

Does the chimpanzee have a theory of mind? 30 years later

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On the 30th anniversary of Premack and Woodruff's seminal paper asking whether chimpanzees have a theory of mind, we review recent evidence that suggests in many respects they do, whereas in other respects they might not. Specifically, there is solid evidence from several different experimental paradigms that chimpanzees understand the goals and intentions of others, as well as the perception and knowledge of others. Nevertheless, despite several seemingly valid attempts, there is currently no evidence that chimpanzees understand false beliefs. Our conclusion for the moment is, thus, that chimpanzees understand others in terms of a perception-goal psychology, as opposed to a full-fledged, human-like belief-desire psychology.

Introduction

In 1978 Premack and Woodruff asked, 'Does the chimpanzee have a theory of mind?' In this brief review we attempt to answer this question based on much research that has been conducted in the 30 years since that time, particularly in the last decade or so (see Tomasello and Call [1] for the state of the art as of the mid-1990s). The answer will not be a simple yes or no, however, because part of the progress that has been made in recent years is a recognition that there are many different ways in which organisms might understand the psychological functioning of others.

A brief history

Premack and Woodruff's [2] original study was actually about chimpanzees' understanding of human goals. But soon there was new research suggesting that perhaps these results were experimental artifacts [3,4] and other research on social learning that suggested chimpanzees did not have an understanding of human goals [5]. Negative evidence also accrued during the 1990s about chimpanzees' understanding of visual perception, especially from the well-known studies of Povinelli and Eddy [6] in which chimpanzees begged indiscriminately from humans facing them and others with buckets over their heads (see also Ref. [7]). There was also one negative study on chimpanzees' understanding of false beliefs [8].

All of these data led Tomasello and Call [1] to the general conclusion that chimpanzees and other non-human primates do not understand the psychological states of others. That is, they can predict the actions of others in many situations based on past experience (and perhaps specialized cognitive adaptations), but they do not

go beneath the surface to an understanding of the goals, perceptions, knowledge and beliefs that guide action (nor to an understanding of underlying physical forces either). But not all of the data existing at that time were consistent in suggesting this conclusion, and moreover, chimpanzees had been observed doing things that would seem to require more than just an understanding of surface-level behavior, for example, tactical deception [9].

The story since the late 1990s has been one of experimenters finding better ways to tap into what chimpanzees know about the psychological states of others – and so getting many more positive results. In most cases this has been guided by attempts to model the experiments more closely on situations that chimpanzees routinely encounter in their natural environments, for example, presenting them with problems not in situations in which they must cooperate with others but, rather, in situations in which they must compete with others (see Box 1). Skeptics still abound, as represented most prominently by Povinelli and colleagues [10,11]. They cling to the hypothesis that chimpanzees understand only surface-level behavior (forming 'behavioral rules'), and indeed this explanation is almost always possible for any single experiment. But there are now in many cases multiple experimental paradigms all aimed at a single psychological state – each presenting chimpanzees with a highly novel problem – that makes the positing of learned behavioral rules a difficult explanatory strategy [12]. Here, we review current experimental evidence about chimpanzees' understanding of: (i) the goals and intentions of others and (ii) the perception, knowledge and beliefs of others.

Understanding goals and intentions

To compete and cooperate effectively with others in their group, highly social animals, such as chimpanzees, must be able not only to react to what others are doing but also to anticipate what they will do. One way of accomplishing this is by observing what others do in particular situations and deriving a set of 'behavioral rules' (or, in some cases, having those built in). This will enable behavioral prediction when the same or a highly similar situation arises again. But another way to do it – indeed a more flexible way to do it – is to discern directly what the other is trying to do, what state of the environment he is trying to bring about and what his goal is. This enables behavioral prediction not only in previously observed or highly similar situations but also in novel situations.

The methodological problem is that when an actor acts toward a goal successfully, then what he is trying to do and

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Box 1. Assessing visual and auditory perspective taking in chimpanzees

Hare *et al.* [26] had chimpanzees compete for food with a human competitor who was inside a glass booth (see Figure 1). In the main study chimpanzees preferentially chose to approach the food that was on the side of the booth with an opaque barrier so that the human could not see them approaching. They, thus, attempted to influence what the human could see, and they did so from the very first trials. Melis *et al.* [27] went one step further by having a booth with opaque barriers on both sides, but chimpanzees had to choose between reaching through a clear tunnel, in which case the human competitor could see their reaching arm, and an opaque tunnel, in which case she could not. Even though they could not see the human under any conditions, the chimpanzees reached more through the opaque tunnel than the clear tunnel – presumably imagining the perspective of the human. In an extension of this, Melis *et al.* [27] used this same booth arrangement but with two clear tunnels leading to food. Here the experimenter lowered her head between her knees so that she was unable to see the chimpanzee. In this case each tunnel had a small door midway through, one of which was very noisy and one of which was silent (they had learned about the doors' properties earlier in a different context). If the human heard a door opening, she would raise her head and grab the food before the chimpanzee had a chance, but not if she could not hear a door opening. Chimpanzees in this case preferentially reached through the silent door, and again they did so from the very first trials.

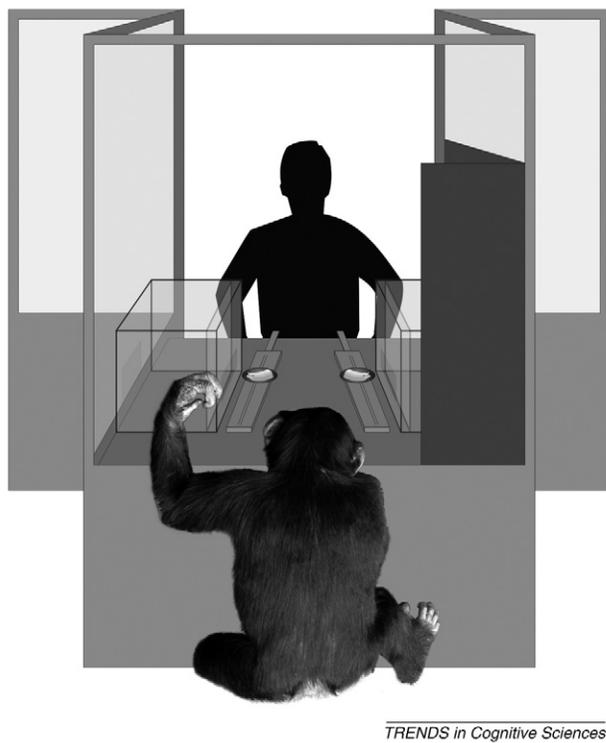


Figure 1. Experimental setup for the studies of Hare *et al.* [26] and Melis *et al.* [27].

what he actually does are the same, and so it is very difficult, if not impossible, to distinguish when an observer is reading the actor's behavior versus reading his goals. But there are situations in which what an actor does does not match his goal, specifically, in unsuccessful attempts and accidents. The best evidence that an observer understands goals, therefore, is when she reacts specifically to the actor's goal and not to his overt behavior when he is trying unsuccessfully or having an accident.

Box 2. Chimpanzees infer a human's intentions

Buttelmann *et al.* [28] used the Gergely *et al.* [29] method to test six human-raised chimpanzees in the so-called rational-imitation paradigm. The chimpanzees were shown how to operate an apparatus to produce an interesting result (e.g. lights or sounds), and then they were given a turn. The most natural behavior for them in all cases was to operate it with their hands. But this obvious behavior was never demonstrated for them; they always saw a human manipulate the apparatus in a novel way with some other body part. The idea was that in some cases the physical constraints of the situation dictated that the human (referred to as 'E' in the figure) had to use that unusual body part; for example, he had to turn on a light with his head because his hands were occupied holding a blanket or he had to operate a light with his foot because his hands were occupied with a heavy bucket (see Figure 1). When the chimpanzees saw this forced use of the unusual body part, they mostly discounted it and used their hands as they normally would (because the constraints were not present for them). However, when they saw the human use the unusual body part when there was no physical constraint dictating this, they quite often copied the unusual behavioral means themselves. If we interpret this experiment the way it is interpreted for human infants, the conclusion is that the chimpanzees understood not only what the experimenter was trying to do (his goal) but also why he was doing it in the way he was doing it – the rationality behind the choice of the plan of action toward the goal. According to Tomasello *et al.* [30], an understanding of the action plan chosen toward a goal constitutes an understanding of the intention.

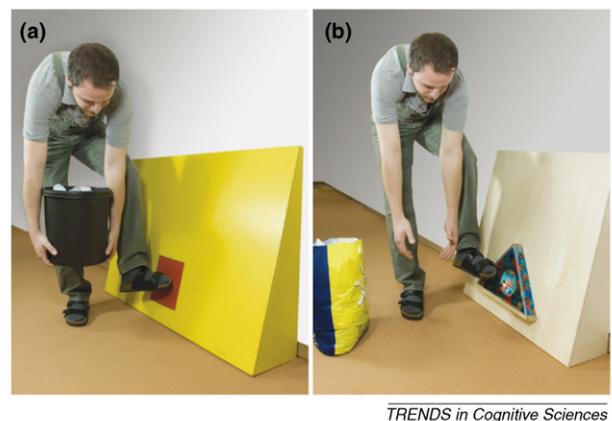


Figure 1. Turning on the light with the foot because (a) E wanted to or (b) E had to (because his hands were occupied) in the Buttelmann *et al.* [28] experiments.

Table 1 lists ten separate studies suggesting that chimpanzees understand others' goals. At least six of these are modeled closely on studies with human infants (see Box 2), which are routinely used as evidence of goal understanding. These ten studies involve several different situations that chimpanzees must understand and several different response measures as well. Thus, in the first seven studies in Table 1 (briefly described there, points 1–7), chimpanzees react not toward the actual behavior of the human but toward his goal, as they attempt to get a reward or anticipate his behavior. For example, they react differently to very similar behaviors when the human is refraining from giving food because he is unwilling versus unable to do so (Table 1, points 1 and 3), when he is doing something on purpose versus by accident (Table 1, point 2) or else when he is an innocent bystander (Table 1, point 7). They also discern that another's goal is to reach an out-of-reach object and then they either help him to reach it (Table 1, point 4) or grab it first if it indicates the location of food (Table 1, point 5). And they anticipate a human's

Table 1. Studies on chimpanzees' and human infants' understanding of goals and intentions

Studies	References	
	Chimpanzees	Infants
Getting/finding food		
1. Leave earlier and beg more intensely from an E who is unwilling as opposed to unable to deliver food (behavior similar in the two cases)	[31]	[32]
2. Select the box acted on intentionally versus accidentally (behavior similar in the two cases)	[33]	[33]
3. Leave earlier when E is playing with as opposed to trying to open a box with food (behavior identical in the two cases)	^a	
Reacting to a partner's actions		
4. Give the object that the E is trying to reach	[34,35]	[34]
5. Take the food that a competitor is trying to reach	[36]	
6. Anticipate where E is going based on potential goals available	^a	
7. When food is stolen retaliate against thief, not against innocent receiver of stolen food	[37]	
Imitation		
8. Produce target action based on observing a failed attempt	[38,39]	[40]
9. Copy intentional actions more often than accidental actions	[38]	[41]
10. Selectively copy freely chosen acts but not those forced by circumstances	[28]	[29]

^a(D. Buttelmann *et al.*, personal communication).

Gaps in the table indicate no information available.

impending actions when he stands and turns in a certain direction based on what goal he is probably pursuing (Table 1, point 6). Importantly, in two of these studies (Table 1, points 3 and 6) the behavior at the time the chimpanzee must react is identical in experimental and control conditions, with the only difference being in the immediately preceding context (e.g. given that the human has been opening boxes, the current ambiguous behavior is probably an attempt to open a new box, whereas without this preceding context the human's goal is unknown).

One could of course attempt to explain any one of these results in terms of behavioral rules that chimpanzees are either born with or learn, and this might be plausible in a particular case. But this explanatory strategy is not plausible across all of the seven studies because of the diversity of situations and reactions required. Moreover, to explain the studies in which the human's behavior is identical in experimental and control conditions at the time of reaction, one would need to also posit something like 'contextual rules' because there is no differential behavior to read in the two situations.

In three further studies in Table 1 (points 8–10) explanations in terms of behavioral or contextual rules are not possible. This is because these all use an imitation paradigm in which the chimpanzee subject actually acts out in her own behavior what she understands the other to be attempting to do, and this does not always correspond to the overt actions (note that all three of these studies use human-raised chimpanzees, who are very probably the only ones capable of copying actions in specific ways [13]). In these three studies (all modeled on similar studies with human infants), chimpanzees imitated what the human was trying to do (not what he did) (Table 1, point 8), his purposeful rather than his accidental actions (Table 1, point 9), and they even selectively imitated actions based on an understanding of why the actor chose this particular action (Table 1, point 10), which might be construed as understanding his intention, in the sense of the action plan he chose for pursuing his goal. Behavioral and contextual rules only help a subject to predict what an actor will do; they provide no guidance whatsoever for social learning.

We believe that there is only one reasonable conclusion to be drawn from the ten studies reviewed here: chimpanzees, like humans, understand the actions of others not just in terms of surface behaviors but also in terms of the underlying goals, and possibly intentions, involved. Behavioral or contextual rules might be concocted to explain the results of any one of the seven studies in which the chimpanzees react to or predict the behavior of others, but this requires many different ad hoc behavioral and contextual rules for which there is absolutely no positive evidence. Indeed consistent use of this explanatory strategy would also deny human children an understanding of goals and intentions because most of the chimpanzee studies are modeled on child studies. Moreover, the three imitation studies would not seem to be amenable to behavioral-rules explanations at all.

Understanding perception and knowledge

To understand how another works as a goal-directed agent, an observer must understand not only his goals but also his perceptions because what he sees and knows helps to determine what he does. Here, we examine what chimpanzees understand about what an actor sees – not just what he is oriented to, but what he registers from the environment in ways that affect his actions – and about what that actor knows in the sense of information he has previously registered that still affects his current actions (e.g. his knowledge of where food is even though he cannot see it now). Understanding false beliefs is the special case in which an observer predicts or explains the behavior of an actor based on a judgment of what that actor believes to be the case, not what really is the case as the observer knows it (e.g. the actor believes the food is in one place when the observer knows that it is really in another).

Again in the current case, the main alternative hypothesis that we must consider is that chimpanzees either are born with or learn certain behavioral or contextual rules that determine how they respond to others' surface behaviors (orienting behaviors in this case) without any understanding of their perception or knowledge. And analogous to the case with goals, the best evidence that an individual understands another's perception is when

Table 2. Studies on chimpanzees' and human infants' understanding of perception and knowledge

Studies	References	
	Chimpanzees	Infants
Gaze following		
1. Follow gaze to distant locations behind self	[42–44]	[45]
2. Follow gaze on the basis of both face and eye direction	[46]	[46,47]
3. Check back with gazer if nothing relevant at the target location	[48,49]	[50]
4. Stop looking after a few trials if nothing relevant at the target location	[51]	
5. Ignore distracting objects on the way to the target location	[52]	[53]
6. Move to the side of opaque barriers to view the target location	[42,49,52]	[54]
7. Understand that gaze stops at an opaque barrier - unless it has a window in it	[55]	[56]
Gestural communication		
8. Use visual gestures mostly when conspecifics or E are oriented to them	[6,14,57,58]	[6]
9. Position oneself to gesture in front of others	[59,60]	[61]
10. Both face and eye orientation of recipient determine gesture production	[62]	[6]
Food competition		
11. Pick the food that the E is not looking at	[26]	
12. Pick the food that a dominant individual or E cannot see because of barrier	[26,63,64]	[65]
13. Visually conceal approach to food (using barrier)	[26,27]	
14. Auditorially conceal approach to food (choosing silent door)	[27]	
15. Take food that a dominant individual did not see being hidden	[15]	[66]
16. Understand that if competitor picks first, he will have chosen the food he saw (not food he did not see) being hidden	^a	^a

^a(J. Kaminski *et al.*, personal communication).

Gaps in the table indicate no information available.

the two individuals' perceptions differ (e.g. they see different sides of a barrier), and the observer acts on the basis not just of what she herself sees or knows but also on the basis of what the other sees or knows.

Table 2 lists 16 different studies relevant to the question of whether chimpanzees understand what others see and know. The first set of studies (Table 2, points 1–7) involve gaze-following behaviors, which are, admittedly, not such powerful evidence of an understanding of perception. The key fact here is that chimpanzees follow the gaze direction of others behind themselves, around barriers and past distractors; they check back with the gazer if nothing interesting is to be found in the indicated direction, and they eventually stop following if an individual always gazes at nothing interesting. These are all characteristics of gaze following shared with human infants, and even though human infants use the eyes, as opposed to the head, more often than chimpanzees do in following gaze direction, chimpanzees do use the eyes to some extent as well (Table 2, point 5).

The second set of studies involves gestural communication. The general finding is that chimpanzees take into account the visual orientation of the recipient when gesturing (Table 2, point 8), even moving themselves in front of the recipient to gesture when necessary (Table 2, point 9). Of particular importance, Kaminski *et al.* [14] found chimpanzees much more sensitive to the recipient than did Povinelli and Eddy [6] in a similar paradigm when the human was actually in a position to deliver food (i.e. facing them bodily). It is true that chimpanzees are not as sensitive to the eyes as are human infants, but still they understand when someone is or is not in a position to receive their communicative act (Table 2, point 10) – again in a manner very similar to human infants.

By far the most powerful evidence comes from the third set of studies, which use food-competition paradigms (Table 2, points 11–16, also Box 1). Each of these studies is a whole experimental paradigm with several control

conditions, that cannot be fully described here. But the basic idea is that when competing with others for food, chimpanzees take into account what their competitor can and cannot see, what he can and cannot hear and even what he does and does not know. In some cases they even attempt to influence what the other can and cannot see and hear by actively concealing their own approach to food either visually or auditorially (Table 2, points 13 and 14). Chimpanzees in these studies also know what others know in the sense that they keep track of what another has just seen a moment before (Table 2, points 15 and 16), just as human infants.

Again, we believe that there is only one reasonable conclusion to be drawn from the totality of the studies reviewed here: chimpanzees, like humans, understand that others see, hear and know things. We have many different methodologies involving several different experimental paradigms and response measures all leading to the same conclusion. Again, behavioral rules might be concocted to explain the results of each of the various studies individually, but again this will require creating a variety of post hoc explanations on the basis of no direct evidence of the requisite past experiences. And again, if one were to use the behavioral rules critique rigorously and fairly across the board, one would have to conclude that human infants and young children also have no understanding of the perception or knowledge of others because many of the studies correspond rather closely to studies conducted with infants.

No understanding of false belief?

Despite all of this positive evidence for chimpanzees' understanding the goals, intentions, perceptions and knowledge of others, there is currently no experimental evidence that they understand false beliefs by, for example, predicting what another will do based on what that other knows (when the subject knows something else to be the case). First are the negative findings of Call and Tomasello [8],

who had positive results with five-year-old children in the same nonverbal paradigm (which correlated with a standard verbal false-belief paradigm). Second, there are now supporting negative results from a competitive version of that task in which subjects were required to infer from a competitor's actions where she believed the hidden food to be, which then led the subject to the actual location (C. Krachun *et al.*, personal communication).

In addition, Hare *et al.* [15] presented two versions of the basic chimpanzee competition task. In one version the dominant chimpanzee either witnessed (informed condition) or not (uninformed condition) the location where the food was placed. In another version, the dominant always witnessed the initial location of the reward but then the reward was moved to a second location. In some trials the dominant witnessed this movement (informed condition), whereas in others she did not (misinformed condition), which created a false belief in the dominant about the reward's location. If subjects understood that in the misinformed condition their competitor had a false belief, they should have performed nearly perfectly in this condition because they would have been able to predict that she should go to the wrong location. However, if they simply understood their competitor to be ignorant, they could make no such specific prediction about where she would go, and so should not perform as well. Results showed that although chimpanzees distinguished between the informed and uninformed conditions (thus showing an understanding of their competitor's knowledge versus ignorance), they did not distinguish between the uninformed and the misinformed conditions (thus providing no evidence for understanding that their competitor had a false belief).

Recently, J. Kaminski *et al.* (personal communication) found a very similar pattern of results in a totally different experimental paradigm. They presented both chimpanzees and six-year-old children with a back-and-forth conspecific competition game with both knowledge-ignorance and false-belief versions. The basic idea was that food was placed in the opaque buckets such that in some cases the location of the food was known to both competitors (who watched the other witnessing the hiding as well), in other cases only the subject witnessed the hiding of the food (the competitor was thus ignorant) and in still other cases both participants watched the hiding of the food but then only the subject saw it being moved to a new location (the competitor thus had a false belief). The overall finding was that children passed both the knowledge-ignorance and the false-belief versions of the task, whereas chimpanzees treated both versions as involving knowledge-ignorance only and not false beliefs. Together with the results of Hare *et al.* [15], the conclusion is clear: chimpanzees understand knowledge-ignorance, but not false belief. This seeming lack of understanding is all the more striking given mounting evidence that even one- and two-year-old human children understand something in the direction of false beliefs [16–19].

Conclusions

It is time for humans to quit thinking that their nearest primate relatives only read and react to overt behavior.

Obviously, chimpanzees' social understanding begins with the observation of others' behavior, as it does for humans, but it does not end there. Even if chimpanzees do not understand false beliefs, they clearly do not just perceive the surface behavior of others and learn mindless behavioral rules as a result. All of the evidence reviewed here suggests that chimpanzees understand both the goals and intentions of others as well as the perception and knowledge of others. Moreover, they understand how these psychological states work together to produce intentional action; that is, they understand others in terms of a relatively coherent perception-goal psychology in which the other acts in a certain way because she perceives the world in a certain way and has certain goals of how she wants the world to be. There is much less evidence overall, but it is possible that other non-human primate species also have a similar understanding [20,21], and as do, perhaps, some bird species as well [22–25].

In a broad construal of the phrase 'theory of mind', then, the answer to Premack and Woodruff's pregnant question of 30 years ago is a definite yes, chimpanzees do have a theory of mind. But chimpanzees probably do not understand others in terms of a fully human-like belief-desire psychology in which they appreciate that others have mental representations of the world that drive their actions even when those do not correspond to reality. And so in a more narrow definition of theory of mind as an understanding of false beliefs, the answer to Premack and Woodruff's question might be no, they do not. Why chimpanzees do not seem to understand false beliefs in particular – or if there might be some situations in which they do understand false beliefs – are topics of ongoing research.

References

- 1 Tomasello, M. and Call, J. (1997) *Primate Cognition*, Oxford University Press
- 2 Premack, D. and Woodruff, G. (1978) Does the chimpanzee have a theory of mind? *Behav. Brain Sci.* 1, 515–526
- 3 Savage-Rumbaugh, E.S. *et al.* (1978) Sarah's problems in comprehension. *Behav. Brain Sci.* 1, 555–557
- 4 Povinelli, D.J. *et al.* (1998) Young and juvenile chimpanzees' (*Pan troglodytes*) reactions to intentional versus accidental and inadvertent actions. *Behav. Processes* 42, 205–218
- 5 Tomasello, M. (1996) Do apes ape? In *Social Learning In Animals: The Roots Of Culture* (Galef, B.G. and Heyes, C., eds), pp. 319–346, Academic Press
- 6 Povinelli, D.J. and Eddy, T.J. (1996) What young chimpanzees know about seeing. *Monogr. Soc. Res. Child Dev.* 61, 1–152
- 7 Povinelli, D.J. *et al.* (1994) Absence of knowledge attribution and self-recognition in young chimpanzees (*Pan troglodytes*). *J. Comp. Psychol.* 108, 74–80
- 8 Call, J. and Tomasello, M. (1999) A nonverbal false belief task: the performance of children and great apes. *Child Dev.* 70, 381–395
- 9 Byrne, R.W. and Whiten, A. (1990) Tactical deception in primates: the 1990 database. *Primate Rep.* 27, 1–101
- 10 Povinelli, D.J. and Vonk, J. (2003) Chimpanzee minds: suspiciously human? *Trends Cogn. Sci.* 7, 157–160
- 11 Povinelli, D.J. and Vonk, J. (2006) We don't need a microscope to explore the chimpanzee's mind. In *Rational Animals* (Hurley, S. and Nudds, M., eds), pp. 385–412, Oxford University Press
- 12 Whiten, A. (1996) When does smart behaviour-reading become mind-reading? In *Theories Of Theories Of Mind* (Carruthers, P. and Smith, P.K., eds), pp. 277–292, Cambridge University Press

- 13 Tomasello, M. *et al.* (1993) Imitative learning of actions on objects by children, chimpanzees and enculturated chimpanzees. *Child Dev.* 64, 1688–1705
- 14 Kaminski, J. *et al.* (2004) Body orientation and face orientation: two factors controlling apes' begging behavior from humans. *Anim. Cogn.* 7, 216–223
- 15 Hare, B. *et al.* (2001) Do chimpanzees know what conspecifics know? *Anim. Behav.* 61, 139–151
- 16 Clements, W.A. and Perner, J. (1994) Implicit understanding of belief. *Cogn. Dev.* 9, 377–395
- 17 Csibra, G. and Southgate, V. (2006) Evidence for infants' understanding of false beliefs should not be dismissed. *Trends Cogn. Sci.* 10, 4–5
- 18 Onishi, K.H. and Baillargeon, R. (2005) Do 15-month-old infants understand false beliefs? *Science* 308, 255–258
- 19 Surian, L. *et al.* (2007) Attribution of beliefs by 13 month olds. *Psychol. Sci.* 18, 580–586
- 20 Flombaum, J.I. and Santos, L.R. (2005) Rhesus monkeys attribute perceptions to others. *Curr. Biol.* 15, 447–452
- 21 Santos, L.R. *et al.* (2006) Rhesus monkeys (*Macaca mulatta*) know what others can and cannot hear. *Anim. Behav.* 71, 1175–1181
- 22 Dally, J.M. *et al.* (2004) Cache protection strategies by western scrub-jays (*Aphelocoma californica*): hiding food in the shade. *Proc. Biol. Sci.* 271, S387–S390
- 23 Dally, J.M. *et al.* (2005) Cache protection strategies by western scrub-jays, *Aphelocoma californica*: implications for social cognition. *Anim. Behav.* 70, 1251–1263
- 24 Dally, J.M. *et al.* (2006) Food-caching western scrub-jays keep track of who was watching when. *Science* 312, 1662–1665
- 25 Emery, N.J. and Clayton, N.S. (2001) Effects of experience and social context on prospective caching strategies by scrub jays. *Nature* 414, 443–446
- 26 Hare, B. *et al.* (2006) Chimpanzees deceive a human by hiding. *Cognition* 101, 495–514
- 27 Melis, A.P. *et al.* (2006) Chimpanzees conceal visual and auditory information from others. *J. Comp. Psychol.* 120, 154–162
- 28 Buttelmann, D. *et al.* (2007) Enculturated chimpanzees imitate rationally. *Dev. Sci.* 10, F31–F38
- 29 Gergely, G. *et al.* (2002) Rational imitation in preverbal infants. *Nature* 415, 755
- 30 Tomasello, M. *et al.* (2005) Understanding and sharing intentions: the origins of cultural cognition. *Behav. Brain Sci.* 28, 675–691
- 31 Call, J. *et al.* (2004) Unwilling or unable? Chimpanzees' understanding of intentional action. *Dev. Sci.* 7, 488–498
- 32 Behne, T. *et al.* (2005) Unwilling versus unable: infants' understanding of intentional action. *Dev. Psychol.* 41, 328–337
- 33 Call, J. and Tomasello, M. (1998) Distinguishing intentional from accidental actions in orangutans (*Pongo pygmaeus*), chimpanzees (*Pan troglodytes*) and human children (*Homo sapiens*). *J. Comp. Psychol.* 112, 192–206
- 34 Warneken, F. and Tomasello, M. (2006) Altruistic helping in human infants and young chimpanzees. *Science* 31, 1301–1303
- 35 Warneken, F. *et al.* (2007) Spontaneous altruism by chimpanzees and young children. *PLoS Biol.*, 5, e184 DOI: 10.1371/journal.pbio.0050184 (<http://biology.plosjournals.org>)
- 36 Hare, B. and Tomasello, M. (2004) Chimpanzees are more skillful in competitive than in cooperative cognitive tasks. *Anim. Behav.* 68, 571–581
- 37 Jensen, K. *et al.* (2007) Chimpanzees are rational maximizers in an ultimatum game. *Science* 318, 107–109
- 38 Tomasello, M. and Carpenter, M. (2005) The emergence of social cognition in three young chimpanzees. *Monogr. Soc. Res. Child Dev.* 70, 1–132
- 39 Myowa-Yamakoshi, M. and Matsuzawa, T. (2000) Imitation of intentional manipulatory actions in chimpanzees (*Pan troglodytes*). *J. Comp. Psychol.* 114, 381–391
- 40 Meltzoff, A. (1995) Understanding the intentions of others: re-enactment of intended acts by 18-month-old children. *Dev. Psychol.* 31, 1–16
- 41 Carpenter, M. *et al.* (1998) Fourteen-through 18-month-old infants differentially imitate intentional and accidental actions. *Infant Behav. Dev.* 21, 315–330
- 42 Povinelli, D.J. and Eddy, T.J. (1996) Chimpanzees: joint visual attention. *Psychol. Sci.* 7, 129–135
- 43 Okamoto, S. *et al.* (2004) Looking back: the “representational mechanism” of joint attention in an infant chimpanzee (*Pan troglodytes*). *Jpn. Psychol. Res.* 46, 236–245
- 44 Tomasello, M. *et al.* (1998) Five primate species follow the visual gaze of conspecifics. *Anim. Behav.* 55, 1063–1069
- 45 Butterworth, G. and Jarred, N. (1991) What minds have in common is space: spatial mechanisms serving joint visual attention in infancy. *Br. J. Dev. Psychol.* 9, 55–72
- 46 Tomasello, M. *et al.* (2007) Reliance on head versus eyes in the gaze following of great apes and human infants: the cooperative eye hypothesis. *J. Hum. Evol.* 52, 314–320
- 47 Brooks, R. and Meltzoff, A.N. (2002) The importance of eyes: how infants interpret adult looking behavior. *Dev. Psychol.* 38, 958–966
- 48 Call, J. *et al.* (1998) Chimpanzee gaze following in an object choice task. *Anim. Cogn.* 1, 89–100
- 49 Bräuer, J. *et al.* (2005) All four great ape species follow gaze around barriers. *J. Comp. Psychol.* 119, 145–154
- 50 Bates, E. (1979) *The Emergence Of Symbols*, Academic Press
- 51 Tomasello, M. *et al.* (2001) The ontogeny of gaze following in chimpanzees and rhesus macaques. *Anim. Behav.* 61, 335–343
- 52 Tomasello, M. *et al.* (1999) Chimpanzees follow gaze direction geometrically. *Anim. Behav.* 58, 769–777
- 53 Butterworth, G. and Grover, L. (1990) Joint visual attention, manual pointing, and preverbal communication in human infancy. In *Attention and Performance 13: Motor Representation And Control* (Jeannerod, M., ed.), pp. 605–624, Lawrence Erlbaum Associates
- 54 Moll, H. and Tomasello, M. (2004) 12- and 18-month-olds follow gaze to hidden locations. *Dev. Sci.* 7, F1–F9
- 55 Okamoto-Barth, S. *et al.* (2007) Great apes understanding of others' line of sight. *Psychol. Sci.* 18, 462–468
- 56 Caron, A. *et al.* (2002) Comprehension of the referential intent of looking and pointing between 12 and 15 months. *J. Cogn. Dev.* 3, 445–464
- 57 Tomasello, M. *et al.* (1994) The learning and use of gestural signals by young chimpanzees: a trans-generational study. *Primates* 35, 137–154
- 58 Leavens, D.A. *et al.* (2004) Tactical use of unimodal and bimodal communication by chimpanzees, *Pan troglodytes*. *Anim. Behav.* 67, 467–476
- 59 Liebal, K. *et al.* (2004) To move or not to move: how apes adjust to the attentional state of others. *Interaction Studies* 5, 199–219
- 60 Povinelli, D.J. *et al.* (2003) Chimpanzees spontaneously alter the location of their gestures to match the attentional orientation of others. *Anim. Behav.* 66, 71–79
- 61 Lizskowski, U. *et al.* Infants' visual and auditory communication when a partner is or is not visually attending. *Infant Behav. Dev.* (in press)
- 62 Gómez, J.C. (1996) Non-human primate theories of (non-human primate) minds: some issues concerning the origins of mind-reading. In *Theories Of Theories Of Mind* (Carruthers, P. and Smith, P.K., eds), pp. 330–343, Cambridge University Press
- 63 Hare, B. *et al.* (2000) Chimpanzees know what conspecifics do and do not see. *Anim. Behav.* 59, 771–785
- 64 Bräuer, J. *et al.* (2007) Chimpanzees really know what others can see in a competitive situation. *Anim. Cogn.* 10, 439–448
- 65 Moll, H. and Tomasello, M. (2006) Level 1 perspective-taking at 24 months of age. *Br. J. Dev. Psychol.* 24, 603–613
- 66 Tomasello, M. and Haberl, K. (2003) Understanding attention: 12- and 18-month-olds know what's new for other persons. *Dev. Psychol.* 39, 906–912