. Mirror neurons have been located here, which fire when a monkey looks in the preferred direction of the neuron and also when observed monkeys look in this direction (Shepherd et al. 2009). In addition, the observer must believe that gaze following is likely to lead to a valuable outcome. Here again LIP neurons seem relevant because they signal the value of social (and nonsocial) information, but only when this information is relevant to decisions about orienting (Klein et al. 2008).

## Mirroring

The aspect of learning through observation that has been most extensively investigated at the neural level relates to action. When we learn about actions from observing others, we are effectively learning to copy them. Forms of copying are often referred to as imitation, mimicry, and emulation, each emphasizing different aspects of copying a model. The process underlying these forms of copying has recently been reinterpreted as a direct result of a specifically social neural mechanism associated with mirror neurons. Rizzolatti & Craighero (2004) were the first to identify such neurons in the ventral premotor cortex (F5) of the rhesus monkey. Although there is still some controversy about the role of this mechanism as a facilitator or a product of imitation (Heyes 2001), the

discovery of mirror neurons has had a major impact on our understanding of the nature and role of imitation. The tendency to imitate the actions of others is likely to be automatic. This is shown by the finding that a high working-memory load facilitates rather than hinders behavioral imitation (van Leeuwen et al. 2009). Nevertheless, imitation can be controlled in a top-down fashion, and we do not imitate the actions of everyone we observe (Spengler et al. 2010).

Perceiving an emotional response of another person elicits the same emotional response in ourselves. This is also called emotional contagion and allows us to share the emotion of the person we are observing (de Vignemont & Singer 2006), a prerequisite of empathy. Emotional contagion supplies a basic conditioning mechanism through which we can learn from others on the basis of their emotional expressions.

## COSTS AND BENEFITS OF OBSERVATIONAL LEARNING

### Self-Interest and Copying

How important is observational learning in comparison with nonsocial alternatives such as trial-and-error learning? Laland and colleagues (Rendell et al. 2010) assessed this question by means of a computer tournament in which participants proposed strategies for combining learning by observation (copying) with learning by direct experience (trial and error) in order to acquire adaptive behavior in a complex environment. The most successful strategy relied almost exclusively on copying. Why was copying so successful in this context? First, the observer avoids having to make errors that are an essential part of trial-and-error learning. In addition, demonstrators selectively perform the actions that they have found to be most beneficial for themselves. Therefore, they effectively and inadvertently act as a filter to provide the information that is most useful for an observer. Copying is a highly adaptive means of gaining knowledge (Rendell et al. 2010).



## Prosocial Effects of Copying

While learning from observation can serve purely short-term self-interest, contagion and copying can also bias us toward the long-term interests of our group (which also serves self-interest). This effect is seen in experiments that reveal subtle effects of copying. If we are covertly mimicked, we tend to like that person. Furthermore, we become more helpful to people in general (van Baaren et al. 2004). Similar effects have been demonstrated in monkeys, who are more likely to approach and share food with an imitator (Paukner et al. 2009). These effects are likely to be unconscious. In contrast, when people are aware that they are being imitated (see Bailenson et al. 2008), they experience high levels of discomfort and thus the prosocial effects do not occur. At the neural level there is evidence that mimicry is rewarding. When we observe someone else being imitated, activity increases in reward-related regions such as vmPFC (Kühn et al. 2010). When others choose the same song that we have just chosen ourselves, because we liked it, a reward area of our brain is activated. Furthermore it is exactly the same area in the vSTR that is activated when we actually receive the desired song (Campbell-Meiklejohn et al. 2010). Thus, there is reward in being endorsed by others, and this may result in reinforcing group-oriented behavior and conformity.

When is it a good idea to stop learning by observation and learn instead by trial and error? This will depend upon an implicit cost-benefit analysis. As long as our own knowledge is sufficient for achieving success (e.g., knowing the location of a food source), we will continue to exploit that knowledge. Once that knowledge becomes unreliable (e.g., the food source at that location is depleted), we switch to learning by observing others. Finally, when the knowledge acquired by observation becomes unreliable, we start to explore innovative choices on our own (Laland 2004). This is an extension into the social world of the exploit/explore dichotomy developed in models of reinforcement learning (Sutton

& Barto 1998). In observational learning, this may become a trichotomy of exploit own knowledge–exploit others’ knowledge–explore.

## Alignment

A necessary consequence of learning by observation is the formation of behavioral similarity across a population. This is most obviously the case when learning about actions. When we interact with others, we often automatically imitate their behavior (Chartrand & Bargh 1999). In the case of verbal interactions this alignment can occur at many levels. During a productive discourse, speakers will automatically tend to align their posture, their speech rate, their choice of words, and their syntactic forms (Garrod & Pickering 2009). This alignment enhances communication (e.g., Adank et al. 2010). But language does not always have to be involved. Alignment has a similar advantage for any joint action, where two players need to coordinate their behavior (Sebanz et al. 2006). Alignment in synchronized tapping can be manifest in mutual adjustments occurring at the level of 1 or 2 ms (Konvalinka et al. 2010).

## Group Decisions

Social insects, such as ants and bees, make successful group decisions by collating information from several individuals (Couzin 2009). One way in which such group decisions can be achieved relies on learning through observation, e.g., the process through which a swarm of honeybees uses information from scouts to locate a new nesting site (Visscher 2007).

The mechanism by which a group decision can be made in the absence of any central coordination is an example of the more general principle of herding, through which complex group behavior can emerge from simple local interactions, which can occur automatically and without awareness (Raafat et al. 2009). In humans, Dyer and colleagues (2008) have shown how a few informed individuals, the equivalent of scouts in the case of bees, can guide a group to

a target without verbal communication or any obvious signaling.

## Group Identity

There is a value to learning about people as types as opposed to people as individuals. It provides prior knowledge to guide our behavior when confronted with someone we have never met before. Inevitably, this prior knowledge feeds into stereotypes and prejudices, and these play a major role in in-group cohesion and, conversely, in out-group hostility.

A child might observe her mother being gracious when approached by a member of an in-group and ungracious when approached by a member of an out-group. Thus, through emotional contagion, human infants can learn to favor members of the in-group. The use of stereotypes is already present by age three (Hirschfeld 1996). At the neural level, prejudice and stereotyping are likely to be underpinned by brain areas associated with evaluative processing (vmPFC and amygdala; Quadflieg et al. 2009). As mentioned already, conformity itself is rewarding and thus may provide a basis for both producing and confirming stereotypic behavior (Richerson & Boyd 2001).

Of great relevance for the study of group conformity is “overimitation.” Children and chimpanzees have been studied when they learn, by observation, how to open a puzzle box to get a reward. The model in these studies performs additional actions that are irrelevant for getting to the reward. Nevertheless, children of three to five years persist in imitating the irrelevant actions, even in situations when there are countervailing task demands and even in the face of direct warnings (Lyons et al. 2011). Adults perform the task with even more emphasis on conformity with the irrelevant actions (McGuigan et al. 2011). Chimpanzees, on the other hand, are much less likely to imitate the irrelevant components of the action and go to the reward as quickly as possible (Horner & Whiten 2005). The faithful copying of actions, which overrides getting a primary reward

by other means, is a striking feature of human culture and provides a means for creating distinct group identities, emphasizing not so much what we do but rather the way we do it.

## LEARNING ABOUT OTHER MINDS

### Taking Account of Other Individuals

Arguably the most important and valuable aspect of social cognition is learning about other agents not just as types but also as individuals. Stereotypes often result in inaccurate predictions and do not take account of changeable predispositions. The relevant cognitive processes in dyadic interactions have been extensively investigated by social psychologists, and an account of their likely neural basis can be found in a review by Liebermann and colleagues (2002). Here we consider changeable attributes of others, such as their current status and their beliefs, knowledge, and intentions, all attributes that need to be continually updated.

How is it possible to keep track of the status of several individuals at the same time? The term “keeping track of” is a spatial metaphor. However, it may actually reflect the evolutionary origins of the mechanism involved. Many animal species, including, for example, monkeys and dolphins, emit sounds as they move about in groups, foraging for food (see Boinski & Garber 2000 for many examples). It is important for their survival that everyone in the group keeps in close contact, but they cannot necessarily see each other. The problem can be solved if all the group members emit frequent calls. If these calls are sufficiently individualistic, then each member of the group knows roughly where the other individuals are. The implication of this idea is that each individual has an internal map of the relative locations of the other members of the group that is continually updated.

A similar principle can be applied to aspects of individuals in the group other than their positions in space. For example, the relative status of the individuals in a group can be represented

spatially by distances along a line. For humans at least, status does seem to be represented this way. Differences in both numerical magnitude and social status scale with activity in the inferior parietal cortex (Chiao et al. 2009). Knowledge of status also helps us to keep track of who is currently allied with whom (Fiske 2010). We also need to keep track of who has the most relevant knowledge. Young children at first are mainly concerned with learning by observing their parents, whom they trust implicitly. However, from about age eight, they switch to copying the local expert instead (Henrich & Broesch 2011).

### **Tracking Past Behavior to Predict Future Actions**

The human face provides many clues as to how a person will behave. First there is the emotional expression that is reflected in the continually changing configuration of a face. From this information we can tell whether a person is fearful or happy even if we have never met that person before. Many studies have now demonstrated that this can happen in the absence of any awareness of the expression (e.g., Dimberg et al. 2000). Another kind of information can also be inferred from the faces of unfamiliar people through fixed configurations of the face, such as the width of the jaw. This information relates to dispositions such as dominance and trustworthiness (Oosterhof & Todorov 2008).

The third kind of information relates to the faces of people we know. When we recognize that this is the face of Fred, we know from past experience with this individual how he is likely to behave. Through our interactions we continually update this knowledge, and it is our knowledge of the person that is more important than his facial appearance (Todorov et al. 2007).

There is some validity to the beliefs we have about the personality of our friends. There is much greater agreement between close acquaintances about the personality traits of an individual (and with the individual's self-ratings) than between strangers who have interacted

with the individual only once (Funder & Colvin 1988). This ability may depend on association learning mechanisms through which we locate everyone we know in a "personality space," with these locations being continually updated (Todorov 2011).

We also implicitly learn from subtle cues in social interactions. Imagine playing the game of stone-paper-scissors. In some cases, the behavior of your opponent enables you to predict what his response would be. For example, a very brief eyebrow movement might consistently precede the choice of stone. Participants can learn to use such a cue because it makes them more likely to win on these trials (Heerey & Velani 2010). This effect was observed even when participants had no idea which cue had been predictive, as revealed in a debriefing session after the game.

Learning about people can certainly occur without awareness (see also Todorov & Uleman 2003). Such learning is likely to be procedural and semantic (i.e., association learning) rather than episodic. This is suggested by the observation that patients with amnesia associated with hippocampal damage can still acquire person knowledge, but only if the damage does not extend into the amygdala and the temporal pole (Todorov & Olson 2008).

There is also some evidence that person knowledge is accessed automatically whenever we see a familiar face (Todorov et al. 2007). If a particular kind of behavior has been associated with a particular face, then the mere presentation of that face elicits stronger brain activity compared with a novel face. Such activity was observed in anterior paracingulate cortex and the STS regardless of the nature of the specific behavior associated with the face. We speculate that this reflects taking an intentional stance toward people we know (see **Table 1**). As yet, however, we lack models of how person representations are rapidly updated in the brain.

### **Reputation and Audience Effect**

Species whose interactions are characterized by indirect reciprocity benefit from keeping track

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**Audience effect/  
reputation  
management:**

behavior of agents to indicate that they are cooperative and trustworthy while being observed

**mOFC:** medial orbitofrontal cortex

**mPFC:** medial prefrontal cortex

**TPJ:** temporo-parietal junction

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of reputation. They are more likely to cooperate with a partner who has a reputation for cooperativeness. For example, clients of the reef cleaner fish, *labroides dimidiatus*, eavesdrop on cleaning sessions and spend more time next to cleaners known to be cooperative. Furthermore, the cleaners behave more cooperatively when they are being observed (Bshary & Grutter 2006).

The audience effect means that we behave differently when we believe ourselves to be observed. For example, to ensure that others will continue to cooperate with us we need to maintain our own reputation for being cooperative (Tennie et al. 2010). Cooperative behavior rapidly declines in trust games where the players are anonymous (Milinski et al. 2002). Under conditions of anonymity, there is no longer any need to guard one's reputation. On the other hand, a watching pair of eyes, even in the form of a photograph, is sufficient to increase prosocial behavior (Bateson et al. 2006). This is presumably an automatic effect because people would be well aware that a photograph cannot record their behavior or damage their reputation.

The evidence for audience effects in cleaner fish suggests that these effects need not depend upon complex cognitive processes. However, such high-level processes are likely to have an additional role in humans (Bshary & Bergmuller 2008). Social psychologists have long studied the processes by which the presence of an audience improves performance (Zajonc 1965). This may in part be due to an increase in arousal when others are present, but there is also evidence that the presence of others increases reflective self-focus and attention to ideal behavioral standards (Carver & Scheier 1981).

How do humans keep track of the trustworthiness of others? This question has been investigated using economic games, such as iterated prisoner's dilemma or trust games. These studies show that the brain's reward system [vSTR and medial orbitofrontal cortex (mOFC)] (see **Table 1**) is activated by reciprocated cooperation (Rilling et al. 2004) and also by fair behavior (Tabibnia et al. 2008). Participants in

the study of Phan and colleagues (2010) rapidly learned about the cooperativeness and fairness of the people they were playing with during a trust game involving iterative exchanges. Positive reciprocity robustly activated vSTR and mOFC. In an earlier study by Singer and colleagues (2004a) using a similar paradigm, the mere presentation of the face of a cooperative partner elicited activity in reward areas. Izuma and colleagues (2010b) scanned participants while they made self-disclosures. Activity in medial prefrontal cortex (mPFC) during self-disclosure was greatly enhanced by the presence of an audience, as was activity in vSTR.

It seems plausible from these observations that we keep track of others' reputation for cooperativeness on the basis of the same fundamental learning mechanisms that we use to learn about objects. Behrens and colleagues (2008) specifically investigated the mechanism by which we update this knowledge. This was a learning study, where a human advisor provided information about where a reward was likely to be found. However, the reliability of the advice was continually varied. The results suggest that the same computational mechanism was engaged for tracking the location of the reward as for tracking the reliability of the advisor: associative learning updated through prediction errors. However, whereas prediction errors associated with reward learning were associated with activity in the vSTR, those relating to social learning were associated with activity in mPFC and temporo-parietal junction (TPJ), regions previously associated with mentalizing (i.e., the ability to attribute mental states to others) (Van Overwalle 2009; see **Table 1**).

## Tracking Mental States

Although experience of their past behavior can help us to predict what people are likely to do next in various situations, we can do better. It is extremely useful to know something about their current intentions, desires, knowledge, and beliefs. Because these mental states are variable, keeping track of them enhances the accuracy of

our predictions. For example, people will not reach for something they cannot see, and their actions will be determined more by what they know, i.e., believe to be the case rather than what is actually the case. Thus, for successful interactions, it pays to keep track of people's continually changing inner states relating to their goals and their knowledge. There is increasing evidence that keeping track of these mental states also occurs automatically and without the need for awareness.

### Tracking Other Points of View

Samson, Apperly, and their colleagues (2010) have shown that observers were slowed down when they had to report the number of dots visible to them in the presence of another agent who could not see all of these dots. In fact, the other agent was an avatar placed in a schematic room with variable numbers of dots on its walls. This result suggests that we automatically take note of the fact that others may have knowledge that differs from our own knowledge due to their different point of view. The idea that this process is automatic was confirmed by a subsequent experiment looking at the effects of cognitive load (Qureshi et al. 2010). Here, the addition of a cognitive load did not stop participants from automatically taking note of the avatar's perspective. However, cognitive load did impair participants' capacity to switch between their own and the avatar's perspective when they were explicitly required to do so. Remarkably, while we automatically keep track of the knowledge of others, it requires cognitive effort to deliberately take their perspective. Awareness into this deliberate process dawns between the ages of two and four years (Flavell 1992).

### Tracking False Beliefs

There is evidence that it is possible not only to automatically keep track of what other people see but also what they (invisible to the eye) believe. The critical insight here is the recognition that people's behavior is determined by their beliefs rather than by physical reality,

even if this belief happens to be false. This insight is a result of mentalizing or having a theory of mind. Although the latter label suggests a conscious process, it is important to bear in mind that there is both an implicit and an explicit version of theory of mind, and this is why we prefer the term mentalizing. Why is it useful to track other people's beliefs about the state of the world? This knowledge allows you to predict what they are going to do much better than if you used your own belief about the world. Children from around the age of four to six years are aware that own beliefs and others' beliefs of the same state of affairs can be interestingly different (Wellman et al. 2001). They can also work out implications. With greater experience, adolescents and adults are increasingly able to manipulate other people's beliefs, for instance through persuasion or deception.

There is now evidence that already in the first and second year of life infants have an implicit recognition of false belief (Kovács et al. 2010). These results suggest that infants (and adults) automatically note when someone has a different belief from themselves. There is also increasing evidence for the ability to keep track of the knowledge of others in nonhuman animals including birds (e.g., Bugnyar 2011), although there is still controversy to what extent this is the case for chimpanzees (Call & Tomasello 2008).

As yet we know very little about the physiological underpinnings of the implicit processes by which we keep track of the mental states of others. There is a large literature on mentalizing tasks implicating mPFC and TPJ/pSTS (e.g., Van Overwalle 2009), but all of these studies involve explicit processes. There are also several studies on visual perspective taking. Many of these also implicate TPJ (see Spengler et al. 2010 for a useful review of links between perspective taking and mentalizing) but, here again, only for explicit processes.

The mechanisms underlying mentalizing are likely to involve the same predictive coding principles as are involved in vision (Kilner et al. 2007). On the basis of an estimated intention, the behavior of the agent is predicted. The



estimated intention can then be updated on the basis of prediction errors. Activity in pSTS reflects such prediction errors (e.g., Behrens et al. 2008). Mechanisms that support explicit forms of mentalizing probably differ from those involved in implicit forms, but systematic distinctions between these forms have yet to be delineated (Apperly & Butterfill 2009).

## **COSTS AND BENEFITS OF LEARNING ABOUT OTHER MINDS**

### **The Dark Side of Mentalizing**

Corvids, who show implicit mentalizing, use this ability in selfish and antisocial ways: Its main purpose seems to be to avoid sharing food with other corvids (Clayton et al. 2007). There are many parallels in human societies. Getting the better of others through scheming and lying is typical for human societies, and Machiavellianism has been used to describe the main outcome of mentalizing (Byrne & Whiten 1988). However, at the same time, mentalizing abilities, both implicit and explicit, are used in the service of reciprocal communication and cooperation.

### **Helping Behavior**

Helping is extremely widespread among social animals and does not depend on keeping track of others' mental states. However, human infants show evidence of a more refined and flexible helping behavior. For example, infants of 18 months spontaneously helped an adult by opening a cupboard door when the adult's hands were full (Warneken & Tomasello 2006). Chimpanzees also showed some evidence of this kind of helping behavior, but in a much reduced form. In another study, Liszkowski et al. (2007) showed that infants age 12 months would point more often to an object whose location an adult did not know than to an object whose location was known. Again, such helpful actions depend upon infants keeping track of what others know.

## **Mutual Trust**

One of the main socially beneficial effects of keeping track of other minds is enhanced and flexible cooperation. As predicted by formal evolutionary theory (Axelrod & Hamilton 1981), we seem to expect, at least to start with, that our partner in a game will be cooperative (Andreoni & Miller 1993). Furthermore, if trust can be established, then players will do better. The mechanism underlying trust building through tracking of partners' intentions to cooperate has been studied using the model of Rousseau's stag and rabbit hunt game (Skyrms 2003). In this game a small reward is gained by catching a rabbit, and this can be obtained regardless of what the other person does. A much bigger reward can be obtained by catching a stag, and this reward is obtained only if both partners choose to cooperate. But there is always the risk that one partner will not cooperate. Successful cooperation in this game depends upon players making inferences about the beliefs of their partner and also making inferences about what their partner believes about them, e.g., they believe that their partner will cooperate when their partner believes that they will cooperate. This is an example of the recursive process that seems to lie at the heart of many human social interactions.

According to a recently developed computational model of this game, players need to estimate the depth of inference being made by their partner in order to optimize success (i.e., achieve cooperation; Yoshida et al. 2008). This suggests that the model is also relevant to reciprocal communication. We have referred to this as "closing the loop" (Frith 2007). Reciprocal communication plays an important role in teaching, as both teacher and learner need to keep track of the differences in their state of knowledge. However, whether these processes are implicit or explicit remains to be determined. A scanning study (Yoshida et al. 2010) found that activity in mPFC was related to participants' uncertainty about their partner's depth of inference. We believe that the approach offered by computational



functional magnetic resonance imaging using models such as the one applied to the stag hunt game could lead to a much more precise formulation of the role of the brain regions involved in mentalizing.

## EXPLICIT PROCESSES IN SOCIAL COGNITION AND THEIR MECHANISMS

Clearly, many processes associated with social cognition occur automatically and without awareness. We have shown that these are typically present in many species including humans and are also present in very young human infants. What is there left to do for explicit processes? We suggest a particular role for explicit processes in fostering social interactions, which may be unique to humans. These processes are characterized not simply by awareness but also by reflective awareness. By this we mean the meta-cognitive ability to think about our thinking. We argue that it is through reflective awareness that humans manage to outstrip the performance of other social species.

### Top-Down Modulation of Competing Implicit Processes

It is a truism that our senses are bombarded by many signals, from which just a few must be selected for controlling our actions. This selection can be achieved bottom-up by direct competition between the many different signals. However, it can also be achieved top-down by prior biases that are applied to some signals and not to others. This is the biased competition model, whose neural basis has been analyzed in some detail (see Beck & Kastner 2009). The same principles as apply to physical information about the world also apply to social information.

### Executive Control of Social Cognition

There is continual competition between the various implicit processes relevant to social interactions, such as self-interest versus group

interest or short-term gain versus long-term gain. This competition can also be biased by top-down, executive processes.

One important role for these executive processes is to overcome biases such as race prejudice. We all tend to have an implicit fear of out-group members (Phelps et al. 2000) and fail to show empathy for people in the out-group (e.g., Avenanti et al. 2010). For example, if white observers are shown the faces of unknown black people for 30 ms, activity is typically elicited in the amygdala. That this result occurs with such a short presentation time suggests that the processing of the face occurs without awareness. Furthermore, the amygdala activity is correlated with measures of the strength of the observer's implicit race prejudice. However, if the faces are shown for 525 ms, then activity is elicited in dorsolateral prefrontal cortex (dlPFC), and the amygdala response is reduced (Cunningham et al. 2004). This result suggests that explicit executive processes, instantiated in frontal cortex, can modulate the automatic evaluation of people.

More direct evidence for a role for executive processes in resolving conflicts between different social processes comes from a study by Zaki and colleagues (2010). Participants were scanned while making inferences about the emotional states of agents. Relevant information was available from two sources: silent video clips of people depicting positive or negative autobiographical events and written sentences describing such events. The idea was that the video clips would activate the brain's mirror system while the sentences would engage the brain's mentalizing system. The pattern of brain activity associated with these different cues confirmed this expectation. In the incongruent condition, activity was elicited in areas associated with executive control [dlPFC and anterior cingulate cortex (ACC)], and there was also evidence that this control was associated with biasing toward a participant's preferred source of information. These results demonstrate that social processes are subject to top-down executive control using the same mechanisms as nonsocial processes (see Table 1).

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**dlPFC:** dorsolateral prefrontal cortex

**ACC:** anterior cingulate cortex

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**Ostensive gestures:** deliberately signaling the intention to communicate; signals can be verbal (call, prosody) and nonverbal (look, touch)

## Verbal Instruction

Just as we can learn by observing others, we can also learn from what others tell us. Work from Milinski's group shows that **reputation, conveyed through word of mouth, can have a strong effect on group behavior.** In a trust game an effect was found even when participants could access the same information by direct observation (Sommerfeld et al. 2007). The same effect can be observed at the neural level. Delgado and colleagues (2005) found that participants would make more risky investment choices with partners when they had been told that the partners had a good reputation. In addition, in this case the activation in the caudate nucleus that normally reflects whether the partner cooperates or defects on a trial-by-trial basis was significantly reduced. The indirect spreading of information about others is known as gossip and is an important part of human communication (Spacks 1982). **It seems that gossip reduces our reliance on the feedback mechanisms underlying trial-and-error learning, as is typical of a top-down mechanism (Li et al. 2011).**

Verbal instruction can also affect how we respond to objects, not just people. The instruction "When you see the blue square, you will receive at least one shock" is sufficient to induce fear of the blue square. But, in this case, the feared object does not elicit a response when presented subliminally (Olsson & Phelps 2007). **It seems that learning through verbal instruction depends upon explicit top-down brain processes.** These do not establish an automatic response to objects that we believe to be threatening but of which we have no direct experience.

## Teaching

Most human learning arguably occurs through deliberate teaching rather than mere observation and is greatly dependent on the use of language. **However, the human advantage of learning from a teacher extends even to situations in which language is not involved.**

Teaching, in a broad sense understood as actively helping a learner to benefit from

the teacher's experience, has been observed in a variety of animals including ants and bees (Hoppitt et al. 2008). Meerkats provide a vivid example (Thornton & Clutton-Brock 2011). To kill and eat a scorpion without being stung requires considerable skill. So the mother prepares this food in line with her pups' gradually increasing abilities. At first, mothers find and kill scorpions, then bring them to the pups. As the young meerkats grow up, their mothers disable the scorpions rather than killing them. They remove their deadly sting and then present the live scorpion. Through such teaching, the young meerkats eventually learn to kill a scorpion. This kind of instruction does not depend on keeping track of constantly changing mental states. Instead it is finely attuned to the **physical states** of the pups, which are signaled by the pitch of their vocalization. It is this **vocalization** that triggers the adult's food preparation behavior.

**We would argue that in humans the continuous tracking of mental states enables a more flexible type of instruction (referred to as natural pedagogy; Csibra & Gergely 2006).** In adult-child interactions in particular, deliberate and explicit teaching occurs, with both adult and child knowing when teaching is intended. This usually involves **ostensive gestures, such as eye contact or the high-pitched speech mode of "motherese" (Senju & Csibra 2008).** In such interactions the child is not simply learning by observation. A **shared intention** has been formed between the adult, the child, and—importantly—also the object of their intention. Intriguingly, we all expect, infants included, that we are taught something important about the object, not about a fleeting and precise moment of interpersonal interaction. In this way we are continuously teaching each other and learning from each other about the world.

**Teaching here is a cooperative activity of which social games would also be examples.** In a study by Warneken and colleagues (2006), 18- to 24-month-old children engaged in cooperative games with adults. At one point in these games the adult partner stopped participating. All of the children made at least one

communicative attempt to re-engage the adult. Here it is the child rather than the adult who is using an ostensive gesture to restart the interaction. In contrast to human children, the chimpanzees in this study never made any communicative attempt to re-engage their partner.

We are aware of only two explorations of the **neural basis of ostensive, communicative gestures**. In our group, Kampe et al. (2003) found that both eye contact with a participant and calling the participant's name elicited activity in anterior rostral **medial prefrontal cortex and in the temporal poles, both regions associated with mentalizing**. Another study investigated brain activity elicited when individuals communicated through pointing at an object compared with just pointing at an object without the intention to communicate (Cleret de Langavant et al. 2011). In this study, when pointing was communicative, the pointers subtly altered their behavior to take account of the point of view of the observer. The brain regions specifically activated by communicative pointing were right pSTS and right mPFC.

As we have seen, activity in mMPFC seems to be elicited in many different situations when we need to think about mental states. In a study by Mitchell and colleagues (2006), participants were presented with a series of sentences describing a person. Some of these sentences were informative as to the personality of the person ("he turned down three parties to study for organic chemistry") whereas others were not ("he photocopied the article"). When the task was to form an impression of the person, both kinds of sentence elicited activity in MPFC. However, when the task was simply to remember the order of the people, only the sentences relevant to personality activated MPFC. We speculate that the instruction to form an impression was a form of ostensive signal, indicating that the sentences that followed would be relevant to this task. The activity in the MPFC reflects the adoption by participants of a mentalizing stance toward all subsequent information. In the absence of such an instruction, only the sentences about personality elicited this stance. This is consistent with the idea that MPFC has a

high-level role in top-down biasing toward treating information as socially relevant. This speculation is also consistent with the various studies in which greater activity was elicited in MPFC when subjects were told that they were interacting with a person rather than a computer (e.g., Gallagher et al. 2002).

An even more specific role for this brain region, consistent with its activation by ostensive gestures and by the presence of an audience, might be in linking mental states of the self and the partner during communicative interactions (Amodio & Frith 2006). In line with these observations, **Saxe (2006) has suggested that cognitive processes supported by mPFC may be a uniquely human form of social cognition (see Table 1).**

## SHARING EXPERIENCES: THE IMPORTANCE OF META-COGNITION

### Reflective Discussion

We have suggested that there is an important **distinction between learning through observation of others, which can occur without explicit awareness, and learning through explicit communication with others**. We have discussed gossip, through which we learn about the reputation of others, and instruction, through which we are taught about objects in the world. In this final section we discuss another major topic of explicit communicative interactions. We refer to it as **reflective discussion**. We frequently talk to each other about our mental states, describing our sensory experiences and justifying our decisions. Such interactions would be impossible without a special high-level ability, meta-cognition, which may well be uniquely human (Metcalfe 2008). **Meta-cognition is the ability to reflect upon our mental states and describe these states to others**. This self-reflection requires taking a step away from the representations of the world and of other people, and this step appears to be a mental "decoupling" (Leslie 1987). We are normally unaware of our representations of the world. Instead, we take for granted that the world is an open book

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**Reflective discussion:** mutual communication of meta-cognitive knowledge; comparison of confidence in own perception increases joint performance

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directly accessible to our experience (Frith 2007). **Meta-cognition allows reflection and can give us a rare glimpse into the fragility of our mental world.** This makes it possible for us to recognize representations as just that, representations (Perner 1991). From this it follows that other minds may have different representations, and even more startling, that our representations of the world might be illusory or false. Since we all are able to have these insights, we can discuss them. Thus, **reflective discussions enable us to compare our views of the world and to create improved shared views of the world.** In this way meta-cognition has a vital role in the generation of cultural values and institutions.

### **Reflective Discussion of Action Changes Behavior**

A major feature of our mental life involves the vivid experience of being in control of our actions and choosing one option rather than another. Yet, this experience seems to be largely post hoc and has little to do with actual control. We believe that the value of this experience arises because we can discuss the sources of our actions with others (Frith 2010). People readily explain and justify their decisions, even though these explanations and justifications may be inaccurate and self-serving. Johansson and colleagues (2005) have shown how readily people will justify a choice even when, unbeknown to them, it was not the choice they actually made. **The importance of such discussions with other people is that they enable us to understand better the factors that determine our own decisions and can change the way we make decisions in the future (e.g., Vohs & Schooler 2008).**

### **Reflective Discussion of Sensations Creates a More Accurate Model of the World**

In humans the explicit meta-cognitive process of **sharing sensory experience enables pairs of participants to enhance their perception of basic sensory signals, even beyond the abilities of the better member of the pair.** In our group,

Bahrami and colleagues (2010) studied pairs of participants collaborating in the performance of a signal detection task. If the pair disagreed as to when the signal was presented, then they had to come up with a joint decision through discussion. **As long as the members of the dyad had relatively similar perceptual abilities, the group performance was significantly better than the better member of the pair.** Furthermore, this group advantage critically depended upon the occurrence of the discussion. We believe that this advantage depends on one or all of the following components. First, the partners need to reflect on their performance; second, they need to be able to convey to each other their confidence in what they have observed, and third, they have to be able to compare their reflections.

### **The Neural Basis of Meta-Cognition**

The exploration of the neural basis of our meta-cognitive abilities (see **Table 1**) has barely begun. However, the frontal cortex is clearly implicated. In relation to perception, the bilateral application of TMS to DLPFC has a specific effect on confidence in perception without affecting discrimination (Rounis et al. 2010). This suggests that **TMS can cause a reduction in meta-cognitive sensitivity, presumably by increasing neural noise in PFC.** Lesions of prefrontal cortex are also associated with greater effects on subjective report than on objective performance (Del Cul 2009). Individuals can differ considerably in their meta-cognitive sensitivity even when they do not differ in perceptual sensitivity. People with greater meta-cognitive sensitivity in a perceptual task have a greater density of gray matter in anterior prefrontal cortex (BA10) (Fleming et al. 2010).

In relation to action and the experience of agency, Lau and colleagues (2004) found that the requirement to make reports about the intention to act was associated with activity in presupplementary motor area (preSMA). A more recent paper (Miele et al. 2011) has taken the study of action considerably further, revealing brain regions relating to a hierarchy of cognitive processes underlying

meta-cognition. In this study, right TPJ activity was associated with the detection of discrepancies between expected and observed states, whereas activity in preSMA and rostral ACC was associated with being in control of one's actions (i.e., few violations of expectations). However, judgments of control (i.e., meta-cognitive reflections upon control) were associated with activity in anterior prefrontal cortex (BA10), a location close to that identified as relevant to perceptual meta-cognition in the study of Fleming and colleagues (2010).

It remains to be explored whether there is an intimate relationship between meta-cognition and the executive processes associated with prefrontal cortex through which competing automatic social processes are modulated. One possibility is that the biasing of competition exerted by top-down control requires explicit representations of the processes that are competing for the control of behavior.

## CONCLUSIONS

In this review we have emphasized the importance of comparisons of different species and the use of an evolutionary framework for understanding social interaction. Much of human social behavior derives from the same range of cognitive processes that can be seen in other social animals. We distinguished mechanisms from processes and suggested that it is largely general mechanisms that enable specifically social processes. That is, many of the underlying mechanisms can also be used to solve problems without social content or social aims. There are many different social processes, from observational learning and copying to mentalizing and reflective discussion. We found that we share some, but not all, with other species and that many of the processes are implicit and automatic. For instance, the mere presence of others biases us toward group-oriented behavior, and our behavior is automatically influenced in the presence of others with a different perspective. We also share with other social species the ability automatically to keep track of the agents we are interacting with,

as well as their status and predispositions. There are hints that this ability may derive from spatial tracking ability. We suggest that mentalizing, that is, tracking the intentions, knowledge, and beliefs of others, may depend on predictive coding mechanisms. In the case of other species, tracking others' mental states appears to be limited to certain domains of interest, for instance, food caching in corvids. In the case of humans, we are continually updating our representations of other people's constantly changing dispositions, emotions, intentions, point of view, knowledge, and beliefs. Though complex, much of this updating also appears to be automatic and implicit.

What then in social cognition is specific to human beings? First, through language, humans have the means of creating processes that are explicit. Second, humans, in comparison with other species, have a much greater ability to exert top-down control over automatic processes. This is particularly important when there is competition between different components of social cognition. Third, humans have the extraordinary ability to reflect upon their own mental states. This is a prime example of meta-cognition, which may well lie at the heart of conscious awareness.

Finally, how do the explicit, controllable, and meta-cognitive abilities that human beings can put to use in the service of social cognition benefit social interaction? We believe that our specific communicative abilities, both verbal and nonverbal, greatly enhance the value of our social interactions. Unlike other animals, humans teach and learn in a deliberately interactive manner and can share intentions and experiences very effectively. Learning by instruction can often be even more efficient than learning by observation. The ability to discuss and share mental states is perhaps the most valuable of the social processes we discussed. This ability to share experiences can enhance the accuracy of the models of the world that we construct and thus our potential to make better decisions. It is this uniquely human kind of social cognition that makes possible joint endeavors, such as cultural institutions, arts, and science.



## SUMMARY POINTS

1. Social cognition needs to explain the use of social cues for selfish interest and for group-directed altruistic behavior. Even altruistic behavior serves self-interest in the long term. The automatic effect of social cues (presence of others, being imitated by others) usually increases prosocial tendencies. The action of social cues is seen in the audience and the chameleon effects.
2. Learning by observation is largely automatic; it is widespread and has many advantages over trial-and-error learning. It has benefits for the individual who can avoid making errors and can make use of others' experience. It is also of benefit for the group by making individuals more similar. However, for exploration of novelty, trial-and-error learning may be necessary.
3. Gossip is an important means to gauge the reliability of potential partners, and it feeds into reputation management. There is pressure for reputation management to facilitate trust and cooperation as well as to punish those who break trust. This is usually an automatic process and is seen in social animals that use the mechanism of indirect reciprocity to balance selfish and group interests. In the framework of neuroeconomics, there is a never-ending arms race between investors and free riders.
4. Mentalizing is likely to be based on predictive coding. This mechanism is carried by a network of frontal and temporo-parietal regions of the brain. An implicit form of mentalizing is observed in infants under 12 months, and homologous forms have been observed in other species, e.g., corvids. The explicit form of mentalizing is linked to the development of meta-cognition and language and is unique to humans, being universally present beginning at about age 4 to 6 years. Classic false-belief tasks test explicit mentalizing; looking behavior is used to test implicit mentalizing.
5. An implicit form of teaching young infants is signaled by ostension. Deliberate instruction, in which both pupil and teacher are aware of the intention to teach, is abundant in human societies from the time that children reach age 4 to 6 years. Many networks of the social brain (mentalizing, meta-cognition, mirroring, language) are involved.
6. Meta-cognition plays a crucial role in human social interactions and provides a basis for human consciousness. Consciously applied top-down processes can control automatic processes. Prefrontal regions of the human brain and their connections to other cortical regions are thought to be crucial in this control.

## FUTURE ISSUES

1. Find a principled distinction between implicit and explicit processes at the cognitive and the experimental level.
2. Find a principled distinction between accidental signals that are broadcast publicly and deliberate signals of communication.
3. Use computational models of mentalizing combined with neuroimaging to lead to a better understanding of the mechanisms involved.



4. Elucidate the relationship between meta-cognition and executive function.
5. Elucidate the role of meta-cognition in social interaction.
6. Comparisons of group decision making in social insects and humans will be important for revealing underlying mechanisms.
7. Study how conflicts are resolved between the use of social signals for an individual's own selfish benefit and for group-oriented behavior.

## DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

## ACKNOWLEDGMENTS

We are very grateful to the following colleagues who gave very constructive comments on a first draft of this paper: Ralph Adolphs, Ian Apperly, Sarah-Jayne Blakemore, Cecilia Heyes, William Hoppitt, Kevin Laland, Matthew Liebermann, Rosalind Ridley, and Matthew Rushworth. Where we have failed to take their advice this is due to our own obduracy and space limitations. We are also grateful to Susan Fiske for her encouragement. Our work is supported by the Danish National Research Foundation through the Interacting Minds project.

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Uses a computational model of cooperation to elucidate the neural basis of mentalizing.

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# Contents

## Prefatory

Working Memory: Theories, Models, and Controversies  
*Alan Baddeley* ..... 1

## Developmental Psychobiology

Learning to See Words  
*Brian A. Wandell, Andreas M. Rauschecker, and Jason D. Yeatman* ..... 31

## Memory

Remembering in Conversations: The Social Sharing  
and Reshaping of Memories  
*William Hirst and Gerald Echterhoff* ..... 55

## Judgment and Decision Making

Experimental Philosophy  
*Joshua Knobe, Wesley Buckwalter, Shaun Nichols, Philip Robbins,  
Hagop Sarkissian, and Tamler Sommers* ..... 81

## Brain Imaging/Cognitive Neuroscience

Distributed Representations in Memory: Insights from Functional  
Brain Imaging  
*Jesse Rissman and Anthony D. Wagner* ..... 101

## Neuroscience of Learning

Fear Extinction as a Model for Translational Neuroscience:  
Ten Years of Progress  
*Mohammed R. Milad and Gregory J. Quirk* ..... 129

## Comparative Psychology

The Evolutionary Origins of Friendship  
*Robert M. Seyfarth and Dorothy L. Cheney* ..... 153

## Emotional, Social, and Personality Development

Religion, Morality, Evolution  
*Paul Bloom* ..... 179

## **Adulthood and Aging**

- Consequences of Age-Related Cognitive Declines  
*Timothy Salthouse* ..... 201

## **Development in Societal Context**

- Child Development in the Context of Disaster, War, and Terrorism:  
Pathways of Risk and Resilience  
*Ann S. Masten and Angela J. Narayan* ..... 227

## **Social Development, Social Personality, Social Motivation, Social Emotion**

- Social Functionality of Human Emotion  
*Paula M. Niedenthal and Markus Brauer* ..... 259

## **Social Neuroscience**

- Mechanisms of Social Cognition  
*Chris D. Frith and Uta Frith* ..... 287

## **Personality Processes**

- Personality Processes: Mechanisms by Which Personality Traits  
“Get Outside the Skin”  
*Sarah E. Hampson* ..... 315

## **Work Attitudes**

- Job Attitudes  
*Timothy A. Judge and John D. Kammeyer-Mueller* ..... 341

- The Individual Experience of Unemployment  
*Connie R. Wanberg* ..... 369

## **Job/Work Analysis**

- The Rise and Fall of Job Analysis and the Future of Work Analysis  
*Juan I. Sanchez and Edward L. Levine* ..... 397

## **Education of Special Populations**

- Rapid Automatized Naming (RAN) and Reading Fluency:  
Implications for Understanding and Treatment of Reading Disabilities  
*Elizabeth S. Norton and Maryanne Wolf* ..... 427

## **Human Abilities**

- Intelligence  
*Ian J. Deary* ..... 453

## **Research Methodology**

- Decoding Patterns of Human Brain Activity  
*Frank Tong and Michael S. Pratte* ..... 483

Human Intracranial Recordings and Cognitive Neuroscience <i>Roy Mukamel and Itzhak Fried</i> .....	511
Sources of Method Bias in Social Science Research and Recommendations on How to Control It <i>Philip M. Podsakoff, Scott B. MacKenzie, and Nathan P. Podsakoff</i> .....	539
<b>Neuroscience Methods</b>	
Neuroethics: The Ethical, Legal, and Societal Impact of Neuroscience <i>Martha J. Farah</i> .....	571
<b>Indexes</b>	
Cumulative Index of Contributing Authors, Volumes 53–63 .....	593
Cumulative Index of Chapter Titles, Volumes 53–63 .....	598

### Errata

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