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Chimpanzee Personhood: Supporting Scientific Documentation

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The Humane Society of the United States

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Chimpanzee Personhood Supporting Scientific Documentation

compiled by Jonathan Balcombe, PhD

March 2012

Background

The aim of this document is to provide scientific support for granting chimpanzees and bonobos the legal status of persons. The studies summarized here have been selected because they show these species to have levels of awareness, cognition, emotionality and virtue that rivals that of their hominid cousins, *Homo sapiens*. Chimps, like other great apes, have long-term relationships, grieve the loss of a loved-one, can solve complex puzzles, display a sense of justice, and can learn hundreds of signs and put them together in logical sentences.

Chimpanzees and bonobos (pygmy chimpanzees) are our closest living relatives, and we (not gorillas or orangutans) are theirs. Our genomes are over 98% identical. In 2003, a group of scientists proposed in the *Proceedings of the National Academy of Sciences* that chimpanzees should be included in the genus *Homo* (Wildman et al. 2003).

In most parts of the world, it is still legal to torture and murder chimps. In research laboratories, for instance, chimps are deliberately infected with potentially lethal diseases, such as HIV and Hepatitis, and sometimes killed in the process. Currently, some 1,200 chimpanzees are kept in US laboratories. Even if they do not die, many are confined in prison-like conditions. Unlike human prisoners, they are granted no rights. In the US and elsewhere, an unknown number of chimpanzees are also enslaved in entertainment, chained to stakes, or incarcerated in zoo exhibits.

A growing list of nations is recognizing the legal consistency of ascribing basic rights to great apes. Bans or severe restrictions on their use in research now exist in the Netherlands, New Zealand, the United Kingdom, Sweden, Germany, Austria, Japan, Spain, and Belgium. In 2011 the United States National Institutes of Health announced that it would no longer fund research on chimpanzees. The climate seems suitable for a challenge to the legal status of great apes as the property of humankind.

CONTENTS

Background	1
CONTENTS	2
Adoption	3
Altruism	4
Amusement	5
Anatomy	5
Attribution	5
Awareness	7
Bartering	9
Celebration	10
Cognition	10
Cognitive development	13
Comfort	14
Communication	15
Concern for others	17
Conflict management	17
Conflict with humans	18
Consolation	18
Cooperation	18
Cruelty	19
Culture	19
Deactivation of snares	21
Deception	21
Emotion	22
Emotional attachment	24
Emotional awareness	24
Emotional development	25
Empathy	25
Fairness/Justice	26
Genocide	26
Gratitude	26
Grief	27
Handedness	27
Human culture	28
Humor	28
Imitation	28
Individual recognition	29
Kinship	29
Language	29
Laughter	31
Learning	32
Leisure	32
Life cycle	33
Memory	33

Mindedness	33
Numerosity	34
Perception	35
Planning	35
Play	36
Pretending	36
Psychological vulnerability	36
Reciprocity	38
Restraint	38
Revenge	39
Self-awareness	39
Self-control	40
Self-medication	40
Sharing	40
Social development	41
Sympathy	41
Teaching	42
Technology transfer	42
Theory of mind	42
Tool use	43
Understanding	44
Warfare	45
REFERENCES	46

Adoption

Some researchers have claimed, based on tenuous captive studies, that chimpanzees are indifferent to the welfare of unrelated group members. However, wild chimpanzees have shown a variety of apparently altruistic behaviors, including food sharing, coalition formation, cooperative hunting, and border patrolling. The current study reports 18 cases of adoption of orphaned youngsters by group members in Tai forest (Ivory Coast) chimpanzees. Half of the adoptions were done by males and remarkably only one of these proved to be the father. Despite how costly is this behavior, adoptions by adults can last for years and thus imply extensive care towards the orphans (Boesch et al, 2010).

If a mother dies, older siblings, including males, may typically adopt younger brothers or sisters (de Waal 1996; Lindsey 1999). In the wild, a sterile adult female was observed to adopt three orphaned infants during a two-year period (Lindsey 1999).

This study reports a unique incident of adoption, in which a grandmother adopted her daughter's infant, the circumstances of which appear to have been to the benefit of all three individuals (Wroblewski 2008).

Altruism

In experiments at the Max Planck Institute, 12 of 18 semi-wild adult chimps went out of their way to help an unfamiliar human who was struggling to perform a task (reach a stick), even when it required having to climb over an 8-foot rope barrier for no reward. Human toddlers will do the same thing. Chimps who had been taught how to unlatch a door also helped unfamiliar chimps struggling to get through the door—by unlatching the door for them. These results indicate that chimpanzees share crucial aspects of altruism with humans, suggesting that the roots of human altruism may go deeper than previous experimental evidence suggested (Warneken et al. 2007).

Reasoning that experiments using food to study altruistic acts in chimpanzees might fail because chimpanzees often compete for food, the authors instead presented young chimpanzees (aged between 3 and 4.5 years) with tasks involving opportunities to help humans who had dropped or misplaced non-food items (e.g., marker, clothespin, book). All three chimps helped in the five tasks involving reaching for an object that had fallen out of reach of the human. On no occasion did the chimps receive any benefit (e.g., reward or praise) for helping (Warneken & Tomasello 2006).

An adult, captive-reared chimpanzee was shown videotaped scenes of a human actor struggling with one of eight problems, then shown two photographs, one depicting an action or object (or both) representing a solution to the problem. On seven of the eight problems, the chimp consistently chose the correct photograph. For example, when the video depicted a human shivering violently while standing next to a disconnected portable heater, the chimp selected a picture of a connected heater. This study demonstrates a) a chimpanzee's problem-solving ability, and b) perhaps also a modicum of empathy for the struggling actor (Premack & Woodruff 1978).

Chimpanzees helped others obtain both food and non-food items in situations when the donor could not get the food herself. The key factor in motivating the helping behavior is the recipients' attempts to either get the food or get the attention of the potential donor. These findings add to the accumulating body of evidence that humans and chimpanzees share the motivation and skills necessary to help others in situations in which they cannot selfishly benefit (Melis et al. 2011).

Pairs of chimpanzees in adjoining booths were given tools to solve problems, but the tools were inappropriate for the task. For instance, when one chimp was given a stick tool to solve a problem that required a straw, and the chimp in the adjacent booth had a straw tool but required a stick, the two apes spontaneously exchanged the two tools, and usually after one requested the other's tool. Even without any hope of reciprocation from the partner, the chimpanzees continued to help the partner as long as the partner required help (Yamamoto et al. 2009).

The authors argue that whereas young children have a biological predisposition to help others achieve their goals, to share resources with others and to inform others of things helpfully, chimpanzees engage in some but not all of these behaviors. Specifically, they help others instrumentally, but they are not so inclined to share resources altruistically and they do not inform others of things helpfully (Warneken & Tomasello 2009).

In trials using "selfish" tokens that reward only the actor, and "prosocial" tokens that reward both the actor and a partner, seven of seven female chimpanzees—each tested with three different partners—showed a significant bias for the prosocial option. Prosocial choices occurred both in response to solicitation by the partner and spontaneously without solicitation. These results draw into question previous conclusions that chimpanzees have a limited sensitivity to the needs of others and behave prosocially only in response to significant prompting (Horner et al. 2011).

Amusement

Chimpanzees at Bossou, Guinea have been observed capturing and toying with western tree hyraxes. In one case, an adolescent female carried a hyrax for 15 hours, slept with it in her nest, and groomed it. In another case, two adolescent males timidly inspected a small hyrax (Hirata et al. 2001). These observations suggest that a chimpanzee can recognize that a member of another species is an individual with a life, and that the behavior of wild chimpanzees is not governed only by opportunistic self-interest.

Captive chimps amuse themselves by taking water into their mouths and squirting it at unsuspecting humans. So convincing is the chimp's ability to hide their intent that even wary caretakers who know they do this can fall prey to a dowsing. The ape will stroll around the cage as if occupied with something else, only to swing around and launch the attack at the right moment (de Waal 1996). The chimps respond to a successful dowsing by shrieking, laughing, jumping and sometimes falling over (de Waal 1997).

Anatomy

The topography of the corpus callosum (CC), a significant part of the mammalian cerebral cortex, was compared for the first time in chimps (n=21) and humans using high-resolution magnetic resonance imaging (MRI) and diffusion tensor imaging (DTI). Similar to humans, tractography identified five clusters of CC fibers: prefrontal; premotor and supplementary motor; motor; sensory; parietal, temporal and occipital. Overall, the results indicate chimpanzees display similar topography of the CC as humans, in terms of distribution of callosal projections and microstructure of fibers as determined by anisotropy measures (Phillips & Hopkins 2012).

Attribution

By the age of 13 months, an infant chimpanzee showed reliable ability to follow a human's orientation cues towards an object, including tapping on the target object with a finger, pointing to the object, gazing at the object with head orientation, and glancing towards the object with no head orientation (Okamoto et al. 2002).

Staged encounters with a model of a dangerous snake show that whether or not he gives an alarm call depends on his perception of another individual's knowledge (Seyfarth & Cheney 2012).

In another study or staged encounters with a model viper placed on wild chimpanzees' travel path, chimps (n=33) were more likely to alarm call in response to the snake in the presence of

unaware group members than in the presence of aware group members. Specifically, alarm calls were significantly more common if the caller was with group members who had either not seen the snake or had not been present when alarm calls were emitted. This suggests that chimps recognize knowledge and ignorance in others (Crockford et al. 2012).

There is strong evidence that the Great Apes, at least both chimpanzee species, can view a situation from the perceptual perspective of others.

European Union Scientific Committee on Animal Health
and Animal Welfare, 2002

Studies of chimpanzees and other great apes have repeatedly shown that they attribute conscious awareness to others of their kind, and to humans. These findings show that chimpanzees are able to attribute awareness, or knowledge, to other chimpanzees., and to use this information to devise effective social-cognitive strategies (Hare et al. 2001).

Four chimpanzees were shown the location of food locked inside a box, but they needed the help of a human trainer who had the key. When the trainer entered the enclosure, the chimps simply led the way and the trainer followed them to the box. But when the trainer entered the room with several blindfolds wrapped around different parts of his/her face, three of the four chimps took the trainer by the hand and physically led him to the box, indicating the attribution of blindness to the trainer. The fourth chimp instead removed the blind-fold covering the trainer's eyes, leaving the decoys, then led him to the box (Page 1999, p 224).

Chimpanzees and gorillas will divert their attention from a hidden source of food when a competitor comes on the scene. To enhance the ruse, they may also take to grooming or some other activity. Only when the competitor has left the scene do they again look at the food and retrieve it (Whiten & Byrne 1988).

In a series of experiments, a subordinate and a dominant chimpanzee competed for food placed in various ways on the subordinate's side of an opaque barrier. In some conditions, the dominant could not see the food baiting; the subordinate always saw the entire baiting procedure and could also monitor the visual access of their dominant competitor. Subordinates preferentially approached and retrieved food that dominants had not seen hidden or moved. Subordinates also recognized, and adjusted their behaviour accordingly, when the dominant individual who witnessed the hiding was replaced with another dominant individual who had not witnessed it, thus demonstrating the ability to keep track of precisely who has witnessed what.

All four species of great ape are known, from both wild observations and carefully designed captive studies, to follow the gaze of another to distant objects and around obstacles. For instance, a recent captive study demonstrated that all four great apes reliably followed a human's gaze direction and sometimes even checked back when they found no target. They also reliably put themselves in positions from which they could see what a human was gazing at behind a barrier (Bräuer et al. 2005).

Chimpanzees produced more behaviors and deserted a testing station sooner when working with a willing but unable human experimenter than with a willing and able experimenter. The

chimpanzees' responses demonstrate an understanding of the intentional actions of others (Call et al. 2004).

Studies have demonstrated that chimpanzees produce more visual signals when the recipient's eyes are uncovered, and acoustic signals are used more when the recipient's eyes are closed than when open. These findings indicate the animals' awareness of another's sensory awareness, and that they use the presence of the eyes as a cue that their own visual signals will be effective (Hostetter et al. 2006).

Studies with captive chimpanzees show that they will gesture, vocalize, and display more often when a nearby human is carrying a tool they could use to access food. Chimps also respond differentially based on the human's attentional state, and when given the wrong tool persist in their communicative efforts (Russell et al. 2005).

Chimpanzees, bonobos and orangutans were presented with a situation in which they had to request food from a human observer who was either staring at the ape, facing the ape with her eyes closed, sitting with her back towards the ape, or left the room. All the apes produced more behaviors when they were being watched, and treated body and face orientation in a manner that indicates that face orientation encodes the observer's perceptual access, while body orientation encodes the observer's disposition to transfer food (Kaminski et al. 2004).

Studies using the looking time measure have been used to demonstrate what appears to be the attribution of goals to others by human infants. An experiment modeled on these studies was carried out on chimpanzees, and the chimpanzees responded the way infants do. Thus, chimpanzees also appear to attribute goals in the manner of human infants (Uller & Nichols 2000).

Studies in which great apes beg for food from human experimenters who systematically vary their body and face orientations show that both body and face orientation affect the apes' begging behavior. In this study, the human could hand over food regardless of body orientation. In response, face orientation became the key factor in the apes' begging behavior. This study presents the first evidence that all great ape species are able to assess the attentional state of a recipient based on the orientation of the face (Tempelmann et al. 2011).

Awareness

Chimpanzees adjust their behaviour according to their awareness of what another chimp knows or doesn't know. A subordinate and a dominant chimpanzee peered through a window on opposite sides of a room while a piece of food was strategically placed (baited) somewhere in the room, then they competed for the food after the doors were opened. The subordinate chimp could always see the baiting, but opaque barriers in the room allowed some baitings to be made out of view of the dominant chimp. The subordinate could also monitor the visual access of their dominant competitor. When baitings were out of view of the dominant chimp, subordinates preferentially approached and retrieved food; they did not do so when the dominant had seen the baiting, because the dominant would know where it was and claim it for him or herself. However, if a dominant individual who witnessed a baiting was replaced with another dominant

individual who had not witnessed it, subordinates went straight to the food, thus demonstrating the ability to keep track of precisely who has witnessed what (Hare et al. 2000).

In an extension of the above (Hare et al. 2000) paradigm to the auditory modality, chimpanzees appeared insensitive to whether a competitor can hear food rewards being hidden. The results suggest that chimpanzees did not take what the competitor had heard into account, despite being able to locate the hiding place themselves by the noise (Bräuer et al. 2008).

Chimpanzees show awareness of another's sensory awareness, and they use the presence of the eyes as a cue that their own visual signals will be effective. When chimpanzees are shown the location of food locked inside a box but are not provided a key to open it, they simply lead the way to the box when a human enters the room. But when the human enters with several blindfolds wrapped around different parts of his/her face, they recognize the handicap. Chimps have shown two solutions to this situation: 1) take the human's hand and physically lead him or her to the box, or 2) remove the blind-fold covering the helper's eyes, leaving the decoys, then leading him/her to the box (Premack & Premack 1984).

Wild female chimpanzees uttered copulation calls more often during copulation bouts with high-ranking males, but suppressed their calls if high-ranking females were nearby. Copulation calling may therefore be one potential strategy employed by female chimpanzees to advertise their receptivity to high-ranked males, and to confuse paternity in this promiscuously mating species as a means of secure future support from these socially important individuals (Townsend et al. 2008).

Great apes appear to be aware of varying likelihoods that they may be wrong. In a study that tested eight chimpanzees and four bonobos (as well as seven gorillas and seven orangutans) involved presenting the animal with two hollow tubes, baiting one of them and letting subject choose. In some conditions the subject had visual access to the baiting. There were variations in the cost associated with seeking information, in the time interval between baiting and choosing, in the food quality, and in the additional information offered regarding the food's location. Although subjects showed a high retrieval accuracy when they had witnessed the baiting, they were more likely to check inside the tube before choosing when high stakes were involved or after a longer period of time had elapsed between the baiting and reward retrieval. In contrast, providing subjects with indirect auditory information about the food's location or increasing the cost of checking reduced checking before choosing. Taken together, these findings suggest that subjects knew that they could be wrong when choosing (Call 2010).

In playback experiments, chimpanzees gazed significantly longer following incongruent sequences (not in accordance with the established social dominance hierarchy), despite their involving fewer call types from fewer individuals than congruent ones. These findings indicate that chimps discriminate the acoustic structure of aggressors versus victim's calls, and understand the nature of out-of-sight social interactions. Thus, chimpanzees are able to categorize apparently simple acoustic signals into victim and aggressor screams and to form inferences about third-party interactions they cannot see (Slocombe et al. 2010).

Just when a male chimpanzee was flashing an erection at a female to show his amorous intentions toward her, a high-ranking male appeared unexpectedly from around a corner. The aroused male immediately placed his hands over his penis to conceal it from view, like an embarrassed schoolboy (de Waal 2005a).

Four captive infant chimpanzees performed as well as human infants in recognizing goal-directed behavior, by responding appropriately to the trajectories of computer-generated objects (Uller 2004).

The eye movements of chimpanzees were recorded as they viewed naturalistic pictures containing a full-body image of a chimpanzee, a human or another mammal. The results showed a striking similarity in viewing patterns between chimpanzees to those found in earlier studies with humans. Both species look at the animal figures for longer than at the background and at the face region for longer than at other parts of the body (Kano & Tomonaga 2009).

Chimpanzees and other great apes showed object individuation but reaching into a box to retrieve a second object more often if a) they had seen two objects placed in the box before one was removed by a demonstrator, and b) if the single object they removed did not match the single object they had seen being placed in the box. These results suggest that earlier methods showing that great apes did not have object individuation were methodologically flawed (Mendes et al. 2008).

Positron emission tomography imaging was used to assess resting-state brain activity in chimpanzees as a potential window onto their mental world and to compare these results with those of a human sample. Like humans, chimpanzees show high levels of activity within default mode areas, including medial prefrontal and medial parietal cortex. Chimpanzees differ from a human sample in showing higher levels of activity in ventromedial prefrontal cortex and lower levels of activity in left-sided cortical areas involved in language and conceptual processing in humans. These results raise the possibility that the resting state of chimpanzees involves emotionally laden episodic memory retrieval and some level of mental self-projection, albeit in the absence of language and conceptual processing (Rilling et al. 2007).

Bartering

Over an observational period of 22 months, female wild chimpanzees copulated more frequently with those males who shared meat with them. These results strongly suggest that wild chimpanzees exchange meat for sex, and do so on a long-term basis (Gomes & Boesch 2006).

Both chimpanzees and bonobos make sex-for-food deals. A lower-ranking male seeking a sexual union with a receptive female will sometimes groom the alpha male to earn credit for that privilege. After grooming for awhile, the suitor approaches the female and begins to mate, all the while keeping an eye on alpha. If alpha gets up and starts swaying with bristling fur, it spells trouble and the suitor may groom alpha again (de Waal 2005a).

A female bonobo, on seeing a male with two oranges, presents herself for sex, and afterwards walks away with one of the fruits (de Waal 2005a).

Celebration

When two female chimpanzees were unexpectedly confronted with an enormous pile of bananas, “they flung their arms around each other’s neck and pressed their open mouths to each other’s shoulders while uttering excited food calls before they took a single fruit” (Goodall 1986, p. 359-60).

Liberation from dreary confinement has been observed to produce expressions of joy in various animal species. When the chimpanzees leave their indoor winter quarters at the captive colony at Arnhem Zoo, The Netherlands, chimpanzee expert Frans de Waal describes it as “the most festive day of the year”:

...All over the enclosure apes can be seen embracing and kissing each other. Sometimes they stand in groups of three or more jumping and thumping each other excitedly on the back. The apes’ delight in regaining their freedom is obvious” (de Waal 1982, p 26).

Cognition

For certain tasks, chimpanzees appear to be more intellectually developed than humans. For instance, chimpanzees can recognize the upside-down faces of other chimpanzees they know, while humans cannot do the same with familiar human faces (Tomonaga et al. 1993). This may relate to the fact that chimps are much more likely than humans to see others’ faces when one of them is hanging upside down—such as during play.

Tetsuro Matsuzawa, who directs research on a community of captive chimpanzees at Kyoto University, Japan, presented chimps with touch-sensitive computer monitors and they soon learned to obtain small food treats by performing tasks on the monitor. One such task is to recall in sequence the numbers 1 to 9 scattered randomly on a computer screen for just one second before being replaced by white squares. Ayumu, a five-year old chimp, excels at this. He casually but quickly points to all the white squares in sequence. Humans barely pass the test with just four or five numbers (Inoue & Matsuzawa 2007). When the British memory champion Ben Pridmore—who can remember the order of a shuffled deck of cards in 30 seconds—competed head-to-head against Ayumu, the chimp performed three times better. When the numbers flashed for just a fifth of a second, Ayumu correctly recalled all nine digits ninety percent of the time, compared to 33 percent for Pridmore (McRae 2008). While Ayumu is the best among his chimp peers, the average chimp scores twice as well as the average human on this short-term memory task.

There is evidence that chimpanzees, like humans, are susceptible to the Stroop effect, which is the conflict that arises in one’s brain when one is asked to name the color of ink that a word is printed in, when that word denotes a different color (for example, GREEN). This suggests that chimps can process two different streams of information at once, and detect a conflict between them (Beran et al. 2007).

Chimpanzees were able to distinguish different quantities of items dropped into a container (out of view and therefore with no visual cues available). Their accuracy was unaffected by the

timing of release of objects into the container, indicating that the chimps were not merely using elapsed time as a means to estimate different quantities (Beran 2012).

Chimpanzees and older children generally performed better than young children at distinguishing ratios between two sets of discrete items, with performance in all groups predictably being best when the difference between sets was greater (Beran et al. 2011).

Chimpanzees observed a series of demonstrations involving the pouring of liquid (juice) quantities from one container to another using different combinations of clear and opaque syringes and containers, and varying the heights from which liquid was poured into containers. Despite these distractions—which produce perceptual illusions of different quantities being poured—chimpanzees accurately compared visible sets to nonvisible sets in all conditions tested (Beran 2010).

A 6 year old female chimpanzee learned to distinguish perfectly every letter of the alphabet in a matching-to-sample task with 26 letters as choice alternatives. These results resemble those obtained from similarity judgements by humans. Using letters of various sizes, a visual acuity test revealed that the chimpanzee's acuity was also comparable to that of normal humans (Matsuzawa 1990).

Studies with human subjects find that people tend to be more averse to choosing ambiguous options than risky options with known probabilities. A study of chimpanzees and bonobos found that they, too, share this bias against ambiguity. First, apes chose between a certain option that reliably provided an intermediately preferred food type, and a variable option that could vary in the probability that it provided a highly preferred food type. When trials were interspersed in which the apes had no knowledge about the probabilities, both species avoided the ambiguous option and favored the risky option (Rosati & Hare 2011).

In a comparison of individual differences of 106 chimpanzees and 105 two-year-old human children using 15 cognitive tasks that posed problems about the physical or social world, a similar factor of spatial cognition was found for the two species. Also, whereas chimpanzees had a single factor in addition to spatial cognition, the children had two distinct additional factors: one for physical cognition and one for social cognition. These findings, in combination with previous research, support the proposal that humans share many cognitive skills with nonhuman apes, especially for dealing with the physical world, but in addition have evolved some specialized skills of social cognition (Herrmann et al. 2010a).

The skills in solving a food-reaching problem was compared among all great ape species, including 22 chimpanzees, 18 bonobos, 18 orangutans, 6 gorillas and 42 children 3-5-year-old children. The test required subjects to avoid reaching directly for food and instead use an indirect reaching method to successfully obtain the food. Overall, orangutans were the most skilful apes, including human children. Sanctuary chimpanzees and bonobos outperformed their zoo counterparts whereas there was no difference between the two orangutan samples. Most zoo chimpanzees and bonobos failed to solve the original task, but improved their performance with additional training. In general, the performance of the older children was far from perfect and comparable to some of the nonhuman apes tested (Vlamings et al. 2010).

Chimpanzees preferred to reach for the lower of two cups balancing on a scale, after a banana had been hidden beneath one cup without the chimp knowing which cup. Chimps showed no intrinsic preference for lower cups in control situations without any movement of the balance. This study demonstrates chimps' ability to make a causal inference based on an object's weight (Hanus & Call 2008).

Chimpanzees recognize that a slanted board is more likely to have food beneath it than a board lying flat. Furthermore, they also know that another chimp knows the connection between the board's orientation and the likely presence of food, indicating that they can determine the inferences another is likely to have made (Schmelz et al. 2011).

Tests involving the presentation of two cups, one of which contains food, show that all great apes will select the baited cup when only the empty cup is shaken (auditory cue) or its contents shown (visual cue), an ability termed “inference by exclusion.” Control tests also show that apes avoid shaken noiseless cups, learn to use auditory information as a cue, and are not simply more attracted to noisy cups—all of which means they understand that the food causes the noise, and not simply that the noise is associated with the food (Call 2004).

Imitation is the basis of cultural learning. It requires a transference of what is observed to oneself, and suggests a sense of self. Young chimpanzees imitate the actions of a human demonstrator in a series of tasks to retrieve a reward from a puzzle-box. Interestingly, the chimps ignore any irrelevant tasks performed by the demonstrator, indicating a cognitive awareness of the goal-relevant steps involved. Human children of similar age (3- to 4-years) imitate both relevant and irrelevant steps, at the expense of efficiency, suggesting a greater susceptibility to cultural conventions (Horner & Whiten 2005).

Chimps understand that a given gesture refers to a conceptual category: e.g., the verb “open” was taught only for a door, but the chimp seamlessly transferred its meaning to book, water faucets, and drawers (Gould & Gould 1994)

Experiments with chimpanzees using arbitrary plastic symbols (lexigrams) to represent objects, qualifiers (e.g., “red”), actions (e.g., “give”), and conditionals (e.g., “same,” “different,” “if-then”) demonstrate comprehension, and a grasp of abstractness. For example, the chimp Sarah recognizes that if a blue chip stands for a red object, she identifies the object as red. She knows that half an apple stands in a “same as” relationship with a half-filled container of liquid, and that “open” can be used in conjunction with a can of food or a box of toys (Premack's work, described in Page 1999).

Chimps were shown a scene of someone hiding an object in a room on a closed-circuit television. When they were later released into the room they went directly to the hidden object. This simple experiment illustrates the use of mental maps by chimps. (one of many examples, and in many species) (source Page 1999, describing EW Menzel's experiments from the 1970s).

Chimps also excel at the “conservation test,” which stumps most children under the age of seven. When two identical glasses are filled with identical amounts of water, chimps and young

children will answer “yes” to the question: Is the amount of water in each glass the same? But when the water from one glass is then poured into a taller and narrower glass, most children answer “no” to the same question, whereas chimps correctly answer “yes,” because they understand the concept of conservation regarding quantity. (Page 1999)

An adult female chimpanzee's cognitive performance was shown to be compromised during the ovulation period of her menstrual cycle, probably due to a decrease in attention and/or motivation (Inoue & Matsuzawa 2011).

Two- to 3-year old human children and juvenile chimpanzees had to stack four wooden blocks, and in which one of the blocks was shaped (with bumps) such that it had to be the highest block. Both groups performed poorly at first but experienced juvenile chimpanzees and humans older than 3 years became proficient at solving the task. Behavioral strategies adopted to succeed in the task were common to both species (Hayashi & Takeshita 2009).

"We [sic] follow this approach in examining eight cognitive cases--teaching, short-term memory, causal reasoning, planning, deception, transitive inference, theory of mind, and language--and find, in all cases, that similarities between animal and human abilities are small, dissimilarities large. There is no disparity between brain and mind." (Premack 2007)

In a captive study, bonobos were more skilled at solving tasks related to theory of mind or an understanding of social causality, while chimpanzees were more skilled at tasks requiring the use of tools and an understanding of physical causality. These species differences support the role of ecological and socio-ecological pressures in shaping cognitive skills over relatively short periods of evolutionary time (Herrmann et al. 2010b).

In a study of relationality using cups connected to tubes, all five species of great apes (including human children) performed better when provided with logico-causal cues than with non-logico-causal cues. Also, only children above 4 years of age, and bonobos and chimpanzees (unlike younger children, gorillas and orangutans) displayed some mastery of reasoning by non-causal relational similarity. The study authors conclude that recognizing relational similarity is not unique to the human species, and that the lack of a human sort of language capability does not preclude recognition of simple relational similarities (Haun & Call 2009).

Cognitive Development

The Brazelton Neonatal Behavioral Assessment Scale (NBAS) was administered to 13 nursery-reared chimpanzees every other day during their first month of life, and to 42 humans, twice, on the third and thirtieth day of life. Orientation items included social stimuli (a human face and both human and chimpanzee sounds) and nonsocial stimuli (a red ball and a red rattle). Results revealed that chimpanzee neonates have the capacity for sustained attention to all stimuli, both social and nonsocial, indistinguishable from that of human neonates. Significant improvements in orientation performance from Day 2 to Day 30 were found for both species. These striking similarities in early orientation ability are viewed as a challenge to notions of unique human propensities (Bard et al. 1992).

Chimpanzee and human newborns were compared on a standardised human neonatal assessment scale at both 3 days and 1 month of age. Human infants scored significantly higher on the orientation cluster at both ages, and scored lower in motoric maturity. The two chimpanzee infants who were human-reared scored as well as did the human infants at 1 month, suggesting that differences were attributable to the care-giving environment and not innate abilities (Hallock et al. 1989).

In a study of object-permanence involving 7 juvenile and adult chimpanzees, five orangutans and 24 19- and 26-month-old children, all three species showed comparable levels of problem solving (Call 2001).

Chimpanzees, orangutans, and 2.5-year-old children were presented with a finding game in which food or stickers were hidden in one of two or three tubes, with variations on whether subjects saw the baiting of the tubes, whether subjects could see through the tubes, and whether there was a delay between baiting and presentation of the tubes to subjects. All three species appropriately looked into the tubes before choosing one more often when they had not seen the baiting than when they had seen the baiting, and in general they used efficient search strategies more often than insufficient or excessive ones (Call & Carpenter 2001).

Chimpanzees differed in their ability to discriminate appearance from reality in a test in which magnifying lenses manipulated the relative size of two grapes so that the larger one appeared smaller. However, some chimps figured out the task and this was shown not to be merely by applying a reverse-contingency rule. Four-year-old human children typically fail this task, but pass it at 4.5 years (Krachun et al. 2009).

The cultural intelligence hypothesis argues that humans' advanced cognition is mainly a product of culture. This hypothesis was tested by giving a comprehensive battery of cognitive tests to large numbers of chimpanzees and orangutans, as well as to 2.5-year-old human children before literacy and schooling. Supporting the cultural intelligence hypothesis and contradicting the hypothesis that humans simply have more "general intelligence," the children and chimpanzees were found to have very similar cognitive skills for dealing with the physical world but that the children had more sophisticated cognitive skills than either of the ape species for dealing with the social world (Herrmann et al. 2007).

Comfort

Wild chimpanzees in Bossou, Guinea, were observed using a set of leaves as a cushion while sitting on wet ground (Hirata et al. 1998).

A study of tree nests built by wild chimpanzees found that chimpanzees may place additional leaves or twigs over hard branches, protruding from the nest surface after construction, to increase comfort of the central nest area. Authors conclude that the functions of chimpanzee nest building are likely to be several, but their findings suggest that comfort is a factor in nest building behavior (Stewart et al. 2007).

Communication

The screams uttered by chimpanzees on winning a fight are very different from those losing a fight. In interactions involving severe aggression, victim screams are sometimes much longer and more intense when there is an audience present compared to no audience. However, this audience effect was only seen when one of the audience members ranked higher than the aggressor chimp (Slocombe & Zuberbuhler 2007). This dynamic reflects both keen awareness of who is watching whom, and the capacity to manipulate others through emotive cues (screams).

A research team was able to acoustically five different types of call uttered by bonobos during interactions with food. These calls were not given singly, but usually as part of long and complex call sequences. After establishing food preference hierarchies for 10 captive bonobos, it was found that the composition of call sequences produced by these individuals was related to the desirability of the food encountered by the caller (Clay & Zuberbuhler 2009). The research team only considered these calls in terms of a communication function to other group members, but an additional, proximate interpretation might be an expression of the emotional state of the calling bonobo.

Chimpanzees uttered acoustically distinct forms of a call called the "rough grunt" when they encountered different foods. Playback experiments revealed that chimpanzees could use the information conveyed by these calls to guide their search for different food, indicating that the different grunt types were meaningful to the listener. This study provides experimental evidence that our closest living relatives can produce and understand functionally referential calls as part of their natural communication (Slocombe & Zuberbuhler 2005).

Observational studies with bonobos suggest that they shake their head to communicate a desire that the signal recipient not do something. This finding suggests a possibly shared origin to a functional head-shake in humans and bonobos (Schneider et al. 2010).

Observational study of captive infant and juvenile chimpanzees found that a) the same gesture were often used in different contexts, and different gestures were often used in the same context, b) individuals adjusted their choice of gestures depending on the attentional state of the recipient, and c) gestural use varied highly across individuals, including d) a number of idiosyncratic gestures used by individuals at each observational time point. Although the chimpanzees showed no indication of having any sort of gestural "grammar," they clearly gestured intentionally, and combined different modes of communication (e.g., limb movements with facial expressions) to convey greater meaning (Tomasello et al. 1994).

Through a variety of sounds used in specific contexts chimpanzees communicate messages and express particular emotions that are understood by other chimps (Lindsey 1999).

Jane Goodall recounts a key moment in her acceptance by the wild chimpanzees of Gombe:

I had been following David [Greybeard, a dominant male in the troop] one day, struggling through dense undergrowth near a stream. I was thankful when he stopped to rest, and I sat near him. Close by I noticed the fallen fruit of an oil nut palm, a favourite food of chimpanzees. I picked it up and held it out to David on the palm of my hand. For

a moment I thought he would ignore my gesture. But then he took the nut, let it fall to the ground and, with the same movement, very gently closed his fingers around my hand. He glanced at my face, let go of my hand, then turned away. I understood his message: 'I don't want the nut, but it was nice of you to offer it.'" (from Page 1999, p 260-61)

Touch and gesture are important in chimpanzee communication. A mother chimp will gently touch her child when she is ready to move on, or tap the trunk of a tree when she wants the youngster to come down (Lindsey 1999). When chimps greet, they embrace, hold hands, kiss and pat each other's backs (Lindsey 1999).

In experiments where captive chimpanzees were either given a whole banana (successful communication), part of a banana (partially successful communication), or undesirable processed primate chow (failed communication), the chimps exhibited persistence in and elaboration of their communication in every condition except when the whole banana was delivered. These findings indicate that communication is about a specific item, and that chimps show both intentionality and nonverbal reference in their communications with others (Leavens et al. 2005).

Chimpanzees use individual gestures and gesture sequences to communicate with others. They also show sensitivity to the attentional state of the recipient, using visually-based gestures mostly when others are already paying attention, and tactile gestures regardless of the attentive state of the recipient (Liebal et al. 2004). Chimpanzees have also been shown to use visual cues to indicate the location of an unreachable food item to another who has access to the food. Caged chimps used directed gestural cues (begging, pointing with whole hand or with index finger) to signal to a human experimenter the location of a banana, as well as gaze alternation (looking back and forth from human to banana). The apes deployed the same types of referential communication when the banana was visible or hidden from view. These findings illustrate the capacity for chimps to try to influence the state of knowledge of an observer (in this case, a member of another species) (Leavens et al. 2004).

When juvenile chimpanzees play, they increase their play signaling (visual cues that convey a playful spirit or mood) in the presence of the mothers of younger partners, particularly as the intensity of play increases. The authors of this study interpret these findings to suggest that play signaling is increased to prevent termination of play bouts by mothers of younger partners (Flack et al. 2004). Behavior of this sort suggests acute awareness of subtle aspects of one's social environment, and of the different interests of others.

Another study monitored chimpanzee play-panting during play bouts, and found that a) chimpanzees play-panted more often when on the receiving end of boisterous actions, and b) chimpanzees tended to continue to play boisterously when their partner uttered play-pants. Thus, it appears that play-panting provides positive feedback to the play partner to encourage the continuation of boisterous play, which may otherwise risk excessive arousal and blur the line between boisterous play and aggression (Matsusaka 2004).

An analysis of 355 scream vocalizations recorded from 12 chimpanzees in two captive groups showed that screams vary both by the context in which they are made (e.g., chasing or being

chased), and by sex of the screamer. Thus, screams appear to reflect the motivations of the caller, and to convey his or her emotional state (Siebert & Parr 2003).

An 11-year-old female chimpanzee, trained to communicate using a display board with 256 lexigram signals, watched as an object was hidden in the woods outside her outdoor enclosure. Following a delay of up to 16 hours, a naïve human was introduced, the chimp did whatever it took to get the human's attention, then consistently and effectively used the lexigram display, combined with pointing and vocalizations, to direct the human to the hidden object. The chimp indicated over 20 food items as well as non-food objects (Menzel 1999).

Concern for Others

Frans de Waal was at a zoo once where keepers were trying to retrieve a monkey who had escaped into a tree. A group of chimps were watching from their enclosure. One of the males who was watching gave a little yelp, and held the hand of another chimp as the darted monkey fell out of the tree and into the net (NPR [Jon Hamilton] Morning Edition, Research Shows Mice May have Feelings Too, July 5 2006).

In August 1996, a three-year-old boy climbed the wall adjoining the gorilla exhibit at Illinois's Brookfield Zoo, and fell 20 feet onto the concrete below. A nearby mother gorilla named Binti Jua—with her own 17-month-old infant clinging to her back—rushed to the boy's side. She lifted his limp body and him to a log in a stream, where she sat cradling him and patting his back. She then carried him to one of the exhibit doorways, where she gently put him down. A keeper soon arrived to retrieve the boy, who later recovered (de Waal 1997).

Reconciliation and reassurance are routine behaviors by social primates, and probably most highly developed in chimps and bonobos. For example, one who has wounded another in a fight will often approach the victim afterwards to inspect and tend to the wound. As de Waal (1996) describes, this is very deliberate behaviour—if the wound was inflicted on the left foot, the former attacker very deliberately lifts the left foot and inspects it.

Conflict management

In a captive colony of 19 chimpanzees, the frequency of grooming among adults increased significantly in the period just before regular scheduled feeding times (Palagi et al. 2004). Pre-feeding and feeding times are contexts in which conflict of interest is known to reach peak levels, and grooming is known to benefit participants by reducing tension and fostering good feelings among members of the group. Thus, the authors of this study conclude that pre-feeding grooming is a conflict management strategy to increase levels of tolerance around food. Another study documented the same phenomenon, and also noted that the effect was more marked when food was clumped (ergo more likely to cause disputes) than when it was dispersed (Koyama & Dunbar 1996).

Conflict with humans

A total of 11 known chimpanzee attacks on local humans has occurred at Bossou, Republic of Guinea, from 1995 to 2009. Most of the targets were children. The attacks varied in their severity, but none were fatal. Attacks took place on a road and narrow paths that bordered the forest or in cultivated fields and orchards where opportunities for human-chimpanzee contact are high. Attacks also occurred between the months of March and October, coinciding with wild fruit scarcity, increased levels of crop-raiding, and periods of human cultivation with likely increased human usage of paths (Hockings et al. 2010).

Consolation

Apes will hover around the victim of an aggressor's attack, offering consolation with hugs and kisses (de Waal 2005a).

Consoled chimpanzees engage in less stress behaviors such as scratching or self-grooming (Fraser et al. 2008).

A study of a large captive chimpanzee database revealed that consolation behavior happened more often in the absence of reconciliation between former opponents, suggesting that consolers are sensitive to the contact need of victims of aggression, which may be greater if the aggressor ignores them. Also, consolation tends to be reciprocated, suggesting that it is an integrated part of close mutual relationships in chimpanzees (Romero et al. 2010).

In a study of 22 adult chimpanzees kept at Chester Zoo, consolation was more likely to occur in the absence of reconciliation than after reconciliation, and reconciliation was more likely to occur in the absence of consolation than after consolation. These findings supporting the idea that consolation acts as a substitute for reconciliation when the latter fails to occur (Fraser & Aureli 2008).

Cooperation

In a series of experiments involving eight semi-free-ranging chimpanzees, when presented with a food-retrieval problem, an ape would recruit a partner to collaborate with only when the problem required assistance. In such cases, they recruited the more effective of two available collaborators based on their experience with them the previous day. These experiments show that recognizing when collaboration is necessary and determining who is the best collaborative partner are skills shared by both chimpanzees and humans (Melis et al. 2006a).

In feeding situations among conspecifics, bonobos were found to be more tolerant of others in their midst than were chimpanzees. Only bonobos exhibited socio-sexual behavior, and they played more than co-feeding chimps. When presented with a task of retrieving food that was difficult to monopolize, bonobos and chimpanzees were equally cooperative, but when one individual could monopolize a food-source, bonobos were more successful than chimpanzees at cooperating to retrieve it. These results suggest that temperament may in part explain the

variance in cooperative ability across species, including great apes and humans (Hare et al. 2007).

Cruelty

Like boys who throw rocks at ducks in a pond, chimps can be cruel, particularly when confronted with the boredom of prolonged confinement. In one instance, captive chimps would lure chickens by proffering bread crumbs through a chain-linked fence, then hit the birds with a stick or poke them with a piece of wire when they got close enough. Sometimes they worked in pairs, one being the enticer, the other the hit-man (de Waal 2005a).

“Wife-beating” has been witnessed repeatedly in a population of chimpanzees living in Kibale Forest, Uganda. A male, Imoso, was seen repeatedly thumping an estrus female with a stick. He was eventually repelled by the female’s little daughter, who pummelled Imoso’s back with her fists until he gave up. The behaviour has since been observed in several other males in this population. Researchers view the use of wooden weapons as a sign of restraint, for rocks would maim or injure the victims, who usually end up being mated by the offending males (de Waal 2005a).

Culture

Wild chimpanzees are known to have a different repertoire of tool use unique to each community. For example, "ant-dipping" is a tool use behavior known in several chimpanzee communities across Africa targeted at driver ants (*Dorylus* spp.) on the ground, whereas "ant-fishing," which is aimed at carpenter ants (*Camponotus* spp.) in trees, has primarily been observed among the chimpanzees of Mahale in Tanzania (Yamamoto et al. 2008).

A study of ant-dipping behavior among thirteen wild mother-offspring pairs (1-10 years old) demonstrates the important role of mothers and learning opportunity in the acquisition of a hazardous tool-use behavior, and suggests that chimpanzee material culture is a product of a complex interaction between social processes and ecological factors (Humble et al. 2009).

Cultural traits are those which are not genetically passed on, but learned by observation and apprenticeship. A recent review of 151 combined years of chimpanzee field studies revealed cultural variations in thirty-nine different behaviour patterns or traditions, including tool use, grooming, greetings, and courtship behaviours (Whiten et al. 1999).

For example, drumming by male chimps has varied meanings in different populations. In one troop, drumming codes instructions for how long the group should rest and where to move to next (Whiten et al. 1999). A comparison of drumming on tree buttresses between populations in the Ivory Coast and in Uganda found differences in number of beats and duration, and in integration with pant-hoot calls (Clark Arcadi et al. 2004).

Chimpanzees studied by Jane Goodall in Gombe, East Africa, and chimps from the Tai forest in West Africa studied by Christoph Boesch, use different methods to fish termites from logs. The Gombe chimps use a long wand, and a brisk hand sweep to gobble the insects down. The Tai

chimps use shorter sticks, plucking each insect from the stem with their lips. Mothers from each population teach their children, passing their “tool culture” through the generations (Page 1999).

Chimpanzees show cultural conformity. One female chimp from each of two captive groups was taught a technique for removing food from a complicated apparatus. One chimp was taught to poke the barrier with a stick, and the other to lift the barrier. Each chimp’s group was then allowed to watch the new experts use their skills. When these groups were given the opportunity to try the food extraction by themselves, they used the technique of their own group’s expert, not the other; i.e., the poker’s group preferred to poke and the lifter’s group tended to lift. Furthermore, even though the poking method was more efficient, and some of the lifting chimps learned to use it, they tended to revert to the lifting method, demonstrating conformity to their own group (Whiten et al. 2005). When retested 2 months later, they still overwhelmingly used their leader’s method.

The transmission of cultural behaviour through multiple generations has also been demonstrated in captive studies, by introducing a foraging technique to a chimpanzee then allowing single individual members of the same group successively to observe and learn the technique. One chimp from each of two separate family groups learned to remove fruit from a special testing box, either by lifting or sliding the door. Once the first chimp was proficient in one of these techniques, another chimp from the same group was allowed to observe the process before interacting with the test box. Once the second animal succeeded, a third would enter and observe the technique, and so on down the chain. The particular behavior was transferred accurately along a chain of up to six chimps, representing six simulated generations, and approximately 90 years culture in the wild. The fidelity of transmission within each chain was notable given that several individuals in a no-model control group were able to discover either method by individual exploration. This study shows that chimpanzees have the capacity to sustain local traditions over multiple simulated generations (Horner et al. 2006).

Handclasp-grooming, in which a pair of chimpanzees face each other and each raises one arm and clasps the other’s hand or wrist, is a unique social custom that occurs regularly in some wild chimpanzee populations but is absent in others (Bonnie & de Waal 2006).

A study of nut-cracking techniques in a wild population of chimpanzees in Guinea found that population-specific differences in tool-use and nut-selection cannot be explained solely by ecological differences. Experiments with unfamiliar species of nuts demonstrate key aspects of cultural innovation and transmission. Chimps were also highly specific in their selection of fellow chimps as models for observation, preferentially attending members of their own group who are the same age or older. These findings demonstrate a mechanism for the emergence of culture in wild chimpanzees (Biro et al. 2003).

In a series of trials in which subjects were required to track the displacement of objects placed visibly or invisibly under one or two of three cups, great apes (chimpanzees, bonobos, gorillas, and orangutans) and 30-month-old children performed at comparable levels, except in the transposition task (wherein cups are switched while the platform remains stationary), in which apes performed better than children (Barth & Call 2006).

Orangutan researchers have documented 19 clearly defined cultural traditions, with five more tentatively identified (van Schaik et al. 2003).

A captive study of chimpanzees living in sanctuary in Austria documented conformity and conservatism in regard to the adoption and use of specific techniques to acquire food from a wooden puzzle board. Most chimps used sticks to acquire the food, but five chimps independently invented a novel technique that involved rattling the board. While almost all group members eventually tried the rattling technique, which was more efficient, they nevertheless continued to favor the stick method. Similarly, after the board was manipulated to render useless the rattle technique, rattlers still favored rattling despite their knowledge of the stick technique. These patterns of behavior are hallmarks of cultural conformity and stability (Hrubesch et al. 2009).

Deactivation of Snares

Snare injuries in the wild population of chimpanzees living in Bossou, Guinea, are much rarer than elsewhere, despite active snaring efforts by regional poachers. Here, researchers report six observations of chimpanzees attempting to break and deactivate snares. On two occasions they were successful in doing so. The behavior was seen in five males ranging from juveniles to adults. This study suggests a link between de-snaring efforts and incidence of snare injury (Ohashi & Matsuzawa 2011).

Deception

Deception is widespread in animals. Once thought to be merely instinct, recent studies show it to be flexible and calculating. Because deceitful acts rapidly lose effectiveness if employed too often, striking instances of deception tend to be rare, and mostly anecdotal. Nevertheless, there are many examples. When two British primatologists invited experts on primate behaviour to send them instances of spontaneous deception, they compiled 253 accounts, the most complex of which involved chimpanzees (de Waal 1996).

Studies suggest that chimpanzees will manipulate the visual and auditory perception of others by concealing information from them. In trials where chimpanzees could approach a human competitor unseen and reach through either an opaque or a clear tunnel to grab food that was observable and reachable to a human competitor, chimpanzees (n=7) chose the opaque tunnel. In separate trials where the human was facing away from the food but one of two clear tunnels made a loud noise when opened, chimpanzees chose the silent tunnel (Melis et al. 2006b).

For example, in three novel tests in which they were competing with a human for access to a contested food item, eight individually tested chimpanzees chose to approach the food via a route (sometimes circuitous) hidden from the human's view. This result supports other studies demonstrating chimpanzees' skill at manipulating, to their own advantage, whether others can or cannot see them (Hare et al. 2006).

Keeping up appearances is something we share with other apes. When Yeroen was injured by his alpha comrade Nikkie, he adopted an exaggerated limp whenever he was in sight of his attacker,

apparently to encourage sympathy and to remind Nikkie that it is never a good idea to hurt a buddy whom you depend on (de Waal 2005a).

A juvenile chimp saw an apple roll away from his mother's food pile. Seemingly aware that he would get into trouble if he picked it up, he approached his younger sister, with an exaggerated play-face. They began to wrestle, during which activity the male moved closer and closer to the apple. Once they got close enough, he grabbed it with a sudden movement, and all interest in the play vanished (Page 1999, p 238).

When out on patrol, chimpanzees can maintain almost total silence, despite the presence of dry leaves and rustling bushes. On one occasion Jane Goodall noted that they maintained total vocal silence for three hours: acoustic deception of a high and calculated order (from Page 1999).

Emotion

In a captive study in which pairs of male chimpanzees or pairs of male bonobos shared food, males of both species showed an anticipatory decrease (relative to baseline) in steroid hormones in a situation in which the two individuals shared food, and an anticipatory increase in a situation in which the dominant individual obtained more food. The species differed, however, in terms of which hormone was affected; in bonobo males the shifts occurred in cortisol, whereas in chimpanzee males the shifts occurred in testosterone. Thus, in anticipation of an identical competition, bonobo and chimpanzee males showed differential endocrine shifts, perhaps due to differences in perception of the situation, that is, viewing the event either as a stressor or a dominance contest, respectively (Wobber et al. 2010). The physiological measures documented here likely also reflect discrete and complex emotional changes experienced in the different situations.

A study of 59 orphaned chimpanzees of all ages living at an African sanctuary (Chimfunshi, Zambia) showed that individuals produced laugh-elicited laughter in response to another's laughter that is distinct in form and occurrence from their spontaneous laughter. The study also showed that chimps can replicate the expressions of others and produce expressions that differ in their underlying emotions and social implications. Also, laughter-elicited laugh responses were closely linked to play maintenance, indicating an important social function with cooperative and communicative benefits (Davila-Ross et al. 2011).

When her volunteer human teacher became pregnant, captive-reared chimpanzee Washoe became more attentive than usual and regularly asked questions (using sign language) about the baby. Washoe had had two pregnancies of her own, both of which had resulted in the infants' deaths. When the teacher returned after an extended absence, Washoe acknowledged her return but was aloof. The teacher explained that she had had a miscarriage and signed to Washoe: "My baby died." Washoe looked at the teacher and signed "Cry," then signed "Please person hug" as the teacher was leaving (Fouts & Mills 1993).

Chimpanzees have been shown to yawn in response to seeing other chimps yawn in a manner highly reminiscent of the contagious yawning of humans. Contagious yawning is thought to be

based on the capacity for empathy, and in chimpanzees provides further evidence that these apes may possess advanced self-awareness and empathic abilities (Anderson et al. 2004).

A mother chimpanzee has been observed repeatedly sucking water into her mouth, then delivering it to her whimpering two-year-old (Page 1999, p 197).

Kidogo, an elderly male bonobo at the Milwaukee Zoo, has heart disease and labours mightily to get around by himself. He is routinely aided by others (Page 1999, p 197). For example, when Kidogo was first introduced to the colony in Milwaukee, he was confused by the keepers' shifting commands inside the unfamiliar building. Resident bonobos stepped in, taking Kidogo by the hand and leading him to where the keepers wanted him, thus showing they understood both the keepers' commands and Kidogo's predicament (de Waal 2005a).

When a shipment of materials was loaded into an unused trolley and pulled past the chimpanzees now residing at a sanctuary for chimps formerly used in laboratory experiments, two of the chimps—Tom and Pablo—simultaneously let out a piercing shriek. At that point, all fifteen chimps lunged forward and clung to the bars of their enclosure, rocking back and forth while screaming and staring at the trolley. It later came to light that this trolley had been used to transport unconscious chimpanzees from their cages to the surgery room in the same laboratory from which they had come two years earlier (Hall & Waters 2000).

Chimpanzees showed significant decreases in skin temperature (a physiological response associated with negative emotional arousal in humans) when viewing three categories of emotionally negative video scenes: other chimps receiving injections, images of darts and needles alone, and another chimp in conflict with veterinarians. When the subjects were required to use facial expressions to categorize emotional video scenes—such as favorite food and objects, and veterinarian procedures—according to their positive and negative valence, they spontaneously matched the emotional videos to chimpanzee expressions according to their shared emotional meaning. This study indicates that chimpanzees process facial expressions emotionally, as do humans (Parr 2001).

Chimpanzees' heart rates accelerated when exposed to recordings of other chimps engaged in laughter, and cardiac activity decelerated in response to other chimpanzees shown screaming (Berntson et al. 1989).

When they watched videotapes of emotional stimuli (severe aggression), six chimpanzees' right-brain temperatures (monitored non-invasively via the tympanic membranes) were significantly higher than baseline temperature. This effect was relatively stable, long lasting, and consistent across the six chimpanzee subjects. Less emotive stimuli (scenes of play, scenery) did not evince any temperature differences. These findings support leading theories regarding the lateralization of emotions in the brain, and provide physiological support for emotional arousal in chimpanzees (Parr & Hopkins 2000).

Six universally recognized and biologically determined facial expressions of emotion have been documented in humans: anger, disgust, fear, happiness, sadness, and surprise. Studies of facial expressions in non-human primates have shown that they are evolutionarily homologous with

those of humans, both in their physiological structure and their social function (Preuschoft and van Hooff 1995).

Objective and subjective measures indicate that both human and chimpanzee facial expressions are asymmetric, and that the left side of the face (right hemisphere) is more involved in production of emotional responses. Thus, chimpanzees, like humans, show a right hemisphere specialization for facial expression of emotions, supporting homologous emotional origins in these species (Fernandez-Carriba et al. 2002).

Among humans and the other great apes, elaborate facial communication is accompanied by specializations in brain areas controlling facial movement. The evolution of empathy, or emotional awareness, might be attributed to specialized cells in the neocortex. Specifically, spindle cells have been associated with self-conscious emotions, and mirror neurons have been shown to activate in response to communicative facial gestures (Parr et al. 2005).

Chimpanzees, like children, actively distract themselves to cope with waiting for a desired but delayed reward. Self-control may thus be a capacity we share with our nonhuman primate relatives (Heilbronner & Platt 2007).

Chimpanzees display a complex, flexible facial expression repertoire with many physical and functional similarities to humans (Parr & Waller 2006).

Emotional attachment

In several primate species, mothers have been observed carrying the bodies of their infants for days or even weeks following the infant's death. In 1992, Matsuzawa observed a mother chimpanzee, Jira, carrying her 2.5 year old son Jokro for 27 days following his death from a respiratory illness. Jira exhibited extensive care of the body, grooming it regularly, sharing her day- and night-nests with it, and showing distress whenever they became separated. This behavior is a "poignant testament to the close mother-infant bond which extends across different primate taxa" (Biro et al. 2010).

Emotional awareness

In a study involving 17 chimpanzees and five bonobos (as well as five gorillas and five orangutans), subjects preferred to investigate the hidden contents of a box after a human had expressed happiness when opening it, than a box that had elicited an expression of disgust. In a second experiment involving two containers, only one of which contained food, apes opted to open the container with food after seeing a human subject express disappointment on opening the other container. These findings suggest that great apes understand both the directedness and the valence of some human emotional expressions, and that they can use this information to infer desires (Buttelmann et al. 2009).

Emotional development

Forty-six nursery-reared chimpanzee infants received either Standard Care (ST, $n=29$) or Responsive Care (RC, $n=17$), the latter involving an additional twenty hours per week of interaction time with human care-givers trained to provide species appropriate socio-emotional and communicative development. At age 12 months, subjects were tested using the Strange Situation Procedure (SSP), and all exhibited clear patterns of distress, proximity-seeking and patterns of exploration characteristic of human infants. However, whereas the ST group showed patterns similar to human infants from Greek or Romanian orphanages, RC chimps showed less disorganized attachment to their caregivers, more advanced cognitive development and less object attachment. This study shows that a more socialized and loving rearing environment enhances cognitive and emotional development in institutionalized young chimpanzees (van Ijzendoorn et al. 2008).

Chimpanzee and human infants appear to experience similar emotions in similar contexts. For example, they smile to the face of familiar caregivers, and laugh when tickled. By age one year, socialization experiences have exerted themselves onto emotional experience and expression (Bard 2008).

Empathy

“It is not uncommon that, after one chimpanzee has attacked another, a bystander will go over to embrace the victim. We have documented hundreds of cases.” (de Waal, 2006, p 60)

The early twentieth-century Russian psychologist Nadie Ladygina-Kohts raised a young male chimpanzee named Yoni. As is a young chimp’s way, Yoni was often unruly, delighting in defying Nadie’s authority. One of his favorite spots was the roof of her house, and Nadie’s firm commands and entreaties to get him to come down were fruitless. Eventually, the psychologist discovered that the only way to get Yoni to come down was to appeal to the chimp’s concern for her. By closing her eyes and pretending to weep, Yoni would leave his perch and hasten to Nadie’s side to comfort her while looking around indignantly for the source of her upset. Appealing to Yoni’s empathy turned out to be the only way to circumvent his defiant nature (de Waal 2005a).

Twenty-three chimpanzees from two separate groups watched videos of familiar and unfamiliar individuals yawning or at rest (control). Chimpanzees yawned more when watching yawns of familiar chimps than when watching either the familiar control or the unfamiliar yawns. These results suggest that contagious yawning is a measure of empathy (Campbell & De Waal 2011).

When presented with 3-D computer-animated chimpanzees yawning, 24 chimpanzees yawned significantly more in response to the animated yawns than to non-yawn mouth opening control animations. This finding implies that, like humans, chimpanzees identify emotionally to representations of their kind that are obviously artificial (Campbell et al. 2009).

Fairness/Justice

In an ultimatum game, chimpanzees were rational maximizers and not sensitive to fairness, whereas people will take into account the interests of others and are sensitive to norms of cooperation and fairness. Authors conclude that humans have other-regarding preferences and show aversion to inequitable outcomes, which play key roles in human social organization, and that this distinguishes us from our closest living relatives (Jensen et al. 2007a).

Primates of many species appear to have a sense of right and wrong, fair and unfair. One expert has suggested that “reciprocity among chimps is governed by the same sense of moral rightness and justice as it is among humans” (de Waal 1982, p 107). Chimpanzees, and many other primate species, resent others who do not reciprocate a favor. There is evidence for similar behavior in other species, too

Chimpanzees are more likely to refuse an exchange (token for food) if they can observe another chimpanzee receiving a more favorable reward (grape) than they are being offered (slice of cucumber). Furthermore, this inequity awareness (IA) is only robust in subjects with limited familiarity with the chimp receiving the grapes. If the other chimp is part of the subject’s tightly knit social structure—which in chimps is characterized by intense integration and social reciprocity—inequity is for the most part tolerated (Brosnan et al. 2005). This finding parallels human responses in close relationships (Clark & Grote 2003).

Genocide

In 1970, seven males and three females with young split off from the main (Kasakela) community of chimps at Gombe, Tanzania. For a time, the two groups maintained a civil, if somewhat tense neighbourly relationship, with males displaying and calling loudly whenever the neighbors met. Then, in early 1974, violence broke when five chimpanzees from the Kasekela community caught and murdered a single male of the Kahama group. Thus began a seemingly directed campaign of extermination by the Kasakela group, and by the end of 1977, only one Kahama male survived (Lindsey 1999).

Gratitude

Roosje, a chimpanzee infant born at the Arnhem Zoo to a mother whose deafness hampered her ability to properly care for him (e.g., she couldn’t hear his cries for help or attention), was reluctantly removed by Frans de Waal to safety. Kuif, another chimp in the same colony had lost more than one of her own infants and had suffered deep depression each time, marked by rocking, self-clutching, refusing food, and heart-wrenching screams. De Waal decided to train Kuif to bottle-feed Roosje through the bars of the chimps’ compound. Kuif took well to this, and was eventually allowed to have Roosje to rear by herself. Taking someone else’s infant isn’t well regarded among chimps, and Kuif glanced between Roosje and de Waal, kissing each, as if asking permission. She was the most caring and protective mother that could have been hoped for. Up to that time, Kuif had had a rather neutral relationship with de Waal, but from that day onward she has showered him with the utmost affection whenever he shows his face. Three decades on, Kuif’s gratitude is undiminished (de Waal 2005a).

Like us, chimps are not particularly fond of being out in the rain, and Jane Goodall recounts the expression of joy witnessed by the primatologist Wolfgang Köhler when two chimps were locked out of their artificial den. Köhler went out in the pouring rain to let them in, and describes how, before entering, the grateful chimps “turned to me and put their arms around me, one round my body, the other round my knees, in a frenzy of joy.” (Goodall 1986 cit. Köhler 1925, p. 242)

Grief

When the elderly female chimp Flo died, her 8-year-old son Flint sank into a profound depression, and died three weeks later of apparent grief (Lindsey 1999).

Handedness

Nut-cracking behavior requires long-term learning of the fine manipulation of stones and nuts by both hands. Each hand has a separate role, and the hands work together in nut cracking. A study of wild chimpanzees in their natural habitat at Bossou, Republic of Guinea, documented a small difference in left/right hand use for the purposes of food picking and carrying. However, in the more complex task of nut-cracking, the chimpanzees showed strong individual preference for either the right or left hand. The differential and complementary use of both hands may be a prime factor promoting exclusive hand preference in chimpanzees comparable to that of humans (Sugiyama et al. 1993).

Of four tool-use skills (ant-dipping, algae-scooping, pestle-pounding and nut-cracking) practiced by wild chimpanzees of Bossou, Guinea, nut-cracking is the most cognitively complex and the only one requiring complementary coordination of both hands. Nut-cracking yielded the greatest strength in hand use with all adults expressing exclusive use of one hand over the other. The least lateralized behavior was pestle-pounding, which required bimanual coordination but also imposed fatigue constraints. Bossou chimpanzees demonstrated a tendency for a population-level right-hand use (Humble & Matsuzawa 2009).

Population-level handedness in wild chimpanzees’ use of tools for termite-fishing has recently been shown, and a broader survey of the literature on handedness for nut-cracking and wedge-dipping found task-specific differences in handedness. Studies of tool-use in chimpanzees indicate that hand preferences are heritable. These findings suggest that the antecedents of lateralization of function associated with human hand use were present at least 5 million years ago, before the Pan-Homo split (Lonsdorf & Hopkins 2005).

Observations of 70 captive chimpanzees revealed a predominance of right-handedness for species-typical gestures when directed to both humans and conspecifics. Furthermore, hand preferences during intra-species communication were significantly and positively correlated with gestures directed toward humans. By contrast, hand preferences for gestures did not significantly correlate with hand use for a non-communicative self-directed action. These findings suggest that the typically left-brain lateralization for language is not a unique trait to humans (Meguerditchian et al. 2010).

Human Culture

Human subjects (n=165) watched a series of advertisements, into which was embedded one of three categories of chimpanzee videos: 1) a chimpanzee conservation commercial, 2) commercials containing "entertainment" chimpanzees or 3) control footage of the natural behavior of wild chimpanzees. A post-viewing questionnaire revealed that subjects who watched the conservation commercial showed a greater understanding that chimpanzees were endangered and unsuitable as pets than did the control group, and that viewers of the "entertainment" chimpanzee commercial showed less understanding of these facts. These results firmly support the hypothesis that use of entertainment chimpanzees in the popular media negatively distorts the public's perception and hinders chimpanzee conservation efforts (Schroepfer et al. 2011).

Humor

All of the hominoids—humans, chimps, bonobos, gorillas, and orangutans—share the tickle spot under the arms (Goodall 1986). In her early observations of the chimps of Gombe, Jane Goodall described playful interactions between the adult males Goliath and David Graybeard, which began with hand tickling, then body tickling, tumbling and “laughing,” then chasing, followed by a 21 minute grooming session (Goodall 1986)

Michael, one of the gorillas at The Gorilla Foundation, plays a tugging and chewing game with his caregiver through the bars of his enclosure. Michael occasionally gets what we might refer to as “the giggles,” and may laugh continuously for up to 10 minutes during this game. Laughter’s contagious quality extends to gorillas; once he and DeeAnn (his human teacher) get laughing they “feed off each other’s joyous mood for quite some time” (Balcombe 2006).

Koko also makes plays on words. She has signed ‘Koko + nut = coconut,’ and put a straw to her nose, calling herself a ‘thirsty elephant’. When Koko was a youngster and she was asked by her teachers to do something funny, she responded by feeding an M&M chocolate to a bird puppet in its eye rather than its mouth, and she put a toy key on her head and called it a ‘hat’ (Balcombe 2006). These are instances of ‘incongruity humor,’ a form known from child development studies. Bongo, a gorilla at Columbus Zoo, ‘would run along with keeper running outside, then stop suddenly and then laugh as the keeper whizzed past outside the bars’.

Imitation

Five captive infant chimpanzees aged 7-15 days were tested on two imitation paradigms and found to match modeled facial actions, sounds, and series of actions. In a communicative paradigm, all subjects imitated mouth-opening, most imitated tongue-protrusion, and most the tongue-click, including the sound. These findings suggest that neonatal chimpanzees have an innate capacity for imitation comparable to that of humans (Bard 2007).

Great apes demonstration imitation recognition—that is, they recognise when they are being imitated by showing increased visual attention to imitators (implicit recognition) and by engaging in so-called testing behaviours (explicit recognition). Imitation recognition is thought

to foster understanding of social causality, intentionality in others and the formation of a concept of self as different from other (Haun & Call 2008).

Individual Recognition

Earlier studies concluded that chimpanzees had poor face recognition. But there was a problem: researchers presented chimps with human faces, presuming that they are easier to distinguish. It wasn't until chimp faces were used that chimps showed face recognition on par with our recognition abilities. Clearly, chimp faces are just as distinct, and chimps have a natural talent for reading chimp faces, as we do human faces. Chimps also recognize the marks of kinship, being able to link faces of unfamiliar chimps with relatives (de Waal 2005a).

A study of five captive chimpanzees showed that they were able to match digitized black-and-white portraits of unfamiliar females with their male offspring significantly above chance. These findings indicate that chimpanzees are able to perceive similarities in the faces of related chimpanzees that they have never before seen (Parr & de Waal 1999).

Kinship

Chimpanzees can catch and be affected with all human contagious diseases except cholera (Lindsey 1999). Humans and chimpanzees can also exchange blood of the same type (Lindsey 1999).

Language

A study with a 12-year-old female chimpanzee named Ai demonstrates that a chimpanzee can be trained to use the personal pronouns ME, YOU, HIM, and HER in a way similar to that used by humans, even when the referent individuals are shifted with respect to the "speaker" (Itakura & Matsuzawa 1993).

Positron emission tomography (PET) was used on four chimpanzee subjects, two of whom produced attention-getting vocalizations directed towards a human experimenter in addition to manual communicative gestures. These two subjects showed greater mean metabolic activity in the Broca's area homologue of the human brain as compared to a baseline scan. These data contradict an exclusive "gestural origins" theory of human language, for they suggest that it is vocal signaling that selectively activates the Broca's area homologue in chimpanzees. In other words, the activity observed in the Broca's area homologue reflects the production of vocal signals by the chimpanzees, suggesting that this critical human language region was involved in vocal signaling in the common ancestor of both modern humans and chimpanzees (Tagliatela et al. 2011).

A chimpanzee who recognizes 128 spoken words was presented with recordings of 48 individual words whose sound quality had been corrupted to a) simulate the input of a hearing aid, and b) to limit sounds to just three moving tones. Although receiving rewards randomly and only intermittently, the chimpanzee performed well above chance level, including when hearing synthetic versions for the first time. The authors conclude that *"the chimpanzee's ability to*

spontaneously recognize acoustically reduced synthetic words suggests that experience rather than specialization is critical for speech-perception capabilities that some have suggested are uniquely human" (Heimbauer et al. 2011).

Patterns of brain activation during the production of communicative signals by chimpanzees show strong parallels with those of human brains during speech. This suggests that the neurological substrates underlying language production in the human brain may have been present in the common ancestor of humans and chimpanzees (Tagliatela et al. 2008).

Chimpanzees are famous for having taught to use sign language, after attempts to teach them to speak failed repeatedly due not to a limited intellect but to their unsuited vocal anatomy. The ability of great apes including chimpanzees and gorillas to communicate by human sign language and computers, not only with humans but also among each other in private, effectively demolishes the old idea that language is a dividing line between humans and other animals. Ample evidence shows that primate communications, like human speech, encode both semantic and emotional information. Two captive bonobos, Kanzi and his little sister, Panbanisha, who studied and were taught American sign-language by Sue Savage-Rumbaugh, each understand thousands of words, use sentences, talk on the phone, and enjoy gossiping (Hamilton 2006). (Koko, the 35-year-old gorilla matriarch of The Gorilla Foundation, has mastered more than 1,000 signs in American Sign Language, understands several thousand English words, and scores between 70 and 95 on human IQ tests (Balcombe 2006).

Captive chimpanzees who are not taught sign language by their human caregivers nevertheless learn to sign from other chimps in their group who have been taught sign language. Loulis, for example, picked up fifty signs from his stepmother, Washoe, even though no humans taught Loulis directly (Page 1999).

Captive chimpanzee Sarah understands the difference between these two strings:

If/Sarah/take/apple/then/Mary/give/Sarah/chocolate
If/Sarah/take/banana/then/Mary/no/give/Sarah/chocolate

Much of the communications among animals are too subtle for us to notice. A prime example from a captive situation involved six young chimpanzees. One of them (we'll call him the "leader") was introduced alone into an outdoor enclosure and shown either a hidden source of food or a stuffed snake. When this chimp was reunited with his fellows outside the enclosure, they quickly resumed their normal activities: playing, wrestling, grooming, etc. There was no sign that the leader communicated his important knowledge of the situation to the other chimps. Yet, when all six were allowed into the enclosure, they headed straight for the food if this was a "food" experiment, and sometimes the five preceded the leader to the exact location of the food. In the "snake" experiment, the chimps all entered the enclosure with fur erected and approached the danger zone with extreme caution, sticks at the ready (Emil Menzel's experiments, described in Page 1999).

The creative, novel word combinations animals may use to describe new objects indicates the conceptual element in their use of language: "metal hot" for cigarette lighter, "listen drink" for Alka Seltzer, "candy drink" for watermelon (Gould & Gould 1994).

Language studies by the likes of David Premack and Sue Savage-Rumbaugh with Duane Rumbaugh using chimps and bonobos have found that language trained individuals who had learned to use symbols on a display board perform far better on logic tests than do non-trained individuals. For instance, language-trained animals learned to solve an analogy problem like “lock is to key as can is to can-opener, whereas those without language training failed to solve even the simplest of analogies, like “apple is to apple as banana is to _____”. It is not as if the latter group are less smart, for they solve real-world problems as well as their trained counterparts. Instead, success in these problems, it seems, depends both on native intelligence and on knowing how to take such tests. It appears that human language skills just aren’t powerful intellectual tools for chimps in the wild.

Four cross-fostered chimpanzees taught American sign-language responded appropriately to four types of probes issued by a human interlocutor: general requests for more information, on-topic questions, off-topic questions, or negative statements. Chimps reiterated, adjusted, and shifted the signs in their signed “utterances” in conversationally appropriate rejoinders, and their reactions resembled patterns of conversation found in similar studies of human children (Jensvold & Gardner 2000).

In trials of declarative signals in an object-choice task, chimpanzees and bonobos reared in a sociolinguistically complex environment performed significantly better than did relatively impoverished conspecifics. These results demonstrate that environmental factors, particularly access to a sociolinguistically rich environment, directly influence great apes' ability to comprehend declarative signals and suggest that, contrary to the recent claims of human language supremacists, apes have the biological capacity to use purely informative communication (Lyn et al. 2010).

Analysis of two chimpanzees' conversations with their teacher during a tool-use training task demonstrated that chimps use lexigrams (a human-devised visual symbol system), selectively to represent perceived variability. Specifically, they generally used the symbols to differentiate alternative possibilities or to represent change or novelty in a situation. In contrast, they tended to leave unsaid what was unchanging, repetitive, or the unique possibility in a situation. In addition to symbol choice, utterance length was varied according to the complexity of the situation; multi-lexigram utterances were associated with multi-dimensional situations. Thus, an absence of formal grammatical structure in chimp language does not imply that utterances beyond one word in length are either rote strings or imitations. The chimps' tendency to mention the variable while leaving the constant or redundant unsaid is, moreover, strong support for the position that their use of a humanly devised symbol system is more than a series of conditioned responses (Greenfield & Savage-Rumbaugh 1984).

Laughter

Analyses of the vocalizations of humans, chimpanzees, orangutans, bonobos and gorillas while being tickled reveal strong evidence of common evolutionary origins (Davila Ross et al. 2009).

Learning

Infant chimpanzees did not ingest novel food immediately, but always sniff-licked it first. Furthermore, infants tended to pay attention to their mothers before mouthing or ingesting novel foods themselves, but never did so with familiar ones. These findings suggest that infant chimps refer to their mother before attempting to ingest unfamiliar foods (Ueno & Matsuzawa 2005).

While chimpanzee infants did not show habituation to objects as human infants did, they nevertheless showed significant novelty-preference on par with human infants when presented with an unfamiliar object (example: vehicle) that didn't match a familiar object category (example: mammal). Thus, infants of both species form categorical representations of a global-like level, suggesting parallels in the origins and species-specificity of categorization abilities, and the cognitive operations underlying categorization (Murai et al. 2005).

A review of 31 experimental studies of social learning in chimpanzees, gorillas and orangutans affirms that all three species do, in fact, ape. Moreover, these studies suggest that apes ape in flexible, adaptive ways using various social-learning strategies (Whiten et al. 2004).

Three young chimpanzees and bonobos (between 4 and 10 years) raised by humans (i.e., “enculturated chimps”) imitated simple and complex actions with a novel object shown them by their human caregivers at a proficiency rate much higher than did three chimpanzees and bonobos (aged 3 years 7 months, 4 years, and 21 years) raised mostly with other chimpanzees, and at rates equivalent to those of eight 18 and 30 month-old human children. On a separate test in which subjects were given a demonstration of an action with a novel object, then given the opportunity to imitate it after a delay of 48 hours, the enculturated chimpanzees significantly outperformed the other three groups (Tomasello et al. 1993). This study suggests that a human-like rearing environment is crucial to the development of human-like social-cognitive and imitative learning skills, and that performance deficits in wild chimps are attributable to learning environment and not to intelligence.

This study involved 13 male chimpanzees living at Chimpanzee Sanctuary Uto, five of whom were wild-born and 8 captive-born. Tests of problem-solving ability consistently revealed superior sophistication in the skills of wild-born male chimpanzees. Rearing conditions affected both the behavior acquisition and the execution of behaviors that had already been acquired (Morimura & Mori 2010).

Leisure

Like human children, chimpanzee infants romp and play for much of the time that they're not eating or sleeping. They are highly curious, and learn by observation and imitation, and need constant reassurance and attention. Affectionate physical contact is vital to healthy, normal development (Lindsey 1999).

Life cycle

The chimpanzee life cycle resembles that of humans. Infancy lasts about 5 years, followed by childhood, then adolescence. A chimpanzee's first tooth appears at about three months, and permanent teeth start coming in during the fifth year. Tottering steps begin at around four months and the infant walks unsteadily for the first two years. Not until age three will solid food become an important part of the diet. Sexual maturity occurs between nine and thirteen years old. Females usually have babies every five years. The onset of old age occurs at about forty years (Lindsey 1999). Wild chimps often live into their fifties, and captives longer still.

Memory

Chimpanzees were fed preferred but perishable food (frozen juice) and less preferred but non-perishable food (grape). After the food items were hidden, subjects could choose one of them either after 5 min or 1 h. The frozen juice was still available after 5 min but melted after 1 h and became unobtainable. Apes chose the frozen juice significantly more after 5 min and the grape after 1 h. In a second experiment, subjects faced two baiting events happening at different times, yet they formed an integrated memory for the location and time of the baiting event for particular food items. These results demonstrate episodic memory in great apes—that is, the ability to remember the what, when and where of a past event (Martin-Ordas et al. 2010).

Humans are commonly believed to be the only species to have memory that spans decades (many species are ineligible to this claim owing to their shorter lifespans); recent study of captive chimpanzee Lana found that she remembered the meanings of coded word symbols (lexigrams) that she had not seen for more than 20 years (Beran et al. 2000).

Chimps are xenophobic, and in captivity will normally attack unfamiliar individuals when attempts are made to introduce them to the group. But when an adult male named Jimoh was introduced to the resident troop at Yerkes Primate Center, two older females approached peacefully and groomed him. When other females began to threaten, they defended him fiercely. Years later, during a routine background check, it was discovered that young Jimoh had been housed 14 years earlier with the same two females who now defended him (de Waal 2005a).

Experiments with captive chimpanzees have demonstrated their ability to remember the value of different values of Arabic numerals (up to the number 7) over long periods (3.5 years), during which they had no exposure to numbers (Beran 2004a).

Mindedness

Trials were conducted in which pairs of chimpanzees were introduced to an arena in which food had been hidden, wherein only one of the chimps could see where it was being hidden but the other chimp could observe the witnessing chimp. Over the course of days, each chimp adopted tactics and counter-tactics to improve their chances of getting the food. For example, the witness misled the witness-of-witness in several cases by taking a route to an empty container. These interactions illustrate the high social intelligence of chimpanzees (Hirata & Matsuzawa 2001) and their possession of a theory of mind.

In a series of experiments, great apes (chimpanzees, bonobos, gorillas, and orangutans) were able to use a variety of experimenter-given cues associated with foraging actions to locate hidden food, and thereby were partially sensitive to the general purpose underlying these actions.

In a situation where a human experimenter examined two eggs—only one of which contained food—by smelling or shaking them, but only made a failed attempt to open (via biting) the egg containing food, the apes significantly preferred the egg that was first examined and then bitten, and had no preference when there were no cues. In a modified experiment using an unfamiliar clue (experimenter attempting to pull apart the egg), the subjects significantly preferred eggs presented with this novel cue, but did not prefer eggs presented with a novel but functionally irrelevant action. In a third experiment, apes did not interpret human actions as cues to food-location when they already knew that the eggs were empty (Buttelmann et al. 2008a).

Unlike 14-month-old human infants (and domestic dogs), most great apes (orangutans were an exception) failed to imitate rationally by copying an adult's unusual action more often when it was freely chosen than when it was forced by some constraint. (For example, dogs usually favor their mouth to perform a motor task, but a dog will perform an action [e.g., pull down a horizontal bar to release food] using her foreleg if a demonstrator dog had performed the same action when the demonstrator's mouth was empty [irrational condition], but will use her mouth to pull the chain if the demonstrator dog had had a ball in his mouth [rational condition]) (Buttelmann et al. 2008b).

Whereas 6-year-old children understood two mental states—knowledge-ignorance, and false belief—chimpanzees understood knowledge-ignorance but not false belief. After ruling out various alternative explanations of these and related findings, the authors conclude that in at least some situations chimpanzees know what others know (Kaminski et al. 2008).

Chimpanzees (n=17) but not bonobos, orangutans or gorillas showed a statistically significant preference for approaching a "nice" human (who gave grapes to a beggar in preliminary encounters that the subject could observe) over approaching a "nasty" human (who kept grapes to themselves) (Russell et al. 2008).

Numerosity

Four chimpanzees were highly accurate in selecting the larger of two concurrent accumulations of bananas in two opaque containers during a 20 minute period. Bananas were dropped into the containers one at a time, in view (but not reach) of the chimps, and there were no other clues as to the number of bananas in a given container. Accumulations of up to 6 vs 10 bananas were discriminated by the apes, in a performance that matched human infants and young children in similar tests (Beran & Beran 2004). Chimpanzees are also able to select the largest accumulations in three sets of opaque containers, including after a single item is removed from one of the containers (Beran 2004b).

Perception

Responses to sweet and bitter tastes were strongly similar in quality and duration across infant humans and infant primates (including chimpanzees). These results show that both the quality and intensity of affective reaction are similar and share common evolutionary origins in human and non-human primates (Steiner et al. 2001).

Like adult humans, chimpanzees (and monkeys) also exhibit the Regular-Random Numerosity Illusion (RRNI), or the tendency to overestimate the number of items in regularly arranged stimulus sets compared to randomly arranged sets (Beran 2006).

Results of a conditional-discrimination task in which various complex figures were presented to human and chimpanzee subjects suggest that chimpanzees and humans perceive such figures similarly. Outer-contour elements were perceived most dominantly by both species, and straight-line elements least dominantly. Both species showed the same perceptual hierarchy or dominance among perceptual categories (Tomonaga & Matsuzawa 1992).

A four year old chimpanzee successfully used symbols to name 11 colors: black, white, blue, red, yellow, orange, green, grey, purple, pink and brown. Using formal color classification (Munsell) charts, the chimp and a human divided the color space into clusters of a broad area within which a single color was assigned consistently. Furthermore, in intermediate areas that might be assigned to either of two color groups, both the chimp and the human subject showed prolonged hesitation, and tended to use both adjacent color names (Matsuzawa 1985). These experiments indicate that color perception and cognition are similar in chimpanzees and humans.

Planning

Chimpanzees sometimes collect suitable sticks and stems hours before they arrive at a site where they will be fishing for ants and termites (de Waal 2005a). Wild orangutan expert Carel van Schaik reports that orangutans often give “long calls” to let others know the direction in which they’re going to travel a couple of hours later (Jaffe 2006).

Chimpanzees are now known to supplement their diets with substantial amounts of vertebrate meat, which they acquire with premeditated, carefully orchestrated hunts. Red colobus monkeys are a favored prey, but in some areas they are so difficult to catch that hunting skills take years to develop, and pursuing males reportedly adopt a role division (e.g., driver, blocker and ambusher). As with humans, the most difficult tasks tend to be taken on by the oldest males (de Waal 2005b).

Research at the Max Planck Institute of Evolutionary Anthropology in Germany shows both bonobos and orangutans remember to carry the right tools to retrieve treats one to 14 hours later (Mulcahy & Call 2006). Having learned to use a particular tool (a piece of plastic pipe) as a key to open a container with grapes inside, each ape was led, one at a time, into a test room where each saw the grape-holding container and four objects: a dowel, a plastic dish, a bowl, and the slot-fitting pipe. A Plexiglas panel blocked the container, but each animal was free to take away an object when leaving the room, and wasn’t permitted to return for an hour, by which time the

Plexiglas and other tools had been removed. Three bonobos and three orangutans were tested 16 times each, and on an average of 7 occasions each (range: 2 to 15), the correct tool was selected and later used to open the grape container. In an unexpected incident, an orangutan brought back the wrong tool and then shaped it into a usable key.

Santino, an adult male chimpanzee housed at a Swedish zoo, made headlines in 2009 when it was discovered he was stashing stones to later be used to throw at human visitors. He collected the stones in a calm state in the morning hours before the zoo opened (Osvath 2009).

Play

In staged play encounters between captive bonobos and humans, bonobos behaved in many ways similar to human children. They were more interested in the joint activity than the play objects themselves, and they used communicative gestures to encourage reluctant partners to engage in the play, which indicates an awareness of others' intentions (Pika & Zuberbuhler 2008).

A study of wild chimpanzee populations in the Ivory Coast suggests that play behavior by young chimpanzees might be an important vector for the spread of infectious disease and resulting mortality—and a basis of cyclic disease/mortality outbreaks like those seen in humans (Kuehl et al. 2008).

Chimpanzee play shows patterns of development, with different developmental trajectories for solitary and social play. Solitary play peaks in infancy, whereas social play shows strong temporal variations in complexity, asymmetry, and playmate choice. Like laughter in humans, chimpanzees' playful expressions seem to advertise readiness to cooperate and likelihood of engaging in solid social relationships (Cordoni & Palagi 2011).

Young chimps and other species tested in the laboratory will choose play over food unless they are very hungry (Goodall & Bekoff 2002).

Pretending

Analyses of the playful interactions between three captive chimpanzees and two bonobos (aged 2-5 years), and their human care-givers, showed that the apes progressed through the stages of pretend play in the same way that human children do. The most impressive observation was of a female chimp named Panpanzee who pretended to groom a doll, then pretended to pluck bugs off the doll's body and feed them to the doll. She also offered some bugs to the caregiver, Liz, and when Liz offered some imaginary bugs back to Panpanzee, the chimp pretended to eat them (Lyn et al. 2006).

Psychological vulnerability

Infant chimpanzees confined in laboratory conditions exhibited stereotyped behaviors characterized by frequent, almost mechanical, repetition of a posture or movement which varies only slightly in form from time to time, and which apparently serves no obvious function. These

behaviors are also commonly seen in mentally defective, blind, and psychotic humans (Davenport & Menzel 1963).

Six adult chimpanzees who had spent their first 1-2 years in impoverished laboratory living conditions showed inferior cognitive compared to eight wild-born control chimpanzees, despite the fact that both groups shared the same cages and living conditions after 3-4 years of age. This study illustrates the vulnerability of chimpanzees to early environmental deficits (Davenport et al. 1973).

Chimpanzees subjected to social and perceptual restrictions during early life are strikingly different from animals reared by their mothers in a natural habitat. By adolescence their behavior includes avoidance of social contact, little species-typical behavior; and infrequent play and copulatory behavior, and absence of grooming. These abnormalities are highly resistant to modification by contact with normal social partners, drugs, or experimental manipulation (Corbett et al. 1969).

This study involved 11 chimpanzees living at Fauna, a sanctuary outside Montreal, Canada. These animals have a history of trauma-inducing conditions, including: captivity for sustained periods, painful and stressful biomedical procedures, and traumatic disruptions (e.g., mother-infant separation, sensory-motor deprivation, social isolation). Documented behavioral and psychological disturbances include: self-injury (biting, hitting, hair-pulling), excessive emotional outbursts (e.g., anger), withdrawal, persistent dysphoria, severe anxiety, depression (with whimpering, rocking), hyper-arousal, startle-response, mood swings, hypervigilance, inability to tolerate touch, dissociative episodes (e.g., violent attacks on hand or foot), trance with ritualistic circling, extreme responses to minor stressors, repetitive movements (e.g., self-poking for hours), hand and foot tremors, seizures, insomnia, eating disorders, and anorexia. A diagnosis of Complex PTSD in chimpanzees is consistent with descriptions of trauma-induced symptoms as described by the DSM-IV and human trauma research (Bradshaw et al. 2008).

Many captive great apes show gross behavioral abnormalities (e.g., stereotypies, self-mutilation, inappropriate aggression, fear or withdrawal) that resemble symptoms associated with psychiatric disorders in humans such as depression, anxiety disorders, eating disorders, and post-traumatic stress disorder. As intensely social animals with a prolonged period of infantile and juvenile dependence, chimpanzees are vulnerable to human intrusions such as early separation of infants from mothers, solitary housing, and sensory deprivation, which are in turn recognized sources of psychopathology in these apes. Interventions such as enrichment of living conditions and careful introduction of new physical and social environments are therapeutic, though not usually to the point of full recovery. This article proposes the need to expand research into ape psychopathology as a legitimate phenomenon, ultimately to the benefit of both humans and other great apes (Brüne et al., 2004).

An examination of published case reports of 20 chimpanzees found that a small number of these chimpanzees met DSM-IV criteria for PTSD and depression. The authors used the DSM-IV criteria and ethograms to develop behaviorally anchored alternative criteria for PTSD and depression. In a separate analysis of chimpanzees living in wild sites in Africa (n = 196) and chimpanzees living in sanctuaries with prior histories of experimentation, orphanage, illegal

seizure, or violent human conflict (n = 168) 58% of the chimpanzees living in sanctuaries met the alternative criteria for depression, compared with 3% of chimpanzees in the wild. Also, 44% of chimpanzees in sanctuaries met the alternative criteria for PTSD, compared with 0.5% of chimpanzees in the wild (p = 0.04) (Ferdowsian et al. 2011).

In a study of chimpanzees retired from biomedical research and resocialization after long-term social isolation, chimpanzees who had been separated from their mothers at a younger age and kept in isolation for more years appeared to be more timid personalities, less socially active, less dominant and more susceptible to stress, as compared to chimpanzees with a less severe deprivation history. However, permanent retirement from biomedical research in combination with therapeutic resocialization resulted in lower levels of stress hormones. Results indicate that chimpanzees can recover from severe social deprivation, and may experience resocialization as less stressful than solitary housing (Reimers et al. 2007).

Reciprocity

Mutual dependence is important to many primate societies, and it is fundamental to the social dynamics of chimps. Chimpanzees are aware of their debts to others, and they display reciprocity in diverse situations from obvious to subtle.

One of the more subtle expressions of chimp reciprocity was observed by primatologist Frans de Waal at the Arnhem Zoo. After Luit had deposed Yeroen as the alpha male, Yeroen's mating privileges with the colony's females were cut off by Luit. Subsequently, Yeroen supported Nikkie's bid to displace Luit. When Nikkie eventually succeeded in dethroning Luit, Yeroen immediately made his intentions plain, openly trying to mate with females under Nikkie's nose. Because Nikkie was dependent on Yeroen's support to keep his place above Luit, Nikkie had to let Yeroen have his way. This is just one of thousands of observed chimp alliances in which individuals support each other in fights and other conflicts (de Waal 2005a).

Restraint

Chimpanzees (n=4) showed the ability to delay gratification for 3 minutes when watching a human placing candies from a transparent container to a bowl in front of the chimpanzee. The chimps showed equal levels of restraint when the candies were dropped automatically into the bowl with no human present. A final experiment with the automated dispenser revealed that chimps can delay gratification up to 11 minutes (Beran & Evans 2006).

Bonobos and chimpanzees exhibit a degree of patience not seen in other animals tested thus far. Humans are less willing to wait for food rewards than are chimpanzees. Humans are more willing to wait for monetary rewards than for food, and show the highest degree of patience only in response to decisions about money involving low opportunity costs. These findings suggest that core components of the capacity for future-oriented decisions evolved before humans diverged evolutionarily from other apes. Moreover, the different levels of patience that humans exhibit might be driven by fundamental differences in the mechanisms representing biological versus abstract rewards (Rosati et al. 2007).

Chimpanzees (4) and an orangutan performed at least as well as human children do in showing restraint in an experiment in which up to 20 chocolate pieces were placed one-at-a-time into a bowl. An ape could consume the treats at any time during the placement, but provisioning was immediately curtailed at that point. The apes quickly learned to wait until all 20 chocolate pieces had been placed in the bowl (Beran 2002).

Revenge

When two adolescent chimpanzees refused to enter their night building, preferring instead to stay outside to enjoy the fresh air and the space to themselves, the rest of the captive colony was thrown into a grumpy mood, for it delayed their usual feeding time. To prevent reprisals, the keeper kept the two dawdlers in a separate room overnight. The next morning, the rest of the group chased the two culprits and delivered a beating. The pair were the first to enter the night building that evening (de Waal 2006).

Captive chimpanzees did not inflict costs on other chimps by knocking food away if the outcome alone was personally disadvantageous, but they did retaliate against conspecifics who actually stole the food from them. Thus, like humans, chimpanzees retaliate against personally harmful actions, but unlike humans, they appear indifferent to simply personally disadvantageous outcomes and are therefore not spiteful (Jensen et al. 2007b).

Revenge, a negative form of reciprocity, is also widely observed in chimps, who are able and willing to wait days or weeks to exact payback for an earlier wrong. For example, when Arnhem Zoo chimp Tepel, a female, was injured by another female, Jimmie, their human observer (de Waal 2005a) waited to see if and when Tepel would square her accounts with Jimmie. Later in the week, Jimmie was on the receiving end of a fight with alpha female Mama. Tepel took the opportunity to add her two cents to Jimmie's defeat, thus reminding her to pick her enemies with care.

Self-awareness

When confronted with a mirror, chimpanzees will immediately touch and inspect a dot of paint or other mark placed on their forehead while they had been anesthetized or asleep. This famous "mirror test" illustrates self-awareness (Gallup 1982).

Acute awareness of how signals sent by their own bodies affect others also indicates self-awareness in chimps. A male chimpanzee who was sitting with his back to his challenger had a grin on his face, having just heard hooting sounds in the distance. Before turning around to face his rival, he used his fingers three times to push his lips back over his teeth again, literally wiping the smile off his face so as to avoid sending the wrong signal to his rival (de Waal 1996). Another male chimp used his hands to hide an erect penis display directed at a nearby female, on the sudden appearance of a higher-ranking male (de Waal 1982, 1996).

The standard mirror self-recognition test has also been passed by bonobos, orangutans and gorillas. Monkeys facing a mirror show the ability to recognise that another animal is approaching from behind (Suddendorf & Whiten 2001).

Self-control

Chimpanzees spent more time playing with available toys in a situation where they had to continually inhibit responses to accumulating candies in order to earn a greater amount of those rewards. Thus, chimpanzees engaged in self-distraction with the toys when such behavior was most beneficial as a coping mechanism (Evans & Beran 2007).

Self-medication

A study of food choices in a community of over 40 wild chimpanzees at Kibale National Park, Uganda, found that many of the plants they consume aren't for nutrition but are likely ingested for medicinal purposes. The chimpanzee medicine chest includes leaves that fight tumors, plant pith with anti-malarial and anti-bacterial properties, bark that acts as an anti-diarrheal, the use of fig leaves as a de-worming agent), and many more. The primates seemed to strategically go for the medicinal parts of these plants, and would consume them even when other more nutritious and palatable foods were available. The researchers also documented similar patterns of behavior in about a dozen wild western gorillas in Dzanga-Ndoki National Park, Central African Republic (Masi et al. 2012).

Wild chimpanzees swallow the rough, hispid leaves of certain plant species as a means of physically expelling intestinal parasites. Studies in which naïve captive-reared chimpanzees are presented with these leaves find that some individuals spontaneously exhibit the same behavior. Leaf swallowing appears to have originated in the wild from opportunistic feeding behavior and was later passed down in the form of a self-medicative behavioral tradition (Huffman & Hirata 2004).

Sharing

While sharing of plant foods, unlike meat, is quite rare among chimpanzees, sharing of cultivated human crops is curiously not so rare, at least among chimps living in Bossou, Guinea. Of 59 plant food sharing events observed in this study, 58 were of cultivated plants. A changing human-dominated landscape presents chimpanzees with fresh challenges, and observations suggest that crop-raiding provides adult male chimpanzees at Bossou with highly desirable food commodities that may be traded for other currencies (Hockings et al. 2007).

Comparisons between chimpanzees and humans have led to the hypothesis that only humans voluntarily share their own food with others. However, when unrelated bonobos were given a choice of either monopolizing food or actively sharing it, they preferred to release a recipient from an adjacent room and feed together instead of eating all the food alone, independent of kinship and in the absence of any harassment (Hare and Kwetuenda 2010).

Sharing is widely practiced in chimpanzees, for which important social bonds and alliances are bolstered and rewarded by acts of kindness.

In experiments in which two chimps must cooperate to access food, they do so. In one such experiment, Sherman had access to several locked boxes containing food. Austin, in an adjoining room connected by a small window, had tools to open the boxes. That Sherman and Austin learned to cooperate to gain access to the food was not surprising. Chimp societies are renowned for the formation of alliances and reciprocity, so such behaviour comes naturally to them. More revealing was that after the correct tool was passed to Austin, he opened the container and passed food to Sherman (Griffin 1992). This controlled experiment illustrates consideration for the wants and needs of another.

Luit, the dominant chimp at the Arnhem Zoo colony, would break a branch from a dead tree, drag it to a live tree and with great skill and bravery, use it as a ladder to leap-frog the electric wires girdling the trunk. Once up among the branches, rather than merely having his fill, Luit would break off leafy stems and toss them down to his grateful comrades below (de Waal 1982, 1996).

In staged situations where mothers and offspring chimpanzee pairs exchanged limited numbers of tokens for food from a human provider, mothers sometimes acquiesced to their offspring's scrounging efforts, and in one pair, a young chimp gave tokens to a begging mother (Tanaka & Yamamoto 2009).

A study found that children of around three years of age share with others much more equitably in collaborative activities than they do in either windfall or parallel-work situations. By contrast, one of humans' two nearest primate relatives, chimpanzees (*Pan troglodytes*), 'share' (make food available to another individual) just as often whether they have collaborated with them or not (Hamann et al. 2011).

Social Development

In a study of 17 captive chimpanzees aged 1-3 years, subjects received facial expressions of happiness and fear from their human care-givers in arbitrary but consistent association with different novel objects presented to them. Each chimpanzee looked referentially at their caregiver, and their resulting aversion and gaze behavior was different for the happy and fear-inducing objects. It is concluded that chimpanzees use social referencing to acquire information about their complex social and physical environments (Russell et al. 1997).

Sympathy

There are many observations of chimpanzees showing care and sympathy for others who are in pain or suffering. Robert Yerkes observed in the 1920s the frolicsome play of three young chimps while another lay mortally ill nearby. Not only were the players careful not to bump into or otherwise disturb their ailing conspecific, from time to time one would go to her and touch her gently or caress her. Yerkes himself summed it up thus: "*A certain solicitude, sympathy, and pity, as well as a most human expression of consideration were thus manifested by these little creatures.*" (Yerkes & Yerkes 1929, pg 297, from de Waal 1996, p 57).

Maurice Temerlin, who with his wife Jane raised and studied chimpanzee Lucy, described her sympathy for Jane when she was sick. Lucy would “*become very disturbed, running into the bathroom, standing by Jane, comforting her by kissing her and putting her arm around her as she vomited.*” (Temerlin 1975, p. 165, from de Waal 1996)

Teaching

The bonobo Kanzi, who is gifted with understanding and interpreting human speech, observed a human trainer trying unsuccessfully to teach Kanzi’s younger and un-taught sister, Tamuli, to respond to simple verbal commands. When the trainer asked Tamuli to groom Kanzi, Kanzi took Tamuli’s hand and placed it on his chest, looking into Tamuli’s eyes with a questioning expression (de Waal 2005a).

Technology Transfer

When a Mitumba chimp joined the Kasekela group, one of the younger Kasakela females suddenly began using the Mitumba technique of catching carpenter ants with twigs. This was the first observation of technology transfer between chimpanzee communities (Lindsey 1999).

Theory of Mind

Note: to have a *theory of mind* is to be aware that others are autonomous individuals with thoughts and intentions of their own.

Chimpanzees are sensitive to the attentional and intentional states of others. Thus, enculturation does not appear to be a necessary condition to develop some components of theory of mind. Chimpanzees are already sensitive to some of the psychological states of others in the first place (Call 2006).

A study of chimpanzees, orangutans, and 2- and 3-year-old children found that all three species preferentially selected a box that the experimenter had marked intentionally over a box that had been marked “accidentally,” with 3-year-old children presenting the most robust results. These findings suggest that subjects understood something about the experimenter’s intentions (Call & Tomasello 1998).

Chimpanzees can gauge the motives of human experimenters and distinguish their intentional from accidental actions. Thus chimpanzees appear able to interpret the perceptions and actions of others from a psychological perspective—they seem to know what others can and cannot see and what goals others pursue (Call 2005).

Enculturated chimpanzees watched a human demonstrator perform routine tasks (e.g., operating a light switch) in an unusual way (e.g., using the forehead). When the demonstrator performed the unusual task while his/her hands were empty, the apes were more likely to imitate the unconventional action than if they watched the task performed while the demonstrator’s hands were full (e.g., carrying blankets). Thus, chimpanzees, like humans, have some understanding of the rationality of another’s actions (Buttelmann et al. 2007).

Tool use

An examination of the use of stone anvils and hammers by wild chimpanzees found that anvils tended to be larger than hammers. Tools are transported distinguished and substituted in a flexible manner that appears rooted in the chimpanzees' understanding of the relationship between tools and referents (i.e., the function of tools (Sakura & Matsuzawa 1991).

An apparatus was set up that provided orange juice in an outdoor compound for a group of 9 chimpanzees. Although they could reach the juice with their hands, eight of the nine chimps used natural tools. In total, fifteen kinds of tools were used, including straw, twigs, and some kinds of leaves. Individual chimpanzees showed high selectivity with regard to tool type. The use of White cedar was initiated by two females, then adopted by five other individuals who observed them (Tonooka et al. 1997).

A young male chimpanzee at Bossou, Guinea, exhibited the first observed instance of ant-fishing behavior. During the first session, at the age of 5, he employed wands of similar length when ant-fishing in trees to those used for ant-dipping on the ground, which is a customary tool use behavior of this community. Two years later, at the age of 7, his tools for ant-fishing were shorter and more suitable for capturing carpenter ants. This observation is a rare example of innovation in the wild and provides insights into problem-solving and learning processes in chimpanzees (Yamamoto et al. 2008).

New examples of tool use and other technology are being regularly discovered in wild chimpanzee populations. A recent example is the discovery of percussive technology in food processing by chimpanzees in the Nimba Mountains, Guinea: *Treculia* fracturing. The technique deploys stone or wooden "cleavers" as tools as well as stone outcrop "anvils" as substrates to fracture the large and fibrous fruits of *Treculia africana*, a rare but prized food source. This newly described form of percussive technology is distinctive, as the apparent aim is not to extract an embedded food item, as is the case in nut cracking, baobab smashing, or pestle pounding, but rather to reduce a large food item to manageably sized pieces. It is also the first instance of two types of percussive being used for the same purpose in a chimpanzee population (Koops et al. 2010).

Six young chimpanzees (2-4 years) were presented with a wooden tool that could be used to extract food from within a plastic cylinder, and could observe a model subject demonstrating how to solve the problem. Only 3-4 year old chimpanzees were influenced by the model. Patterns of onset of cognition, imitation, and comprehension of cause-effect relation compare favorably with those of human cognitive development (Bard et al. 1995).

Wild chimpanzees at Goulougo Triangle, Republic of Congo apply a set of deliberate, distinguishable actions to modify herb stems to fashion a brush-tipped probe, which is different from the form of fishing tools used by chimpanzees in East and West Africa. The specialized modifications to prepare the tool for termite fishing, measures taken to repair non-functional brushes and appropriate orientation of the modified end suggest that these wild chimpanzees are

attentive to tool modifications. Separate tests of the brush-tipped tool show that it is a more effective tool than an unmodified fishing probe (Sanz et al. 2009).

A problem called the "trap-tube problem" is very difficult for chimpanzees to solve, with only a small minority succeeding in most studies of it. However, when chimpanzees were withheld a tool normally given them to "help solve" the problem, all chimps (n=8) solved the problem, suggesting that the tool had been masking the chimps' problem-solving abilities (Seed et al. 2009). This study should caution anthropocentrically-driven conclusions about chimpanzee problem-solving abilities.

In experiments involving six orangutans and five bonobos, the apes successfully and spontaneously used pointing gestures to guide a human experimenter to the hiding place of a fork which was needed to retrieve food, by pointing to it when it was necessary. Other trials indicated that the subjects can take into account whether it is relevant or not to guide the human (Zimmermann et al. 2009).

At least 39 types of tool manufacture and use have been described in wild chimpanzees (e.g., Goodall 1968, McGrew 1992, Whiten et al. 1999). Examples include stripping leaves from twigs to make a tool to fish termites from their mounds, fashioning grass stems and sticks to prescribed lengths for probing for ants and dipping for honey, chewing up leaves to use as a sponge to soak up water that can't be reached with the mouth, using rocks and stones as anvils and hammers to crack open hard nuts, frayed-end sticks as brushes, and leaves as cushions to sit on wet ground.

Chimpanzee mothers patiently teach their children in the subtle arts of using stone tools and anvils to crack up tree nuts. Much of the learning is through observation, but mothers also assist their kids in the manipulation of the tools and the particular placement of the target nut (C Boesche, cited in Page 1999).

Six months of continuous remote video monitoring of chimpanzees in the forests of the Goualougo Triangle, Republic of Congo, confirmed that these apes use a tool set to puncture and fish at subterranean termite nests, and a different tool set to perforate and fish at above-ground nests. These observations illustrate levels of complexity in the material culture of chimpanzees: strict adherence to tool forms at different nest types, tool selectivity, reusable wood tool assemblages, and inter-community tool culture differences (Sanz et al. 2004).

Chimpanzees regularly hunt mammals, but use only their hands and teeth. For the first time, chimpanzees have now been found to make tools in order to spear mammalian prey (Byrne 2007).

Understanding

An adult, captive-reared chimpanzee was shown videotaped scenes of a human actor struggling with one of eight problems, then was shown two photographs, one depicting an action or object (or both) representing a solution to the problem. On seven of the eight problems, the chimp consistently chose the correct photograph. For example, when the video depicted a human shivering violently while standing next to a disconnected portable heater, the chimpanzee

selected a picture of a connected heater. This test problem-solving comprehension permits the animal's knowledge about problem-solving--its ability to infer the nature of problems and to recognize potential solutions to them--to be examined (Premack & Woodruff 1978).

Warfare

Chimpanzees are known to set out in a coordinated fashion and deliberately kill members of a neighboring population. This behavior has strong parallels to human warfare, and may be attributed to two factors: 1) a state of intergroup hostility, and 2) a sufficient imbalance of power that the attacking group can carry out its aim with relative impunity. Further study would be needed, but current evidence suggests that coalition killing has a long history in both humans and chimpanzees (Wrangham 1999).

REFERENCES

- Anderson JR, Myowa-Yamakoshi M, Matsuzawa T. 2004. Contagious yawning in chimpanzees. *Proc Biol Sci* 271 Suppl 6:S468-70.
- Balcombe JP. 2006. *Pleasurable Kingdom: Animals and the Nature of Feeling Good*. London: Macmillan.
- Bard KA. 2007. Neonatal imitation in chimpanzees (*Pan troglodytes*) tested with two paradigms. *Animal Cognition* 10:233-242.
- Bard KA. 2008. Development of emotional expressions in chimpanzee and human infants. *Psychological Bulletin of Novosibirsk State University, Russia*. 2:98-105.
- Bard KA, Frigaszy D, Visalberghi E. 1995. Acquisition and comprehension of a tool-using behavior by young chimpanzees, *Pan troglodytes*: Effects of age and modeling. *International Journal of Comparative Psychology* 8:47-68.
- Bard KA, Platzman KA, Lester BM, Suomi SJ. 1992. Orientation to social and nonsocial stimuli in neonatal chimpanzees and humans. *Infant Behavior and Development* 15:43-56.
- Barth J, Call J. 2006. Tracking the displacement of objects: a series of tasks with great apes (*Pan troglodytes*, *Pan paniscus*, *Gorilla gorilla*, and *Pongo pygmaeus*) and young children (*Homo sapiens*). *Journal of Experimental Psychology: Animal Behavior Processes* 32:239-252.
- Beran MJ. 2002. Maintenance of self-imposed delay of gratification by four chimpanzees (*Pan troglodytes*) and an orangutan (*Pongo pygmaeus*). *J Gen Psychol* 129:49-66.
- Beran, M J. 2004a. Long-term retention of the differential values of Arabic numerals by chimpanzees (*Pan troglodytes*). *Animal Cognition* 7:86-92.
- Beran M J. 2004b. Chimpanzees (*Pan troglodytes*) respond to nonvisible sets after one-by-one addition and removal of items. *Journal of Comparative Psychology* 118:25-36.
- Beran MJ. 2006. Quantity perception by adult humans (*Homo sapiens*), chimpanzees (*Pan troglodytes*), and rhesus macaques (*Macaca mulatta*) as a function of stimulus organization. *International Journal of Comparative Psychology* 19:386-397.
- Beran MJ 2010. Chimpanzees (*Pan troglodytes*) accurately compare poured liquid quantities. *Animal Cognition* 13:641-649.
- Beran MJ. 2012. Quantity judgments of auditory and visual stimuli by chimpanzees (*Pan troglodytes*). *Journal of Experimental Psychology: Animal Behavior Processes* 38:23-29.
- Beran MJ, Beran MM. 2004. Chimpanzees remember the results of one-by-one addition of food items to sets over extended time periods. *Psychological Science* 15:94-99.

- Beran MJ, Evans TA. 2006. Maintenance of delay of gratification by four chimpanzees (*Pan troglodytes*): The effects of delayed reward visibility, experimenter presence, and extended delay intervals. *Behavioural Processes* 73:315-324.
- Beran MJ, Johnson-Pynn JS, Ready C. 2011. Comparing children's (*Homo sapiens*) and chimpanzees' (*Pan troglodytes*) quantity judgments of sequentially presented sets of items. *Current Zoology* 57:419-428.
- Beran MJ, Pate JL, Richardson WK, Rumbaugh DM. 2000. A chimpanzee's (*Pan troglodytes*) long-term retention of lexigrams. *Animal Learning & Behavior* 28: 201-207.
- Beran MJ, Washburn DA, Rumbaugh DM. 2007. The Stroop Effect in color-naming of color-word lexigrams by a chimpanzee (*Pan troglodytes*). *Journal of General Psychology* 134:217-228.
- Berntson GG, Boysen ST, Bauer HR, Toretto MS. 1989. Conspecific screams and laughter: cardiac and behavioral reactions of infant chimpanzees. *Developmental Psychobiology* 22: 771-787.
- Biro D, Inoue-Nakamura N, Tonooka R, Yamakoshi G, Sousa C, Matsuzawa T. 2003. Cultural innovation and transmission of tool use in wild chimpanzees: evidence from field experiments. *Animal Cognition* 6:213-223.
- Biro D, Humle T, Koops K, Sousa C, Hayashi M, Matsuzawa T. 2010. Chimpanzee mothers at Bossou, Guinea carry the mummified remains of their dead infants. *Current Biology* 20:R351-352.
- Boesch C, Bolé C, Eckhardt N, Boesch H. 2010. Altruism in Forest Chimpanzees: The Case of Adoption. *PLoS ONE* 5(1): e8901. doi:10.1371/journal.pone.0008901
- Bonnie KE, de Waal F B. 2006. Affiliation promotes the transmission of a social custom: handclasp grooming among captive chimpanzees. *Primates* 47:27-34.
- Bradshaw GA, Capaldo T, Lindner L, Grow G. 2008. Building and inner sanctuary: Complex PTSD in chimpanzees. *Journal of Trauma and Dissociation* 9:9-34.
- Bräuer J, Call J, Tomasello M. 2005. All great ape species follow gaze to distant locations and around barriers. *Journal of Comparative Psychology* 119:145-154.
- Bräuer J, Call J, Tomasello M. 2008. Chimpanzees do not take into account what others can hear in a competitive situation. *Animal Cognition* 11:175-178.
- Brosnan SF, Schiff HC, de Waal FBM. 2005. Tolerance for inequity may increase with social closeness in chimpanzees. *Proceedings of the Royal Society B: Biological Sciences* 272: 253-258.

- Brüne M, Brüne-Cohrs, McGrew, WC. 2004. Psychiatric treatment for great apes? *Science* 306:2039.
- Buttelmann D, Carpenter M, Call J, Tomasello M. 2007. Enculturated chimpanzees imitate rationally. *Developmental Science* 10:F31-F38.
- Buttelmann D, Call J, Tomasello M. 2008a. Behavioral cues that great apes use to forage for hidden food. *Animal Cognition* 11:117-128.
- Buttelmann D, Carpenter M, Call J, Tomasello M. 2008b. Rational tool use and tool choice in human infants and great apes. *Child Development* 79:609-626.
- Buttelmann D, Call J, Tomasello M. 2009. Do great apes use emotional expressions to infer desires? *Developmental Science* 12:688-698.
- Byrne RW. 2007. Animal cognition: bring me my spear. *Current Biology* 17:R164-165.
- Call J. 2001. Object permanence in orangutans (*Pongo pygmaeus*), chimpanzees (*Pan troglodytes*), and children (*Homo sapiens*)". *Journal of Comparative Psychology* 115:159-171.
- Call J. 2004. Inferences about the location of food in the great apes (*Pan paniscus*, *Pan troglodytes*, *Gorilla gorilla*, and *Pongo pygmaeus*). *Journal of Comparative Psychology* 118:232-241.
- Call J. 2005. Chimpanzees are sensitive to some of the psychological states of others. *Interaction Studies* 6:413-427.
- Call J. 2006. Can the chimpanzee mind be upgraded? *Anthropological Psychology* 17:31-33.
- Call J. 2010. Do apes know that they could be wrong? *Animal Cognition* 13:689-700.
- Call J, Carpenter M. 2001. Do chimpanzees and children know what they have seen? *Animal Cognition* 4:207-220.
- Call J, Hare B, Carpenter M, Tomasello M. 2004. 'Unwilling' versus 'unable': chimpanzees' understanding of human intentional action. *Developmental Science* 7: 488-498.
- Call J, Tomasello M. 1998. Distinguishing intentional from accidental actions in orangutans (*Pongo pygmaeus*), chimpanzees (*Pan troglodytes*), and human children (*Homo sapiens*). *Journal of Comparative Psychology* 112:192-206.
- Campbell MW, de Waal FBM. 2011. Ingroup-outgroup bias in contagious yawning by chimpanzees supports link to empathy. *PLoS ONE* 6(4): e18283. doi:10.1371/journal.pone.0018283

- Campbell MW, Carter JD, Proctor D, Eisenberg ML, de Waal FB. 2009. Computer animations stimulate contagious yawning in chimpanzees. *Proceedings in Biological Science* 276:4255-4259.
- Clark MS, Grote NK. 2003. Close relationships. In *Handbook of psychology: Personality and social psychology* (ed. T. Millon & MJ Lerner), pp. 447-461. New York: Wiley.
- Clark Arcadi A, Robert D, Mugurusi F. 2004. A comparison of buttress drumming by male chimpanzees from two populations. *Primates* 45:135-9.
- Clay Z, Zuberbuhler K. 2009. Food-associated calling sequences in bonobos. *Animal Behaviour* 77:1387-1396.
- Cordoni G, Palagi E. 2011. Ontogenetic Trajectories of Chimpanzee Social Play: Similarities with Humans. *PLoS ONE* 6(11): e27344. doi:10.1371/journal.pone.0027344
- Crockford C, Wittig R., Mundry R, Zuberbühler K. 2012. Wild Chimpanzees Inform Ignorant Group Members of Danger. *Current Biology* 22:142-146.
- Davenport RK Jr, Menzel EW Jr. 1963. Sterotyped behavior of the infant chimpanzee. *Archives of General Psychiatry* 8:99–104.
- Davenport RK, Rogers CM, Rumbaugh DM. 1973. Long-term cognitive deficits in chimpanzees associated with early impoverished rearing. *Developmental Psychology* 9:343–347.
- Davila Ross M, Owren MJ, Zimmermann E. 2009. Reconstructing the Evolution of Laughter in Great Apes and Humans. *Current Biology* 19:1106-1111.
- Davila-Ross M, Allcock B, Thomas C, Bard KA. 2011. Aping expressions? Chimpanzees produce distinct laugh types when responding to laughter of others. *Emotion* 11:1113-1120.
- de Waal, FBM. 1982. *Chimpanzee Politics: Power and Sex Among Apes*. Harper and Row, New York.
- de Waal FBM. 1996. *Good Natured: The Origins of Right and Wrong in Humans and Other Animals*. Harvard Univ Press, Cambridge, Mass.
- de Waal, FBM. 1997. Are we in anthropodenial? *Discover* 18:50-53.
- de Waal, FBM. 2005a. *Our Inner Ape*. New York: Riverhead Books.
- de Waal, FBM. 2005b. A century of getting to know the chimpanzee. *Nature* 437:56-59.
- de Waal, FBM. 2006. The animal roots of human morality. *NewScientist* 192:60-61.

Evans TA, Beran MJ. 2007. Chimpanzees use self-distraction to cope with impulsivity. *Biology Letters* 3:599-602.

Ferdowsian HR, Durham DL, Kimwele C, Kranendonk G, Otali E, Akugizibwe T, Mulcahy JB, Ajarova L, Johnson CM. 2011. Signs of Mood and Anxiety Disorders in Chimpanzees. *PLoS ONE* 6(6): e19855. doi:10.1371/journal.pone.0019855

Fernandez-Carriba S, Loeches A, Morcillo A, Hopkins WD. 2002. Functional asymmetry of emotions in primates: new findings in chimpanzees. *Brain Research Bulletin* 57:561-564.

Flack JC, Jeannotte LA, de Waal FB. 2004. Play signaling and the perception of social rules by juvenile chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology* 118:149-159.

Fouts R, Mills ST. 1997. *Next of Kin: My Conversations with Chimpanzees* New York: William Morrow.

Fraser ON, Stahl D, Aureli F. 2008. Stress reduction through consolation in chimpanzees. *Proceedings of the National Academy of Science* 105:8557-8562.

Fraser ON, Aureli F. 2008. Reconciliation, consolation and postconflict behavioral specificity in chimpanzees. *American Journal of Primatology* 70:1114-1123.

Gallup GE. 1982. Self-awareness and the emergence of mind in primates. *American Journal of Primatology* 2:237:248.

Gomes CM, Boesch C. 2009. Wild Chimpanzees Exchange Meat for Sex on a Long-Term Basis. *PLoS ONE* 4(4): e5116. doi:10.1371/journal.pone.0005116

Goodall, Jane. 1968. The behaviour of free-living chimpanzees in the Gombe Stream Reserve. *Animal Behaviour Monographs* 1: 161-311.

Goodall, Jane. 1986. *The Chimpanzees of Gombe: Patterns of Behavior*. Belknap Press, Cambridge, Massachusetts.

Goodall J, Bekoff M. 2002. *The Ten Trusts: What We Must do to Care for the Animals We Love*. San Francisco: HarperSanFrancisco.

Gould JL, Gould CG. 1994. *The Animal Mind*. New York: Scientific American . Library.

Greenfield PM, Savage-Rumbaugh ES. 1984. Perceived variability and symbol use: a common language-cognition interface in children and chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology* 98:201-218.

Griffin, DR. 1992. *Animal Minds*. Chicago: University of Chicago Press.

- Hall L, Waters AJ. 2000. From property to person: The case of Evelyn Hart. *Seton Hall Constitutional Law Journal* 11(1).
- Hallock MB, Worobey J, Self PA. 1989. Behavioural development in chimpanzee (*Pan troglodytes*) and human newborns across the first month of life. *International Journal of Behavioural Development* 12:527-540.
- Hamann K, Warneken F, Greenberg JR, Tomasello M. 2011. Collaboration encourages equal sharing in children but not in chimpanzees. *Nature* 476:328-31.
- Hanus D, Call J. 2008. Chimpanzees infer the location of a reward based on the effect of its weight. *Current Biology* 18:R370-372.
- Hare B, Call J, Agnetta B, Tomasello M. 2000. Chimpanzees know what conspecifics do and do not see. *Animal Behaviour* 59:771-785.
- Hare B., Call, J. & Tomasello, M. 2001. Do chimpanzees know what conspecifics know? *Animal Behaviour* 61:139-151.
- Hare B, Call J, Tomasello M. 2006. Chimpanzees deceive a human competitor by hiding. *Cognition* 101:495-514.
- Hare B, Melis AP, Woods V, Hastings S, Wrangham R. 2007 Tolerance allows bonobos to outperform chimpanzees on a cooperative task. *Current Biology* 17:619-623.
- Hare B, Kwetuenda S. 2010. Bonobos voluntarily share their own food with others. *Current Biology* 20:R230-R231.
- Haun D, Call J. 2008. Imitation recognition in great apes. *Current Biology* 18,:288-290.
- Haun D, Call J. 2009. Great apes' capacities to recognize relational similarity. *Cognition* 110:147-159.
- Hayashi M, Takeshita H. 2009. Stacking of irregularly shaped blocks in chimpanzees (*Pan troglodytes*) and young humans (*Homo sapiens*). *Animal Cognition* Supplement 1:S49-58.
- Heilbronner SR, Platt ML. 2007. Animal cognition: time flies when chimps are having fun. *Current Biology* 17:R1008-1010.
- Heimbauer LA, Beran MJ, Owren MJ. 2011. A chimpanzee recognizes synthetic speech with significantly reduced acoustic cues to phonetic content. *Current Biology* 21:1210-1214.
- Herrmann E, Call J, Hernandez-Lloreda MV, Hare B, Tomasello M. 2007. Humans have evolved specialized skills of social cognition: the cultural intelligence hypothesis. *Science* 317:1360-1366.

- Herrmann E, Hernández-Lloreda MV, Call J, Hare B, Tomasello M. 2010a. The structure of individual differences in the cognitive abilities of children and chimpanzees. *Psychological Science* 21:102-110.
- Herrmann E, Hare B, Call J, Tomasello M. 2010b. Differences in the cognitive skills of bonobos and chimpanzees. *PloS One* 27:e12438.
- Hirata S, Myowa M, Matsuzawa T. 1998. Use of leaves as cushions to sit on wet ground by wild chimpanzees. *American Journal of Primatology* 44:215-220.
- Hirata S, Yamakoshi G, Fujita S, Ohashi G, Matsuzawa M. 2001. Capturing and toying with hyraxes (*Dendrohyrax dorsalis*) by wild chimpanzees (*Pan troglodytes*) at Bossou, Guinea. *American Journal of Primatology* 53:93-97.
- Hirata S, Matsuzawa T. 2001. Tactics to obtain a hidden food item in chimpanzee pairs (*Pan troglodytes*). *Animal Cognition* 4:285-295.
- Hockings K, Humle T, Anderson J, Biro D, Sousa C, Ohashi G, Matsuzawa T. 2007. Chimpanzees share forbidden fruit. *PLoS ONE* 9:1-4.
- Hockings KJ, Yamakoshi G, Kabasawa A, Matsuzawa T. 2010. Attacks on local persons by chimpanzees in Bossou, Republic of Guinea: long-term perspectives. *American Journal of Primatology* 72:887-896.
- Horner V, Whiten A. 2005. Causal knowledge and imitation/emulation switching in chimpanzees (*Pan troglodytes*) and children (*Homo sapiens*). *Animal Cognition* 8:164-81.
- Horner V, Whiten A, Flynn E, de Waal FBM. 2006. Faithful replication of foraging techniques along cultural transmission chains by chimpanzees and children. *Proceedings of the National Academy of Sciences, U.S.A.* 103:13878-13883.
- Horner V, Carter JD, Suchak M, de Waal FB. 2011. Spontaneous prosocial choice by chimpanzees. *Proceedings of the National Academy of Sciences, U.S.A.* 108:13847-13851.
- Hostetter AB, Russell JL, Freeman H, Hopkins WD. 2006. Now you see me, now you don't: evidence that chimpanzees understand the role of the eyes in attention. *Animal Cognition* 10:55-62.
- Hrubesch C, Preuschoft S, van Schaik C. 2009. Skill mastery inhibits adoption of observed alternative solutions among chimpanzees (*Pan troglodytes*). *Animal Cognition* 12:209-216.
- Huffman, M. A. & Hirata, S. 2004. An experimental study of leaf swallowing in captive chimpanzees: insights into the origin of a self-medicative behavior and the role of social learning. *Primates*, 45, 113-118.

- Humle T, Matsuzawa T. 2009. Laterality in hand use across four tool-use behaviors among the wild chimpanzees of Bossou, Guinea, West Africa. *American Journal of Primatology* 70:40–48.
- Humle T, Snowdon CT, Matsuzawa T. 2009. Social influences on ant-dipping acquisition in the wild chimpanzees (*Pan troglodytes verus*) of Bossou, Guinea, West Africa. *Animal Cognition* 12:S37–S48.
- Inoue S, Matsuzawa T. 2007. Working memory of numerals in chimpanzees. *Current Biology* 17:R1004–R1005.
- Inoue S, Matsuzawa T. 2011. Correlation between menstrual cycle and cognitive performance in a chimpanzee (*Pan troglodytes*). *Journal of Comparative Psychology* 125:104-111.
- Itakura S, Matsuzawa T. 1993. Acquisition of personal pronouns by a chimpanzee. Roitblat H, Herman L, Nachtigall P. (eds) *Language and Communication: Comparative Perspectives*. Lawrence Erlbaum 347-363.
- Jaffe E. 2006. What apes can teach us about the human mind. *Science News* 170. Accessed online 10 March 2011 at <http://www.network54.com/Forum/235380/thread/1158157000/last-1158157000/What+apes+can+teach+us+about+the+human+mind>
- Jensen K, Call J, Tomasello M. 2007a. Chimpanzees are rational maximizers in an ultimatum game. *Science* 318:107-109.
- Jensen K, Call J, Tomasello M. 2007b. Chimpanzees are vengeful but not spiteful. *Proceedings of the National Academy of Sciences USA* 104:13046-13050.
- Jensvold ML, Gardner RA. 2000. Interactive use of sign language by cross-fostered chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology* 114:335-346.
- Kaminski, J., Call, J. & Tomasello, M. 2004. Body orientation and face orientation: two factors controlling apes' begging behavior from humans. *Animal Cognition*, 7, 216-223.
- Kaminski J, Call J, Tomasello M. 2008. Chimpanzees know what others know but not what they believe. *Cognition* 109:224-234.
- Kano F, Tomonaga M. 2009. How chimpanzees look at pictures: a comparative eye-tracking study. *Proceedings in Biological Science* 276:1949-1955.
- Koops K, McGrew W, Matsuzawa T. 2010. Do chimpanzees (*Pan troglodytes*) use cleavers and anvils to fracture *Treculia africana* fruits? Preliminary data on a new form of percussive technology. *Primates* 51:175–178.
- Koyama NF, Dunbar RIM. 1996. Anticipation of conflict by chimpanzees. *Primates* 37:79-86.

- Krachun C, Call J, Tomasello M. 2009. Can chimpanzees (*Pan troglodytes*) discriminate appearance from reality? *Cognition* 112:435-450.
- Kuehl HS, Elzner C, Moebius Y, Boesch C, Walsh PD. 2008. The price of play: self-organized infant mortality cycles in chimpanzees. *PLoS ONE* 3(6): e2440.
doi:10.1371/journal.pone.0002440
- Leavens, D. A., Hopkins, W. D. & Thomas, R. K. 2004. Referential communication by chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, 118, 48-57.
- Leavens DA, Russell JL, Hopkins WD. 2005. Intentionality as measured in the persistence and elaboration of communication by chimpanzees (*Pan troglodytes*). *Child Development* 76:291-306.
- Liebal K, Call J, Tomasello M. 2004. Use of gesture sequences in chimpanzees. *American Journal of Primatology* 64:377-396.
- Lindsey, Jennifer. *Jane Goodall: 40 Years at Gombe*. New York: Stewart, Tabori & Chang.
- Lonsdorf DV, Hopkins WD. 2005. Wild chimpanzees show population-level handedness for tool use. *Proceedings of the National Academy of Sciences* 102:12634-8.
- Lyn H, Greenfield P, Savage-Rumbaugh S. 2006. The development of representational play in chimpanzees and bonobos. *Cognitive Development* 21:199-213.
- Lyn H, Russell JL, Hopkins WD. 2010. The impact of environment on the comprehension of declarative communication in apes. *Psychological Science* 21:360-365.
- Martin-Ordas G, Haun D, Colmenares F, Call J. 2010. Keeping track of time: evidence for episodic-like memory in great apes. *Animal Cognition* 13:331-340.
- Masi S, Gustafsson E, Saint Jalme M, Narat V, Todd A, Bomsel M-C, Krief S. 2012. Unusual feeding behavior in wild great apes, a window to understand origins of self-medication in humans: Role of sociality and physiology on learning process. *Physiology & Behavior* 105:337-349.
- Matsusaka T. 2004. When does play panting occur during social play in wild chimpanzees? *Primates* 45:221-229.
- Matsuzawa T. 1985. Colour naming and classification in a chimpanzee (*Pan troglodytes*). *Journal of Human Evolution* 14:283-291
- Matsuzawa T. 1990. Form perception and visual acuity in a chimpanzee. *Folia Primatologica* 55:24-32.
- McGrew WC. 1992. *Material culture in chimpanzees*. Cambridge: Cambridge University Press.

- McRae F. 2008. I'm the champion! Ape trounces the best of the human world in memory competition. *Daily Mail*, January 26.
- Meguerditchian A, Vauclair J, Hopkins WD. 2009. Captive chimpanzees use their right hand to communicate with each other: implications for the origin of the cerebral substrate for language. *Cortex* 46:40-48.
- Melis AP, Hare B, Tomasello M. 2006a. Chimpanzees recruit the best collaborators. *Science* 311:1297-1300.
- Melis AP, Call J, Tomasello M. 2006b. Chimpanzees (*Pan troglodytes*) conceal visual and auditory information from others. *Journal of Comparative Psychology* 120:154-162.
- Melis AP, Warneken F, Jensen K, Schneider AC, Call J, Tomasello M. 2011. Chimpanzees help conspecifics obtain food and non-food items. *Proceedings in Biological Science* 278:1405-1413.
- Mendes N, Rakoczy H, Call J. 2008. Ape metaphysics: object individuation without language. *Cognition* 106:730-749.
- Menzel CR. 1999. Unprompted recall and reporting of hidden objects by a chimpanzee (*Pan troglodytes*) after extended delays. *Journal of Comparative Psychology* 113:426-434.
- Morimura N, Mori Y. 2010. Effects of early rearing conditions on problem-solving skill in captive male chimpanzees (*Pan troglodytes*). *American Journal of Primatology* 72:626-633.
- Mulcahy NJ, Call J. 2006. Apes save tools for future use. *Science* 312: 1006-7.
- Murai C, Kosugi D, Tomonaga M, Tanaka M, Matsuzawa T, Itakura S. 2005. Can chimpanzee infants (*Pan troglodytes*) form categorical representations in the same manner as human infants (*Homo sapiens*)? *Developmental Science* 8:240-254.
- Ohashi G, Matsuzawa T. 2011. Deactivation of snares by wild chimpanzees. *Primates* 52:1-5
- Okamoto S, Tomonaga M, Ishii K, Kawai N, Tanaka M, Matsuzawa T. 2002. An infant chimpanzee (*Pan troglodytes*) follows human gaze. *Animal Cognition* 5:107-114.
- Osvath M. 2009. Spontaneous planning for future stone throwing by a male chimpanzee. *Current Biology* 19:R190-191.
- Page G. 1999. *Inside the Animal Mind*. New York: Doubleday.
- Palagi, E., Cordoni, G. & Tarli, S. M. B. 2004. Immediate and delayed benefits of play behaviour: New evidence from chimpanzees (*Pan troglodytes*). *Ethology*, 110, 949-962.

- Parr LA. 2001. Cognitive and physiological markers of emotional awareness in chimpanzees (*Pan troglodytes*). *Animal Cognition* 4:223-229.
- Parr LA, de Waal FBM. 1999. Visual kin recognition in chimpanzees. *Nature* 399:647.
- Parr LA, Hopkins WD. 2000. Brain temperature asymmetries and emotional perception in chimpanzees, *Pan troglodytes*. *Physiol Behav* 71:363-371.
- Parr LA, Waller BM, Fugate J. 2005. Emotional communication in primates: implications for neurobiology. *Current Opinions in Neurobiology* 15:716-720.
- Parr LA, Waller BM. 2006. Understanding chimpanzee facial expression: insights into the evolution of communication. *Social Cognition and Affective Neuroscience* 1:221-228.
- Phillips KA, Hopkins WD. 2012. Topography of the Chimpanzee Corpus Callosum. *PLoS ONE* 7(2): e31941. doi:10.1371/journal.pone.0031941
- Premack D, Woodruff G. 1978. Chimpanzee problem-solving: a test for comprehension *Science* 202:532-35.
- Premack D, Premack AJ. 1984. *The Mind of an Ape*. New York: Norton.
- Premack D. 2007. Human and animal cognition: continuity and discontinuity. *Proceedings of the National Academy of Sciences, U.S.A.* 104:13861-13867.
- Pika S, Zuberbuhler K. 2008. Social games between bonobos and humans: Evidence for shared intentionality? *American Journal of Primatology* 70:207-210.
- Reimers M, Schwarzenberger F, Preuschoft S. 2007. Rehabilitation of research chimpanzees: stress and coping after long-term isolation. *Hormones and Behavior* 51:428-435.
- Rilling JK, Barks SK, parr LA, Preuss TM, Faber TL, Pagnoni G, Bremner JD, Votaw JR. 2007. A comparison of resting-state brain activity in humans and chimpanzees. *Proceedings of the National Academy of Sciences, U.S.A.* 104:17146-17151.
- Romero T, Castellanos MA, de Waal FB. 2010. Consolation as possible expression of sympathetic concern among chimpanzees. *Proceedings of the National Academy of Sciences, U.S.A.* 107:12110-12115.
- Rosati AG, Hare B. 2011. Chimpanzees and bonobos distinguish between risk and ambiguity. *Biology Letters* 23:15-18.
- Rosati AG, Stevens JR, Hare B, Hauser MD. 2007. The evolutionary origins of human patience: temporal preferences in chimpanzees, bonobos, and human adults. *Current Biology* 17:1663-1668.

- Russell DR, Adamson LB, Bard KA. 1997. Social referencing by young chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology* 111:185-193.
- Russell JL, Braccini S, Buehler N, Kachin MJ, Schapiro SJ, Hopkins WD. 2005. Chimpanzee (*Pan troglodytes*) intentional communication is not contingent upon food. *Animal Cognition* 8:263-272.
- Russell YI, Call J, Dunbar, R.I.M. 2008. Image scoring in great apes. *Behavioural Processes* 78:108-111.
- Sanz C, Morgan D, Gulick S. 2004. New insights into chimpanzees, tools, and termites from the Congo Basin. *The American Naturalist* 164:567-81.
- Sanz C, Call J, Morgan D. 2009. Design complexity in the tool use of chimpanzees (*Pan troglodytes*) in the Congo basin. *Biology Letters* 5:293-296.
- Sakura O, Matsuzawa T. 1991. Flexibility of wild chimpanzee nut-cracking behavior using stone hammers and anvils: an experimental analysis. *Ethology* 87:237-248.
- Schmelz M, Call J, Tomasello M. 2011. Chimpanzees know that others make inferences. *Proceedings of the National Academy of Sciences, U.S.A.* 108:3077-3079.
- Schneider C, Call J, Liebal K. 2010. Do bonobos say NO by shaking their head? *Primates* 51:199-202.
- Schroepfer KK, Rosati AG, Chartrand T, Hare B. 2011. Use of "entertainment" chimpanzees in commercials distorts public perception regarding their conservation status. *PloS One* 6:e26048
- Scientific Committee on Animal Health & Welfare. 2002. *The Welfare of Non-Human Primates used in Research*. Publications of the European Commission, Health & Consumer Protection. DG.
- Seed AM, Call J, Emery NJ, Clayton NS. 2009. Chimpanzees solve the trap problem when the confound of tool-use is removed. *Journal of Experimental Psychology: Animal Behavior Processes* 35:23-34.
- Seyfarth RM, Cheney DL. 2012. Animal cognition: Chimpanzee alarm calls depend on what others know. *Current Biology* 22:R51-R52.
- Siebert ER, Parr LA. 2003. A structural and contextual analysis of chimpanzee screams. *Annals of the New York Academy of Science* 1000:104-109.
- Slocombe K, Zuberbuhler K. 2005. Functionally referential communication in a chimpanzee. *Current Biology* 15:1779-1784.

- Slocombe K, Zuberbühler K. 2007. Chimpanzees modify recruitment screams as a function of audience composition. *Proceedings of the National Academy of Sciences, U.S.A.* 104:17228-17233.
- Slocombe KE, Kaller T, Call J, Zuberbühler K. 2010. Chimpanzees Extract Social Information from Agonistic Screams. *PLoS ONE* 5(7): e11473. doi:10.1371/journal.pone.0011473
- Steiner JE, Glaser D, Hawilo ME, Berridge KC. 2001. Comparative expression of hedonic impact: affective reactions to taste by human infants and other primates. *Neuroscience and Biobehavioral Reviews* 25:53-74.
- Stewart FA, Pruett JD, Hansell MH. 2007. Do chimpanzees build comfortable nests? *American Journal of Primatology* 69:930-939.
- Suddendorf T, Whiten A. 2001. Mental evolution and development: evidence for secondary representation in children, great apes and other animals. *Psychol. Bull.* 127:629-650.
- Sugiyama Y, Fushimi T, Sakura O, Matsuzawa T. 1993. Hand Preference and tool use in wild chimpanzees. *Primates* 34:151-159.
- Tagliatalata JP, Russell JL, Schaeffer JA, Hopkins WD. 2008. Communicative Signaling Activates 'Broca's' Homolog in Chimpanzees. *Current Biology* 18:343-348.
- Tagliatalata JP, Russell JL, Schaeffer JA, Hopkins WD. 2011. Chimpanzee vocal signaling points to a multimodal origin of human language. *PLoS ONE* 6(4): e18852. doi:10.1371/journal.pone.0018852
- Tanaka M, Yamamoto S. 2009. Token transfer between mother and offspring chimpanzees (Pan troglodytes): mother-offspring interaction in a competitive situation. *Animal Cognition* Supplement 1:S19-26.
- Temerlin MK. 1975. *Lucy: Growing up Human*. Palo Alto, Calif.: Science and Behavior Books.
- Tempelmann S, Kaminski J, Liebal K. 2011. Focus on the essential: all great apes know when others are being attentive. *Animal Cognition* 14:433-439.
- Tomasello M, Savage-Rumbaugh S, Kruger AC. 1993. Imitative learning of actions on objects by children, chimpanzees, and enculturated chimpanzees. *Child Development* 64:1688-1705.
- Tomasello M, Call J, Nagell K, Olguin R, Carpenter M. 1994. The learning and use of gestural signals by young chimpanzees: A trans-generational study. *Primates*, 35:137-154.
- Tomonaga M, Matsuzawa T. 1992. Perception of complex geometric figures in chimpanzees and humans: Analysis based on choice reaction time. *Journal of Comparative Psychology* 106:43-52.
- Tomonaga M, Itakura S, Matsuzawa T. 1993. Superiority of conspecific faces and reduced inversion effect in face perception by a chimpanzee. *Folia Primatologica* 61:110-114.

- Tonooka R, Tomonaga M, Matsuzawa T. 1997. Acquisition and transmission of tool making and use for drinking juice in a group of captive chimpanzees (*Pan troglodytes*). *Japanese Psychological Research* 39:253-265.
- Townsend S, Deschner T, Zuberbuhler K. 2008. Female chimpanzees use copulation calls strategically to prevent social competition. *PLoS One* 3:e2431.
- Ueno A, Matsuzawa, T. 2005. Response to novel food in infant chimpanzees: Do infants refer to mothers before ingesting food on their own? *Behavioural Processes* 68:85-90.
- Uller C. 2004. Disposition to recognize goals in infant chimpanzees. *Animal Cognition* 7:154-161.
- Uller C, Nichols S. 2000. Goal attribution in chimpanzees. *Cognition* 76:B27-B34.
- van Ijzendoorn MH, Bard KA, Bakermans-Kranenburg MJ, Ivan K. 2008. Enhancement of attachment and cognitive development of young nursery-reared chimpanzees in responsive versus standard care. *Developmental Psychobiology*: 51:173-185.
- van Schaik CP et al. 2003. Orangutan cultures and the evolution of material culture. *Science* 299:102-105.
- Vlamings PH, Hare B, Call J. 2010. Reaching around barriers: the performance of the great apes and 3-5-year-old children. *Animal Cognition* 13:273-285.
- Warneken F, Tomasello M. 2006. Altruistic helping and human infants and young chimpanzees. *Science* 311: 1301-1303.
- Warneken F, Hare B, Melis A, Hanus D, Tomasello M. 2007. Spontaneous altruism by chimpanzees and young children. *PLoS Biology* 5:1-7
- Warneken F, Tomasello M. 2009. Varieties of altruism in children and chimpanzees. *Trends in Cognitive Science* 13:397-402.
- Whiten A, Byrne RW. 1988. Tactical deception in primates. *Behavioral and Brain Science* 11:233-244.
- Whiten A, Goodall J, McGrew WC, Nishida T, Reynolds V, Sugiyama Y, Tutin CEG, Wrangham RW, Boesch C. 1999. Culture in chimpanzees. *Nature* 399:682-685.
- Whiten, A., Horner, V., Litchfield, C. A. & Marshall-Pescini, S. 2004. How do apes ape? *Learning & Behavior*, 32, 36-52.
- Whiten A, Horner V, de Waal FBM. 2005. Conformity to cultural norms of tool use in chimpanzees. *Nature* 437:737-740.

- Wildman DE, Uddin M, Liu G, Grossman LI, Goodman M. 2003. Implications of natural selection in shaping 99.4% nonsynonymous DNA identity between humans and chimpanzees: enlarging genus Homo. *Proceedings of the National Academy of Science, U.S.A.* 100:7181-7188.
- Wobber V, Hare B, Maboto J, Lipson S, Wrangham R, Ellison PT. 2010. Differential changes in steroid hormones before competition in bonobos and chimpanzees. *Proceedings of the National Academy of Science, U.S.A.* 107:12457-62.
- Wrangham RW. 1999. Evolution of coalitionary killing. *American Journal of Physical Anthropology* 29:1-30.
- Wroblewski EE. 2008. An unusual incident of adoption in a wild chimpanzee (*Pan troglodytes*) population at Gombe National Park. *American Journal of Primatology* 70:995-998.
- Yamamoto S, Yamakoshi G, Humle T, Matsuzawa T. 2008. Invention and modification of a new tool use behavior: Ant-fishing in trees by a wild chimpanzee (*Pan troglodytes verus*) at Bossou, Guinea. *American Journal of Primatology* 70:699–702.
- Yamamoto S, Humle T, Tanaka M. 2009. Chimpanzees Help Each Other upon Request. *PLoS ONE* 4: e7416. doi:10.1371/journal.pone.0007416
- Zimmermann F, Zemke F, Call J, Gómez JC. 2009. Orangutans (*Pongo pygmaeus*) and bonobos (*Pan paniscus*) point to inform a human about the location of a tool. *Animal Cognition* 12:347-358.