

## Chapter 5

# The Evolution of Social Cognition

Nathan J. Emery

Appeared in: Easton, A & Emery, NJ (2005; Eds.) *Cognitive Neuroscience of Social Behaviour*, pp. 151-156, Psychology Press: Hove, UK.

### **INTRODUCTION**

Although this book is focused on the cognitive neuroscience of *human* social behaviour, an understanding of social cognition in *non-human* animals is critical for unravelling the neural basis of social cognition in humans as well as the selective pressures that have shaped the evolution of complex social cognition. Thanks to methodological limitations, we know little about the relationships between certain biochemical and electrophysiological properties of the human brain and how they compute the behaviour and mental states of other individuals. Traditional techniques for examining neural function in humans, such as event-related potentials (ERP), positron emission tomography (PET), and functional magnetic resonance imaging (fMRI), are constrained by the fact that subjects are placed either into an immovable scanner with a lot of background noise or wired up with dozens of electrodes that are sensitive to slight movements. The possibility of scanning or recording brain waves from two individuals that are physically interacting socially is technically impossible at present (however, see Montague et al, 2002 for a new method for simultaneously scanning two individuals interacting via a computer).

The only way to understand the neurocognitive architecture of human social behaviour is to examine similar social processes in both human and non-human animal minds and make comparisons at the species level. An additional argument is that traditional human socio-cognitive tasks are dependent on the use of stories, cartoons and verbal cues and instructions (Heberlein & Adolphs, this volume) which themselves will elicit specific neural responses that have to be eliminated from neural responses specifically related to mindreading. Therefore, the development of non-verbal tasks would provide a breakthrough for studies in non-linguistic animals, pre-verbal human infants and human cognitive neuroimaging.

### **SOCIAL COGNITION & EVOLUTION OF THE SOCIAL BRAIN**

Before we discuss comparative approaches to social cognition, it is important to assess how such lines of thinking have developed and why such questions may be of interest to cognitive neuroscientists. In discussing the evolution of human intellect and by association the evolution of the human brain, both Humphrey (1976) and Jolly (1966) independently proposed that living in a social group and predicting the behaviour of conspecifics required unprecedented levels of cognitive processing, not displayed in non-primates. This 'social intelligence hypothesis' as it later became known was proposed as an alternative to the more traditional candidates for the evolution of primate and human intelligence; tool use, hunting, enhanced spatial memory or extractive foraging (Humphrey, 1976). Due to the anthropocentric bias of those working in this area at the time, focusing solely on the evolution of human intelligence, the experimental and theoretical work in the area was really only concerned with comparing non-human and human primates.

A classic example of these types of study was de Waal's observations of the social life of a group of chimpanzees at the Arnhem Zoo, which highlighted the Machiavellian strategies employed by certain male group members (de Waal, 1982). This study in particular, developed the idea that there were benefits in understanding and remembering the previous interactions and relationships of conspecifics and that this information could be used to predict or manipulate their behaviour in the future. de Waal observed that there were clear similarities between the complex social behaviour of the chimpanzees

and the political shenanigans that were rife in human affairs of state, something which he subsequently called ‘chimpanzee politics’.

Byrne and Whiten later encapsulated this idea as ‘Machiavellian intelligence’ (Byrne & Whiten, 1988; Byrne, 1999), based on Nicoli Machiavelli’s “The Prince”, where the prince of the title would use any deceptive and manipulative means possible to retain political power. They further suggested that the ability to ‘intentionally’ deceive another individual, so-called ‘tactical deception’ (TD), formed the basis for this form of social intelligence, relegating cooperative behaviour to the sidelines. Byrne and Whiten collected ‘evidence’ for TD, not through rigorous experimentation, but through the collation of anecdotes from a wide variety of field primatologists. They found that TD appeared to be widespread throughout the primate order, however it was most prevalent in the cercopithecine monkeys and the great apes (although this tended to be biased by the greater number of field studies performed in these species). Some examples of experimental studies of TD will be described in the relevant section below.

Other social mammals, such as dolphins, killer whales, wolves, wild dogs, horses, hyenas, lions, elephants, and social birds, such as corvids and parrots, appear to demonstrate many of the sophisticated traits of complex social behaviour, such as coalition and alliance formation, reciprocity and interchange, understanding of third party relationships and reconciliation (Connor et al, 2001; Emery, 2004; Feh, 1999; Grinnell et al, 1995; Smale et al, 1995; see also papers in de Waal & Tyack, 2003). We therefore argue that the study of mental attribution in nonhuman animals should be extended to all social animals that demonstrate these traits.

Also relevant to this discussion (particularly for neuroscientists) is the finding that the size of the primate brain (Sawaguchi, 1990), and more specifically the neocortex as a ratio against the rest of the brain (Dunbar, 1992; Barton & Dunbar, 1997), was correlated with mean group size, i.e. those primates with relatively larger brains were usually found in larger social groups. (It was suggested that the larger the social group, the greater the number of potential relationships that can occur between individuals and thus the size of the group may indicate the level of social complexity. However, the notion that group size may provide a useful indication of the social complexity of a species has recently been refuted, because there is no correlation between social learning, innovation and group size in primates, although there is a significant correlation between social learning and neocortex size; Reader & Laland, 2002.) No such relationship has been found between brain (or neocortex) size and various ecological variables, such as home range size or percentage fruit in the diet. These findings are consistent with a link between the evolution of the primate neocortex (the seat of cognition) and social intellect, and importantly not based on the accumulation of anecdotes. However, the relationship between social intelligence and primate brain size at this stage was correlational, not causal. As we have already seen in Chapters 2-4, there is now significant evidence that distinct regions of the non-human primate brain are essential for social behaviour, and that these areas may also be important for social cognition (Brothers, 1990).

At the same time that the ‘social brain hypothesis’ was being developed (Brothers, 1990; Dunbar, 1992, 1998), a mechanism for *how* primates (human and non-human) and other large-brained social animals performed such complex social operations was proposed by Premack and Woodruff (1978), which they named ‘theory of mind’. However, there was an immediate backlash from behavioural scientists who suggested that interpretations of chimpanzee mentalizing abilities by the language-trained chimpanzee, Sarah were nothing more than ‘mere’ associative learning (Savage-Rumbaugh et al, 1978). This had the devastating effect of stifling studies on comparative social cognition for many subsequent years.

At the same time, however, more productive empirical lines of research into ToM were being developed by developmental psychologists (Perner, 1991; Premack & Premack, 2002; Frith & Frith, 2003). Some of this work will be reviewed in a later section. Of particular note, was the development of the ‘false belief’ task which appeared to be a nail in the coffin of comparative social cognition. In brief, the ‘false belief task’ tests whether children understand that another individual can have different beliefs

from themselves. A classic example of this is the Sally-Anne test. Here a child is presented with two dolls; Sally & Anne who both witness a candy being placed into one of two boxes. Anne is then removed from the room, but during which time the candy is moved to the second box in the presence of Sally and the child. Anne then re-enters the room and the child is asked “Where does Anne think the candy is?” or “Where will Anne search for the candy?”. If the child has understood the question and understands that because Anne did not witness the change in the candy’s location, then Anne would believe that the candy is located in the first, rather than the second box, then they should say the first box. Wimmer & Perner (1983) who first developed a version of this test based on a suggestion by Dennett (1978), found that 4 year old children answered correctly, whereas those of 3 years of age and younger based their response purely on their own knowledge that the candy had been moved. As we will see later, the development of an equivalent test for non-human animals has so-far proved futile.

The ‘false belief task’ is believed by many developmental psychologists to be the benchmark test for ToM in human children (Wimmer & Perner, 1983), but it is highly dependent on the use of language. Does this therefore suggest that animals without the benefit of human language could never possess a ‘theory of mind’? There has been a recent backlash against the importance of the ‘false-belief’ task for demonstrating ToM in human children (and therefore by necessity non-human animals), suggesting that it is too difficult a task (Siegal & Beattie, 1991) or that younger children demonstrate implicit understanding of belief (Clements & Perner, 1994). However, in a recent meta-analysis of all studies tackling the problem of false-belief development in human children, Wellman et al (2001) found that the general consensus that false-belief develops in human children around 4 yr old is robust.

## **THEORY OF MIND**

Theory of mind (ToM), also called *folk psychology*, *mindreading*, *mentalizing*, *metarepresentation* or *secondary representation*, is the ability to understand the psychological or mental states of other individuals, such as their beliefs, desires, and knowledge (Premack & Woodruff, 1978).

### **The mechanics of mindreading**

It is important from an empirical and theoretical viewpoint to discuss how an understanding of animal mindreading could translate to studies of neurobiology. Two concepts that are extremely important to an understanding of the mechanisms of mentalizing are ‘the intentional stance’ (Dennett, 1983) and ‘intervening variables’ (Whiten, 1996).

Many animals appear to act intentionally. However, the important questions are whether their behaviour is actually intentional or merely reflexive. If it is intentional, can they understand that the behaviour of others is also intentional? Dennett (1983) formulated a scheme based on different levels of intentionality which an agent (animal or human) may possess in relation to the presence and understanding of their own or another’s mental states:

- *Zero-order intentionality* – an agent possesses no beliefs or desires, and therefore responds to events and stimuli in the environment through reflexes; such as producing a scream vocalization when frightened or running to evade a predator.
- *First-order intentionality* – an agent possesses beliefs and desire, but not beliefs about beliefs; such as producing an alarm call because they *believe* a predator is present, or *want* others to run into the trees.
- *Second-order intentionality* – an agent possesses mental states about another’s mental states; such as producing an alarm call because they *want* others to *believe* there is a predator nearby.
- *Third-order intentionality* – an agent possesses mental states about another’s mental states about their mental states; such as producing an alarm call because they *want* others to *believe* that they *think* that they should run into the trees.

One difficulty with previous attempts to understand ToM is the fact that it is a ‘theory’ based on unobservables (mental states; Premack & Woodruff, 1978). For example, I do not know for sure what

you feel or believe, but I can make a guess based on your actions, your facial expression, and in the human case, your language. (The use of language as a cue to internal states, however, is fraught with additional problems, as the speaker may be intentionally deceptive, may speak a different language, or may be unable to transfer their thoughts and feelings into appropriately colourful language.) Whiten (1996) therefore suggested that a productive way to think about mental states are as intervening variables between causes and outcomes. For example, depriving an animal of water, injecting it with saline and feeding it with dry food will produce an animal that increases its rate of bar pressing to gain liquid, it will drink a large volume of liquid and it has a significant tolerance to quinine. This animal in all intents and purposes can be said to be in a motivational state of thirst between the causes of its thirst and the outcomes of its thirst (Miller, 1959). Whiten suggests that a similar notion can be applied for mental states. For example, an individual A may behave as if it has the intention of gaining bananas (such as reaching towards them, moving towards them, affiliating with those that have bananas, begging towards those that already have bananas, etc.). In addition, the behaviour of other individuals may also provide clues to individual A's mental state in regard to the bananas, such as providing them with bananas, stopping them gain access to their bananas. This collection of behaviours, as a whole, may therefore be interpreted that individual A 'wants' or 'desires' bananas. As such, mental states are intervening variables between behavioural causes and outcomes, and experiments designed to provide evidence for an understanding of mental states should be based on these types of variables. Importantly, only an examination of *multiple* intervening variables should be used as evidence for the existence of ToM.

Intervening variables may be useful not only for providing evidence for ToM in animals, but may also provide a useful theoretical framework for investigating the neural basis of mindreading. For example, neurons in the superior temporal sulcus (STS) of rhesus monkeys respond to particular social stimuli, such as faces, eye gaze direction, body postures and movements (see Chapter 4). These neurons have been suggested to form the basis for a neurophysiological system coding for an understanding of another's intentions (Perrett & Emery, 1994; Emery & Perrett, 2000; Chapter 4). Using the example above, we can imagine a scenario in which the *same* ensembles of neurons code for a) actions used by Individual A to acquire a goal, such as walking and reaching towards bananas, b) actions of Individual B protecting the bananas from Individual A and c) actions of Individual A after attaining the goal, such as eating the bananas. From these three response profiles, we may state that the neural ensemble formed a representation that Individual A *wanted* the bananas.

Mental states come in different forms, therefore any investigation attempting to discover whether animals understand another's mental states should differentiate between the different types. Premack (1988) separated the different forms of ToM into three classes; perceptual (understanding seeing and attention), motivational (understanding desires, goals and intentions) and informational (understanding knowledge and beliefs). I will attempt to discuss all previous studies on each of the three classes, and where possible compare an associative learning account of the data with a mentalistic account. This is important, as the ability to *read* behaviour may be a precursor to, but independent of, the ability to represent mental states.

### **Understanding attention: Perceptual ToM 1**

Gaze is an important social signal that may provide information about an individual's knowledge of the external environment and the state of their internal environment, such as their emotions (Emery, 2000). Social gaze is especially important for non-human primates and other social animals that rely on visual communication. Gaze cues may also function in complex forms of social cognition, such as visual perspective-taking, deception, empathy and theory of mind.

Many animals appear to perceive that eye-like shapes, such as a small black circle within a larger white circle represent 'eyes'. A number of prey species can also discriminate between two circles representing a forward facing predator compared to a single circle representing a predator facing away, and therefore less of a threat (as all predators have forward facing eyes; Coss, 1978; Burger et al, 1992; Hampton,

1994;). A more complex use of another's eyes is that they provide an indication of what another can see; either reflexively in response to another's gaze direction (visual co-orienting; VCO), or more specifically tracing another's line of sight to interesting objects in the environment (gaze following). Visual co-orienting (VCO) has been demonstrated in a number of primates, such as stump-tailed macaques (Anderson & Mitchell, 1999; however see Itakura, 1996) and cotton-top tamarins (Neiworth et al, 2002), but not black lemurs (Anderson & Mitchell, 1999; see also Itakura, 1996). Note that lemurs and other prosimians do not have a visually-based communication system.

Povinelli & Eddy (1996b) were the first to examine gaze following in non-human animals; in a group of young chimpanzees. The chimpanzees were first trained to produce a natural begging gesture towards an experimenter in order to receive food at the end of a trial. Once trained to do this, the experimenters produced specific attention cues for the subjects, either using the eyes only or the eyes and head directed towards various locations, such as behind and to the left or right of the subject, or behind a barrier or as a control the experimenter made no change in the direction of their attention and remained focused on the subject. In the eyes and head condition, 50% trials elicited a gaze-following response to the correct side, and in the eyes-only condition, 30% trials elicited a correct response. From this, Povinelli & Eddy suggested that chimpanzees do not follow gaze with an understanding of the mental states of the individual whose gaze they followed; they follow gaze reflexively until they come across an object or event of interest within the line of sight (low-level explanation). However, the percentage of correct responses reported (30-50%) are not greater than chance, yet reflexive responding should surely produce results closer to 100%. So perhaps the chimpanzees can follow gaze with an understanding of the reasons why the individual looked at a particular point in space (see later).

Further evidence against the argument that chimpanzees follow gaze reflexively was reported by Tomasello et al (1999). In this study, human experimenters gazed at objects hidden behind different types of barriers (gutter, board, another room or around a wall). The chimpanzees could perceive what the experimenters were looking at by looking around the barrier. All subjects looked around all types of barrier. In an additional test, Tomasello et al (1999) set up a situation in which an experimenter looked at a target object far behind the subject. In one condition, the target object only was present (Target only trials); in a second condition, a distracter object only was present between the chimpanzee and the target (Distracter only trials) and in a final condition, both the target and distracter were present (Target + Distracter trials). If chimpanzees follow gaze reflexively then the subjects would attend only the distracter object in the Distracter only trials, and in the Target + Distracter trials. By contrast, a mentalistic account would predict that the subjects should attend the target in both the Target only and Target + Distracter trials. Tomasello et al found that although the target and distracter were equally salient in the Target only and Distracter only trials, the subjects looked at them both equally in the Target + Distracter trials. Therefore, the distracter object was relatively salient to the chimpanzees, but not entirely sufficient to distract the chimpanzees from the object of the experimenter's gaze. These results are comparable to those of 18 month human infants, who demonstrate 'geometric' gaze following (Butterworth & Jarrett, 1991).

A further study examining the relative contributions of low-level versus high-level gaze processing was reported for rhesus monkeys. Monkeys' eye movements were recorded as they watched videotapes of conspecifics looking at one of two identical, moving objects (animal puppets). The rhesus monkeys appeared to respond specifically to the gaze direction of conspecifics, looking more towards the direction in space, and towards the specific object compared to other locations and objects that were presented (Emery et al, 1997). However, when the attention cue was removed (i.e. the monkey in the videotape disappeared whilst the objects remained), the observing monkeys looked at the two objects at the same frequency, suggesting that once the cue had been removed, the salience of the attended object disappeared. These two results seem at odds with one another. The first result that monkeys reliably look to the specific object of the conspecific's attention (compared to just looking in the general direction in which they were attending, e.g. to the left) suggests a high-level interpretation, whereas the second result that the monkeys do not continue to select the target object once the conspecific is

removed, possibly suggests a low-level reflexive interpretation. However, the objects were present on screen unchanging for almost 20 sec, and so the subjects may have 'decided' that objects were not of interest. Interestingly, an additional analysis of the temporal pattern of inspections (eye movements) demonstrated that the observing monkeys consistently looked back to the conspecific after looking towards the attended object (Emery, unpublished observations), presumably in order to determine that the objects were still of interest.

Similar results in socially-housed chimpanzees, sooty mangabeys, rhesus macaques, stump-tailed macaques and pigtailed macaques using conspecifics as the sources of social information were reported by Tomasello et al (1998). The description of gaze following in monkeys is particularly interestingly because neurons in the superior temporal sulcus of the rhesus monkey brain are selectively responsive to faces, and eye direction (Emery & Perrett, 2000). However, a sub-set of these neurons did not respond selectively to faces looking at objects compared to away from objects (Emery, 2000). This was a small population of cells and so requires further study (see chapter by Jellema & Perrett for an overview of the neurophysiology of goal-directed behaviour in monkeys).

More complex processing of another's gaze may be that an individual with open eyes or eyes that are not occluded can perceive objects in the world. This cognitive level implies an understanding of the mental state; *seeing*. In a protracted series of experiments, Povinelli & Eddy (1996a) examined the ability of young chimpanzees (5-6 years old) to beg towards one of two experimenters with different types of visual occlusion; one that could see them versus a second that could not. In all cases, the chimpanzees were presented with a conditional discrimination problem; if the chimpanzee begged towards the experimenter that could see them, they were rewarded. One of the experimenters always had their eyes open or free from occlusion, with a second whose eyes were covered with different barriers, such as blindfolds, buckets, or tinted goggles, or their back was turned, their head was turned or their eyes were closed. In almost all cases, the chimpanzees did not differentiate between the two experimenters based on their ability to see. The only discrimination the chimpanzees made was between an experimenter who was facing towards them compared to another whose back was turned. However, the chimpanzees failed to discriminate between two experimenters facing away, but one of them had one turned their head towards the subject. Povinelli and Eddy concluded that chimpanzees may use a more sophisticated level of gaze following than purely reflexive, but that their gaze following abilities do not extend to a concept of seeing or understanding another's mental states from their gaze cues.

There have been a number of criticisms of this study. Because Povinelli and Eddy tested the ability of chimpanzees to follow human eye gaze as opposed to conspecifics one can argue that chimpanzees might have an understanding of seeing as a mental state, but one that does not generalise to people. Clearly the experiment should be repeated using conspecifics. A second issue is age of the chimpanzees tested in these studies. It has been suggested that because the chimpanzees were only 5 years of age they were not old enough to have developed a ToM. But subsequent tests when the same chimpanzees had reached adolescence have continued to show negative results, so even those individuals that were most adept at these tasks continued to use stimulus-based rules about the frontal orientation of the face and eyes rather than using the attribution of seeing (Reaux et al, 1999).

A final test for whether animals understand another's mental states from gaze (understanding attention as a mental state or Level-1 perspective-taking; Flavell et al, 1981) is the 'object-choice' paradigm. In this paradigm, animals are first trained that food can be located under boxes or cups. An experimenter then baits one of two inverted cups behind a screen. When the cups are revealed, the experimenter looks at (or points; see later) the cup covering the food. The animal is then required to displace the cup that hides the food. Many species of primates perform this task with ease or after training, and respond to different pointing cues, and head direction close to the correct choice, but do not use head direction far from the cup or eye gaze alone (Anderson et al, 1995; 1996; Call et al, 1998; Itakura & Anderson, 1996; Povinelli et al, 1999; however, see Peignot & Anderson, 1999 for controversial results in gorillas which appear to use all available human social cues, except glancing).

There are inconsistencies between the results of different laboratories which are largely the consequence of positive findings in enculturated apes and domestic dogs (see later section on “the domestication of social cognition”). Itakura & Tanaka (1998), for example, found that human infants, an enculturated chimpanzee and an enculturated orang-utan could use Point, Tap, Distal and Proximal Gaze and Glancing (eyes only) cues with accuracy levels between 70-100% (all significantly above chance).

The basic failure of monkeys and apes to use distal head and eye gaze cues, but with general success in the use of proximal head and pointing cues, suggests that these species are probably basing their decisions on low-level, proximity-based social information, such as stimulus and local enhancement, to locate hidden food, rather than a high-level interpretation that a human experimenter is looking at one of the two cups because they have knowledge that the cup hides food. Additional behavioural cues or nuances of the experiment appear to enhance the ability of chimpanzees to locate hidden food. Itakura et al (1999) found that producing a vocalization (chimpanzee-like food call or a human vocalization) accompanying gaze cues increased performance on the object-choice task. Did the vocalization enhance the effect of the gaze cues, or did it attract the subject to the experimental situation providing an aid to use of the cues? Call et al (2000) tested chimpanzees using the same paradigm as Itakura et al (1999), however the temporal order of the gaze and vocalization cues was manipulated, with either the gaze produced before vocalization, or vice versa. The chimpanzees produced above chance performances on the object-choice task independent of when the gaze and call cues occurred. In addition, the type of call did not affect performance, and amazingly, when other sounds were used, such as snapping the fingers, slapping the hand on the floor or playing a recording of a bicycle horn, they also produced significant responses. Other important behavioural cues related to local enhancement such as moving towards the correct container and staring at it, lifting the container and looking into it and approaching the container (Call et al, 2000; Itakura et al, 1999) all enhance performance of chimpanzees on the object-choice task.

Finally, Call et al (1998) examined whether the type of occluder influenced responses on this task. They found that chimpanzees could utilise the experimenter’s gaze cues when the occluders were tubes or barriers that did not prevent the experimenter seeing the location of the food after baiting, but not when the occluder was an overturned bowl. This suggests that the chimpanzees do not understand that other individuals know that objects remain in their original place even when they are out of sight, akin to a lack of social ‘object-permanence’. It remains to be tested whether other animals can use these types of behavioural cues or occluders to enhance their performance on object-choice tasks.

Of particular relevance here, are an additional class of neurons in the macaque superior temporal sulcus which respond to the sight of humans walking or reaching towards objects (Emery & Perrett, 2000) and such goal-directed actions combined with cues to another’s attention (Jellema & Perrett, this volume). This neurophysiological data is highly suggestive of a propensity for rhesus monkeys to solve the object-choice task with the aid of additional behavioural cues, such as those used by chimpanzees.

### **The domestication of social cognition**

We have already seen that apes’ abilities at gaze following, understanding seeing and object-choice tasks are some-what limited. Indeed, recent studies have found that domestic dogs (*Canis familiaris*) may be superior to apes in these tasks. Dogs can use human attention cues to locate hidden food (Miklosi et al, 1998; Hare & Tomasello, 1999; McKinley & Sambrook, 2000), use novel cues, such as markers, to find food (Agnetta et al, 2000), use conspecific cues (Hare & Tomasello, 1999) and use cues themselves to direct humans to food (Hare et al, 1998). Dogs have also demonstrated an understanding of seeing that is significantly better than chimpanzees (Cooper et al, 2003). Recently, Hare et al (2003a) found that when compared directly on the same object-choice task, dogs outperform chimpanzees with 9/11 dogs choosing correctly compared to 2/11 chimpanzees. Hare and colleagues have suggested that it was the long domestication of dogs by humans that has selected for this skill in utilising human social cues.

Indeed, these paradigms are dependent on the reading of *cooperative* signals produced by humans. As such, animals that have been selected for their close relationship to humans should demonstrate a clear propensity to read such signals. This is in contrast to primates, which have not been selected for these skills. Although the data is scant, there is some suggestion that many working dogs which have been directly bred to understand human gestures or produce gestures comprehensive to humans, for example, during sheep herding and pointing towards a kill during a shoot, perform better in social cognition experiments than other dogs (McKinley & Sambrook, 2000; Hare et al, 2003a; Miklosi et al, 2003).

To directly test the domestication of social cognition hypothesis, Hare et al (2003a) compared domestic dogs and wolves on the same tasks. In the object-choice task, dogs located food correctly when provided with Gaze + Point + Tap, Gaze + Point and Point cues, whereas wolves were correct only when using the Gaze + Point cue. On a non-social food-finding study that was not dependent on the use of human social cues, there was no difference in the performance of dogs and wolves. Finally, dog puppies at different ages (9-12 weeks; 13-16 weeks and 17-26 weeks old) and with different rearing histories (litter-reared or human-reared) were tested on the object-choice task using Gaze and Gaze + Point cues. There was no difference between the litter-reared and the human-reared puppies, and no difference between the three age groups in their use of human social cues. This final result suggests that there was no effect of age or experience of humans in the use of human attention cues, therefore reinforcing the premise that the process of domestication was the key to the enhancement of socio-cognitive abilities in domestic dogs.

There are some potential problems with this hypothesis. First, Miklosi et al (2003) have performed similar experiments to Hare and colleagues (although focusing only on comprehension of human pointing) in dogs and socialized wolves. They found that 4 wolves could utilise touching cues to locate hidden food, 2 wolves could use proximal pointing (5-10 cm away from the object) and 1 wolf could use distal pointing (50 cm away from the object). Therefore, some socialized wolves could learn to use some human gestures. In two further, non-social tasks used to gain access to food, a rope-pulling task and a bin-opening task, there were no differences in the ability of wolves and dogs to solve this task. The tasks were then made insolvable, i.e. the bin was locked, so the food could not be reached or the rope was tied to a post, rather than to the food. When faced with insolvable problems, the dogs, but not the wolves, looked back at their owner and spent more time gazing at their owner than the wolves. Miklosi et al (2003) suggested that the dogs were looking back at their owners either in an attempt to communicate with them that the food was not accessible or to derive information from their owners about how to solve the task (see also Gomez, 1991).

Second, general domesticity is often confounded with specific use as a working animal. In the 20<sup>th</sup> century, dogs are primarily kept as pets, however, throughout most of the period of domesticity, dogs were kept and trained as working animals. Interestingly, another domestic working animal, the horse (*Equus caballus*), has demonstrated some basic understanding of human-given social cues to locate food (McKinley & Sambrook, 2000). To remove the effects of domesticity and working, experiments should be performed on domestic animals which only function as pets, and thus should not have been selected to use human social cues. A good example would be the domestic cat. Relatives of domestic cats, such as lions, are successful pack hunters (Scheel & Packer, 1991) and so we would predict that if domestic cats have retained this trait then they should be able to utilise conspecific social cues (as would have been useful during a hunt), but they should fail to use human social cues because they have not been bred as working animals.

### **Visual perspective-taking: Perceptual ToM 2**

Distinguishing another individual's visual perspective from one's own is thought to be an important step in interpreting others' intentions and thoughts about the world (Level-2 perspective-taking; Flavell et al, 1981). It may also be a useful skill when used to manipulate another's behaviour and intentions, so-called tactical deception. The classic example of tactical deception is the observation of a female



hamadryas baboon grooming a subordinate male behind a rock out of view of the dominant male. In hamadryas society, dominant males mate and control a harem of females, and so have sole access to them, with subordinate males sneaking copulations out of the sight of the alpha male. It would therefore seem to be advantageous for the subordinate and his consort to hide their clandestine meetings from the alpha male. In this example, the female remains in view of the dominant, but the dominant cannot see what she is doing, and the recipient of what she is doing (Whiten & Byrne, 1988). One interpretation is that the female processed the dominant's line of sight, and positioned herself so that the rock was between the subordinate she was grooming and the dominant male, so that he was completely out of view. But this behaviour could have been learned by differential reinforcement without having any understanding of what looking means.

To test whether animals can understand another individual's visual perspective, long-tailed macaques were given a choice of where to drink a juice reward. One bottle of juice was hidden from the view of a threatening human experimenter whereas a second bottle was in full view of the experimenter (Kummer et al, 1996). The macaques failed to discriminate between the two bottles, choosing randomly, therefore failing to demonstrate an understanding of the human experimenter's visual perspective. Of course, there were little costs associated with taking the juice in the open as the monkey gained as much juice at that bottle as the bottle which was hidden from view.

Many investigators have suggested that laboratory experiments based on an animal's natural history (i.e. with high ecological validity) are likely to be more productive in eliciting mentalizing abilities than artificial paradigms. Examples of naturalistic laboratory studies include using conspecifics as protagonists, or basing studies on an animal's species-specific behavioural repertoire (Matheson et al, 1998; Purdy & Domjan, 1998; Hare, 2001; Emery & Clayton, 2004). A more ecologically valid test for visual perspective-taking in chimpanzees based on competition for food has recently been designed by Hare and colleagues (Hare et al, 2000). A subordinate and a dominant chimpanzee were allowed access to an arena where food had been previously hidden. The subordinate chimp could see both pieces of food, whereas the dominant chimp could only see one of them. The question was asked whether the subordinate chimp would make a decision about which food to approach based on the visual perspective of the dominant animal (i.e. go for the food that the dominant could not see)? When released into the arena together, the subordinate chimp did exactly this. To eliminate the possibility that the subordinate was not reasoning about the dominant's visual perspective, but only responding to simple behavioural cues (such as gaze direction, and direction of movement), the subordinate was released a few seconds before the dominant. As before, the subordinate tended to retrieve the hidden food. Hare and colleagues have suggested that these positive results were due to implementation of a competitive rather than a cooperative paradigm, a more natural behavioural state for chimpanzees. The use of a conspecific as a protagonist rather than a human experimenter would also account for the positive results. The same paradigm has been used successfully in capuchins, in which the subordinates also preferred to choose food that was hidden from dominants. The subordinate capuchins, however, did not preferentially approach the hidden food first when given a head start (in contrast to the chimpanzees), suggesting that the capuchins were predicting the dominant's behaviour based on gaze and movement cues, but did not appreciate their perspective (Hare et al, 2003b).

A recent alternative explanation to the understanding of another's visual perspective is that most animals prefer to feed at the periphery of a clearing to avoid potential predation, and so any preference for feeding behind a barrier may be due solely to fear of eating in the open rather than an appreciation of another's line of sight. This is termed the 'peripheral feeding hypothesis' (PFH; Karin-D'Arcy & Povinelli, 2002). A second argument was that dominants will always go for the piece of food that is in view, and so the subordinate has no other choice but to go for the food which only they can see. For the sake of the 'visual perspective-taking' argument, only the food that is reached for first is important, as just reporting the total amount eaten or which food is eaten could be due to the subordinates having no other choice available. This is exactly what Karin-D'Arcy & Povinelli (2002) found, when attempting to replicate Hare et al's (2000) study, namely that the subordinate chimpanzees tended to

retrieve the hidden food rather than the food that could be seen by both chimpanzees, but that the subordinates did not selectively reach or move towards the hidden piece of food first. In all possible scenarios where only the subordinate was party to the location of the hidden food (and in a geometric position to retrieve it first, it gained the highest percentage of food. Even when the experimental design abolished all possibility of the dominant injuring the subordinate, the subordinate did not selectively retrieve the hidden food. When the PFH was tested using barriers fully occluding or half occluding food, transparent barriers in front of the food or opaque barriers located to the side of the food (and so not removing the food from sight), Karin-D'Arcy & Povinelli (2002) found that the subordinate did not differentiate between the hidden or visible food in which they reached for, touched or retained, thereby supporting the PFH. Of course, there are many possible reasons for the discrepancies between these two research groups. Povinelli and colleagues have begun to report a number of negative findings with respect to ToM in chimpanzees (also causal understanding of tool use; Povinelli, 2000). This could be due to interference effects between the different types of cognitive experiments (using the same chimpanzees throughout), or detrimental effects in the lack of conspecific socialization during development.

An additional ecologically-valid situation in which food is competed for, and which may also provide a good model for examining visual perspective-taking in animals is food-caching and cache protection. Cachers that either live in a social group or have to defend territories may have to cache in front of conspecifics (and heterospecifics), some of which are potential cache pilferers. Many corvids, such as scrub-jays, magpies and ravens have demonstrated sophisticated cache protection strategies, such as delaying caching until a competitor has left the scene, making 'false' caches, switching from larder hoarding (one large defendable cache site) to scatter hoarding (many smaller cache sites spread over a wide area) or vice versa, and re-caching food items when competitors have left (Vander Wall, 1990; Heinrich & Pepper, 1998; Emery & Clayton, 2001; Emery et al, 2004; see later section). Ravens have also been shown to cache selectively behind large obstacles, such as rocks and tree stumps, positioning the obstacle between themselves and the would-be thief (Bugnyar & Kotrschal, 2002). Ravens also tend to cache as far from competitors as possible (Bugnyar & Kotrschal, 2002) and possibly use distraction techniques (Heinrich, 1999).

An experimental investigation of scrub-jay caching revealed similar strategies to the ravens. If the jays were presented with caching locations near to or far from an observing conspecific, they chose to cache in locations far from the conspecific, but they did not make this discrimination when they cached in private (Dally et al, in press). When presented with caching locations either behind barriers or in the open (removing distance as a factor), jays consistently chose to cache in locations out of sight of the observer (Dally et al, in press). This result did not appear to be because the jays were fearful of the presence of another jay, and so ceased caching or eating in the open, as the jays did not discriminate between caching locations when they were only given powdered (non-cacheable) food. Future studies will examine whether jays can understand that the view of observer's can either be completely or partially occluded depending on their position, and that different observers have different views of the same event. These studies should provide stronger tests of whether scrub-jays can appreciate what conspecifics can and cannot see.

Watve and colleagues (Smitha et al, 1999; Watve et al, 2002) suggested that another species of bird, the bee-eater, may also be a good candidate for ToM. Bee-eaters appear to respond to what a predator can see, as they do not tend to enter their nest (and so lead a predator to their offspring) if the nest is being watched. They therefore attempted to set up an experimental situation mimicking this in the wild, using human experimenters as 'predators'. They examined whether bee-eaters would be more likely to enter a nest if the view between the predator and the nest was blocked by a barrier, compared to a position in full-view of the nest or in a position in view of the nest, but a great distance from it. A bee-eater was always positioned on a perch at an angle between the nest and the predator. Watve et al (2002) found that the time taken before the subject made their first entry into the nest was greatest when the distance from the predator was small and the view was unimpeded. Distance appeared to have the least effect

on the tendency to enter the nest. The bee-eaters also seemed to appreciate the gaze direction of the predator, entering the nest more frequently when the experimenter was looking away compared to looking at the nest (Watve et al, 2002), and may have understood something about the predator's knowledge (had they seen the nest before; Smitha et al, 1999). Although there are many methodological problems, this semi-natural paradigm certainly warrants further investigation.

### **Intentional communication: the bridge between perceptual and motivational ToM**

During intentional communication “the behaviour of the sender must involve a goal and some flexibility in the means for attaining it” (Tomasello & Call, 1997, p. 243). As such, the sender may use different types of ‘gestures’, vocalizations or behavioural strategies in order to achieve a goal. These may include ‘attention-getting’ behaviours which are used to capture the attention of the potential recipient so that they are ready to receive the communicative gesture, gaze alternation between the recipient and the object or event of interest, and the gesture itself, such as proto-imperative or proto-declarative pointing towards the goal. Based on these criteria, intentional communication may form a bridge between two forms of ToM; perceptual and motivational. In this section, I will only deal with intentional communication of visual signals, however the reader is directed to Tomasello & Call (1997) for a discussion of intentional communication of vocalizations, such as alarm calls.

### **Attention-getting behaviours**

The use of visually-based gestures to communicate intentions to a second party are largely dependent on the recipient being in an attentional state conducive to receiving the signal; i.e. attending the signal sender. In their natural social interactions, chimpanzees will tailor the type of gesture directed to a conspecific based on whether they are facing the sender, or looking away. Tomasello et al (1994) found that the chimpanzees were more likely to use visual signals if the conspecific was looking at them, compared to using more auditory and tactile gestures when the conspecific was looking away. The issue of whether chimpanzees understand that their gestures should fit with the attentional state of the recipient has been examined in three laboratory studies.

Gomez (1996) tested the attention-getting behaviours of a group of hand-reared and human-experienced chimpanzees. The chimpanzees were required to request food from an experimenter that was inattentive (eyes closed, back turned, head turned towards a corner or gaze over the chimpanzee's head). The chimpanzees used attention-getting behaviours, such as touching the experimenter or attempting to make eye contact in 68% of the inattentive trials. The hand-reared chimpanzees used attention-getting behaviours more frequently than the human-experienced chimpanzees.

Theall & Povinelli (1999) performed a similar experiment in chimpanzees, however the experimenter did not provide the food reward immediately after the chimpanzees made a begging gesture, but waited for 20 sec. The experimenter's attentional state differed in four conditions; eyes open (EC) and following the movements of the subject, head movement (HM), attention above the subject (AC) and eyes closed (EC). Therefore, the subjects should have been more likely to use attention-getting behaviours (touching and vocalizations) during the AC and EC conditions, where the experimenter was inattentive. However, Theall & Povinelli (1999) did not find a difference between the conditions in the frequency of touching and vocalizations.

In a study of 49 captive chimpanzees, Hostetter et al (2001) examined a larger number of attention-getting behaviours than in previous studies (vocalizations, gestures, banging the cage, throwing objects, spitting, displaying, clapping and pouting). Rather than examine responses of chimpanzees to an inattentive human experimenter, based on the eyes, Hostetter et al only used facing the subject and back turned away from the subject as conditions (as Povinelli & Eddy, 1996 had reported that chimpanzees only appear to understand that a human facing away is inattentive, not when their eyes were covered). The chimpanzees emitted vocalizations faster, and made their first gesture more frequently when the experimenter was oriented away from the subject. These studies suggest that chimpanzees may understand something about the attentional state of a human experimenter, however,

this ability only develops after prolonged interactions with humans during early development (see later section). As chimpanzees do not understand the special relationship between the eyes and seeing, it is important to provide the subjects with cues that they do comprehend, such as discriminating between a forward facing experimenter and an experimenter with their back turned.

### **Gaze alternation**

The second criteria for the intentional communication of visually-based gestures is that the sender continues to communicate with the recipient until their goal is achieved or the recipient leaves. Human infants, for example, do this by gaze alternation, i.e. constantly looking between the recipient and the object of interest (Gomez et al, 1993). Gomez (1991) examined whether a hand-reared young gorilla used similar gaze alternation when confronted with a series of problems that were outside of its behavioural repertoire, such as opening a door to leave a room or gaining an out of reach banana. Gomez found that initially, the gorilla would physically attempt to move the experimenter towards the goal object, such as pulling them towards the door. Gomez reports that the gorilla would frequently touch the experimenter first, awaiting eye contact, and then lead the experimenter to the goal once eye contact had been made. Eventually, the gorilla would 'signify their intentions' by alternating their gaze between the experimenter's eyes and the goal (door handle or banana).

Emery (2000) has discussed this issue in relation to the behaviour of some pet animals, which display behaviours which may be interpreted as gaze alternation (and attention-getting):

“Many pet owners discuss the abilities of cats and dogs to look at the location of a food source or to the door to outside, then back to the pet owner, then back to the food or the door... This behaviour is usually associated with vocalizations. Although this behaviour is identical to that described above for gorillas, the domesticated pets would not be described as intentionally communicating with their owners. The pets are more likely to have been looking at the location of the food or outside at an earlier occasion and vocalizing because of the motivation to gain food or entry to outside. The pet owner happened to initiate the required action (get food or open the door) independent of the intentions of the cat or dog. The pet therefore learnt through association that looking and vocalizing at an object of interest leads to access to that resource by the actions of the owner” (p. 593).

Miklosi et al (2000) have investigated whether pet dogs alternate their gaze with their owner's gaze and the location of a hidden piece of food or favourite toy. After controlling for baseline levels of gazing and attention-getting behaviours (by examining the levels of these behaviours when the dog was alone or when a second human familiar to the dog pets them), the subjects' gaze alternation behaviour was examined when food was hidden in their presence, but not in the presence of the owner. The dogs increased the frequency of vocalizations, sniffing the location of the food or toy, and increased the frequency of gazing at the owner and the food or toy compared to baseline conditions. These results suggest that dogs can communicate the location of hidden objects to their owners (see also Hare et al, 1998) using gaze alternation.

### **Pointing**

Pointing has been proposed as a method by which human infants begin to communicate (non-verbally) with others (Baron-Cohen, 1991). There are two types of pointing described in the developmental psychology literature that may be present in animals; proto-imperative and proto-declarative (referential) pointing (Leavens & Hopkins, 1999). Proto-imperative pointing takes the form of reaching using the whole-hand towards an out-of-reach object of interest which the agent wants or desires, whereas proto-declarative pointing typically takes the form of pointing using the index finger to show or notify others of the presence and location of objects and events (Povinelli & Davis, 1994). Leavens & Hopkins (1999) have suggested that pointing in apes (and likely other animals) resembles human pointing as although apes tend to point with their whole-hand, they have been recorded pointing with the index finger, young children frequently point with the whole hand, chimpanzees point significantly more when others are present than when alone (Leavens et al, 1996), chimpanzees vocalize less when

pointing than young children (Leavens & Hopkins, 1998) and chimpanzees alternate their gaze between the object of interest and the human they are attempting to communicate with more frequently than children (Leavens et al, 1996; Krause & Fouts, 1997). Therefore, although ape pointing may be equivalent structurally and functionally to human pointing (but see arguments against this view by Povinelli & Davis, 1994), there is little evidence that apes use other body parts to point with, which humans readily do (Leavens & Hopkins, 1998; leg, shoulders, head or chin).

Proto-imperative pointing has been reported for many captive species (Blaschke & Ettliger, 1987; Hess et al, 1993; Povinelli et al, 1992a, 1992b), human infants, but not apes in the wild (Plooij, 1978). A similar gesture is holding out the hand, in the form of begging or solicitation (Bygott, 1979). By contrast, proto-declarative pointing has only been described for some enculturated apes (Call & Tomasello, 1994; Krause & Fouts, 1997), language-trained dolphins (Xitco et al, 2001) and normal human infants, but not infants with autism (Baron-Cohen, 1989). These examples may be party to alternative explanations, in particular the dolphin case seems like a over-interpretation; with dolphin pointing described thus: “a dolphin would stop his forward progress, often less than 2m from an object, and align the anterior-posterior axis of his body with the object for several seconds” (Xitco et al, 2001; p. 117).

Many species also appear able to comprehend other’s pointing as a referential gesture, such as during the object-choice task (apes – Itakura & Tanaka, 1998; Peignot & Anderson, 1999; monkeys, Anderson et al, 1995, 1996; dogs - Hare & Tomasello, 1998; McKinley & Sambrook, 2000; Miklosi et al, 2003; Soproni et al, 2001, 2002; dolphins – Herman et al, 1999; Tschudin et al, 2001). The possibility arises that the response to pointing may be due to the distance between the hand and the object (local enhancement; Povinelli & O’Neill, 2000) rather than understanding (for example, Itakura & Tanaka, 1998). This has been controlled in experiments in dogs (Soproni et al, 2002; Miklosi et al, 2003) and gorillas (Peignot & Anderson, 1999), comparing responses to proximal and distal pointing cues.

### **Understanding intentional actions: Motivational ToM**

The term theory of mind first appeared in a paper by Premack and Woodruff in 1978. However, Premack and Woodruff were referring to understanding another’s intentions or goals or *motivational ToM*. They examined whether a language-trained chimpanzee, Sarah, could appreciate the correct solution to a problem given to a human demonstrator. Sarah was presented with a video sequence of either an actor locked in a cage, or shivering next to an unlighted heater, or unable to clean a dirty floor, or unable to listen to music on an unplugged stereo. After each sequence, the video was paused and Sarah was then provided with a number of alternative answers to the problems (as photographs), such as a key, a lighted paper wick, a connected hose and a plugged in cord, and she had to match the correct image with the appropriate video. Sarah was highly accurate in her selection of the photographs, and so it was argued that she understood the actor’s intentions (“he wanted to get out of the cage”, “he intended to listen to music”, etc.). Needless to say, this interpretation has been criticized. Perhaps Sarah merely understood the relationship between objects (e.g. lock and key) that had been associated previously during her life in captivity. Savage-Rumbaugh et al (1978), for example, presented their language-trained chimpanzees with different sets of cards, which included pairs of objects that were related, such as lock and key, and the chimpanzees correctly matched the two related cards far above chance. The fact that some of the solutions provided to Sarah were novel, however, suggests that this explanation cannot account for all Sarah’s abilities.

A more explicit method for examining the ability to understand intentions was first developed by Povinelli (1991), and then tested more extensively by Povinelli et al (1998) and Call & Tomasello (1998). Povinelli (1991) examined whether a language-trained chimpanzee, Sheba could discriminate between a ‘bad’ experimenter who deliberately poured juice in front of her whilst simultaneously threatening her and a ‘clumsy’ experimenter who dropped the juice on the floor accidentally. Sheba predominantly chose the clumsy experimenter, however this may have been due to the fact that Sheba avoided choosing the nasty experimenter. Using a larger sample of laboratory-housed, but not

enculturated chimpanzees, Povinelli et al (1998) repeated these experiments. The subject had to beg or indicate towards one of the trainers to give them juice. One of the trainers then approached the subject and tripped over spilling the juice on the floor, a second trainer deliberately poured the juice on the floor in front of the subject and a third aggressively poured the juice on the floor before the subject. Povinelli et al (1998) found that their subjects did not discriminate between any of the trainers, suggesting that they did not understand the difference between intentional and accidental acts. By comparison, Call & Tomasello (1998) tested orang-utans, chimpanzees and human children. The subjects were initially trained that a marker placed onto the top of a box denoted that food was hidden inside. The box containing food was baited in private, then the subject was presented with three boxes (including the baited box). The experimenter then marked two boxes in turn; one intentionally (placing the marker carefully on top of the box), one accidentally (dropping the marker onto the box). All three species chose the box that was intentionally marked. It should be noted that the older human children (> 3yr old) and an enculturated orang-utan (Chantek) were consistently better than the other apes.

Although the field of ToM began with the study of understanding intentions, very few studies have approached this subject experimentally. It is clear from these results that, at least, some apes can understand a human experimenter's intentions and that this ability is enhanced after extensive human contact during early development. It remains to be tested whether other species understand intentions, especially the intentions of conspecifics. Certainly neurophysiological evidence of neurons responding to goal-directed actions suggests that monkeys (and probably other animals) may appreciate another's purposive behaviour. What is perhaps the most difficult empirical problem is clearly differentiating between what are perceived as goal-directed actions (Dickinson & Balleine, 2000), and the mental state of intention. For example, Menzel (1974) described a series of studies based in a large enclosure, in which one chimpanzee had witnessed the hiding of food. When the entire group was released, Menzel recorded the groups' accuracy in locating the hidden food using only the behavioural cues (direction and speed of travel, body orientation and gaze direction) provided by the individual that was party to the location of the food. However, were the other group members responding to the knowledgeable chimpanzee's goal-directed movements or understanding their intentions?

### **Knowledge attribution: Informational ToM 1**

The third type of mentalizing that we will discuss is *informational ToM* or the mental state of *knowledge*, which is linked to perceptual ToM, in that knowledge states cannot exist without access to perception. This has been called the 'seeing leads to knowing' relationship, but it is the same for all the senses. Cheney & Seyfarth (1990) were the first to examine whether non-human animals would attribute knowledge or ignorance to other individuals based on whether they had visual access to events or objects that would lead to knowledge. Female Japanese and rhesus macaques were shown food or a predator (a technician with a net), either in the presence of their offspring or when alone. Two questions were addressed: did the females attempt to alert their offspring of the presence of either food or a predator (through the use of food or alarm calls) and did they differentiate between those offspring that had been present during exposure to these stimuli (knowledgeable) and those that were separated from their mothers (and so were ignorant)? The macaque mothers did not appear to differentiate knowledge from ignorance in their infants as they did not produce a higher frequency of alarm or food vocalizations towards the ignorant offspring.

Povinelli et al (1990), adapting a paradigm designed by Premack (1988), examined the ability of chimpanzees to attribute different knowledge states to human experimenters, asking the question 'do chimpanzees understand that seeing leads to knowing?' A chimpanzee was present whilst one of four containers was baited with food (although they could not see which container was baited). In the first condition, the 'Knower' baited the container whilst the 'Guesser' left the room. Once the container had been baited, the 'Guesser' re-entered the room and both the 'Knower' and 'Guesser' pointed to a container. To receive the food reward the chimp had to point to the container that the 'Knower' pointed to. The chimps pointed towards the 'Knower' on the majority of the trials, however they only did this greater than 70% correct after 200-300 trials. During a transfer phase, a third experimenter

baited a container, whilst the 'Knower' observed and the 'Guesser' did not leave the room, but remained with a bag over their head. In this condition, the chimpanzees pointed significantly more towards the 'Knower'. However, a re-analysis of the data found that the subjects only did this consistently after the first 5 trials (Povinelli, 1994). Importantly, the subjects in this study were 6 years old and above. Povinelli et al (1994) replicated the study using 3-4 year old chimpanzees, and all failed to distinguish between the 'Knower' and 'Guesser'.

One potential problem with this study is the fact that chimpanzees do not understand that humans with bags, buckets or blindfolds on their heads cannot see (Povinelli & Eddy, 1996b). Therefore, the chimpanzees' inability to discriminate between the 'Knower' and 'Guesser' during the first 5 trials of the transfer phase could be attributed to a lack of understanding at this level, rather than a failure to relate seeing to knowing. Call et al (2000) attempted to control for this possibility by replicating Povinelli et al (1990) but instead of the 'Guesser' leaving the room or remaining in the room with a bag over their head during baiting, both the 'Knower' and the 'Guesser' remained in the room, but the 'Guesser' turned their back to the subject, whilst the 'Knower' faced the subject. As an additional control, either the 'Knower' or a third experimenter baited the container with food. Only two enculturated chimpanzees chose the cue provided by the 'Knower' when the 'Knower' was the baiter, but not when the third experimenter baited the container.

An additional criticism of Povinelli et al (1990) is the fact that the chimpanzee had to be taught to make begging gestures towards a human experimenter when they wanted food. Chimpanzees very rarely beg to others in the wild, and only infants to their parents; chimpanzees usually fight for access to food. Therefore, ToM may be more likely to have been selected for a role in competition rather than cooperation. In an extension of their earlier studies on visual perspective-taking, Hare et al (2001) examined knowledge attribution in chimpanzees using conspecifics. In this situation, a dominant and a subordinate chimp were present in cages to the side of an arena that contained two barriers, with food located behind one of the barriers on the subordinate's side. Compared to the earlier experiment, the dominant individuals either saw the food being hidden or moved (i.e. were informed) or did not see the food being hidden or moved (i.e. were uninformed). Subordinates on the other hand were always informed. If the subordinates were aware of what the dominants did or did not see during baiting, they should have preferred to go towards food that dominants did not know the location of, and that is what they did. In a second experiment, one dominant observed the food baiting, and then they were switched with a second individual that had not seen the baiting. The subordinates tended to go for food that the switched animal had not seen being baited. Finally, however, when two pieces of food were baited, one that the dominant had seen and one that they had not, the subordinates did not make a preference for which one they went for.

Monkeys have not demonstrated any ability to attribute knowledge to others. Povinelli et al (1992) tested rhesus monkeys using the same paradigm as used with the chimpanzees (Povinelli et al, 1990), and no subject reliably chose the 'Knower' compared to the 'Guesser' (Povinelli et al, 1992). Kuroshima et al (2002), by comparison found that capuchin monkeys learned (over 330 to 470 trials) to chose one of three containers indicated by a 'Knower' compared to a 'Guesser'. One difference in this study was that the 'Knower' looked into each container, whereas the 'Guesser' either did not look into the containers, or only touched them. A second difference was that the subject had to choose the container hiding food rather than indicate the experimenter who would then give them the food if correct. This may have removed an additional level of complexity inherent in the Povinelli experiment.

There is some evidence that western scrub-jays may attribute knowledge to conspecifics. As I discussed earlier, many food-caching animals have to compete with conspecifics to protect their caches from theft. During caching, storsers need to assess whether a conspecific can see them, and if so whether they possess information as to the location of their caches. Emery & Clayton (2001) examined whether scrub-jays would treat their caches differently depending on whether they had cached in view of a conspecific or whether they had cached when the observer's view was occluded. To distinguish

between responses based on to the observer's mental states, rather than learning a simple behavioural cue, the birds recovered their caches in private. When the birds had been observed by another bird during caching, they recovered and re-hid their caches, all in new places unbeknown to the observer (see earlier). By contrast, they did little re-caching when they had previously cached in private and certainly did not discriminate where they re-cached. The jays also re-cached in new sites when they were presented with interleaved trials; first given a visuospatially unique caching tray in which to cache when observed, then a second visuospatially unique tray in which to cache in private, again recovering the caches in private. These results suggest that the jays understood that the observer had knowledge of the location of their caches, and therefore should protect them by moving them to new places, whereas the bird that did not witness caching (in private condition) would be ignorant to their location, and so re-caching would not be required.

The only other species to have been examined for their understanding that seeing leads to knowing are domestic pigs (Held et al, 2001). Subjects were trained to locate food in one of four boxes baited by an experimenter, and given the reward if they chose the correct box. In non-rewarded probe tests, these subjects were then tested for their ability to follow one of two pigs that either did or did not have visual access to a baiting event (i.e. were knowledgeable or ignorant). Almost all subjects failed to follow the knowledgeable conspecific, however one subject did. This may have been attributed to previously learned associations prior to the experiment (although this seems unlikely based on the design). Uninformed pigs can also locate hidden food by utilising the behavioural cues of an informed pig that had previously witnessed the food being hidden by an experimenter (Held et al, 2000), however, the pigs did not have a choice between a knowledgeable and an ignorant pig.

### **Tactical deception & 'false belief': Informational ToM 2**

Tactical deception refers to the intentional manipulation of another's beliefs leading to them to believe something contrary to the truth. Unfortunately, most of the data on tactical deception is based on anecdotes, reported in response to a questionnaire sent to field primatologists. Byrne & Whiten (1988) accumulated all the anecdotes they were sent and sorted them into certain categories that would represent different forms of tactical deception. One classic case of potential tactical deception is as follows:

“Subadult male ME attacks one of the young juveniles who screams. Adult male HL and several other adults run over the hill into view, giving aggressive pan grunt calls; ME seeing them coming, stands on hindlegs and stares into the distance across the valley. HL and the other newcomers stop and look in this direction; they do not threaten or attack ME” (Byrne & Whiten, 1988, p. 237)

Byrne and Whiten have suggested that ME may be staring into the distance with the 'intention' of forming the 'false belief' in the 'minds' of the other baboons that there is a predator located close to them. Of course, this actual scenario could have happened previously in which there was a predator present, or ME may actually have heard something in the bushes to divert his attention, that couldn't be perceived by the researcher. Although Byrne has stated that he could not see anything, he may not have been in the appropriate position to have. Whilst anecdotes are important for formulating testable hypotheses, direct evidence requires an interventionist approach.

### **Experimental studies of deception**

There have been few experimental studies of tactical or intentional deception largely due to difficulties in designing a paradigm that will produce enough data from an infrequent behavioural strategy. (Such strategies are low frequency events probably because their over-use would reduce their power as a competitive strategy.) The earliest experimental study which described deception within a competitive social framework was Menzel (1974; see earlier). Although the informed chimpanzee tended to share food with the other members of their group, the dominant male chimp (Rock), increasingly monopolised the food bonanza, not sharing with any others. The informed chimp (Belle) became less likely over time to move towards, or indicate the location of food if Rock was present. Rock countered



this by moving her off a patch if she was down for too long, and examined the locations where she had previously been or used her body orientation to determine where the food might be located. Belle finally learned to lead the group off in completely the wrong direction to the food, and quickly tail back to retrieve it when the others' attention was elsewhere. This could be interpreted as intentional deception (see also Hirata & Matsuzawa, 2001). Coussi-Korbel (1994) replicated this study in a more controlled manner with sooty mangabeys. She found that Rapide, a subordinate male, when informed of the location of food, was often attacked by the dominant male, Boss, who stole his food. Instead of moving directly towards the food, Rapide quickly changed strategies and followed an increasingly indirect route to the food when Boss was observing.

Bugnyar & Kotrschal (2002) have suggested that caching and raiding ravens may present an example of intentional deception through an attempt to manipulate another individual's attention, either to prevent opponents from gaining opportunities for stealing or to gain opportunities for learning socially from their opponents. They examined two forms in which another's attention may be manipulated; withholding information and directing another's attention away from caches (object of interest). During caching, ravens tended to withdraw from conspecifics, and were often found at a greater distance from conspecifics during caching than during other activities, such as feeding and resting. The storers also cached close to large objects, with 80% of the caches being placed between the storers and the observers, and outside the view of the observers. Cachers moved their caches if an observer moved towards them, and they also protected their cache sites. Cache raiders also employed a number of strategies to increase the potential for learning about cache sites, and for stealing caches. In 33% of cases, the observers changed their position relative to the structures that blocked their view of the cache sites and in 32% of cases the observers changed their orientation and distance away from the cachers (see visual perspective-taking section). If a storer was close to a cache site, the observers delayed pilfering until the cacher had moved away from the caches, usually within 1-min of the cacher leaving the cache site.

Such behaviours suggest that ravens not only appreciate the visual perspective of conspecifics, but they also may use deceptive strategies and counter-strategies in an arm's race to gain another's food caches or protect their own caches. Such strategies may be good candidates for intentional deception as they need to be applied flexibly, they are used in novel contexts or they need to be newly created. Bugnyar & Kotrschal (2004) have recently described a novel strategy in ravens, not described within the context of protecting food caches; leading others away from cache sites.

A different paradigm, which was not based on the natural history of apes, was developed by Woodruff & Premack (1979) in which subjects had to first learn to 'point' towards a container in which they had observed food being hidden by an experimenter to obtain that food. The subject was then presented with a condition in which a second trainer entered the room, and again the subject had to point to the food. One trainer was cooperative (CoopT) who always shared the food with the subject and a second trainer was competitive (CompT) who always kept food for themselves. Woodruff & Premack (1979) were interested in whether the chimpanzee subjects would a) point to the correct location of the food when presented with the CoopT, b) refrain from indicating any container when presented with the CompT, and c) actively mislead the CompT by indicating the container which did not contain food. All four subjects learned to point to the baited container in the presence of CoopT, and learned to withhold information as to the location of hidden food. Additionally, two subjects also began to point towards the empty container. Although Woodruff & Premack (1979) interpreted these results as evidence for intentional deception, the subjects had experienced hundreds of trials across 3 years, and so may have developed sophisticated social strategies to gain the food. Indeed, the subjects could have quickly learned a rule that producing an error with the CompT trainer, i.e. indicating the location of the hidden food, resulted in loss of food, and so rapidly transferred to either withholding any response, or indicating any container except from the one in which the food was actually hidden.

Mitchell & Anderson (1997) and Anderson et al (2001) have replicated this design using capuchin monkeys and squirrel monkeys respectively. Mitchell & Anderson (1997) found that 1 capuchin monkey learn over many hundreds of trials to withdraw responding towards the correct container in the presence of the CompT, whereas the second monkey pointed towards the empty container in the presence of the CompT. Similarly, a squirrel monkey learned over hundreds of trials to point to the incorrect container on CompT trials. However, once the containers were coloured to indicate the presence or absence of food (i.e. green for food present, black for food absent), two subjects reached towards the positive container on CoopT trials, and decreased the frequency with which they reached for the positive container on CompT trials. Further control conditions indicated that these same monkeys could switch strategies appropriately and flexibly from trial-to-trial depending on the type of trainer. Squirrel monkeys have not previously demonstrated sophisticated social strategies during interactions, so these results should be viewed with caution. Indeed, the monkeys received thousands of trials across the entire study, and so some learning process cannot be discounted. The high rate of 'correct' responding by the subjects suggests that the use of deceptive strategies may have not been intentional, as deceptive acts lose their effectiveness when used frequently and predictably. Anderson et al (2001) provided further evidence to suggest that the monkeys were not utilising intentionally deceptive strategies, as the subjects did not appear to take the trainer's knowledge state into account when deciding to be deceptive. The CompT observed where the food was located before the subject had to point to one of the containers, and they continued to point to the incorrect location or withhold pointing to the correct container. In a final study, the experimenter hid the food in the opposite container from the one expected (black instead of green). They found that the subjects continued to reach for the green container, and refrained from reaching towards the black container, in the presence of the CoopT. These results all provide evidence that although the squirrel monkeys can use deceptive strategies during competitive situations, they do not base these strategies on an understanding of the mental states of the protagonist.

A recent experiment examining whether capuchin monkeys would spontaneously deceive conspecifics has produced ambiguous results which are worthy of future study (Fujita et al, 2002). Subordinate-dominant pairs were placed into a food competition situation. Two feeder boxes were located between the two subjects, with the food visible and accessible to the subordinate, but invisible and not accessible to the dominant (until the subordinate had opened the box). Fujita et al (2002) found that two out of four subordinate monkeys spontaneously started to open the unbaited box first, however they only did this on 10% of the total trials.

Although the results of these various experimental studies (in semi-natural environments and the laboratory; using humans or conspecifics as protagonists) provide strong evidence that ravens, monkeys and apes use extremely sophisticated tactics to deceive opponents, they do not provide evidence that these species use such strategies within an intentional framework.

### ***False belief task: The gold standard for ToM?***

Commentators to Premack & Woodruff's 1978 paper made the suggestion that the most convincing evidence for ToM would be produced through an understanding of an agent's beliefs (Bennett, 1978; Dennett, 1978; Harman, 1978). However, as we discussed earlier, understanding that another individual may have *different* beliefs about the world from yourself and that sensory information can be unreliable, may provide better evidence, so-called 'false-belief'. This form of mental attribution has been examined extensively in human children using the 'Sally-Anne' task (or variants of this task). Language is a necessary feature of false belief tasks used in human children. This does not mean that creatures without access to language, such as non-human animals and pre-verbal infants are not in possession of an understanding of false belief. However, it does make the creation of non-verbal false belief tasks challenging. Premack (1988) was the first to develop a non-verbal false belief task for apes and children, but failed to produce any positive results.

Gomez (1998) also developed a false belief task, which has been used in a female orang-utan. During training, the subject was placed into a cage, with two boxes in front of the cage. The boxes were padlocked and the keys were kept in a container elsewhere. One experimenter (Caterer) entered the room, and used the keys to open one of the padlocks, then returned the key to the container and left. A second experimenter (Giver) then entered the room and 'asked' the subject where the food was. The subject was previously trained to point to the box containing food, and once they had pointed to one of the boxes, the Giver retrieved the keys and opened the box indicated by the subject. The Giver then gave the food to the subject if they made the correct choice of box, returned the keys and exited the room. In experimental probe trials, in-between the occasion when the Caterer left the room and the Giver entered the room, a third experimenter (Provider) entered the room and hid the keys in a new location. Therefore, when the Giver entered the room, if they had attributed ignorance to the Giver, they should have pointed to the keys as well as the food. To ensure that this was a test of ignorance, two control conditions were performed; the Giver sees the keys being hidden or hides the keys themselves. Gomez found that although the orang-utan failed the first 6 probe trials, she was successful from then on (see also Gomez, 1996).

Although at initial glance, this appears to be a well-controlled test for false belief, Heyes (1998) has suggested that subjects could solve this problem through associative learning. She states that the subject could have learned that pointing towards the keys in the training trials lead to reward and so transferred this learning to the probe trials in which the Provider hid the keys. However, Gomez stated that the subject was not required to point to anything except the food during training. Heyes also stated that an absence of pointing in the control trials, where the Giver should not be ignorant of the keys' location, may reflect a generalization decrement, i.e. that the subject failed to transfer learning from one context to another. These objections perhaps leave very little possibility for a mentalistic interpretation under any circumstances, and so are hard to reconcile without further experimental information. Whiten (2000a) replicated this experiment with language-trained chimpanzees, and also found that they pointed to the keys before the food during the probe trials (Provider present). The subject's behaviour during control trials suggests that they were not attributing false beliefs. In control trials, the Provider was present when the Hider moved the keys to a new location, but was distracted. In this case, the subjects did not point to the new location of the keys, and so may have been basing their decisions on presence versus absence of the Provider.

The only other non-verbal test for false belief in non-human animals was adapted by Call & Tomasello (1999) which was used in chimpanzees, orang-utans and human children. One experimenter hid food out of the subject's view in one of two identical boxes. A second communicator (who had seen the baiting of the box) indicated which of the boxes contained food, and in control trials, the subjects learned to choose the box that was marked by the communicator. They also learned in additional control trials to choose the unmarked box if they saw the hider move the food from one box to another when the communicator was out of the room. Call & Tomasello suggested that if the subject knew where the food was located (but the communicator did not) they should ignore the communicator's pointing, as he had a false belief that the food remained in the box he saw it placed into. Only 5 year old children passed the 'false belief' component of this experiment, where the hider swapped the boxes around, without showing the food, after the communicator had left the room and the communicator returned and pointed at the wrong box. An understanding of false belief represents a case for third-order intentionality (I *know* that you *believe* that you *know* X) and may therefore be beyond the cognitive capacities of animals, and may be completely dependent on a complex symbolic communication system, such as displayed by human language.

### **Role-taking & experience projection: Simulation ToM**

One aspect of mental attribution that has not been examined seriously in animals until recently is 'simulation' theory (role-taking and experience projection). Simulation 'theory' has been proposed as an alternative to the 'theory' theory of mind approach so far discussed in this chapter. 'Theory' theory is a so-called 'cold' theory which posits that a mindreader is a passive observer of the world, recognizing

another's mental states in the same way as physical forces, such as gravity. One can predict the effects of gravity on objects, and it is proposed that the effects of mental states on another's behaviour are predicted in the same way (by constructing a theory). 'Theory' ToM has no requirement for introspection. By contrast, 'simulation' ToM posits that the mindreader uses her own mind to simulate the mental processes of another individual (i.e. 'putting herself in another's shoes'). As such 'simulation' ToM does require introspective processes, and so may be related to self-awareness (Gallup, 1982). At present, philosophers of mind and psychologists are divided as to the relative contributions of 'theory' ToM and 'simulation' ToM to human mental state attribution (Gordon, 1986; Goldman, 1992; Currie & Ravenscroft, 1997; see also papers in Carruthers & Smith, 1996). Recent proposals suggest that different aspects of 'theory' ToM and 'simulation' ToM contribute to mindreading (Perner, 1996); indeed different aspects of these two theories appear to be compromised in autism (Currie, 1996).

'Simulation' ToM has been examined in animals in two forms; role-taking or cognitive empathy (Povinelli et al, 1992, Povinelli, 1993), and experience projection (Emery & Clayton, 2001). Both Gallup (1982) and Whiten (1996, 2000) have made the suggestion that demonstrating experience projection would provide good evidence for ToM in animals. However, in both cases, only a single experience or role is projected or transferred, whereas 'simulation' theory attempts to cover the entire range of mental experience (Whiten, 2000). Projecting one's own experiences to another, however may also be different from representing another's mental states, in fact, the specific experiences are not necessarily tied to a particular mental state, such as attention, desire or belief. As such, experience projection may not be strictly dependent on language, and so individual behaviour may be used as an index to performance and as such may provide an unambiguous technique with which to investigate mentalizing in nonhuman animals.

Role-taking has been examined in both chimpanzees and rhesus monkeys (Povinelli et al, 1992a, b). Subjects were presented with an apparatus first developed by Mason & Hollis (1962), in which an operator could control levers which moved food bowls from one side of the apparatus to the other. The 'informant' could see whether one of the 4 food bowls was baited, but did not have access to the controls used to gain access to the food. The 'operator' however, could not see which bowl was baited, but were able to control the apparatus. The informants therefore had to indicate, through pointing, which of the bowls contained food, so that the operator would use the controls to move the bowls towards the informant and the operator, so that they both received the food. The chimpanzees and rhesus monkeys were trained to perform one of the roles, and then they transferred to the opposing, new role. Three out of 4 chimpanzees transferred immediately to their new role, whereas the rhesus monkeys were never able to transfer to their new role. Unfortunately, the second task was not learned faster than the first task, thus providing an argument against role-taking (Heyes, 1998). Heyes also suggested that experience projection may be ruled out, as the subjects' experiences outside of the experiment cannot be ruled out, especially their comprehension and/or production of pointing, and the effects of pre-training.

Experience projection has only been examined once in a non-human animal, a food-caching corvid, not a great ape. As discussed earlier, western scrub-jays utilise different cache protection strategies depending on whether or not they had been watched during caching. Of particular relevance here to an understanding of the evolution of mental attribution is the fact that birds only re-cached when they themselves had previous experience of pilfering another bird's caches, again in new locations. Birds without this experience failed to re-cache, irrespective of whether they had previously cached in front of an observer or in private. This result raises the exciting possibility that birds with pilfering experience can project their own experience of being a thief onto the observing bird, and so counter what they would predict a thief would do in relation to their hidden food.

### **Experience projection, cognitive empathy & mirror neurons.**

In the mid-1990s, a startling neurophysiological finding was published that has had an incredible influence on social cognition research; namely the finding of 'mirror-neurons' in the macaque

pre-motor cortex (area F5; Rizzolatti & Craighero, 2004 for review). Mirror-neurons are cells that respond selectively to the (visual) perception of another individual's motor action pattern (such as an experimenter reaching towards an object) AND the action itself performed by the monkey in which the neurons are being recorded. Gallese & Goldman (1998) have made a connection between 'simulation' theory and mirror neurons, and Preston & de Waal (2002) have made the connection between empathy and mirror neurons. However, I would like to suggest that experience projection is the most neurobiologically plausible candidate for future investigations of the neural basis of social cognition, particularly in non-verbal creatures using single-cell neurophysiological techniques (see chapter by Jellema & Perrett). Of course, this does not preclude the existence of complex neuronal circuits (or neural ensembles) representing different aspects of 'simulation' theory. This is similar to the argument that mirror neurons are unlikely to represent imitation per se, as imitation is the copying of a series of novel actions, not individual actions (as represented by mirror neurons). As such, imitation may function through a circuit including area F5, but also such regions as the supplementary motor area (SMA), which contains neurons responsive to the physical motor performance of sequences of actions (Halsband et al, 1994; Tanji & Shima, 1994). As such, mirror neurons in area F5 may also be one-stage in a 'social cognition pathway', which will also include superior temporal sulcus, amygdale, and medial prefrontal cortex, amongst others.

### **Arguments against ToM in animals**

Some authors, in particular Heyes (1998), state that there is no evidence as yet, that any animal has been unequivocally shown to possess a theory of mind (although to be fair these statements were made before the recent competitive paradigm studies of Emery & Clayton, 2001 and Hare et al, 2001). The basis for Heyes' standpoint is that many of these experiments could be interpreted in both mentalistic (i.e. understanding mental states) and nonmentalistic (i.e. associative learning) terms. For example, in Povinelli's knowledge attribution experiment (Povinelli et al, 1990), the chimps may have formed an association between the 'Knower' and the baited food, as the 'Knower' initially baited the food, whilst the 'Guesser' was out of the room. In the transfer condition, the 'Guesser' has a bag over their head, therefore the chimps may have learned a new discrimination, or may have developed an aversive reaction to the bag, as we do not know whether the chimpanzees had experience of this stimulus prior to the experiment. In many respects, the Hare et al (2001) study largely eliminates these simple discrimination based arguments by using chimpanzees that have either been misinformed about the location of food, or using different individuals from the ones that had witnessed the baiting.

In another example, the role-taking experiment (Povinelli et al, 1992a, b), there was no difference in the rate of learning between the pre-switch and post-switch condition, i.e. the problem in the second condition was not learned any faster than the initial problem. A mentalistic explanation would have predicted the opposite of this, with a correct response on the first trial after the switch. Finally, in the visual perspective-taking experiment (Povinelli & Eddy, 1996a), the chimps did not selectively discriminate between trainers based on various natural and artificial occluders to sight. In the one case where there was a successful discrimination (facing versus back turned), the chimpanzees may have been responding to a simple discrimination based on previous experience (experimenters never had their backs turned when they gave food to the chimpanzees). The other discriminations (such as changes in eye gaze) may have been too difficult (or subtle) for the chimpanzees.

Heyes (1993, 1998) has also suggested that any attempt to assess ToM in animals must use *triangulation*, where an animal is trained on one set of conditions and is then tested in conditions that are conceptually, but not physically similar so that it makes it difficult for the animal to solve the new task by associative learning and stimulus generalisation. Unfortunately, few tests for ToM have done this. Clearly what is needed is a series of tests in which an animal that relied on associative learning would show the opposite result to that of an animal that used ToM. Only one study has attempted such a distinction, but has only been examined using human subjects. Gagliardi et al (1995) showed college students short video clips of similar situations similar to the 'Knower-Guesser' experiments, and the students were rewarded with money for each correct response. For one group, the Guesser (whose

back was turned while the container was baited) always pointed to the correct container, while the second group received the typical procedure in which the Knower always pointed to the correct container. Thus, for one group associative learning was inconsistent with ToM, and for the other group it was consistent. Interestingly, there was no difference between the two groups in speed of task acquisition, showing that subjects may use associative learning to solve the task even if they possess a ToM. This might be a productive approach that could be developed for non-human species.

Heyes (1993) also suggested that the most convincing evidence for ToM in non-human animals would be converging evidence from different experiments using the same animals, for example, visual perspective-taking, knowledge attribution and role-taking. Interestingly, there is good evidence for these abilities in both chimpanzees and scrub-jays. This approach is certainly more powerful than positive results from a single experiment in a single language-trained animal.

One argument against ToM in primates has been proposed by Povinelli, who now suggests that the evidence is thin or non-existent (Povinelli et al, 2000; Povinelli & Vonk, 2003). Povinelli now takes the radical standpoint that primate researchers are mistaken in their positive view of primate ToM and base their positive reasoning on the 'argument by analogy', or the popular opinion that chimpanzees and the other great apes must have complex cognitive abilities, such as ToM because they are our closet living relatives (Povinelli et al, 2000). This view is starkly contrasted to that of Tomasello and Call who have changed their own position from 'no evidence' (Tomasello & Call, 1997) to 'positive evidence' (Tomasello et al, 2003ab). In both cases, the change in position seems to have been driven by the results of one critical experiment. Povinelli's position has changed after finding that chimpanzees could not discriminate between a human that could see them compared to another that could not (Povinelli & Eddy, 1996b). Tomasello and Call's position has changed after finding that chimpanzees know what conspecifics can and cannot see, and what they do and do not know (Hare et al, 2000, 2001). Although a prolonged discussion of these issues is outside the scope of this chapter, I would like to caution against restricting views of the evidence for and against ToM in animals to a sub-set of researchers. Research in species which are not closely related to humans, such as western scrub-jays, cannot be guilty of the 'argument by analogy', and as such may present the best evidence for ToM in non-human animals so far.

## **SUMMARY & CONCLUSIONS**

In this chapter, I have reviewed and discussed all the evidence for and against the view that non-human animals possess the ability to represent other individual's mental states (ToM). Although I have attempted to cover all known studies of non-human mentalizing, I have particularly focused on those aspects of comparative social cognition which may be of interest to neuroscientists working with non-human animals and humans alike. First, I discussed the requisites for complex social cognition; a large brain, complex social groups, and enhanced longevity, so that the correct species are targeted for future research. Second, I described a couple of theoretical tools which may be particularly useful in thinking about the neurobiology of social cognition; intentional stance and intervening variables. Third, I described the different types of social cognition that have been examined in non-human animals; understanding attention, knowledge attribution, intentional communication, understanding beliefs and false beliefs, and simulation ToM (role-taking and experience projection). Finally, I described some of the arguments against ToM in animals. In conclusion, the only positive evidence for ToM in non-human animals has been provided by recent experiments in chimpanzees and western scrub-jays. The available evidence is for multiple types of social cognition, and is presented as convergent evidence. The aspect of ToM which has yet to be demonstrated by any non-human animal is an understanding of false belief. This ability requires third-order intentionality which may be outside the capacity of the animal mind.

As a final word, I would like to stress that we may never determine the neurocognitive mechanisms of how humans and other animals understand each other as social agents, and why these abilities fail,

without collaborations between comparative and developmental psychologists, cognitive and behavioural neuroscientists, psychopathologists, psychiatrists, geneticists and even philosophers.

### **ACKNOWLEDGEMENTS**

I would like to thank Nicky Clayton for her insightful comments on an earlier draft of this manuscript, and for extensive discussions of these issues. During the writing of this chapter, I was funded by a Royal Society University Research Fellowship.

### **REFERENCES**

- Agnetta, B., Hare, B., & Tomasello, M. (2000). Cues to food location that domestic dogs (*Canis familiaris*) of different ages do and do not use. *Animal Cognition*, 3, 107-112.
- Anderson, J. R. & Mitchell, R. W. (1999). Macaques, but not lemurs, co-orient visually with humans. *Folia primatologica*, 70, 17-22.
- Anderson, J. R., Kuroshima, H., Kuwahata, H., Fujita, K. & Vick, S-J. (2001). Training squirrel monkeys (*Saimiri sciureus*) to deceive: acquisition and analysis of behaviour toward cooperative and competitive trainers. *Journal of Comparative Psychology*, 115, 282-293.
- Anderson, J. R., Montant, M. & Schmit, D. (1996). Rhesus monkeys fail to use gaze direction as an experimenter-given cue in an object-choice task. *Behavioral Processes*, 37, 47-55.
- Anderson, J. R., Sallaberry, P. & Barbier, H. (1995). Use of experimenter-given cues during object-choice tasks by capuchin monkeys. *Animal Behaviour*, 49, 201-208.
- Baron-Cohen, S. (1989). Perceptual role-taking and protodeclarative pointing in autism. *British Journal of Developmental Psychology*, 7, 113-127.
- Baron-Cohen, S. (1991). Precursors to a theory of mind: Understanding attention in others. In: *Natural Theories of Mind: Evolution, development and simulation in everyday mindreading* (Whiten, A., ed.), pp. 233-251, Blackwell: Oxford.
- Baron-Cohen, S., Leslie, A. M. & Frith, U. (1985). Does the autistic child have a 'theory of mind'? *Cognition*, 21, 37-46.
- Barton, R. & Dunbar, R. I. M. (1997). Evolution of the social brain. In: *Machiavellian intelligence II: evaluations and extensions* (Whiten, A. & Byrne, R. W., eds.), pp. 240-263, Cambridge University Press: Cambridge.
- Bennett, J. (1978). Some remarks about concepts. *Behavioural & Brain Science*, 1, 557-560.
- Blaschke, M. & Ettliger, G. (1987). Pointing by monkeys. *Animal Behaviour*, 35, 1520-1523.
- Brothers, L. (1990). The social brain: a project for integrating primate behavior and neurophysiology in a new domain. *Concepts in Neuroscience*, 1, 27-51.
- Bugnyar, T. & Kotrschal, K. (2002). Observational learning and the raiding of food caches in ravens, *Corvus corax*: is it 'tactical' deception? *Animal Behaviour*, 64, 185-195.
- Bugnyar, T. & Kotrschal, K. (2003). Leading a conspecific away from food in ravens (*Corvus corax*)? *Animal Cognition*, 7, 69-79.
- Burger, J., Gochfield, M. & Murray, B. G. (1992). Risk discrimination if eye contact and directness of approach in black iguanas (*Ctenosaurus similis*). *Journal of Comparative Psychology*, 106, 97-101.
- Butterworth, G. & Jarrett, N. (1991). What minds have in common is space: Spatial mechanisms serving joint visual attention in infancy. *British Journal of Developmental Psychology*, 9, 55-72.
- Byrne, R. W. (1999). Human cognitive evolution. In: *Descent of Mind: Psychological perspectives on hominid evolution* (Corballis, M. C & Lea, S. E. G., eds.), pp. 71-87, Oxford University Press: Oxford.
- Byrne, R. W. & Whiten, A. (1988, eds.). *Machiavellian Intelligence: Social expertise and the evolution of intellect in monkeys, apes and humans*. Clarendon Press: Oxford.
- Call, J. & Tomasello, M. (1994a). Production and comprehension of referential pointing by orangutans (*Pongo pygmaeus*). *Journal of Comparative Psychology*, 108, 307-317.
- Call, J. & Tomasello, M. (1996). The effects of humans on the cognitive development of apes. In: *Reaching Into Thought: the minds of the great apes* (Russon, AE, Bard, KA & Parker, ST, eds.), pp. 371-403, Cambridge University Press: New York.

- Call, J. & Tomasello, M. (1998). Distinguishing intentional from accidental actions in orangutans (*Pongo pygmaeus*), chimpanzees (*Pan troglodytes*) and human children (*Homo sapiens*). *Journal of Comparative Psychology*, 112, 192-206.
- Call, J. & Tomasello, M. (1999). A nonverbal false belief task: the performance of children and great apes. *Child Development*, 70, 381-395.
- Call, J., Agnetta, B. & Tomasello, M. (2000). Cues that chimpanzees do and do not use to find hidden objects. *Animal Cognition*, 3, 23-34.
- Call, J., Hare, B. & Tomasello, M. (1998). Chimpanzee gaze following in an object-choice task. *Animal Cognition*, 1, 89-99.
- Carruthers, P. & Smith, P. K. (1996; eds.). *Theories of Theories of Mind*. Cambridge University Press: Cambridge.
- Cheney, D. & Seyfarth, R. (1990). Attending to behaviour versus attending to knowledge: examining monkeys' attribution of mental states. *Animal Behaviour*, 40, 742-753.
- Clements, W. A. & Perner, J. (1994). Implicit understanding of belief. *Cognitive Development*, 9, 377-397.
- Connor, R. C., Heithaus, M. R. & Barre, L. M. (2001). Complex social structure, alliance stability and mating access in a bottlenose dolphin 'super-alliance'. *Proceedings of the Royal Society of London: B*, 268, 263-267.
- Cooper, J. J., Ashton, C., Bishop, S., West, R., Mills, D. S., & Young, R. J. (2003). Clever hounds: Social cognition in the domestic dog (*Canis familiaris*). *Applied Animal Behaviour Science*, 81, 229-244.
- Coss, R. G. (1978). Perceptual determinants of gaze aversion by the lesser mouse lemur (*Microcerbus murinus*): The role of two facing eyes. *Behaviour*, 64, 248-267.
- Coussi-Korbel, S. (1994). Learning to outwit a competitor in mangabeys (*Cercocebus t. torquatus*). *Journal of Comparative Psychology*, 108, 164-171.
- Currie, G. (1996). Simulation-theory, theory-theory and the evidence from autism. In: *Theories of Theories of Mind* (Carruthers, P. & Smith, P. K., eds.), pp. 242-256, Cambridge University Press: Cambridge.
- Currie, G. & Ravenscroft, I. (1997). Mental simulation and motor imagery. *Philosophy of Science*, 64, 161-180.
- Dally, J. M., Emery, N. J. & Clayton, N. S. (2004). Cache protection strategies by western scrub-jays (*Aphelocoma californica*): Implications for social cognition. *Animal Behaviour*, in press.
- de Waal, F. B. M. (1982). *Chimpanzee politics: sex and power among apes*. John Hopkins University Press: Baltimore, MD.
- de Waal, F. B. M. & Tyack, P. (2003). *Animal Social Complexity*. Harvard University Press: Harvard, MA.
- Dennett, D. C. (1978). Beliefs about beliefs. *Behavioural and Brain Sciences*, 1, 568-570.
- Dennett, D. C. (1983). Intentional systems in cognitive ethology: The 'Panglossian paradigm' defended. *Behavioural and Brain Sciences*, 6, 343-390
- Dickinson, A. & Balleine, B. W. (2000). Causal cognition and goal directed action. In: *Evolution of Cognition* (Heyes, C. M. & Huber, L., eds.), pp. 185-204. MIT Press: Cambridge, MA.
- Dunbar, R. I. M. (1992). Neocortex size as a constraint on group size in primates. *Journal of Human Evolution*, 20, 469-493.
- Dunbar, R. I. M. (1998). The social brain hypothesis. *Evolutionary Anthropology*, 6, 178-190.
- Emery, N. J. (2000). The eyes have it: the neuroethology, function and evolution of social gaze. *Neuroscience & Biobehavioral Reviews*, 24, 581-604.
- Emery, N. J. (2004). Are corvids 'feathered apes': Cognitive evolution in crows, jays, rooks and jackdaws. In: Watanabe, S (Ed.) *Comparative Analysis of Minds* (pp. 181-213), Keio University Press: Tokyo.
- Emery, N. J. & Clayton, N. S. (2001). Effects of experience and social context on prospective caching strategies by scrub jays. *Nature*, 414, 443-446.



- Emery, N. J. & Clayton, N. S. (2004). Comparing the complex cognitive abilities of birds and primates In: Rogers, L. J. & Kaplan, G (Eds.) *Comparative Vertebrate Cognition: Are primates superior to non-primates?* Pp. 3-55. Kluwer Academic/Plenum Press: New York.
- Emery, N. J., Dally, J. M. & Clayton, N. S. (2004). Western scrub-jays (*Aphelocoma californica*) use cognitive strategies to protect their caches from thieving conspecifics. *Animal Cognition*, 7, 37-43.
- Emery, N. J., Lorincz, E. N., Perrett, D. I., Oram, M. W. & Baker, C. I. (1997). Gaze following and joint attention in rhesus monkeys (*Macaca mulatta*). *Journal of Comparative Psychology*, 111, 286-293.
- Feh, C. (1999). Alliances and reproductive success in Camargue stallions. *Animal Behaviour*, 57, 705-713.
- Flavell, J. H., Everett, B. A., Croft, K. & Flavell, E. R. (1981). Young children's knowledge about visual perception: further evidence for the level 1-level 2 distinction. *Developmental Psychology*, 17, 99-103.
- Frith, U. & Frith, C. D. (1999). Development and neurophysiology of mentalizing. *Philosophical Transactions of the Royal Society of London: Biological Sciences*, 358, 459-473.
- Fujita, K., Kuroshima, H. & Masuda, T. (2002). Do tufted capuchin monkeys (*Cebus apella*) spontaneously deceive opponents? A preliminary analysis of an experimental food-competition contest between monkeys. *Animal Cognition*, 5, 19-25.
- Gagliardi, J. K., Kirkpatrick-Steger, K. K., Thomas, J., Allen, G. J. & Blumberg, M. S. (1995). Seeing and knowing: knowledge attribution versus stimulus control in adult humans (*Homo sapiens*). *Journal of Comparative Psychology*, 109, 107-114.
- Gallese, V. & Goldman, A. (1998). Mirror neurons and the simulation theory of mind-reading. *Trends in Cognitive Sciences*, 493-501.
- Goldman, A. (1992). In defence of the simulation theory. *Mind & Language*, 7, 104-119.
- Gomez, J-C. (1991). Visual behaviour as a window for reading the minds of others in primates. In: *Natural Theories of Mind: evolution, development and simulation of everyday mindreading* (Whiten, A., Ed.), pp. 195-207, Blackwell: Oxford.
- Gomez, J-C. (1996). Nonhuman primate theories of (nonhuman primate) minds: some issues concerning the origins of mindreading. In: *Theories of theories of mind* (Carruthers, P. & Smith, P. K., Eds.), pp. 330-343, Cambridge University Press: Cambridge.
- Gomez, J-C. (1998). Assessing theory of mind with non-verbal procedures: Problems with training methods and alternative "key" procedure. *Behavioural & Brain Sciences*, 21, 119-120.
- Gomez, J-C., Sarriá, E., & Tamarit, J. (1993). The comparative study of early communication and theories of mind: Ontogeny, phylogeny and pathology. In: *Understanding Other Minds: Perspectives from autism* (Baron-Cohen, S., Tager-Flusberg, H., & Cohen, D., Eds.), pp. 397-426, Oxford University Press: Oxford.
- Gordon, R. M. (1986). Folk psychology as simulation. *Mind & Language*, 1, 158-171.
- Grinnell, J., Packer, C. & Pusey, A. E. (1995). Cooperation in male lions: kinship, reciprocity or mutualism? *Animal Behaviour*, 49, 95-105.
- Halsband, V., Matsuzaka, Y. & Tanji, J. (1994). Neuronal activity in the primate supplementary, pre-supplementary, and pre-motor cortex during externally and internally instructed sequential movements. *Neuroscience Research*, 20, 149-155.
- Hampton, R. R. (1994). Sensitivity to information specifying the line of gaze of humans in sparrows (*Passer domesticus*). *Behaviour*, 130, 41-51.
- Hare, B. (2001). Can competitive paradigms increase the validity of experiments on primate social cognition? *Animal Cognition*, 4, 269-280.
- Hare, B. & Tomasello, M. (1999). Domestic dogs (*Canis familiaris*) use human and conspecific social cues to locate hidden food. *Journal of Comparative Psychology*, 113, 173-177.
- Hare, B., Addessi, E., Call, J., Tomasello, M. & Visalberghi, E. (2003b). Do capuchin monkeys, *Cebus apella*, know what conspecifics do and do not see? *Animal Behaviour*, 65, 131-142.
- Hare, B., Brown, M., Williamson, C. & Tomasello, M. (2003a). The domestication of social cognition in dogs. *Science*, 298, 1634-1636.

- Hare, B., Call, J., & Tomasello, M. (1998). Communication of food location between human and dog (*Canis familiaris*). *Evolution of Communication*, 2, 137-159.
- Hare, B., Call, J., Agnetta, B. & Tomasello, M. (2000). Chimpanzees know what conspecifics do and do not see. *Animal Behaviour*, 59, 771-785.
- Hare, B., Call, J. & Tomasello, M. (2001). Do chimpanzees know what conspecifics know? *Animal Behaviour*, 61, 139-151.
- Harman, G. (1978). Studying the chimpanzee's theory of mind. *Behavioural & Brain Sciences*, 1, 576-577.
- Hauser, M. D. (2000). *Wild Minds*. Henry Holt Publishers: London.
- Heinrich, B. (1999). *Mind of the Raven*. Harper Collins: London
- Heinrich, B. & Pepper, J. W. (1998). Influence of competitors on caching behaviour in the common raven, *Corvus corax*. *Animal Behaviour*, 56, 1083-1090.
- Held, S., Mendl, M., Devereux, C. & Byrne, R. W. (2000). Social tactics of pigs in a competitive foraging task: the 'informed forager' paradigm. *Animal Behaviour*, 59, 569-576.
- Held, S., Mendl, M., Devereux, C. & Byrne, R. W. (2001). Behaviour of domestic pigs in a visual perspective taking task. *Behaviour*, 138, 1337-1354.
- Herman, L. M., Abichandani, S. L., Elhaji, A. N., Herman, E. Y. K., Sanchez, J. L. & Pack, A. A. (1999). Dolphins (*Tursiops truncatus*) comprehend the referential character of the human pointing gesture. *Journal of Comparative Psychology*, 113, 347-364.
- Hess, J., Novak, M. A. & Povinelli, D. J. (1993). 'Natural pointing' in a rhesus monkey, but no evidence of empathy. *Animal Behaviour*, 46, 1023-1025.
- Heyes, C. M. (1993). Anecdotes, training, trapping and triangulating: do animals attribute mental states? *Animal Behaviour*, 46, 177-188.
- Heyes, C. M. (1998). Theory of mind in nonhuman primates. *Behavioural & Brain Sciences*, 21, 101-148.
- Hirata, S. & Matsuzawa, T. (2001). Tactics to obtain a hidden food item in chimpanzee pairs (*Pan troglodytes*). *Animal Cognition*, 4, 285-295.
- Hostetter, A. B., Cantero, M. & Hopkins, W. D. (2001). Differential use of vocal and gestural communication by chimpanzees (*Pan troglodytes*) in response to the attentional status of a human (*Homo sapiens*). *Journal of Comparative Psychology*, 115, 337-343.
- Humphrey, NK (1976). The social function of intellect. In: *Growing points in ethology* (Bateson, P. P. G. & Hinde, R. A., eds.), pp. 303-317. Cambridge University Press: Cambridge.
- Itakura, S. (1996). An exploratory study of gaze-monitoring in nonhuman primates. *Japanese Psychological Research*, 38, 174-180.
- Itakura, S. & Anderson, J. R. (1996). Learning to use experimenter-given cues during an object-choice task by a capuchin monkey. *Current Psychology of Cognition*, 15, 103-112.
- Itakura, S. & Tanaka, M. (1998). Use of experimenter-given cues during object-choice tasks by chimpanzees (*Pan troglodytes*), an orang-utan (*Pongo pygmaeus*), and human infants (*Homo sapiens*). *Journal of Comparative Psychology*, 112, 119-126.
- Itakura, S., Agnetta, B., Hare, B. & Tomasello, M. (1999). Chimpanzee use of human and conspecific social cues to locate hidden food. *Developmental Science*, 2, 448-456.
- Jolly, A. (1966). Lemur social behaviour and primate intelligence. *Science*, 153, 501-506.
- Karin-D'Arcy, M. R. & Povinelli, D. J. (2002). Do chimpanzees know what each other see? A closer look. *International Journal of Comparative Psychology*, 15, 21-54.
- Kummer, H., Anzenberger, G. & Hemelrijk, C. K. (1996). Hiding and perspective taking in long-tailed macaques (*Macaca fascicularis*). *Journal of Comparative Psychology*, 110, 97-102.
- Kuroshima, H., Fujita, K., Fuyuki, A. & Masuda, T. (2002). Understanding of the relationship between seeing and knowing by tufted capuchin monkeys (*Cebus apella*). *Animal Cognition*, 5, 41-48.
- Leavens, D. A. & Hopkins, W. D. (1998). Intentional communication by chimpanzees: A cross-sectional study of the use of referential gestures. *Developmental Psychology*, 34, 813-822.
- Leavens, D. A. & Hopkins, W. D. (1999). The whole-hand point: the structure and function of pointing from a comparative perspective. *Journal of Comparative Psychology*, 113, 417-425.

- Leavens, D. A., Hopkins, W. D. & Bard, K. A. (1996). Indexical and referential pointing in chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, 110, 346-353.
- Lorincz, E. N., Baker, C. I. & Perrett, D. I. (1999). Visual cues for attention following in rhesus monkeys. *Current Psychology of Cognition*, 18, 973-1003.
- McKinley, J. & Sambrook, T. D. (2000). Use of human-given cues by domestic dogs (*Canis familiaris*) and horses (*Equus caballus*). *Animal Cognition*, 3, 13-22.
- Mason, WA & Hollis, JH (1962). Communication between young rhesus monkeys. *Animal Behaviour*, 10, 211-221.
- Matheson, M., Cooper, M., Weeks, J., Thompson, R. & Frigaszy, D. (1998). Attribution is more likely demonstrated in more natural contexts. *Behavioural & Brain Sciences*, 21, 124-126.
- Menzel, E. W. Jr. (1974). A group of young chimpanzees in a one-acre field. In: *Behavior of non-human primates* (Eds. Schrier, A. M. & Stollnitz, F.). Vol. 5. (pp. 83-153). Academic Press: New York.
- Miklosi, A., Kubinyi, E., Topal, J., Gacsi, M., Viranyi, Z. & Csanyi, V. (2003). A simple reason for a big difference: wolves do not look back at humans, but dogs do. *Current Biology*, 13, 763-766.
- Miklosi, A., Polgardi, R., Topal, J. & Csanyi, V. (1998). Use of experimenter-given cues in dogs. *Animal Cognition*, 1, 113-121.
- Miklosi, A., Polgardi, R., Topal, J. & Csanyi, V. (2000). Intentional behaviour in dog-human communication: an experimental analysis of "showing" behaviour in the dog. *Animal Cognition*, 3, 159-166.
- Miller, N. E. (1959). Liberalization of basic S-R concepts: Extension to conflict, motivation, and social learning. In: *Psychology: A study in science* (Koch, S., Ed.), pp. 196-292, McGraw Hill: New York.
- Mitchell, R. W. & Anderson, J. R. (1997). Pointing, withholding information and deception in capuchin monkeys (*Cebus apella*). *Journal of Comparative Psychology*, 111, 351-361.
- Montague, P. R., Berns, G. S., Cohen, J. D., McClure, S. M., Pagnoni, G., Dhamala, M., Wiest, M. C., Karpov, I., King, R. D., Apple, N. & Fisher, R. E. (2002). Hyperscanning: simultaneous fMRI during linked social interaction. *NeuroImage* 16, 1159-1164.
- Neiworth, J. J., Burman, M. A., Basile, B. M. & Licktig, M. T. (2002). Use of experimenter-given cues in visual co-orienting and in an object-choice task by a New World monkey species, cotton top tamarins (*Saguinus oedipus*). *Journal of Comparative Psychology*, 116, 3-11.
- Peignot, P. & Anderson, J. R. (1999). Use of experimenter-given manual and facial cues by gorillas (*Gorilla gorilla*) in an object choice task. *Journal of Comparative Psychology*, 113, 253-260.
- Perner, J. (1991). *Understanding the representational mind*. MIT Press: Cambridge, MA.
- Perner, J. (1996). Simulation as explicitation of predication-implicit knowledge about the mind: arguments for a simulation-theory mix. In: *Theories of theories of mind* (Carruthers, P. & Smith, P. K., Eds.), pp. 90-104, Cambridge University Press: Cambridge.
- Plooij, F. X. (1978). Some basic traits of language in wild chimpanzees? In: *Action, gesture & symbol* (Lock, A., Ed.), pp. 111-131, Academic Press: London.
- Povinelli, D. J. (1991). *Social intelligence in monkeys and apes*. Unpublished doctoral dissertation, Yale University.
- Povinelli, D. J. (1993). Reconstructing the evolution of mind. *American Psychologist*, 48, 493-509.
- Povinelli, D. J. (1994). Comparative studies of animal mental state attribution: a reply to Heyes. *Animal Behaviour*, 48, 239-241.
- Povinelli, D. J. (2000). *Folk Physics for Apes*. Oxford University Press: New York.
- Povinelli, D. J., Bierschwale, D. T. & Cech, C. G. (1999). Comprehension of seeing as a referential act in young children, but not juvenile chimpanzees. *British Journal of Developmental Psychology*, 17, 37-60.
- Povinelli, D. J. & Davis, D. R. (1994). Differences between chimpanzees (*Pan troglodytes*) and humans (*Homo sapiens*) in the resting state of the index finger: implications for pointing. *Journal of Comparative Psychology*, 108, 134-139.
- Povinelli, D. J. & Eddy, T. J. (1996a). Chimpanzees: joint visual attention. *Psychological Science*, 7, 129-135.

- Povinelli, D. J. & Eddy, T. J. (1996b). What young chimpanzees know about seeing. *Monographs of the Society for Research in Child Development*, 61, Serial No. 247. Chicago: University of Chicago Press.
- Povinelli, D. J. & Eddy, T. J. (1997). Specificity of gaze-following in young chimpanzees. *British Journal of Developmental Psychology*, 15, 213-222.
- Povinelli, D. J. & O'Neill, D. K. (2000). Do chimpanzees use their gestures to instruct each other? In: *Understanding Other Minds: Perspectives from developmental cognitive neuroscience*. (Baron-Cohen, S., Tager-Flusberg, H. & Cohen, D., Eds.), pp. 459-487. Oxford University Press: Oxford.
- Povinelli, D. J. & Vonk, J. (2003). Chimpanzee minds: suspiciously human? *Trends in Cognitive Sciences*, 7, 157-160.
- Povinelli, D. J., Bering, J. M. & Giambrone, S. (2000). Toward a science of other minds: escaping the argument by analogy. *Cognitive Science*, 24, 509-541.
- Povinelli, D. J., Nelson, K. E. & Boysen, S. T. (1990). Inferences about guessing and knowing by chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, 104, 203-210.
- Povinelli, D. J., Nelson, K. E. & Boysen, S. T. (1992a). Comprehension of role reversal in chimpanzees: evidence of empathy? *Animal Behaviour*, 43, 633-640.
- Povinelli, D. J., Parks, K. A., & Novak, M. A. (1992b). Role reversal by rhesus monkeys, but no evidence of empathy. *Animal Behaviour*, 44, 269-281.
- Povinelli, D. J., Parks, K. A. & Novak, M. A. (1991). Do rhesus monkeys (*Macaca mulatta*) attribute knowledge and ignorance to others? *Journal of Comparative Psychology*, 105, 318-325.
- Povinelli, D. J., Perilloux, H. K., Reaux, J. E. & Bierschwale, D. T. (1998). Young and juvenile chimpanzees' (*Pan troglodytes*) reactions to intentional versus accidental and inadvertent actions. *Behavioural Processes*, 42, 205-218.
- Povinelli, D. J., Rulf, A. B. & Bierschwale, D. T. (1994). Absence of knowledge attribution and self-recognition in young chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, 108, 74-80.
- Premack, D. (1988). "Does the chimpanzee have a theory of mind?" revisited. In: *Machiavellian Intelligence: Social expertise and the evolution of intellect in monkeys, apes and humans*. (Eds. Byrne, R. W. & Whiten, A.), pp. 160-179, Oxford University Press: Oxford.
- Premack, D. & Premack, A. J. (2002). *Original Intelligence*. McGraw Hill Inc.: New York.
- Premack, D. & Woodruff, G. (1978). Does the chimpanzee have a theory of mind? *Behavioural & Brain Sciences*, 1, 515-526.
- Purdy, J. E. & Domjan, M. (1998). Tactics in theory of mind research. *Behavioural & Brain Sciences*, 21, 129-130.
- Reader, S. M. & Laland, K. N. (2002). Social intelligence, innovation, and enhanced brain size in primates. *Proceedings of the National Academy of Sciences USA*, 99, 4436-4441.
- Reaux, J. E., Theall, L. A. & Povinelli, D. J. (1999). A longitudinal investigation of chimpanzees' understanding of visual perception. *Child Development*, 70, 275-290.
- Rizzolatti, G. & Craighero, L. (2004). The mirror-neuron system. *Annual Review of Neuroscience*, 27, 169-192.
- Savage-Rumbaugh, E. S., Rumbaugh, D. M. & Boysen, S. T. (1978). Sarah's problems in comprehension. *Behavioural & Brain Sciences*, 1, 555-557.
- Scheel, D. & Packer, C. (1991). Group hunting behaviour of lions: a search for cooperation. *Animal Behaviour*, 41, 697-708.
- Siegal, M. & Beattie, K. (1991). Where to look first for children's understanding of false beliefs. *Cognition*, 38, 1-12.
- Smale, L., Holekamp, K. E., Weldele, M., Frank, L. G. & Glickman, S. E. (1995). Competition and cooperation between litter-mates in the spotted hyena, *Crocuta crocuta*. *Animal Behaviour*, 50, 671-682.
- Smitha, B., Thakar, J. & Watve, M. (1999). Do bee-eaters have a theory of mind? *Current Science* 76, 574-577.

- Soproni, K., Miklosi, A., Topal, J. & Csanyi, V. (2001). Comprehension of human communicative signs in pet dogs (*Canis familiaris*). *Journal of Comparative Psychology*, 115, 122-126.
- Soproni, K., Miklosi, A., Topal, J. & Csanyi, V. (2002). Dogs' (*Canis familiaris*) responsiveness to human pointing gestures. *Journal of Comparative Psychology*, 116, 27-34.
- Tanji, J. & Shima, K. (1994). Role of supplementary motor cells in planning several movements ahead. *Nature*, 371, 413-416.
- Theall, L. A. & Povinelli, D. J. (1999). Do chimpanzees tailor their gestural signals to fit the attentional state of others? *Animal Cognition*, 2, 207-214.
- Tomasello, M. & Call, J. (1997). *Primate Cognition*. Oxford University Press: New York.
- Tomasello, M., Call, J. & Hare, B. (1998). Five primate species follow the visual gaze of conspecifics. *Animal Behaviour*, 55, 1063-1069.
- Tomasello, M., Call, J. & Hare, B. (2003a). Chimpanzees understand psychological states – the question is which ones and to what extent. *Trends in Cognitive Science*, 7, 153-156.
- Tomasello, M., Call, J. & Hare, B. (2003b). Chimpanzees versus humans: it's not that simple. *Trends in Cognitive Science*, 7, 239-240.
- Tomasello, M., Call, J., Nagell, K., Olguin, K. & Carpenter, M. (1994). The learning and use of gestural signals by young chimpanzees: A trans-generational study. *Primates*, 35, 137-154.
- Tomasello, M., Hare, B. & Agnetta, B. (1999). Chimpanzees follow gaze direction geometrically. *Animal Behaviour*, 58, 769-777.
- Tschudin, A., Call, J., Dunbar, R. I. M., Harris, G., and van der Elst, C. (2001). Comprehension of signs by dolphins (*Tursiops truncatus*). *Journal of Comparative Psychology*, 115, 100-115.
- Vander Wall, SB (1990). *Food Hoarding in Animals*. University of Chicago Press: Chicago.
- Watve, M., Thakar, J., Kale, A., Puntambekar, S., Shaikh, I., Vaze, K., Jog, M. & Paranjape, S. (2002). Bee-eaters (*Merops orientalis*) respond to what a predator can see. *Animal Cognition*, 5, 253-259.
- Wellman, H. M., Cross, D. & Watson, J. (2001). Meta-analysis of theory of mind development: The truth about false belief. *Child Development*, 72, 655-684.
- Whiten, A. (1996). When does smart behaviour-reading become mind-reading? In: *Theories of Theories of Mind* (Carruthers, P. & Smith, P. K., eds.), pp. 277-292. Cambridge University Press: Cambridge.
- Whiten, A. (2000). Theory of mind in non-verbal apes: conceptual issues and the critical experiments. *Philosophy*, S49, 199-223.
- Whiten, A. & Byrne, R. W. (1988). Tactical deception in primates. *Behavioural & Brain Sciences*, 11, 233-244.
- Wimmer, H. & Perner, J. (1983). Beliefs about beliefs: Representation and constraining function of wrong beliefs in young children's understanding of deception. *Cognition*, 13, 103-128.
- Woodruff, G. & Premack, D. (1979). Intentional communication in the chimpanzee: The development of deception. *Cognition*, 7, 333-362.
- Xitco Jr., M. J., Gory, J. D. & Kuczaj, S. A. (2001). Spontaneous pointing by bottlenosed dolphins (*Tursiops truncatus*). *Animal Cognition*, 4, 115-123.