

# 4.34 Human Cognitive Specializations

F Subiaul, J Barth, S Okamoto-Barth, and D J Povinelli, University of Louisiana at Lafayette, New Iberia, LA, USA

© 2007 Elsevier Inc. All rights reserved.

<b>4.34.1 Introduction</b>	509
<b>4.34.2 The Reinterpretation Hypothesis</b>	510
<b>4.34.3 The Self</b>	511
4.34.3.1 Mirror Self-Recognition	511
4.34.3.2 Episodic Memory: The Self in Time	512
<b>4.34.4 Social Cognition</b>	513
4.34.4.1 Gaze-Following	513
4.34.4.2 Understanding Seeing	515
4.34.4.3 Intentional Communication	517
4.34.4.4 Imitation Learning	518
<b>4.34.5 Physical Cognition</b>	520
<b>4.34.6 Conclusions</b>	522

## Glossary

<i>emulation</i>	A type of social learning characterized by copying a rule pertaining to environmental effects (causes), results, or goals using idiosyncratic movements. Emulation is often contrasted with imitation, which is typically defined as copying specific actions and their respective goals.
<i>episodic memory</i>	Memories about one's personal past; autobiographical recollections.
<i>percept</i>	A representation of something perceived by the senses, regarded as the basic component in the formation of concepts.
<i>proprioception</i>	The perception of bodily movement and the spatial position of limbs relative to the rest of the body arising from internal (bodily) stimuli.
<i>retroduction</i>	A general process of logical inference that generates possible causes (theories) for available facts. Competing (causal) theories are evaluated based on their relative predictive abilities. Also known as hypotheticodeduction.
<i>theory of mind</i>	The ability to reason about unobservable psychological states such as seeing and knowing.

### 4.34.1 Introduction

What makes the human mind 'human'? Arguably, Charles Darwin articulated the most influential answer to this question. In *The Descent of Man*, Darwin (1871) challenged orthodoxy and many of

his champions, including the co-discoverer of the theory of natural selection Alfred Russell Wallace, and argued in favor of the view that the likeness between humans and other primates was not simply skin deep:

...man and the higher animals, especially the primates, have some few instincts in common. All have the same senses, intuitions, and sensations...they practice deceit and...possess the same faculties of imitation, attention, deliberation, choice, memory, imagination, the association of ideas and reason, though in very different degrees...Nevertheless, the difference in mind between man and the higher animals, great as it is, certainly is one of degree and not of kind (Darwin, 1871, p. 82).

This theory, known as the theory of the continuity of mind, made two radical assertions: (1) the mind is like every other morphological feature – subject to selection and change over time and (2) having directly descended from other living organisms, human and nonhuman animal minds evidenced only quantitative but not qualitative differences.

However, from the outset, such an idea was fraught with problems. Principally, the second point articulated by the theory of continuity of mind was more consistent with pre-Darwinian ideas that espoused a Great Chain of Being – the notion that organisms are ranked from the lowest forms, such as bacteria, to the highest forms, such as humans, angels, and God (Mayr, 1985). According to Hodos and Campbell (1969, 1991), the notion of the Great Chain of Being exists today in the form of the phylogenetic scale. That is, the notion that species may be ranked on a single ladder of ascending complexity. In spite of the obvious limitations and

contradictions with neo-Darwinian theory, the idea of psychological continuity continues to influence how scientists think about the evolution of mind and the broader question of human cognitive specialization. As a result, whereas the modern biologist has thrived on understanding the genetic and morphological diversity that exists both within and among populations of species, those interested in the evolution of mind and behavior have largely shunned an exploration of diversity. Perhaps, when compared to the evolution of physiological features, the evolution of mind has significant social and political ramifications. This was true in Darwin's time (Mayr, 1985) and it is certainly true today, as, for example, the academic resistance to socio-biology (Rose *et al.*, 1984; Wilson, 1975/2000; Lewontin *et al.*, 1985; Alcock, 2001). Therefore, we should not be surprised that those scientists who study the minds of both humans and animals – comparative psychologists – have been the most resistant to elucidating phylogenetic psychological differences. Indeed, the resistance to the idea of a significant and qualitative difference between the minds of human and nonhuman animals has been noted by many (e.g., Hodos and Campbell, 1969; Lockard, 1971; Wasserman, 1981; Boakes, 1984; Kamil, 1984; Macphail, 1987).

But why are so many scientists inclined to believe that the mind has escaped evolution? One possibility is that the domains in which comparative psychologists have traditionally searched for qualitative phyletic differences are precisely those in which we should least expect to find them. In this sense, the statement of Macphail (1987) that “causality is a constraint common to all ecological niches” exposes a more general claim that there are no differences in intelligence among vertebrates. Given that causality is a universal feature of biological environments, the types of general-purpose learning mechanisms that early behaviorists championed should be expected to be present in all animals. This approach has come to be known as general process learning theory (Seligman, 1970). This learning theory attempted to account for all learning with the same set of principles (Shettleworth, 1997).

The general process learning theory turned out to be too simplistic and, eventually, untenable. In a series of now classic papers that were adamantly resisted by establishment psychologists, Garcia and Kimeldorf (1957), Garcia *et al.* (1968, 1976) reported that, when rats are made ill from X-rays at the time they ate food pellets, they form associations about the flavor but not the size of the pellets. However, if, while eating, they are treated with a

painful electric shock (rather than X-rays), they form an association with the size but not with the flavor of the pellet. In subsequent tests, rats were systematically treated to electric shock whenever they drank flavored juice. In this condition, rats never learned to avoid the flavored drink. This result perplexed behaviorists but delighted evolutionary thinkers. From an evolutionary perspective it made perfect sense that the consumption of liquids and food does not result in pain in your skin; however, ingesting toxic substances can have damaging internal effects. It follows that animals capable of detecting internal damage and linking these sensory cues with foods or fluids that were recently consumed would have been able to modify their diet adaptively. No such benefit comes from circuitry that enables rats to associate specific foods or fluids with skin pain since ingested substances have no way of acting on external sensors (Alcock, 2001). Refocusing research efforts on ecologically relevant domains in this way might lead to the detection of psychological differences.

Although psychological innovations are rare, rarity should not imply a lack of importance. For instance, in the case of morphological evolution, there have been very few radical transformations in basic animal body plans, yet these core innovations constitute the basis for the classification of distinct phyla (Mayr, 1985, 2001). So, too, radical alterations in psychological forms might occur relatively infrequently. But this is not to state that they never occur. Indeed, comparative psychologists might have already detected the evolution of several such innovations (see Bitterman, 1960, 1975; Gallup, 1982; Rumbaugh, 1990; Itakura, 1996). Thus, in addition to the detection of differing finely scaled psychological dispositions among species, large-scale transformations might also be detectable.

#### 4.34.2 The Reinterpretation Hypothesis

Evidence that has accumulated over the past years suggests that one possible discontinuity between human and nonhuman minds is the ability to interpret observable phenomena, such as an individual's gaze or the propensity for unsupported objects to fall, in terms of unobservable psychological concepts such as desires or physical concepts such as gravity (Povinelli and Preuss, 1995; Povinelli, 2000; Povinelli and Vonk, 2003). For example, when reasoning about behaviors prior to the evolution of a theory of mind system (TOM) in the genus *Homo*, social animals possessed complex nervous systems equipped to detect the various statistical regularities

in the behaviors of others (Heyes, 1997; Povinelli, 2000). The very first social systems were probably quite simple and the information that individual organisms needed to keep track of was relatively limited. However, as some lineages evolved increasingly complicated social interactions, brain systems dedicated to processing information about the regularities of the behaviors of others became increasingly sophisticated as well. The general point is that, for hundreds of millions of years, vertebrates and other taxa have been under steady and unending selection pressures to detect, filter, and process information about the regularities in both their social and physical environments. The hypothesis presented here makes one simple claim: about 3 Mya, one peculiar lineage – the human one – began to evolve the additional ability to interpret these statistical regularities in terms of unobservable causal states. Naturally, this reinterpretation of physical and behavioral events in terms of unseen causal forces was integrated with a pre-existing mechanism for interpreting the observable features of these events.

If this hypothesis (or something like it) is correct, what causal role does the representation of unobservable states play in generating behavior? After all, if complex social behaviors such as self-awareness, gaze-following, social learning, and so forth evolved prior to a TOM and complex technological behaviors such as tool selection, construction, and use evolved prior to an understanding of physical forces, this implies that other psychological systems are independently capable of controlling their execution. Does this mean that the representation of causal forces plays no role in one's actions? We do not think so. Rather, the initial evolutionary advantages of this new psychological system that reinterprets observable phenomenon in terms of imperceptible concepts was that it allowed already existing behaviors (such as social learning or tool use) to be employed in more flexible and proactive ways, without discarding the ancestral psychological systems. As a result, we contend that, for any given behavior, humans will have multiple causal pathways of executing it.

So what evidence exists that phylogenetically ancient behaviors coexist with the uniquely derived ability to interpret these ancient behaviors in terms of invisible causes such as belief and force? A number of laboratories, including our own, have pursued various lines of research in various domains in an effort to answer this and related questions.

Below, we review the results from three general domains: (1) self-awareness, (2) social cognition,

and (3) physical cognition. We conclude with an overarching view of human cognitive uniqueness.

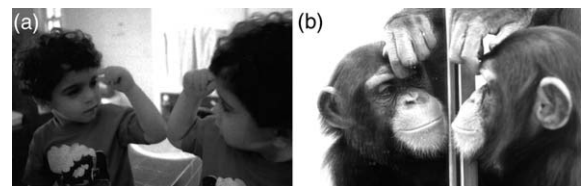
### 4.34.3 The Self

#### 4.34.3.1 Mirror Self-Recognition

In 1970, Gordon Gallup reported that chimpanzees used their mirror reflections to explore body parts difficult to see without the aid of a mirror such as their under arms, teeth, and anogenital region (Gallup, 1970; Figure 1). Gallup also reported that, after lengthy exposures to mirrors, monkeys continued to display social behaviors toward their mirror image, which suggested that they failed to see their reflections as representations of their selves (Gallup, 1970). Following this study, additional research has reported mirror self-recognition in bonobos (Hyatt and Hopkins, 1994; Walraven *et al.*, 1995) and orangutans (Lethmate and Dücker, 1973; Suarez and Gallup, 1981). Gorillas, however, have failed to recognize their mirror image (Suarez and Gallup, 1981; Ledbetter and Basen, 1982; Shillito *et al.*, 1999) with one exception (Patterson and Cohn, 1994; Patterson and Linden, 1981). Subsequent studies with monkeys confirmed Gallup's initial negative findings (e.g., Suarez and Gallup, 1981; Hauser *et al.*, 2001).

Among human infants, evidence of mirror self-recognition first appears around 18 months of age (Amsterdam, 1972; Bertenthal and Fischer, 1978; Johnson, 1982; Anderson, 1994). At this age, infants begin to use their reflection to investigate marks on body parts such as their nose and head much as non-human apes do (Figure 1a). The distribution and development of mirror self-recognition within the primate order suggests that the ability to recognize one's self-image represents an example of a phylogenetic cognitive specialization (see Evolutionary Specializations for Processing Faces and Objects).

The pattern of performance reported for apes in front of mirrors raises an important question: do apes and young human children equally depend upon representing psychological and temporal dimensions of the self? One view of self-recognition has emphasized the role of the kinesthetic dimension



**Figure 1** Mirror self-recognition. Examples of a child (a) and of a chimpanzee (b) using a mirror to explore marks on their faces.

of the self (e.g., Povinelli, 1995; Povinelli and Cant, 1995; Barth *et al.*, 2004). In this view, once an organism can hold in mind a kinesthetic representation of the current state of its body, it is able to match this information with the one seen in the mirror. Accordingly, self-exploratory behaviors arise from an association between proprioception and contingent visual cues provided by the mirror's reflection. This kinesthetic-visual matching can be contrasted with a psychological interpretation of the mirror's reflection (e.g., That's me!). In this case, subjects must reinterpret the association between proprioception and visual perception as an abstract self that guides actions independently of both proprioception and visual perception.

To address important aspects of this question, Povinelli and colleagues used live video feeds to explore the role of temporal contingency in supporting mirror self-recognition in 2- to 5-year-old children (Povinelli *et al.*, 1996; Povinelli and Simon, 1997; Povinelli *et al.*, 1999a, 1999b). In those studies, an experimenter played a game with the children in which the subjects were regularly praised. On some occasions the experimenters used this opportunity to secretly put a sticker on the child's head. One group of children saw a live video feed (i.e., they saw the experimenter placing a sticker on their head), the other group saw a 3 min delayed video showing the placement of the sticker. Most of the children that saw the live images retrieved the sticker, whereas few of the younger children who saw the delayed video retrieved the sticker. However, it is important to note that the younger children did not fail to retrieve the sticker on their head because they failed to recognize themselves in the delayed images. In fact, they would accurately state that they saw themselves in the video, but would refer to him/her (i.e., speaking in the third person) as having a sticker on their head. This suggests that for children younger than 4 years of age it is difficult to link the present self to a past self. This is a remarkable fact when one considers how early in development mirror self-recognition appears (see Amsterdam, 1972).

As has been noted by various scientists, the ability to recognize one's image has a number of implications. Gallup (1977) repeatedly proposed that the evidence of mirror self-recognition may be used as an index of self-consciousness or, as he phrased it, the ability to become the object of one's own attention. This interpretation of the results was premised on the notion that, to recognize an image in a mirror as one's own, one had to have an abstract (unobservable) concept of self. Later, Gallup (1982) speculated further, arguing that, if chimpanzees,

bonobos, and orangutans (and by extension, 18-month-olds) were self-aware in this sense, they might also have the capacity to reflect upon their own experiences and, by inference, the experiences of others; this topic we discuss below at length.

#### 4.34.3.2 Episodic Memory: The Self in Time

Tulving (1983; Tulving and Markowitsch, 1998) named the ability to reflect upon one's experiences as episodic memory. Tulving and Markowitsch (1998, p. 202) defined episodic memory as having to do with "the conscious recollection of previous experiences of events, happenings, and situations." In short, episodic memory concerns events experienced in one's personal past. Such autobiographical memories are, presumably, defined by a concept of self that is not anchored to facts about our lives in the here-and-now, but is free to move seamlessly backward and forward in time while reflecting on its history.

Schwartz and Evans (1994, 2001) have argued that episodic memory is characterized by three critical features: (1) it refers to a specific event in one's personal past; (2) retrieval involves re-experiencing a past event; and (3) it is accompanied by a strong sense of confidence in the veracity of the memory. Clayton and Dickinson (1998) developed criteria to examine features of episodic memory in nonlinguistic animals. In their view, the critical components of episodic memory is the binding of information about the what, where, and when of a given event. Others have included who, as well (Schwartz *et al.*, 2002). These researchers have resorted to the term episodic-like in recognition of the fact that with nonlinguistic animals it is impossible to ascertain whether they are reflecting on or re-experiencing their past.

To date, the strongest evidence of episodic-like memory has been reported in food-storing birds (scrub jays) and in apes (Clayton and Dickinson, 1998; Schwartz and Evans, 2001; Schwartz, 2005). Scrub jays are particularly interesting because in the wild these birds cache extra food. When food is in short supply, they return to the cache sites. In a series of laboratory studies, Clayton and Dickinson measured whether scrub jays remembered the location of cached food on a single and unique trial of learning. In these studies, jays had to encode information about the type of food (what), its freshness (when) and its location (where). In a typical experiment, crickets were stored on one side of an ice tray and peanuts were stored on the other side. Jays naturally prefer to eat crickets, but, whereas peanuts remain edible for long periods of time, crickets do

not. To respond adaptively, jays had to encode when a given food was cached, switching from crickets to peanuts after long delays. This is, in fact, how jays responded. Clayton *et al.* (2001) argued that this is evidence that jays bind information about the what, the where, and the when of events.

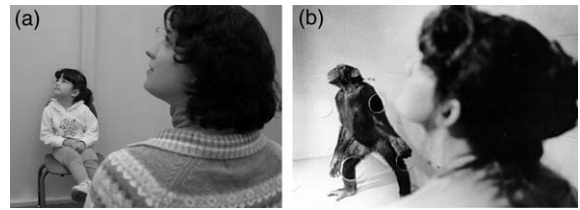
There is only a single published account of a nonhuman primate encoding multiple types of information in a single event. Schwartz and his colleagues have reported that a gorilla named King made what and who judgments in some cases after a 24h delay (Schwartz *et al.*, 2002, 2004, 2005). In one study, King had to select different cards that contained information about a type of food (e.g., banana) or an individual trainer. During training, King learned to respond appropriately to the commands “what did you eat?” and “who gave you the food?” During testing, King was asked both what and who questions. King responded correctly to what and who questions on 43% of the trials (chance was 10%).

While intriguing, the presence of this type of memory binding in species that do not typically evidence spontaneous mirror self-recognition, such as birds and gorillas, suggests that encoding multiple components of an event as described by Clayton and Dickinson and Schwartz and colleagues is independent of a concept of self (kinesthetic or otherwise) free to move forward and backward in time (Tulving, 1983). In this regard, we expect that future studies will show that many animal species are able to bind different facts about an event. Yet, we are doubtful that this paradigm, by itself, will answer whether nonhuman animals are able to re-experience their past in the same way humans do.

#### 4.34.4 Social Cognition

##### 4.34.4.1 Gaze-Following

One of the features that characterize the primate order is its gregariousness. For example, our closest living relative, the chimpanzee, resides in medium-sized groups that consist of males and females (Goodall, 1986). Males patrol the borders of their territories and cooperate when hunting small monkeys (Mitani, 2006). They also engage in complex social struggles for control over valuable resources such as food, mates, and allies. De Waal (1982) has aptly referred to this feature of chimpanzee societies as chimpanzee politics. In order to navigate their social worlds, chimpanzees, like humans, probably form representations of the behavior of others, predict future actions and adjust their own conduct accordingly (see Relevance of Understanding Brain Evolution). For example, when a chimpanzee sees a



**Figure 2** Gaze-following. Examples of a child (a) and of a chimpanzee (b) following the gaze of an experimenter.

conspecific pursing his lips with hair bristling, he need not represent each of these behaviors separately. Rather, a concept of threat display can be formed. In like fashion, primates are likely to form all sorts of concepts based on observable behaviors.

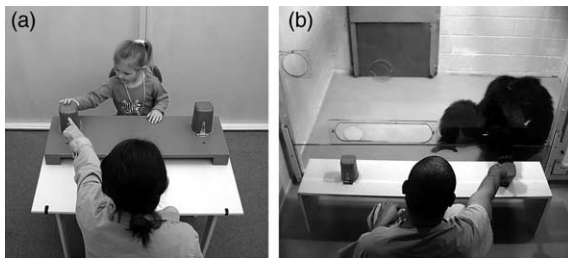
Consider the behavior of gaze-following and joint-attention. Primates in general and apes in particular are acutely sensitive to the direction of gaze (Figure 2). Determining the precise direction of another’s attention is an important ability because it provides salient information about the location of objects such as food and predators. In social settings, a great deal of information is communicated by means of following other individuals’ gaze to specific individuals or to call attention to specific events.

Several field studies suggest that primates can follow the gaze of conspecifics (e.g., Chance, 1967; Menzel and Halperin, 1975; Whiten and Byrne, 1988). However, in field studies, it is difficult to identify which object, individual, or event is the focus of two individuals’ attention and whether they arrived at the focal point by following one another’s gaze. For instance, individuals may come to fixate on the same object because the object is inherently interesting even if they do not follow gaze. Such interpretational confounds can be effectively excluded in laboratory studies. In fact, various studies have demonstrated that many primate species follow the gaze of others to objects (e.g., chimpanzees, mangabeys, and macaques) (Call *et al.*, 2000; Emery *et al.*, 1997; Tomasello *et al.*, 1998; Tomonaga, 1999). They do this even when the target is located above and/or behind them (Itakura, 1996; Povinelli and Eddy, 1996b, 1997). Itakura (1996) studied the ability of various species of prosimians, monkeys, and apes to follow a human experimenter’s gaze. Only chimpanzees and one orangutan responded above chance levels. Neither Old nor New World monkeys (i.e., brown lemur, black lemur, squirrel monkey, brown capuchin, whiteface capuchin, stump-tailed macaque, rhesus macaque, pig-tailed macaque, and Tonkean macaque) responded above chance levels.

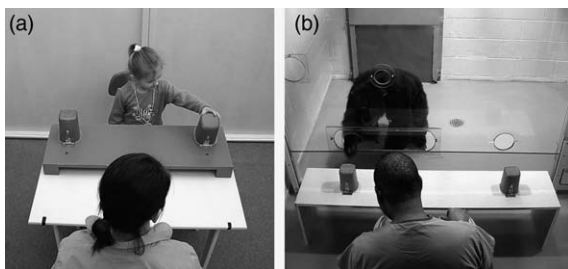
The clearest evidence for the ability to follow gaze in nonhuman primates comes from laboratory work

on great apes, in particular chimpanzees (Figure 2). For instance, Povinelli and Eddy (1996a), in order to investigate how chimpanzees follow another individual's gaze, installed an opaque barrier in a testing room, obstructing subjects' line of sight. In cases where the experimenter looked to an object next to the barrier (outside the immediate line of sight of the subject), chimpanzees followed the experimenter's line of sight around the barrier to the unseen object. These results have been replicated and extended to all four great ape species (Bräuer *et al.*, 2005) and human children (Moll and Tomasello, 2004). This ability might be important when trying to extrapolate information from other's attention, specifically when the focus of attention is out of sight (rhesus monkeys: Emery *et al.*, 1997; chimpanzees: Tomasello *et al.*, 1999). These findings suggest that primates do not reflexively follow gaze to the first available object within their view, but actively track the gaze of others geometrically to locations or objects that are the focus of others' attention.

One method commonly used to investigate nonhuman primates' ability to use gaze cues, is the object-choice task. In this task, subjects must choose one of two containers, only one of which is baited (Figures 3 and 4). In a series of studies, Anderson and his colleagues used this task to investigate



**Figure 3** Using proximate pointing cues. A child (a) and a chimpanzee (b) using an experimenter's proximate pointing cue to locate hidden rewards.



**Figure 4** Using distant gaze cues. A child (a) and a chimpanzee (b) using an experimenter's distant gaze cue to locate hidden rewards.

whether capuchin monkeys (Anderson *et al.*, 1995) and rhesus macaques (Anderson *et al.*, 1996) use human gaze to locate hidden food rewards. Subjects were tested in various conditions: pointing only, gaze only (head orientation and eyes cues), and gaze and pointing. None of the capuchin monkeys or rhesus macaques could be trained to use the gaze-only cue to retrieve a concealed reward. However, some subjects eventually learned to use either the pointing only or the gaze and pointing cue. However, it is likely that local enhancement (Thorpe, 1956) may explain these subjects' success in the gaze and pointing situation (e.g., responses may be guided by the hand's proximity to the container).

Using a similar paradigm, Itakura and Tanaka (1998) found that chimpanzees, an enculturated orangutan, and human infants (18–27 months old) used an experimenter's gaze, including pointing and glancing (without head turning), to choose a baited container. These responses appeared to be spontaneous and independent of training. Povinelli *et al.* (1999), however, found that chimpanzees failed to use the eyes only (glancing) cue when responding in a similar task. These differences may be due to the age, experimental experience, testing design, and developmental history of the different groups of chimpanzees. Nevertheless, the available research suggests that there is a qualitative difference between monkeys' and apes' understanding of gaze cues in the object-choice task (see also Itakura and Anderson, 1996).

Povinelli and Eddy (1996a, 1996b) have offered an explanation for the differences between monkeys and apes in this task. They theorized that following another individual's gaze might be an automatic response and form part of a primitive orienting reflex triggered by a reward. This reflex does not require the attribution of a mental state. The use of an operant task to test gaze-following would fail to test for the presence of a primitive orienting reflex compared to a more complex social cognition mechanism (e.g., a theory of mind). Monkeys, for example, might follow the gaze of conspecifics yet fail to use the same cue in operant tasks.

The development of this ability in chimpanzees and humans closely parallel one another. For instance, Okamoto *et al.* (2002) demonstrated that, starting at 9 months of age, a chimpanzee infant began using various social cues such as tapping or pointing and head turning to direct the attention to an object. By 13 months of age the infant reliably followed eye gaze. Starting at 21 months of age, the infant looked back to targets located behind him, even when there was a distracter in front of him (Okamoto *et al.*, 2004). Research

with human infants has produced similar results. From 3 months of age, human infants are able to discriminate changes in an adult's eye direction (Hains and Muir, 1996). The development of gaze-following in human infants has been widely studied (e.g., Scaife and Bruner, 1975; Butterworth and Cochran, 1980; Butterworth and Jarrett, 1991; Corkum and Moore, 1995; D'Entremont *et al.*, 1997). By 12 months of age, human infants begin to follow their mother's gaze toward particular objects in their visual field, and at around 18 months they can direct their attention to objects outside of their visual field. Although there are some developmental differences in the onset of gaze-following, on the surface the development of gaze-following in human and chimpanzee infants appears to be remarkably conserved.

But alongside these similarities in the gaze-following behavior of humans and nonhuman primates important differences exist. For example, Okamoto *et al.* (2002, 2004) reported that an infant chimpanzee failed to look back at the experimenter after following her gaze to an object located behind him. This triadic interaction between mother, child, and object of interest has been widely reported in the human developmental literature but is largely absent in the animal literature. Researchers have offered various explanations for these differences. Among humans, a number of changes in social communication occur at around 6 to 9 months of age (Carpenter *et al.*, 1998a). By 6 months, human infants interact dyadically with objects or with a person in a turn-taking (or reciprocally exchanging) sequence. However, they do not interact with the person who is manipulating objects (Tomasello, 1999). From 9 months on, infants start to engage in triadic exchanges with others. Their interactions involve both objects and persons, resulting in the formation of a referential triangle of infant, adult, and object to which they share attention (Rochat, 2001; Tomasello, 1999). That is to say, shared attention is an important component of social cognitive skills in human infants 12 months of age and older. These theories suggest that the chimpanzee infant described in Okamoto *et al.* (2004) and the human experimenter jointly attended to the object behind the infant without engaging in shared attention.

Nevertheless, results from our own laboratory (Povinelli and Eddy, 1996c; Povinelli, 2000) have revealed that chimpanzees and humans share many aspects of gaze-following behavior exhibited by 18-month-olds, including: (1) the ability to extract specific information about the direction of gaze from others; (2) the ability to display the

gaze-following response whether it is instantiated by movements of the hand and eyes in concert or the eyes alone; (3) the ability to use another's gaze to visually search into spaces outside their immediate visual field in response to eye plus head/upper torso movement, eye plus head movement, or eye movement alone; (4) no requirement to witness the shifts in another's gaze direction in order to follow it into a space outside their immediate visual field; and (5) the possession of at least a tacit understanding of how another's gaze is interrupted by solid, opaque surfaces.

#### 4.34.4.2 Understanding Seeing

There are two broadly different ways of interpreting the level of social understanding associated with chimpanzees' gaze-following abilities. First, chimpanzees and other nonhuman primate species (and even human infants) may understand gaze not as a projection of attention, but as a direction cue. It is possible that the ancestors of the modern primates evolved an ability to use the head/eye orientation of others to direct their own visual system along a particular trajectory. Once their visual system encountered something novel, the orientation reflex would ensure that two chimpanzees, for example, would end up attending to the same object or event, without attributing an internal (psychological) state to each other. This kind of gaze-following system may have evolved because it provided useful information about predators or social exchanges at little or no cost to individuals involved. A second account is that apes follow gaze because they appreciate its connection to internal attentional states. We will refer to these two accounts as the low-level and the high-level account of gaze-following.

In an effort to distinguish between the low- and the high-level account of gaze-following, Povinelli and colleagues executed a series of studies that measured chimpanzees' and human children's understanding of 'seeing' as a psychological (unobservable) function of eyes. To address this question, they used the chimpanzee's natural begging gesture (Figure 5), a gesture that this species uses in a number of different communicative contexts, including soliciting allies, requesting food, or reconciliation with others after hostile encounters. The apes were trained to use this gesture in a standardized routine: the apes entered a test unit in which they were separated from human experimenters by a Plexiglas partition, and they quickly learned to gesture through a hole directly in front of a single, familiar experimenter who was either standing or sitting to their left or to their right. On each trial that

they gestured through the hole to the experimenter, this person praised them and handed them a food reward. This training set the stage for examining the animals' reactions to two experimenters, one whose eyes were visible and therefore could respond to their gestures, and another whose eyes were covered or closed and therefore could not respond to their gestures. Several treatments recreated this problem (Figure 6).

When first confronted with two experimenters during one of these treatments, the animals' first reaction was to pause. But after noticing the novelty of the conditions, the apes in these studies were as likely to gesture to the person whose eyes were covered/closed as to the person whose eyes were visible/open. In other words, the chimpanzees displayed no preference for gesturing toward the experimenter who could see them. Yet, on trials when subjects were presented with a single



**Figure 5** Chimpanzee begging gesture. Example of a captive chimpanzee gesturing to an experimenter.

experimenter, the apes gestured through the hole directly in front of them on virtually every trial. Thus, despite their general interest and motivation in the test, when it came to the seeing/not seeing treatments, the animals responded indiscriminately seemingly, oblivious to the psychological state of seeing. These same chimpanzees were tested in a number of other experiments, which further manipulated the presence of eyes and/or the orientation of the experimenter's posture (Figure 6). Nevertheless, in all instances, chimpanzees ignored the eyes as cues and relied almost exclusively on global cues such as the back/front posture of the experimenter. These results have now been independently replicated by other comparative psychologists working with captive chimpanzees (Kamisky *et al.*, 2004).

This pattern of performance contrasted sharply with the performance of human children. Children, like the chimpanzees, were trained to gesture to an experimenter for brightly colored stickers. They were tested on several of the conditions used with the apes and it was found that the youngest children (2-year-olds) were correct in most or all of the conditions from their very first trial forward (Povinelli and Eddy, 1996a).

Hare and associates have challenged these results (Hare, 2001; Hare *et al.*, 2000, 2001, *in press*). They used a competitive paradigm (individuals must compete with conspecifics or human experimenters for food) because they argue that this paradigm is more ecologically valid than the cooperative paradigm (in which subjects gesture to an experimenter) used by Povinelli and Eddy (Hare, 2001; Hare and Tomasello, 2004). In the paradigm of Hare *et al.*, a dominant and a subordinate chimpanzee were



**Figure 6** See/not see paradigm. Different experimental manipulations used by Povinelli and Eddy (1996c).

placed in opposite sides of a large enclosure. In certain trials, both the subordinate and the dominant animal were in view of one another and food was placed in a position that was visible to both the subordinate and the dominant animal. In other trials, food was strategically placed in a position that was only visible to the subordinate. Hare and colleagues reported that subordinate animals avoided the food that was visible to the dominant animal but not the food that had been strategically positioned so that only the subordinate animal could see. These results were interpreted as evidence that chimpanzees infer some aspects of mental states such as seeing (Hare, 2001; Hare *et al.*, 2000, 2001, *in press*). Povinelli and colleagues have offered alternative interpretations for these results (see Karin-D'Arcy and Povinelli, 2002; Povinelli and Vonk, 2003, 2004).

However, the see/not-see paradigm (whether competitive or cooperative) poses at least three distinct problems. The first problem involves whether or not the cooperative paradigm of Povinelli and Eddy (1996b, 1996c) or the competitive paradigm of Hare *et al.* (2000, 2001, *in press*) can adequately isolate nonhuman primates' understanding of unobservable psychological states such as seeing from their understanding and/or use of nonpsychological, observable cues associated with the psychological interpretation of seeing, such as the visibility of the face and the eyes. The main concern is that neither of these particular competitive or cooperative paradigms is adequate to answer the question of whether or not chimpanzees understand seeing as a psychological state. In either paradigm, subjects can develop behavioral rules based on observable cues such as the visibility of the competitor's face, or they may develop rules premised on psychological interpretations of these observable (nonpsychological) cues. However, because the psychological inference depends on the availability of observable cues, and the use of either rule would lead to the same behavioral consequence, it is impossible to discern which rule – psychological or behavioral – subjects are using.

The second problem concerns whether competitive paradigms are better than cooperative paradigms in terms of eliciting psychological interpretations of others' behavior(s). If, in fact, the performance of subjects in Hare and colleagues' studies is dependent upon a specific setting or paradigm, it further suggests that observable cues (unique to the setting), rather than unobservable (psychological) inferences, are guiding the subjects' behavior. This possibility is reinforced by the assertions of the senior authors who have stressed that competitive paradigms mimic the type of situations

that might elicit such psychological inferences in the wild (Hare and Tomasello, 2004). But rather than eliciting psychological inferences, such settings can activate arousal/motivational mechanisms that make subjects more sensitive to a competitor's behavior. Regardless, as noted above, because reasoning about what competitors can and cannot see necessarily involves the ability to reason about observable (nonpsychological) variables such as the visibility of the face and eyes, the argument that competitive paradigms are more ecologically valid does not resolve the problem that chimpanzees can use either a behavioristic or mentalistic rule when making a response.

The third problem involves the interpretation of the results and its implication for chimpanzee and human cognition. Despite our skepticism of the studies described above, we do not believe that chimpanzees are mindless automatons. The results reported here and elsewhere speak to the contrary. Chimpanzees use information in a flexible and adaptive manner. In particular, chimpanzees' performance on social (e.g., Hare *et al.*, *in press*) and physical tasks (e.g., Visalberghi *et al.*, 1995; Povinelli, 2000) speaks volumes about this species' problem-solving abilities as well as their unique perception of the world. We should be neither discouraged nor insulted by the suggestion that chimpanzees may reason about the world in a way that's unique and different from our own. Rather, we should celebrate it.

#### 4.34.4.3 Intentional Communication

In the middle of the twentieth century, a number of studies sought to inculcate into nonhuman primates a uniquely human behavior: language (e.g., Hayes, 1951; Kellogg and Kellogg, 1967; Gardner and Gardner, 1969; Terrace, 1979; Terrace *et al.*, 1979). At best, this tradition highlighted what apes might be capable of learning were they trained under ideal circumstances; at worst, it demonstrated that language is a uniquely human trait and of little use to nonhuman primates (Chomsky, 1964; Terrace, 1979; Pinker, 1994). A different tradition has sought to explore how apes naturally communicate with each other. This vein of research explores parallels in the intentional desire to express goals, desires, and intentions through a means other than language.

But what separates intentional communication from other forms of communication? Tomasello and Call (1997) argue that, in order for a signal (or gesture) to be an intentional form of communication, it must involve a goal and some flexibility for attaining it. This entails using the behavior in

different contexts and with different communicative functions, or, conversely, using different signals in the same communicative context. For these authors, this entails learning. But the learning is not of the signal itself – rather, learning the appropriate social contexts in which to use such signals. Another important feature of identifying intentional communication is that the intentional cue has to be directed to a specific individual rather than to a general (i.e., nonspecific) audience. This appears to be the case with the vervet alarm call system. Vervet monkeys have three general calls for three different predators: eagles, leopards, and snakes. Each call is associated with a specific behavioral response: eagles – run to the center of trees and look up; leopards – run to the limbs of trees; snakes – stand up and look at surroundings (Cheney and Seyfarth, 1990).

Tomasello *et al.* (1985, 1989) recorded a number of gestures used by juveniles in a group to solicit food, play, grooming, nursing, etc. Although they collected no systematic data, these investigators reported that the behaviors were flexibly used in different contexts. Tomasello and Call (1997, p. 244) cite two examples of gestures being used to initiate play:

... the initiation of play often takes place in chimpanzees by one juvenile raising its arm above its head and then descending on another, play-hitting in the process. This then becomes ritualized ontogenetically into an ‘arm-raise’ gesture in which the initiator simply raises its arm and, rather than actually following through with the hitting, stays back and waits for the other to initiate the play... In other situations a juvenile was observed to actually alternate its gaze between the recipient of the gestural signal and one of its own body parts... (an invitation to grab it and so initiate a game of chase)...

This view of chimpanzee communication has found support among a number of field researchers. For example, Whiten and a number of other renowned primatologists reported 39 behavioral patterns, including a number of behavioral patterns that the authors described as “patterns customary or habitual at some sites yet absent at others, with no ecological explanation” (Whiten *et al.*, 1999, p. 683). Of those, five are described as having communicative functions: rain dance (display), branch slap (attention-getting), branch din (warn/threat), knuckle-knock (attract attention), leaf-strip (threat). There were two other actions with possible communicative/affiliative functions: stem pull-through (which makes a loud sound like leaf-strip and might be used as a threat), and handclasp (where two individuals clap hands above their heads while grooming as a specific affiliative gesture).

A number of controlled studies, however, suggest that apes have difficulty reasoning about (and hence

communicating) beliefs and desires (Premack and Premack, 1994; Tomasello and Call, 1997). This apparent inability to reason about the beliefs of others may handicap nonhuman primates’ ability to use communicative signals in a meaningful and intentional fashion. Although some studies suggest that chimpanzees might be able to use pointing gestures to located occluded rewards (Menzel, 1971, 1974; Povinelli *et al.*, 1992; Call and Tomasello, 1994; Itakura and Tanaka, 1998), other work has demonstrated that, when humans use pointing gestures to inform chimpanzees about the location of hidden food, chimpanzees appear to rely more on the proximity of the finger or pointing hand than on the referential aspect of the pointing hand/finger (Povinelli *et al.*, 1997; Barth *et al.*, 2005; but see Itakura and Tanaka, 1998).

Chimpanzees may have a more difficult time understanding the referential cues of humans than a conspecific. While no long-term field study on chimpanzee social behavior has ever documented an instance in which a member of this species pointed to something in a referential manner (Nishida, 1970; Goodall, 1986), chimpanzees do use a gesture that topographically resembles pointing: holding out a hand (Bygott, 1979; Figure 5). This gesture does not appear to be used in a referential fashion, rather it appears to be used to solicit food, bodily contact, or as a means to recruit allies during conflicts (De Waal, 1982; Goodall, 1986). In captivity, however, chimpanzees exhibit a number of gestures that look like pointing, but these seem to be restricted to their interactions with humans (Woodruff and Premack, 1979; Savage-Rumbaugh, 1986; Gomez, 1991; Call and Tomasello, 1994; Leavens *et al.*, 1996; Krause and Fouts, 1997). How might we explain such gestures in captivity? One possible explanation is that chimpanzees construct pointing-like gestures from their existing behavioral repertoire because humans consistently respond to their actions (such as reaching) in a manner that the chimpanzees themselves do not understand or intend (Povinelli *et al.*, 2003). A number of people have argued that this is also the case in infancy (Vygotsky, 1962). But whereas human infants begin to redescribe their gestures in an intentional manner between the ages of 18 and 24 months (Karmiloff-Smith, 1992), a similar redescription process might never occur in the development of nonhuman primates.

#### 4.34.4.4 Imitation Learning

As with the attribution of mental states, there has been a long-standing controversy over whether or

not humans are unique in the ability to learn from others. In fact, Aristotle argued in the *Poetics* that humans are “the most imitative creatures in the world and learn first by imitation.” In the past 30 years, interest in imitation has experienced a renaissance, particularly as scientists have found that, from birth, neonates copy the facial expressions of adults (Meltzoff and Moore, 1977), and primatologists have documented various instances of tool traditions in populations of wild chimpanzees (McGrew, 1992, 1994, 2001; Whiten *et al.*, 1999) and orangutans (van Schaik *et al.*, 2003).

To date, seven studies have directly compared imitation learning in human and nonhuman (adult) apes using analogous procedures (Nagell *et al.*, 1993; Tomasello *et al.*, 1993; Call and Tomasello, 1995; Whiten *et al.*, 1996; Horner and Whiten, 2005; Horowitz, 2003; Call *et al.*, 2005). Four of these studies reported that, on an operational task for which a tool had to be manipulated in a certain manner to retrieve a reward, humans reproduce the demonstrator’s actions with greater fidelity (i.e., imitation) than mother-reared apes (Nagell *et al.*, 1993; Tomasello *et al.*, 1993; Call and Tomasello, 1995; Call *et al.*, 2005). The other two studies reported both similarities and differences between humans and peer-reared chimpanzees when executing specific actions on an object following a demonstration (Whiten *et al.*, 1996; Horner and Whiten, 2005); and one found no differences between the performance of adult humans and chimpanzees (Horowitz, 2003).

However, the notion that humans are unique when learning by imitation has been challenged by Subiaul and colleagues. Subiaul *et al.* (2004) have distinguished between motor imitation (the imitation of a motor rule) and cognitive imitation (the imitation of a cognitive rule). In a series of studies, they reported that rhesus macaques – primates that typically do poorly in motor imitation tasks (Chamove, 1974; Thorndike, 1898; Whiten and Ham, 1992; Tomasello and Call, 1997) – excelled in a cognitive imitation task in which the execution of specific motor rules was independent of the execution of specific serial (cognitive) rules. These researchers suggested that human and nonhuman primates may differ fundamentally in the manner in which they plan, coordinate, and represent the actions of others. This conclusion is buttressed by a number of studies showing a dissociation between action and perception (monkeys: Hauser, 2003; Fitch and Hauser, 2004; human infants: Diamond, 1990; Spelke, 1994, 1997; apes: Myowa-Yamakoshi and Matsuzawa, 1999).

Researchers from a number of disciplines have reported that human and nonhuman primates share



**Figure 7** Oral facial imitation. a, Human infants (Meltzoff and Moore, 1977) and b, neonatal chimpanzees (Myowa-Yamakoshi *et al.*, 2004) copying three distinct orofacial movements. Reprinted from Meltzoff, A. N. and Moore, K. W. 1977. Imitation of manual and facial gestures by human neonates. *Science* 198, 75–78. Copyright 1977 AAAS.

a number of homologous mechanisms mediating behavior-matching. For example, Iacoboni *et al.* (1999) and Rizzolatti *et al.* (1988) reported that neurons in the inferior frontal lobe of humans (BA44) and macaques (area F5) are active both when subjects execute a specific action and when they observe a demonstrator execute the same action. Investigators have concluded that BA44 and F5 are evolutionarily homologous (Rizzolatti *et al.*, 2002).

Behavioral research by comparative developmental psychologists has found no significant differences between a human and a chimpanzee infant’s ability to copy the orofacial expressions of a model. Chimpanzees, like human infants (e.g., Meltzoff and Moore, 1977), reproduce tongue protrusions, lip protrusions, and mouth openings in response to a model displaying the same expression (Myowa-Yamakoshi *et al.*, 2004). Figure 7 illustrates the similarities of responses between human infants (e.g., Meltzoff and Moore, 1977) and those of neonatal chimpanzee (Myowa-Yamakoshi *et al.*, 2004).

There are also parallels in the developmental trajectory of orofacial imitation in both of these species. Myowa-Yamakoshi *et al.* (2004) report that, after 9 weeks of age, the incidence of orofacial imitation in chimpanzees slowly disappears. A similar phenomenon has been reported for human infants (Abravanel and Sigafoos, 1984). In short, this study found no qualitative differences between humans infants and infant chimpanzees in orofacial imitation.

Nevertheless, there is considerable evidence suggesting that, when learning from others, humans differ from other primates in significant ways. This has become evident in various imitation experiments with young children who evidence reasoning about unobservable mental concepts such as a model's goals and intentions. For example, in one study, [Carpenter \*et al.\* \(1995, 1998a, 1998b\)](#) exposed children to a model which, while executing a target action, made superfluous movements that were not necessary to achieve the goal. Children only copied the actions that were necessary to achieve the objective, omitting movements that were unnecessary. [Gergeley \*et al.\* \(2002\)](#) has reported a similar phenomenon. No comparable results have been reported for nonhuman primates.

The performance of human subjects also differs from that of nonhuman primates in a ghost control; that is, a treatment in social learning experiments in which target actions are executed in the absence of a demonstrator. A number of studies have employed this control to isolate imitation from emulation learning ([Heyes \*et al.\*, 1992](#); [Fawcett \*et al.\*, 2002](#); [Klein and Zentall, 2003](#); [Subiaul, 2004](#); [Subiaul \*et al.\*, 2004](#); [Thompson and Russell, 2004](#); [Huang and Charman, 2005](#)). However, whereas a number of investigators have reported that human subjects benefit from the standard social learning condition as well as the ghost condition ([Subiaul, 2004](#); [Thompson and Russell, 2004](#); [Huang and Charman, 2005](#)), comparative psychologists have reported that animals that copy a rule executed by a conspecific do not copy a similar rule in the ghost control ([Heyes \*et al.\*, 1992](#); [Atkins \*et al.\*, 2002](#); [Subiaul \*et al.\*, 2004](#)). This difference between the performance of humans and animals suggests that the ghost treatment is a measure of something other than emulation because, at least among primates, emulation appears to be the default social learning strategy ([Horner and Whiten, 2005](#); [Call \*et al.\*, 2005](#)). Although increasing the salience of the target actions in this control treatment might be sufficient for learning in certain paradigms ([Klein and Zentall, 2003](#)), we suspect that learning novel rules in the ghost condition might involve grappling with unobservable concepts. Depending on the experimental context and the task employed, learning in this control condition may require inferring (implicitly or explicitly) actions, intentions, or agency.

The research we have summarized above leads to a number of interesting questions and, potentially,

new avenues of research. Some possible questions for future research in social cognition include:

1. Do human and nonhuman primates differ in their sensitivity to behavioral cues and/or the statistical regularities of behaviors?
2. Does the propensity of a human to reinterpret behavioral regularities in terms of unobservable concepts lead to predictable errors that nonhuman primates do not make?
3. Is there a nonverbal experimental paradigm that can distinguish between the use of a behavioral rule and a psychological rule without confounding the two?

#### 4.34.5 Physical Cognition

We live in a world governed by invisible forces such as gravity, strength, weight, and temperature. Although they are invisible, we reason about these forces constantly. A long-lasting question in the comparative sciences has been: do nonhuman primates similarly reason about these forces that cannot be directly perceived but must be inferred?

From a very young age, humans are predisposed to make these kinds of inferences about the physical world. So, when young children see a ball, hit a stationary ball, and then see this second ball darting away, they insist that the first ball caused the second ball to move. Indeed, as the classic experiments of [Michotte \(1962\)](#) revealed, this seems to be an automatic mental process in humans. But what is it, exactly, that humans believe causes the movement of the second ball? As [Hume \(1739–1740/1911\)](#) noted long ago, this belief goes beyond the mere observation that the balls touched. Rather, humans redescribe this observation in terms of the first ball transmitting something to the second ball. That 'something' is, of course, a theoretical force that is ubiquitous, yet unseen.

At the very least, the earliest comparative studies on physical cognition date back to [Köhler \(1925\)](#). In the past decade, there has been a resurgence of interest in nonhuman primates' folk physics. Empirical attention has focused both on tools and on the conceptual systems that govern their use ([Köhler, 1925](#); [Boesch and Boesch, 1990](#); [Matsuzawa, 1996, 2001](#); [Hauser, 1997](#); [Visalberghi and Tomasello, 1998](#); [Santos \*et al.\*, 1999, 2003](#); [Munakata \*et al.\*, 2001](#); [Santos and Hauser, 2002](#); [Fujita \*et al.\*, 2003](#)). A significant number of studies have investigated how monkeys understand the relationships between means and ends (e.g., [Hauser, 1997](#); [Hauser \*et al.\*, 1999, 2002b](#)). Of these, some have focused on the

question of whether or not the ability to reason about invisible causal forces mediating the behavior and properties of objects represents a human cognitive specialization (see Visalberghi and Trinca, 1989; Visalberghi and Limongelli, 1994, 1996; Visalberghi, 1997; Limongelli *et al.*, 1995; Visalberghi and Tomasello, 1998; Povinelli, 2000; Kralik and Hauser, 2002; Santos and Hauser, 2002).

In a series of studies, Hauser and his colleagues repeatedly demonstrated that a New World monkey – the cotton-top tamarin – once trained how to use a tool, will readily transfer what it has learned to novel tools that differ in terms of shape and color (Hauser, 1997; Hauser *et al.*, 1999, 2002a, 2002b). A more recent study with capuchin monkeys replicated this result, but, in addition, showed that these monkeys, while not being distracted by the irrelevant features of the tools, nevertheless failed to attend to relevant variables of the task. For instance, they did not learn to pull in the appropriate tool to procure a reward when obstacles or traps impeded performance (Fujita *et al.*, 2003).

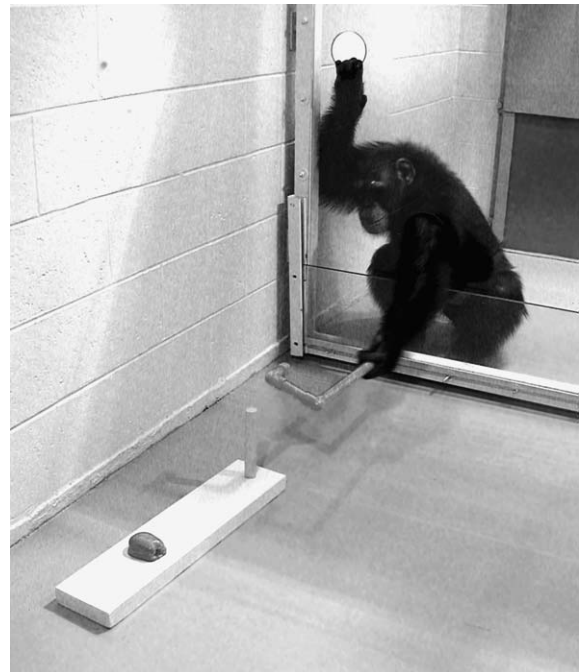
In another study, Hood *et al.* (1999) adapted a paradigm used to test gravity rules in human children (Hood, 1995) for use by cotton-top tamarins. The task involved dropping a food reward down a chimney which was at times clear and at other times opaque. The chimney was connected to various solid containers. Whereas children eventually learned to search in the container connected to the chimney, tamarins always searched in the container where the food was dropped on the first trial, ignoring whether the chimney was connected to that container or not. This result suggests that tamarins do not understand general principles of gravity (or connectedness).

However, some authors have suggested that, whereas the same representational abilities characterize the tool-using capacity of monkeys and apes (Westergaard and Fragaszy, 1987), others have implied that chimpanzees use tools in a more complex and sophisticated fashion than monkeys (Westergaard, 1999). In particular, these researchers have hypothesized that the apes succeed where the capuchin monkeys fail because of apes' ability to represent the abstract causal forces underlying tool use (Visalberghi, 1990; Limongelli *et al.*, 1995; Visalberghi *et al.*, 1995).

In an effort to test this and other hypotheses, Povinelli and colleagues in the mid-1990s systematically explored what they termed chimpanzee folk physics (Figure 8). Specifically, they focused the apes' attention on simple tool-using problems such as those used by Köhler, Hauser, and Visalberghi (Povinelli, 2000). Given chimpanzees' natural proclivity with tools (e.g., Whiten *et al.*, 1999), the goal

was to teach them how to solve simple problems. All the tasks involved pulling, pushing, poking, etc. Carefully designed transfer tests assessed chimpanzees' understanding of why the tools produced the observed effects. In this way, Povinelli and his associates attempted to determine if their subjects reasoned about things such as gravity, transfer of force, weight, and physical connection, or whether they only reasoned about spatiotemporal regularities. Throughout, these researchers contrasted such concepts with their perceptual properties (see Table 1).

For instance, a series of experiments explored in detail the chimpanzees' understanding of physical connection – the idea that two objects are bound together through some unseen interaction such as the force transmitted by the mass of one object resting on another, or the frictional forces of one object against another. Or, conversely, the idea that



**Figure 8** Chimpanzee tool use. One example of a tool task employed by Povinelli (2000) to assess captive chimpanzees' understanding of connectedness, shown here.

**Table 1** Theoretical concepts and their observable properties

<i>Theoretical concept</i>	<i>Paired observable properties</i>
Gravity	Downward object trajectories
Transfer of force	Motion–contact–motion sequences
Strength	Propensity for deformation
Shape	Perceptual form
Physical connection	Degree of contact
Weight	Muscle/tendon stretch sensations

simply because two objects are touching each other does not mean there is any real form of connection. To answer this question, Povinelli and colleagues presented the chimpanzees with numerous problems. In one set of studies chimpanzees were first taught to use a hooked tool to pull a food tray within reach. Chimpanzees quickly mastered this task. In order to address exactly what the chimpanzees had learned, they were presented with two choices: one was consistent with a theory of intrinsic connection (transfer of force); the other choice was consistent with a theory of superficial contact. In all cases, perceptual and/or superficial contact seemed to be chimpanzees' operating concept. In fact, any type of contact was generally sufficient for chimpanzees to think that a tool could move another object.

Bates and colleagues presented 10-month-old children with a battery of tests similar to those Povinelli (2000) presented to chimpanzees. In each case, a fuzzy toy could be attained only with the aid of a tool. The conditions varied in the amount of contact between the tool and the toy, from a toy resting on a cloth, to a toy positioned next to a stick. Children as young as 10 months old successfully retrieved the toy when it was making contact with the tool, but not in instances where the toy did not make direct contact with the tool or in cases where the contact was implied (Bates *et al.*, 1980).

In another group of studies, Brown (1990) trained 1.5-, 2-, and 3-year-old human subjects to use a tool to retrieve a reward. Once they had mastered the task using a training tool, she presented these same subjects with a choice between two tools differing in their functional properties. One of these tools retained the correct functional characteristics; for example, the tool was sufficiently long, rigid, or it had an effective pulling end. The second tool was perceptually more similar to the training tool; that is, it was the same color or shape, but it was functionally ineffective, being too short, made of a flimsy material, or did not have an effective end. Brown reported that children as young as 24 months virtually ignored surface features such as color or the shape of the effective end of the tool. Instead, young children's choices, unlike the choices of chimpanzees, were guided by abstract physical properties such as rigidity, length, and an effective end; that is, the tool properties that were related to the causal structure of the task.

In spite of the fact that chimpanzees attend to statistical regularities associated with objects and events – using these regularities to execute behaviors that are coherent and rule-governed – they fail to reason about these same regularities in terms of invisible causal forces. Indeed, we have speculated

that, for every unseen causal concept that humans may form, chimpanzees will rely exclusively on an analogous concept, constructed from the perceptual invariants that are readily detectable by the sensory systems (see Table 1). Of course, like chimpanzees, humans rely on these same spatiotemporal regularities most of the time, perhaps relying on systems that are homologues of those found in chimpanzees and other primates. But, unlike apes, we believe that humans evolved the unique capacity to form additional, far more abstract concepts that reinterpret observable phenomenon in unobservable terms (such as force, belief, etc.). If this interpretation of the data is correct, future research should address the following:

1. Can animals ever be taught to explicitly reason about unobservable physical forces such as gravity or connectedness?
2. For any given unobservable learned through explicit training, is it stable and generalizable across tasks and domains or restricted to a limited set of problems?
3. Do human and nonhuman primates form different percepts when confronted with identical sensory stimuli? If so, how might these differences affect nonhuman primates' conceptualization of physical unobservables?

#### 4.34.6 Conclusions

The evidence reviewed above demonstrates that various features of the human and nonhuman mind are remarkably conserved. As a result, human and nonhuman primates are remarkably similar in each of the cognitive domains reviewed (see Figures 1–7). However, this same evidence also suggests that the ability to wield abstract theoretical concepts is the basis for much of what is deemed higher-order cognition in humans. We speculate that primate minds come in two forms: minds that are capable of generating predictions about regularities (physical and/or behavioral) alone and minds that are capable of generating predictions about regularities in addition to generating predictions about abstract (theoretical) concepts. For instance, the ability to interpret a given behavior, such as reaching for an object, as intentional depends on the ability to infer from observable behavior an unobservable intervening variable, and to use this intervening variable to describe the behavior in psychological terms. But note that describing a behavior as reaching (for an object) need not be additionally redescribed as wanting (an object). In fact, the same observable behavior – reaching – may lead to predictions

understood in behavioral terms alone (reaching=consumption or possession) or in terms of mental states (reaching=wanting or needing). Note that both types of minds describe the behavior and may respond to an individual reaching for a desirable object such as food in the same way.

Importantly, the system that describes observable phenomena in terms of mental states or physical forces did not replace the older system that only analyzed observable features. Instead, this newer integrated system co-evolved with the existing psychological systems of primates. Because the ability to reason about unobservable concepts such as minds co-evolved with a phylogenetically older behavioral system, we found ourselves in the position of being able to represent ancient behavioral patterns in explicitly psychological terms, and of using these new representations to modulate an existing behavioral repertoire in order to cope with the newly uncovered mental world in addition to the directly observable aspects of the social and physical world with which our ancestors had been coping for millions of years. If this view of human cognitive specializations is correct, the most crucial differences between humans and apes are defined by cognitive, not behavioral, innovations. This view contrasts with a number of hypotheses about the evolution of primate intelligence. First, unlike the social intelligence hypothesis, our theory does not assume that the ability to predict behaviors based on unobservable psychological states produced an entirely new class of behaviors. To the contrary, we believe that the nonlinguistic behaviors of organisms with minds that can generate unobservable concepts and use these concepts to redescribe certain behaviors do not qualitatively differ from the behaviors of organisms with minds that can generate only observable concepts. Second, the ecological (e.g., Parker and Gibson, 1977, 1979) and technical intelligence hypothesis (Byrne, 1997; Parker and Gibson, 1977, 1979), which argues that challenges in the physical environment favor unique behavioral and cognitive traits, has the same limitations. As in the social domain, selection likely favored the ability to successfully and accurately interpret the observable statistical regularities that characterize objects in the environment (e.g., flowering plants or tools). We agree with the assessment of Byrne (1997, p. 293) that, "Rapid learning and efficient memory, having evolved because of social [and physical] profits, evidently also allow benefits in quite different, non-social tasks." But we do not agree that apes' unique technical abilities requires the evolution of an additional system that reinterpret spatiotemporal regularities in terms of unobservable forces. The

sophisticated behaviors that characterize apes in general requires, "efficient learning and large memory capacity. . .and possession of theory of mind [or a system for representing unseen forces] is not necessary for the case" (Byrne, 1997, p. 292).

The ability to reinterpret observable phenomena in terms of unobservable concepts may depend on a specific type of inference which the philosopher Charles Sanders Pierce called retroductive inferences. For Pierce, "Retroduction comes first and is the least certain and. . .the most important kind of reasoning. . .because it is the only kind of reasoning that opens up new ground" (as cited by Kehler, 1911). Pierce viewed retroduction as fundamental to the scientific enterprise because it depended upon the development of hypotheses about observable phenomena. Elsewhere (e.g., Povinelli and Dunphy-Lelii, 2001; Povinelli and Vonk, 2003; Povinelli, 2004), it has been argued that there is a difference between a mind that predicts events and one that seeks to explain them. But, of course, there is nothing trivial about predictions. Note that predictions come in two varieties: forward (e.g., classic conditioning), and backward (e.g., descriptive). If the reinterpretation hypothesis is correct, we can imagine, on the one hand, a mind that responds in a predictive manner to events and cues, and, on the other, a mind that generates rules that makes predictions (from hypotheses) across domains. In other words, a mind that engages in retroductive reasoning.

Thus far we have focused on the aspects of the conceptual systems of humans that may be unique in the primate order. But the human conceptual system may be distinct because fundamental features of the human peripheral nervous system are unique. As noted in the introduction of this article, it has been assumed since time immemorial that the differences between humans and other primates is not only skin deep; as a result, physiologists and psychologists have assumed that basic features of the nervous system (e.g., receptors and effectors) of primates do not meaningfully differ. Yet, differences in the sensory systems of primates will result in the generation of different percepts. If two organisms form different percepts from the same sensory experience, they will develop different concepts of the same event. Imagine the different visual percepts formed by the eyes of prosimians (who are largely nocturnal) versus the eyes of catarrhines (who are diurnal). If these differences at this basic level are real, we can be certain that the percepts that develop from these differences are similarly real.

In short, we should expect that humans and other primates differ in ways large and small. These

differences may be instantiated at the conceptual level as well as in more basic levels. We should not be surprised if differences at more basic levels of information processing (i.e., sensory system) have an effect on cognition. In fact, it is entirely possible that quantitative differences in the sensory systems may result in qualitative differences in the conceptual systems of primates. Only through a systematic exploration of these various problems will we ultimately come to understand human and nonhuman cognitive specializations.

## References

- Abrevanel, E. and Sigafoos, A. D. 1984. Exploring the presence of imitation during early infancy. *Child Dev.* 55, 381–392.
- Alcock, J. 2001. *The Triumph of Sociobiology*. Oxford University Press.
- Amsterdam, B. 1972. Mirror self-image reactions before age two. *Dev. Psychobiol.* 5(4), 297–305.
- Anderson, J. R. 1994. The monkey in the mirror: A strange conspecific. In: *Self-Awareness in Animals and Humans: Developmental Perspectives* (eds. S. T. Parker, R. W. Mitchell, and M. L. Boccia), pp. 315–329. Cambridge University Press.
- Anderson, J. R., Sallaberry, P., and Barbier, H. 1995. Use of experimenter-given cues during object-choice tasks by capuchin monkeys. *Anim. Behav.* 49, 201–208.
- Anderson, J. R., Montant, M., and Schmitt, D. 1996. Rhesus monkeys fail to use gaze direction as an experimenter-given cue in an object-choice task. *Behav. Process.* 37, 47–55.
- Atkins, C. K., Klein, E. D., and Zentall, T. R. 2002. Imitative learning in Japanese quail (*Coturnix japonica*) using the bidirectional control procedure. *Anim. Learn. Behav.* 30(3), 275–281.
- Barth, J., Povinelli, D. J., and Cant, J. G. H. 2004. Bodily origins of SELF. In: *The Self and Memory* (eds. D. Beike, L. Lampinen, and D. A. Behrend), pp. 11–43. Psychology Press.
- Barth, J., Reaux, J. E., and Povinelli, D. J. 2005. Chimpanzees' (*Pan troglodytes*) use of gaze cues in object-choice tasks: Different methods yield different results. *Anim. Cogn.* 8, 84–92.
- Bates, E., Carlson-Lunden, V., and Bretherton, I. 1980. Perceptual aspects of tool using in infancy. *Infant Behav. Dev.* 3, 127–140.
- Bertenthal, B. I. and Fischer, K. W. 1978. The development of self-recognition in the infant. *Dev. Psychol.* 14, 44–50.
- Bitterman, M. E. 1960. Toward a comparative psychology of learning. *Am. Psychol.* 23, 655–664.
- Bitterman, M. E. 1975. The comparative analysis of learning. *Science* 188, 699–709.
- Boakes, R. 1984. *From Darwin to Behaviorism: Psychology and the Minds of Animals*. Cambridge University Press.
- Boesch, C. and Boesch, H. 1990. Tool use and tool making in wild chimpanzees. *Folia Primatol.* 54, 86–89.
- Bräuer, J., Call, J., and Tomasello, M. 2005. All great ape species follow gaze to distant locations and around barriers. *J. Comp. Psychol.* 119(2), 145–154.
- Brown, A. L. 1990. Domain-specific principles affect learning and transfer in children. *Cognitive Sci.* 14, 107–133.
- Butterworth, G. and Cochran, E. 1980. Towards a mechanism of joint visual attention in human infancy. *Int. J. Behav. Dev.* 3, 253–272.
- Butterworth, G. and Jarrett, N. 1991. What minds have in common is space: Spatial mechanisms serving joint visual attention in infancy. *Br. J. Dev. Psychol.* 9, 55–72.
- Bygott, D. 1979. Agonistic behavior and dominance among wild chimpanzees. In: *The Great Apes* (eds. D. Hamburg and E. McCown), pp. 405–427. Benjamin Cummings.
- Byrne, R. W. 1997. Machiavellian intelligence. *Evol. Anthropol.* 5, 289–311.
- Call, J. and Tomasello, M. 1994. The production and comprehension of referential pointing by orangutans, *Pongo pygmaeus*. *J. Comp. Psychol.* 108, 307–371.
- Call, J. and Tomasello, M. 1995. Use of social information in the problem solving of orangutans (*Pongo pygmaeus*) and human children (*Homo sapiens*). *J. Comp. Psychol.* 109, 308–320.
- Call, J., Agnetta, B., and Tomasello, M. 2000. Cues that chimpanzees do and do not use to find hidden objects. *Anim. Cogn.* 3, 23–34.
- Call, J., Carpenter, M., and Tomasello, M. 2005. Copying results and copying actions in the process of social learning: Chimpanzees (*Pan troglodytes*) and human children (*Homo sapiens*). *Anim. Cogn.* 8, 151–163.
- Carpenter, M., Tomasello, M., and Savage-Rumbaugh, S. 1995. Joint attention and imitative learning in children, chimpanzees, and enculturated chimpanzees. *Soc. Dev.* 4, 217–237.
- Carpenter, M., Nagell, K., and Tomasello, M. 1998a. Social cognition, joint attention, and communicative competence from 9 to 15 months of age. *Monogr. Soc. Res. Child Dev.* 63 (4, no. 255).
- Carpenter, M., Akhtar, N., and Tomasello, M. 1998b. Fourteen-through 18-month-old infants differentially imitate intentional and accidental actions. *Infant Behav. Dev.* 21, 315–330.
- Chamove, A. S. 1974. Failure to find rhesus observational learning. *J. Behav. Sci.* 2, 39–41.
- Chance, M. R. A. 1967. Attention structure as a basis of primate rank orders. *Man* 2, 503–518.
- Cheney, D. L. and Seyfarth, R. M. 1990. Attending to behaviour versus attending to knowledge: Examining monkey's attribution of mental states. *Anim. Behav.* 40, 742–753.
- Chomsky, N. 1964. The development of grammar in child language: Formal discussion. *Monogr. Soc. Res. Child Dev.* 29, 35–39.
- Clayton, N. S. and Dickinson, A. 1998. Episodic-like memory during cache recovery by scrub jays. *Nature* 295, 272–274.
- Clayton, N. S., Griffiths, D. P., Emery, N. J., and Dickinson, A. 2001. Elements of episodic-like memory in animals. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 356(1413), 1438–1491.
- Corkum, V. and Moore, C. 1995. The development of joint attention in infants. In: *Joint Attention: Its Origins and Role in Development* (eds. C. Moore and P. J. Dunham), pp. 61–85. Lawrence Erlbaum Associates.
- Darwin, C. 1871/1982. *The Descent of Man and Selection in Relation to Sex*. Modern Library.
- D'Entremont, B., Hains, S. M. J., and Muir, D. W. 1997. A demonstration of gaze following in 3- to 6-month-olds. *Infant Behav. Dev.* 20, 569–572.
- De Waal, F. B. M. 1982. *Chimpanzee Politics: Power and Sex among Apes*. Johns Hopkins University Press.
- Diamond, A. 1990. Developmental time course in human infants and infant monkeys, and the neural bases of, inhibitory control in reaching. *Ann. NY Acad. Sci.* 608, 637–669.
- Emery, N. J., Lorincz, E. N., Perrett, D. I., Oram, M. W., and Baker, C. I. 1997. Gaze following and joint attention in rhesus monkeys (*Macaca mulatta*). *J. Comp. Psychol.* 111, 286–293.
- Fawcett, T. W., Skinner, A. M., and Goldsmith, A. R. 2002. A test of imitative learning in starlings using a two-action

- method with an enhanced ghost control *Anim. Behav.* 64, 547–556.
- Fitch, M. T. and Hauser, M. D. 2004. Computational constraints on syntactic processing in a nonhuman primate. *Science* 303, 377–380.
- Fujita, K., Kuroshima, H., and Asai, S. 2003. How do tufted capuchin monkeys (*Cebus apella*) understand causality involved in tool use? *J. Exp. Psychol. Anim. Behav. Process.* 19, 233–242.
- Gallup, G. G. 1970. Chimpanzees: Self-recognition. *Science* 167, 86–87.
- Gallup, G. G. 1977. Self recognition in primates: A comparative approach to the bidirectional properties of consciousness. *Am. Psychol.* 32, 329–338.
- Gallup, G. G. 1982. Self-awareness and the emergence of mind in primates. *Am. J. Primatol.* 2, 237–248.
- Garcia, J. and Kimeldorf, D. J. 1957. Temporal relationship within the conditioning of a saccharine aversion through radiation exposure. *J. Comp. Physiol. Psychol.* 50, 180–183.
- Garcia, J., McGowan, B. K., Erwin, F. R., and Koelling, R. A. 1968. Cues: Their relative effectiveness as a function of the reinforcer. *Science* 160, 794–795.
- Garcia, J., Hankins, W. G., and Rusiniak, K. W. 1976. Flavor aversion studies (letter). *Science* 192, 265–267.
- Gardner, R. A. and Gardner, B. T. 1969. Teaching sign language to a chimpanzee. *Science* 165, 664–672.
- Gegeley, G., Bekkering, H., and Király, J. 2002. Development psychology: Rational imitation in preverbal infants. *Nature* 415(6873), 55.
- Gomez, J. C. 1991. Visual behavior as a window for reading the minds of others in primates. In: *Natural Theories of Mind: Evolution, Development and Simulation of the Everyday Mindreading* (ed. A. Whiten), pp. 330–343. Blackwell.
- Goodall, J. 1986. *The Chimpanzees of Gombe: Patterns of Behavior*. Harvard University Press.
- Hains, S. M. J. and Muir, D. W. 1996. Infant sensitivity to adult eye direction. *Child Dev.* 67, 1940–1951.
- Hare, B. 2001. Can competitive paradigms increase the validity of experiments on primate social cognition? *Anim. Cogn.* 4, 269–280.
- Hare, B. and Tomasello, M. 2004. Chimpanzees are more skilful in competitive than in cooperative tasks. *Anim. Behav.* 68, 571–581.
- Hare, B., Call, J., and Tomasello, M. 2000. Chimpanzees know what conspecifics do and do not see. *Anim. Behav.* 59, 771–785.
- Hare, B., Call, J., and Tomasello, M. 2001. Do chimpanzees know what conspecifics know? *Anim. Behav.* 61, 139–151.
- Hare, B., Call, J., and Tomasello, M. Chimpanzees deceive a human competitor by hiding. *Cognition* (in press).
- Hauser, M. D. 1997. Artifactual kinds and functional design features: What a primate understands without language. *Cognition* 64, 285–308.
- Hauser, M. D. 2003. Knowing about knowing: Dissociations between perception and action systems over evolution and during development. *Ann. NY Acad. Sci.* 1001, 79–103.
- Hauser, M. D., Kralik, J., and Botto-Mahan, C. 1999. Problem solving and functional design features: Experiments on cotton-top tamarins (*Saguinus oedipus*). *Anim. Behav.* 57, 565–582.
- Hauser, M. D., Miller, C. T., Liu, K., and Gubta, R. 2001. Cotton-top tamarins (*Saguinus oedipus*) fail to show mirror-guided self-exploration. *Am. J. Primatol.* 53, 131–137.
- Hauser, M. D., Pearson, H. M., and Seelig, D. 2002a. Ontogeny of tool-use in cotton-top tamarins (*Saguinus oedipus*): Innate recognition of functionally relevant features. *Anim. Behav.* 64, 299–311.
- Hauser, M. D., Santos, L. R., Spaepen, G. M., and Pearson, H. M. 2002b. Problem solving, inhibition and domain-specific experience: Experiments on cotton-top tamarins (*Saguinus oedipus*). *Anim. Behav.* 64, 387–396.
- Hayes, C. 1951. *The Ape in Our House*. Harper.
- Heyes, C. M. 1997. Theory of mind in nonhuman primates. *Behav. Brain Sci.* 21, 101–114.
- Heyes, C. M., Dawson, G. R., and Nokes, T. 1992. Imitation in rats: Initial responding and transfer evidence. *Q. J. Exp. Psychol. B* 45, 229–240.
- Hodos, W. and Campbell, C. B. G. 1969. Scala naturae: Why is there no theory in comparative psychology? *Psychol. Rev.* 76, 337–350.
- Hodos, W. and Campbell, C. B. G. 1991. The scala naturae revisited: Evolutionary scales and anagenesis in comparative psychology. *J. Comp. Psychol.* 105, 211–221.
- Hood, B. M. 1995. Gravity rules for 2–4-year olds? *Cognitive Dev.* 10, 577–598.
- Hood, B. M., Hauser, M. D., Anderson, L., and Santos, L. R. 1999. Gravity biases in a non-human primate? *Dev. Sci.* 2, 35–41.
- Horner, V. and Whiten, A. 2005. Causal knowledge and imitation/emulation switching in chimpanzees (*Pan troglodytes*) and children (*Homo sapiens*). *Anim. Cogn.* 8(3), 164–181.
- Horowitz, A. C. 2003. Do humans ape? Or do apes human? Imitation and intention in humans (*Homo sapiens*) and other animals. *J. Comp. Psychol.* 117, 325–336.
- Huang, C. and Charman, T. 2005. Gradations of emulation learning in infants' imitation of actions on objects. *J. Exp. Child Psychol.* 92, 276–302.
- Hume, D. 1739–1740/1911. *A Treatise of Human Nature*, vols 1–2. In: (ed. A. D. Lindsay) Dent.
- Hyatt, C. W. and Hopkins, W. D. 1994. Self-awareness in bonobos and chimpanzees: A comparative perspective. In: *Self-Awareness in Animals and Humans: Developmental Perspectives* (eds. S. T. Parker and R. W. Mitchell). Cambridge University Press.
- Iacoboni, M., Woods, R. P., Brass, M., Bekkering, H., Mazziotta, J. C., and Rizzolatti, G. 1999. Cortical mechanisms of human imitation. *Science* 286, 2526–2528.
- Itakura, S. 1996. An exploratory study of gaze-monitoring in non-human primates. *Jpn. Psychol. Res.* 38, 174–180.
- Itakura, S. and Anderson, J. R. 1996. Learning to use experimenter-given cues during an object-choice task by a capuchin monkey. *Cab. Psychol. Cognit.* 15, 103–112.
- Itakura, S. and Tanaka, M. 1998. Use of experimenter-given cues during object choice tasks by chimpanzees (*Pan troglodytes*), and orangutan (*Pongo pygmaeus*), and human infants (*Homo sapiens*). *J. Comp. Psychol.* 112, 119–126.
- Johnson, D. B. 1982. Altruistic behavior and the development of the self in infants. *Merrill-Palmer Q.* 28, 379–388.
- Kamil, A. C. 1984. Adaptation and cognition: Knowing what comes naturally. In: *Animal Cognition* (eds. H. L. Roitblat, T. G. Bever, and H. S. Terrace), pp. 533–544. Lawrence Erlbaum Associates.
- Kaminsky, J., Call, J., and Tomasello, M. 2004. Body orientation and face orientation: Two factors controlling apes' behavior from humans. *Anim. Cogn.* 7(4), 216–223.
- Karin-D'Arcy, R. and Povinelli, D. J. 2002. Do chimpanzees know what each other see? A closer look. *Int. J. Comp. Psychol.* 15, 21–54.
- Karmiloff-Smith, A. 1992. *Beyond Modularity: A Developmental Perspective on Cognitive Science*. Cambridge.
- Kehler, J. H. 1911. A letter. *NEM* 3, 203–204.
- Kellogg, W. N. and Kellogg, L. A. 1967. *The Ape and the Child*. Hafner.

- Klein, E. D. and Zentall, T. R. 2003. Imitation and affordance learning by pigeons. *J. Comp. Psychol.* 117(4), 414–419.
- Köhler, W. 1925. *The Mentality of Apes*. Liveright.
- Kralik, J. D. and Hauser, M. D. 2002. A nonhuman primates' perception of object relations: Experiments on cottontop tamarins, *Saguinus oedipus*. *Anim. Behav.* 63, 419–435.
- Krause, M. and Fouts, R. 1997. Chimpanzee (*Pan troglodytes*) pointing: Hand shapes, accuracy and the role of gaze. *J. Comp. Psychol.* 111, 330–336.
- Leavens, D. A., Hopkins, W. D., and Bard, K. A. 1996. Indexical and referential pointing in chimpanzees (*Pan troglodytes*). *J. Comp. Psychol.* 110, 346–353.
- Ledbetter, D. H. and Basen, J. A. 1982. Failure to demonstrate self-recognition in gorillas. *Am. J. Primatol.* 2, 307–310.
- Lethmate, J. and Dücker, G. 1973. Untersuchungen zum Selbsterkennen im Spiegel bei Orang-Utans und einigen anderen Affenarten (Studies on mirror self-recognition by orangutans and some other primate species). *Z. Tierpsychol.* 33, 248–269.
- Lewontin, R. C., Rose, S., and Kamin, L. 1985. *Not in Our Genes: Biology, Ideology, and Human Nature*. Pantheon Books.
- Limongelli, L., Boysen, S. T., and Visalberghi, E. 1995. Comprehension of cause–effect relations in a tool-using task by chimpanzees (*Pan troglodytes*). *J. Comp. Psychol.* 109, 18–26.
- Lockard, R. B. 1971. Reflections on the fall of comparative psychology: Is there a message for us all? *Am. Psychol.* 26, 168–179.
- Macphail, E. 1987. The comparative psychology of intelligence. *Behav. Brain Sci.* 10, 645–656.
- Matsuzawa, T. 1996. Chimpanzee intelligence in nature and captivity: Isomorphism of symbol-use and tool-use. In: *Great Ape Societies* (eds. W. C. McGrew, L. F. Marchant, and T. Nishida). Cambridge University Press.
- Matsuzawa, T. 2001. Primate foundations of human intelligence: A view of tool use in non-human primates and fossil hominids. In: *Primate Origins of Human Cognition and Behavior* (ed. T. Matsuzawa). Springer.
- Mayr, E. 1985. *The Growth of Biological Thought: Diversity, Evolution, and Inheritance*. Harvard University Press.
- Mayr, E. 2001. *What Evolution Is*. Basic Books.
- McGrew, W. C. 1992. *Chimpanzee Material Culture*. Cambridge University Press.
- McGrew, W. C. 1994. Tools compared: The material of culture. In: *Chimpanzee Cultures* (eds. R. Wrangham, W. C. McGrew, F. de Waal, and P. Heltne). Harvard University Press.
- McGrew, W. C. 2001. The nature of culture: Prospects and pitfalls of cultural primatology. In: *The Tree of Origin: What Primate Behavior Tells us About Human Social Evolution* (ed. F. de Waal). Harvard University Press.
- Meltzoff, A. N. and Moore, K. M. 1977. Imitation of facial and manual gestures by human neonates. *Science* 198, 75–78.
- Menzel, E. W. 1971. Communication about the environment in a group of young chimpanzees. *Folia Primatol.* 15, 220–232.
- Menzel, E. W. 1974. A group of chimpanzees in a one-acre field. In: *Behavior of Non-Human Primates* (eds. A. M. Shrier and F. Stollnitz). Academic Press.
- Menzel, E. W. and Halperin, S. 1975. Purposive behavior as a basis for objective communication between chimpanzees. *Science* 189, 652–654.
- Michotte, A. 1962. *The Perception of Causality*. Methuen.
- Mitani, J. C. 2006. Demographic influences on the behavior of chimpanzees. *Primates* 47(1), 6–13.
- Moll, H. and Tomasello, M. 2004. 12- and 18-month-olds follow gaze behind barriers. *Dev. Sci.* 7, F1–F9.
- Munakata, Y., Santos, L. R., Spelke, E. S., Hauser, M. D., and O'Reilly, R. C. 2001. Visual representation in the wild: How rhesus monkeys parse objects. *J. Comp. Psychol.* 13, 44–58.
- Myowa-Yamakoshi, M. and Matsuzawa, T. 1999. Factors influencing imitation in manipulatory actions in chimpanzees (*Pan troglodytes*). *J. Comp. Psychol.* 113, 128–136.
- Myowa-Yamakoshi, M., Tomonaga, M., Tanaka, M., and Matsuzawa, T. 2004. Imitation in neonatal chimpanzees (*Pan troglodytes*). *Dev. Sci.* 7, 437–442.
- Nagell, K., Olguin, R., and Tomasello, M. 1993. Processes of social learning in the tool use of chimpanzees (*Pan troglodytes*) and human children (*Homo sapiens*). *J. Comp. Psychol.* 107, 174–186.
- Nishida, T. 1970. Social behaviour and relationship among wild chimpanzees of the Mahali Mountains. *Primates* 11, 47–87.
- Okamoto, S., Tomonaga, M., Ishii, K., Kawai, N., Tanaka, M., and Matsuzawa, T. 2002. An infant chimpanzee (*Pan troglodytes*) follows human gaze. *Anim. Cogn.* 5, 107–114.
- Okamoto, S., Tanaka, M., and Tomonaga, M. 2004. Looking back: The 'representational mechanism' of joint attention in an infant chimpanzee (*Pan troglodytes*). *Jpn. Psychol. Res.* 46, 236–245.
- Parker, S. T. and Gibson, K. 1977. Object manipulation, tool use and sensorimotor intelligence as feeding adaptations in cebus monkeys and great apes. *J. Hum. Evol.* 6, 623–641.
- Parker, S. T. and Gibson, K. R. 1979. A developmental model for the evolution of language and intelligence in early hominids. *Brain Sci.* 2, 367–408.
- Patterson, F. and Linden, E. 1981. *The Education of Koko*. Holt, Rinehart and Winston.
- Patterson, F. G. P. and Cohn, R. H. 1994. Self-recognition and self-awareness in lowland gorillas. In: *Self-Awareness in Animals and Humans: Developmental Perspectives* (eds. S. T. Parker, R. W. Mitchell, and M. L. Boccia), pp. 273–290. Cambridge University Press.
- Pinker, S. 1994. *The Language Instinct*. Harper Collins.
- Povinelli, D. J. 1995. The unduplicated self. *Adv. Psychol.* 112, 161–192.
- Povinelli, D. J. 2000. *Folk Physics for Apes: The Chimpanzee's Theory of How the World Works*. Oxford University Press.
- Povinelli, D. J. 2004. Behind the ape's appearance: Escaping anthropocentrism in the study of other minds. *Daedalus Winter* 29–41.
- Povinelli, D. J. and Cant, J. G. H. 1995. Arboreal clambering and the evolution of self-conception. *Q. Rev. Biol.* 70, 393–421.
- Povinelli, D. J. and Dunphy-Lelii, S. 2001. Do chimpanzees seek explanations? Preliminary comparative investigations. *Can. J. Exp. Psychol.* 55, 93–101.
- Povinelli, D. J. and Eddy, T. J. 1996a. Chimpanzees: Joint visual attention. *Psychol. Sci.* 7, 129–135.
- Povinelli, D. J. and Eddy, T. J. 1996b. Factors influencing young chimpanzee's (*Pan troglodytes*) recognition of attention. *J. Comp. Psychol.* 110, 336–345.
- Povinelli, D. J. and Eddy, T. J. 1996c. What young chimpanzees know about seeing. *Monogr. Soc. Res. Child Dev.* 61.
- Povinelli, D. J. and Eddy, T. J. 1997. Specificity of gaze-following in young chimpanzees. *Br. J. Dev. Psychol.* 15, 213–222.
- Povinelli, D. J. and Preuss, T. M. 1995. Theory of mind: Evolutionary history of a cognitive specialization. *Trends Neurosci.* 18, 418–424.
- Povinelli, D. J. and Vonk, J. 2003. Chimpanzee minds: Suspiciously human? *Trends Cogn. Sci.* 7, 157–160.
- Povinelli, D. J. and Vonk, J. 2004. We don't need a microscope to explore the chimpanzee mind. *Mind Lang.* 19, 1–28.

- Povinelli, D., Nelson, K., and Boysen, S. 1992. Comprehension of role reversal in chimpanzees: Evidence of empathy? *Anim. Behav.* 43, 633–640.
- Povinelli, D. J., Landau, K. R., and Perilloux, H. K. 1996. Self-recognition in young children using delayed versus live feedback: Evidence of a developmental asynchrony. *Child Dev.* 67, 1540–1554.
- Povinelli, D. J., Gallup, G. G., Jr., Eddy, T. J., and Bierschwale, D. T. 1997. Chimpanzees recognize themselves in mirrors. *Anim. Behav.* 53, 1083–1088.
- Povinelli, D. J., Bierschwale, D. T., and Cech, C. G. 1999a. Comprehension of seeing as a referential act in young children, but not juvenile chimpanzees. *Br. J. Dev. Psychol.* 17, 37–60.
- Povinelli, D. J., Landry, A. M., Theall, L. A., Clark, B. R., and Castille, C. M. 1999b. Development of young children's understanding that the recent past is causally bound to the present. *Dev. Psychol.* 35, 1426–1439.
- Povinelli, D. J., Bering, J., and Giambrone, S. 2003. Chimpanzee 'pointing': Another error of the argument by analogy? In: *Pointing: Where Language, Culture, and Cognition Meet* (ed. S. Kita), pp. 35–68. Lawrence Erlbaum Associates.
- Premack, D. and Premack, A. J. 1994. Moral belief: Form versus content. In: *Mapping the Mind: Domain Specificity in Cognition and Culture* (eds. L. A. Hirschfeld and S. A. Gelman), pp. 149–168. Cambridge University Press.
- Rizzolatti, G., Camarda, G., Fogassi, L., Gentilucci, M., Luppino, G., and Matelli, M. 1988. Functional organization of inferior area 6 in the macaque monkey. II: Area F5 and the control of distal movements. *Exp. Brain Res.* 71, 491–507.
- Rizzolatti, G., Fadiga, L., Fogassi, L., and Gallese, V. 2002. From mirror neurons to imitation: Facts and speculations. In: *The Imitative Mind: Development, Evolution and Brain Bases* (eds. W. Prinz and A. N. Melzoff). Cambridge University Press.
- Rochat, P. 2001. *The Infant's World*. Harvard University Press.
- Rose, S., Kamin, L. J., and Lewontin, R. C. 1984. *Not in Our Genes: Biology, Ideology and Human Nature*. Random House.
- Rumbaugh, D. M. 1990. Comparative psychology and the great apes: Their competence in learning, language and numbers. *Psychol. Rec.* 40(1), 15–39.
- Santos, L. R. and Hauser, M. D. 2002. A non-human primate's understanding of solidity: Dissociations between seeing and acting. *Dev. Sci.* 5, F1–F7.
- Santos, L. R., Ericson, B., and Hauser, M. D. 1999. Constraints on problem solving and inhibition: Object retrieval in cotton-top tamarins. *J. Comp. Psychol.* 113, 1–8.
- Santos, L. R., Miller, C. T., and Hauser, M. D. 2003. Representing tools: How two non-human primate species distinguish between the functionality relevant and irrelevant features of a tool. *Anim. Cogn.* 6, 269–281.
- Savage-Rumbaugh, E. S. 1986. *Ape Language: From Conditioned Response to Symbol*. Columbia University Press.
- Scaife, M. and Bruner, J. S. 1975. The capacity for joint visual attention in the infant. *Nature* 253, 265–266.
- Schwartz, B. L. 2005. Do animals have episodic memory? In: *The Missing Link in Cognition: Origins of Self-Reflective Consciousness* (eds. H. S. Terrace and J. Metcalfe), pp. 225–241. Oxford University Press.
- Schwartz, B. L. and Evans, S. 1994. Social and cognitive factors in chimpanzee and gorilla mirror behavior and self-recognition. In: *Self-Awareness in Animals and Humans: Developmental Perspective* (eds. S. T. Parker, R. W. Mitchell, and M. L. Boccia), pp. 189–206. Cambridge University Press.
- Schwartz, B. L. and Evans, S. 2001. Episodic memory in primates. *Am. J. Primatol.* 55, 71–85.
- Schwartz, B. L., Colon, M. R., Sanchez, I. C., Rodriguez, I. A., and Evans, S. 2002. Single-trial learning of 'what' and 'who' information in a gorilla (*Gorilla gorilla gorilla*): Implications for episodic memory. *Anim. Cogn.* 5, 85–90.
- Schwartz, B. L., Meissner, C. A., Hoffman, M., Evans, S., and Frazier, L. D. 2004. Event memory and misinformation effects in a gorilla (*Gorilla gorilla gorilla*). *Anim. Cogn.* 7, 93–100.
- Schwartz, B. L., Hoffman, M. L., and Evans, S. 2005. Episodic-like memory in a gorilla: A review and new findings. *Learn. Motiv.* 36, 226–244.
- Seligman, M. E. P. 1970. On the generality of the laws of learning. *Psychol. Rev.* 77, 406–418.
- Shettleworth, S. 1997. *Cognition, Evolution, and Behavior*. Oxford University Press.
- Shillito, D. J., Gallup, G. G., Jr., and Beck, B. B. 1999. Factors affecting mirror behaviour in western lowland gorillas, *Gorilla gorilla*. *Anim. Behav.* 57, 999–1004.
- Spelke, E. S. 1994. Initial knowledge: Six suggestions. *Cognition* 50, 431–445.
- Spelke, E. S. 1997. Nativism, empiricism, and the origins of knowledge. *Infant Behav. Dev.* 21, 181–200.
- Suarez, S. D. and Gallup, G. G. 1981. Self-recognition in chimpanzees and orangutans, but not gorillas. *J. Hum. Evol.* 10, 175–188.
- Subiaul, F. 2004. *Cognitive Imitation in Monkeys and Children*. Unpublished doctoral dissertation, Columbia University.
- Subiaul, F., Cantlon, J., Holloway, R., and Terrace, H. 2004. Cognitive imitation in rhesus macaques. *Science* 305, 407–410.
- Terrace, H. S. 1979. Nim. Alfred A. Knopf.
- Terrace, H. S., Petitto, L. A., Sanders, R. J., and Bever, T. G. 1979. Can an ape create a sentence? *Science* 206, 891–902.
- Thompson, D. E. and Russell, J. 2004. The ghost condition: Imitation versus emulation in young children's observational learning. *Dev. Psychol.* 40(5), 882–889.
- Thorndike, E. L. 1898. *Animal intelligence: An experimental study of the associative processes in animals*. *Psychol. Rev. Monogr. Suppl.* 2, 8.
- Thorpe, W. H. 1956. *Lemming and Instinct in Animals*. Methuen.
- Tomasello, M. 1999. *The Cultural Origins of Human Cognition*. Harvard University Press.
- Tomasello, M. and Call, J. 1997. *Primate Cognition*. Oxford University Press.
- Tomasello, M., Kruger, G. B., Farrar, M., and Evans, A. 1985. The development of gestural communication in young chimpanzees. *J. Hum. Evol.* 14, 175–186.
- Tomasello, M., Savage-Rumbaugh, E. S., and Kruger, A. C. 1993. Imitative learning of objects by chimpanzees, enculturated chimpanzees, and human children. *Child Dev.* 64, 1688–1705.
- Tomasello, M., Call, J., and Hare, B. 1998. Five primate species follow the visual gaze of conspecifics. *Anim. Behav.* 55, 1063–1069.
- Tomasello, M., Hare, B., and Agnetta, B. 1999. Chimpanzees, *Pan troglodytes*, follow gaze direction geometrically. *Anim. Behav.* 58, 769–777.
- Tomonaga, M. 1999. Attending to the others' attention in macaques: Joint attention or not? *Primate Res.* 15, 425.
- Tulving, E. 1983. *Elements of Episodic Memory*. Oxford University Press.
- Tulving, E. 1989. Memory: Performance, knowledge, and experience. *Eur. J. Psychol.* 1, 3–26.

- Tulving, E. and Markowitsch, H. J. 1998. Episodic and declarative memory: Role of the hippocampus. *Hippocampus* 8, 198–204.
- van Schaik, C. P., Ancrenaz, M., Borgen, G., et al. 2003. Orangutan cultures and the evolution of material culture. *Science* 299, 102–105.
- Visalberghi, E. 1990. Tool use in *Cebus*. *Folia Primatol.* 54, 146–154.
- Visalberghi, E. 1997. Success and understanding in cognitive tasks: A comparison between *Cebus apella* and *Pan troglodytes*. *Int. J. Comp. Psychol.* 18, 811–830.
- Visalberghi, E. and Limongelli, L. 1994. Lack of comprehension of cause-effect relations in tool-using capuchin monkeys (*Cebus apella*). *J. Comp. Psychol.* 108, 15–22.
- Visalberghi, E. and Limongelli, L. 1996. Acting and understanding: Tool use revisited through the minds of capuchin monkeys. In: Reaching Into Thought. The Minds of the Great Apes (eds. A. E. Russon and K. A. Bard), pp. 57–79. Cambridge University Press.
- Visalberghi, E. and Tomasello, M. 1998. Primate causal understanding in the physical and psychological domains. *Behav. Process.* 42, 189–203.
- Visalberghi, E. and Trinca, L. 1989. Tool use in capuchin monkeys: Distinguishing between performing and understanding. *Primates* 30, 511–521.
- Visalberghi, E., Fragszy, D. M., and Savage-Rumbaugh, E. S. 1995. Performance in a tool-using task by common chimpanzees (*Pan troglodytes*), bonobos (*Pan paniscus*), an orangutan (*Pongo pygmaeus*), and capuchin monkeys (*Cebus apella*). *J. Comp. Psychol.* 109, 52–60.
- Vygotsky, L. S. 1962. Thought and Language. MIT Press.
- Walraven, V., Elsacker, L., and Verheyen, R. 1995. Reactions of a group of pygmy chimpanzees (*Pan paniscus*) to their mirror-images: Evidence of self-recognition. *Primates* 36, 145–150.
- Wasserman, E. A. 1981. Comparative psychology returns: A review of Hulse, Fowler, and Honig's cognitive precesses in animal behavior. *J. Exp. Anal. Behav.* 35, 243–257.
- Westergaard, G. C. 1999. Structural analysis of tool-use by tufted capuchins (*Cebus apella*) and chimpanzees (*Pan troglodytes*). *Anim. Cogn.* 2, 141–145.
- Westergaard, G. C. and Fragszy, D. M. 1987. The manufacture and use of tools by capuchin monkeys (*Cebus apella*). *J. Comp. Psychol.* 101, 159–168.
- Whiten, A. and Byrne, R. W. 1988. The manipulation of attention in primate tactile deception. In: Machavellian Intelligence: Social Expertise and the Evolution of Intellect in Monkeys, Apes and Humans (eds. R. W. Byrne and A. Whiten), pp. 211–223. Oxford University Press.
- Whiten, A. and Ham, R. 1992. On the nature and evolution of imitation in the animal kingdom: Reappraisal of a century of research. In: Advances in the Study of Behavior (eds. P. B. Slater, J. S. Rosenblatt, C. Beer, and M. Milinsky), pp. 239–283. Academic Press.
- Whiten, A., Custance, D. M., Gomez, J. C., Teixidor, P., and Bard, K. A. 1996. Imitative learning of artificial fruit processing in children (*Homo sapiens*) and chimpanzees (*Pan troglodytes*). *J. Comp. Psychol.* 110, 3–14.
- Whiten, A., Goodall, J., McGrew, W. C., et al. 1999. Cultures in chimpanzee. *Nature* 399, 682–685.
- Wilson, E. O. 1975/2000. Sociobiology: The New Synthesis. Harvard University Press.
- Woodruff, G. and Premack, D. 1979. Intentional communication in the chimpanzee: The development of deception. *Cognition* 7, 333–362.

## Further Reading

- Heyes, C. 2004. Four routes of cognitive evolution. *Psychol. Rev.* 110, 713–727.
- Hayes, K. J. and Hayes, C. 1953. Imitation in a home-reared chimpanzee. *J. Comp. Physiol. Psychol.* 45, 450–459.
- Povinelli, D. J. 2000. Folk Physics for Apes. Oxford University Press.
- Tomasello, M. and Call, J. 1997. Primate Cognition. Oxford University Press.
- Tomasello, M., Gust, D., and Frost, G. T. 1989. A longitudinal investigation of gestural communication in young chimpanzees. *Primates* 30, 35–50.