

What is the Effect of Affect on Bonobo and Chimpanzee Problem Solving?

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Abstract Humans have two close relatives, the bonobo and chimpanzee, whose psychologies differ in ways that will allow for insights into the evolution of our own species. Unfortunately, we know little about bonobos due to their late classification as a species, their scarcity in captivity and the remote location of their natural habitat. Here I review some of the first experimental comparisons of bonobos and chimpanzees, suggesting that their socioecology has shaped their psychology. First, consistent with the observation that bonobos live in more predictable environments, bonobos value future food payoffs less than chimpanzees, while also avoiding the risky foraging decisions that chimpanzees prefer. Second, consistent with the prediction that more predictable environments allow bonobos to be more egalitarian, it was found that bonobos are capable of more flexible cooperative behavior than chimpanzees if the joint problem requires high levels of tolerance. Overall, these comparisons suggest that it is selection on the emotional reactivity of bonobos and chimpanzees that likely played a large role in shaping their differing psychologies, which raises the possibility that changes in human temperament may have also been crucial for the evolution of the unique psychology of our own species as well.

When thinking about human evolution we often encounter comparisons between ourselves and chimpanzees, or *Pan troglodytes*, our closest living relative. However, the species of chimpanzee with which we are all most familiar is only one of our two closest relatives. We actually have two close relatives that are both members of the “chimpanzee” genus, *Pan*, the chimpanzee and the bonobo (*Pan paniscus*). While our own lineage split from the members of the chimpanzee genus *Pan* 5–7 million years ago (Ruvolo 1997), it was only after this split that the two members of the *Pan* genus themselves diverged around 1 million years ago (Won and Hey 2005; see Figure 1A). As a result, both chimpanzees and bonobos share 99.7% of our genome, making both species more closely related to humans than gorillas.

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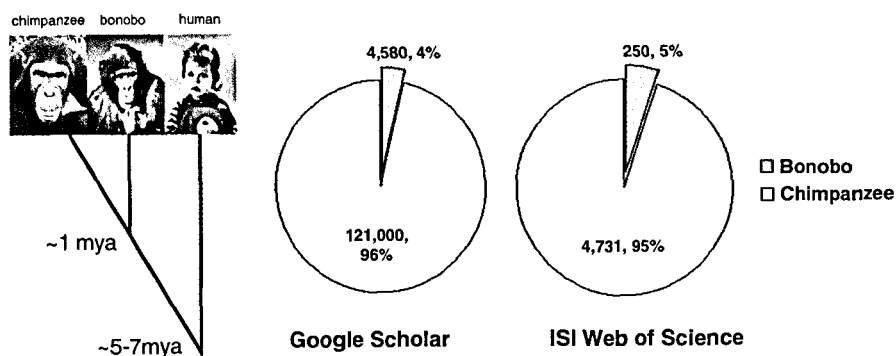


Fig. 1 **a** The phylogeny and estimated divergence times of chimpanzees, bonobos and humans and **b** the absolute number and percentage of citations reported by Google Scholar and ISI Web of science when using either bonobo or chimpanzee as a search term

Our good fortune in having two closest relatives, instead of just one, is often overlooked because our more famous relative, the chimpanzee, has long been the center of attention in science and media alike. This focus is largely due to the fact that bonobos were not even recognized as a species until 1933 and are only found indigenously in one country, the former Zaire or Democratic Republic of Congo. Before the 1970s, hundreds of chimpanzees were taken (or stolen, depending on your perspective) from Africa to fill laboratories, circuses and zoological gardens (the majority from West Africa). Some of these wild-caught animals and their many descendants now live in zoos and labs throughout the developed world. Meanwhile, with little access to the interior of Congo, only a relatively small number of zoos in the U.S, Germany and Belgium have bonobos, approximately two hundred, living in them. Therefore, because of the bonobos' late discovery, remote habitat, and scarcity in captivity, chimpanzees became the relative of choice when comparing the behavior of *Homo* and *Pan*. As a result, instead of being able to split our research efforts more or less equally between our two closest relatives, there has been approximately 20 times more research conducted on chimpanzees than bonobos (see Figure 1B). Due to the paucity of bonobo research, there have been few direct comparisons of bonobos and chimpanzees in any domain of research. This overall skew in the literature led Frans de Waal to dub the bonobo "the forgotten ape" (de Waal and Lanting 1997; Figure 2).

The lack of data on bonobos is particularly problematic when testing phylogenetic hypotheses regarding human evolution. The main goal of comparing humans with chimpanzees is to identify traits that are shared or derived so that we might map out in what ways humans changed since our species split from our last common ancestor with chimpanzees and bonobos. Therefore, when humans possess a trait, say the ability to actively share food, but chimpanzees do not, we feel confident concluding that whatever skill or motivation allows for active sharing in humans must have evolved since the human lineage split (e.g., Jensen et al. 2006). However, while this conclusion may indeed be true, it depends solely on the assumption that our last

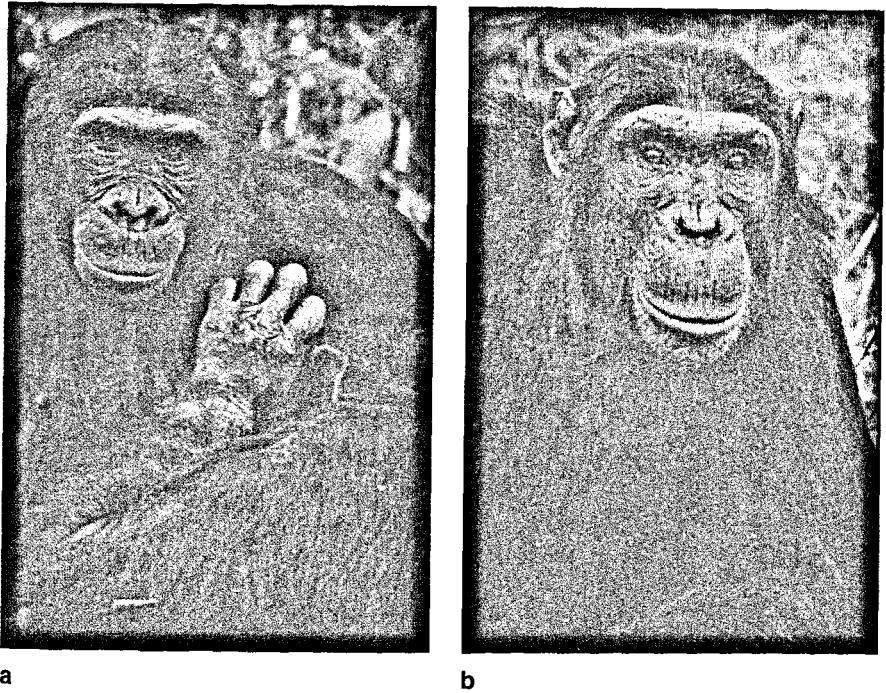


Fig. 2 (a) Bonobos and (b) chimpanzees are our species' two closest living relatives, with both sharing almost 99% of our genome through common descent. This means that the genomes of chimpanzees and bonobos are more similar to humans than that of gorillas. Bonobos and chimpanzees diverged from each other around 1 million years ago and differ in morphology, behavior and perhaps even emotions and cognition in important ways. Bonobos are female dominant, with females forming tight bonds against males through same-sex socio-sexual contact that is thought to limit aggression. In the wild, they have not been seen to cooperatively hunt, use tools or exhibit lethal aggression. Chimpanzees are male dominant, with intense aggression between different groups that can be lethal. Chimpanzees use tools, cooperatively hunt monkeys and will even eat the infants of other chimpanzee groups

common ancestor with chimpanzees and bonobos (or *last common ancestor*) was more chimp-like than bonobo-like. Unfortunately, with no fossil materials available from this ancestor at present, we are left using indirect methods to establish what our common ancestor was like. In agreement with the implicit assumption of many, that the last common ancestor was more chimp-like, some have argued that bonobos are highly divergent and that chimpanzees provide the strongest comparison when identifying derived human traits (e.g., Wrangham and Pilbeam 2001). However, others have argued that, due to certain morphological similarities to humans and lack of climatic fluctuation in the Congo basin, bonobos are likely the species that is more similar to our last common ancestor (de Waal and Lanting 1997). At present there is no definitive proof of which species is more similar to our last common ancestor or whether both species are at the same time highly divergent in some traits but more similar in regard to others (e.g., our last common ancestor possessed a mosaic of bonobo and chimpanzee traits). Therefore, to have the highest level of

confidence when identifying derived human traits, it is desirable to examine this trait in both bonobos and chimpanzees. Moreover, because both chimpanzees and bonobos possess certain traits that are more similar to human traits than they are to one another, direct comparisons between bonobos and chimpanzees can provide a powerful method of testing hypotheses concerning the evolutionary process by which traits have changed between species. To demonstrate the potential power of this comparative approach I first contrast the behavioral ecology of bonobos and chimpanzees, which suggests that the two species may differ in their foraging preferences, temperament and cooperative behavior.

1 Bonobo and Chimpanzee Behavioral Ecology

In many ways, bonobos and chimpanzees are highly similar to each other in their behavior and ecology: Both species are predominantly frugivorous and depend on terrestrial herbs when fruit is scarce; they are semi-terrestrial in that they feed and sleep in trees but range across a relatively large area of tropical forest while traveling on the ground; and they live within large communities (potentially >100 members) that often fissure and fuse into various subgroups depending on the availability of sharable food patches found in large fruiting trees. Like humans, but unlike most other primates, the males of both species stay within their natal group whereas it is females that are more likely to immigrate into a neighboring group around puberty (~9–12 years of age). Finally, the social lives of both species are complicated as they live out life in polygynous multimale-multifemale groups in which mating is promiscuous. Individuals from both species form strong bonds with kin and non-kin within their group, which they must maintain through various affiliative activities so that they might receive support during agonistic interactions (Goodall 1986; Kano 1992; Boesch and Boesch-Achermann 2000).

While it would be easy to concentrate on the many similarities between the two species, there are many striking differences that have also been observed, all of which likely originate from the two species living in geographically distinct habitats for at least one million years (Kano 1992; Boesch et al. 2002). The central difference that has been proposed as driving the speciation of bonobos and chimpanzees is the isolation of bonobos south of the Congo River in forest that allows for a reduction in the intensity of foraging competition due to larger fruit patch size and an increase in the access to terrestrial herbs (White and Wrangham 1988; Wrangham and Peterson 1996; Wrangham 2000). Overall, larger patches of fruit and higher levels of high quality herbs to fall back on when fruit is unavailable reduce the cost of co-feeding and group living for bonobos relative to chimpanzees. Essentially, unlike chimpanzees, bonobos do not need to worry as much about when their next meal will come and whether someone is going to steal it once it does. This difference in food availability across space and time seems to be reflected throughout the social behavior of both species when compared to one another. First, in the wild, it has been observed that reduced foraging competition allows bonobos to form more stable

parties (Kuroda 1980; White 1992; Malenky and Wrangham 1994). It has been suggested that these stable parties, in turn, are associated with lower levels of aggression because females more readily form alliances and are able to prevent male aggression to escalate to the level seen in chimpanzees (Wrangham 1986; Wrangham and Peterson 1996; Wilson et al. 2002). Evidence for less aggression in bonobos relative to chimpanzees can be observed in comparing their dominance style and feeding behavior. First, unlike chimpanzees, where each group has an alpha male, within bonobo groups no single male bonobo or coalition of males has ever been observed to dominate a bonobo social group or coerce females with any measure of success (Kano 1992; Parish 1994; Fuirichi 1997; Vervaecke et al. 1999, 2000; Hohmann and Fruth 2003; Paoli et al. 2006). Meanwhile, unlike chimpanzees, where male-male coalitions are ever-prevalent, a comparison across several captive bonobo groups found that female-female coalitions as opposed to either male-male or male-female coalitions are the most prevalent support pattern observed (Stevens et al. 2006). Finally, unlike chimpanzees, where a male can overpower any female, male bonobos who do occasionally attempt to intimidate females - for example, during food sharing episodes - are in some cases attacked by a coalition of females or in many cases simply ignored in favor of other females or kin (Parish 1994; Vervaecke et al. 1999, 2000; Fruth and Hohmann 2002).

Taken together, these findings indicate that, while bonobos and chimpanzees are similar in many ways, there are major differences between the feeding ecologies and social behaviors of these species that seem to be related to one another causally. It seems likely that the high levels of tolerance and lower levels of competition and aggression in bonobos relative to chimpanzees is a result of the richer environment that bonobos inhabit. One prediction of this hypothesis is that the behavioral differences observed in these two species are a reflection of psychological differences that have evolved to allow each species to make adaptive foraging and social decisions based on the constraints found within the environment in which they evolved. If true, how might one test the prediction that the differing socio-ecologies of these two species have shaped their psychologies?

2 Comparing Bonobo and Chimpanzee Psychology

While it seems plausible that the differing feeding ecologies of bonobos may have led to the higher level of tolerance in this species, at first it might seem unclear how to test this causal relationship directly. In fact there is still dispute about exactly how different bonobos and chimpanzee ecology and behavior really are. Some authors emphasize the differences between bonobos and chimpanzees (De Waal and Lanting, 1997; Wrangham and Pilbeam 2001) whereas other authors argue that many of the purported differences (e.g., high levels of tolerance or higher levels of socio-sexual behavior in bonobos) are actually by-products of captivity (Stanford 1998). One potentially powerful way to resolve such debates is with direct quantitative comparisons of chimpanzees and bonobos using experimental methods.

Below I review recent research comparing the foraging behavior of captive chimpanzees and bonobos in two foraging tasks to test whether their feeding preferences in such games match predicted preferences based on how the natural habitats are believed to differ. In addition, I review experiments that test the causal link between these species' temperaments and social behavior by comparing the ability of each to share food and cooperate.

3 Divergent Foraging Psychology in Bonobos and Chimpanzees

Two of the biggest variables that any animal must contend with when finding food are time and risk. First, foraging requires decisions about how long to exploit resources. Animals must frequently decide whether they wish to continue feeding on an immediately available resource or begin searching for another resource that might be more desirable (i.e., less depleted). Second, finding food also requires choices regarding the level of risk animals are willing to accept when foraging. For example, should a primate take a chance of obtaining the most ripe fruit at the branch tips in tree tops where fruit is of highest quality but more dangerous to obtain or should they remain supported by larger limbs and eat lower quality fruit in order to minimize the risk of falling and serious injury?

While all animals must deal with time and risk when foraging, the best foraging strategy will in large part depend on the environmental niche that a species exploits. In some feeding environments, it may in general be advantageous to be more patient and risk averse, whereas in others, a lower return might be received for these same preferences. For example, common marmosets as gumivores likely need more patience when foraging than cotton top tamarins, which are predominantly insectivores. Stevens et al. (2005) tested this prediction with individuals from each species by giving them the choice between two and six pieces of food that were presented simultaneously. Initially, regardless of their choice, they received either option immediately; however, as the test progressed, a delay was introduced that increased across sessions when the larger option was chosen. Both species preferred the larger option if they could have either option immediately, but as delay to obtaining the large food options increased, different preferences developed. Tamarins quickly lost their preference for the larger option when obtaining it required waiting little more than five seconds, whereas marmosets maintained a preference for the larger option even when the delay was twice as long as that which the tamarins were willing to incur. This species difference in patience likely reflects the fact that the psychology of the two species as it relates to foraging evolved under very different conditions. For tamarins, patience does not pay when food is visible (i.e., mobile insect prey), whereas for marmosets it does (immobile gum). Moreover, this research highlights a potentially powerful way to test for differences in the psychology of animals as they relates to suspected differences in their feeding ecology, with the main premise being that, if two species differ in their feeding ecology, then so too should their psychology involved with making foraging decisions (see also Rosati et al. 2006).

Therefore, we used similar techniques to provide an experimental test of the hypothesis that chimpanzees and bonobos evolved in environments with different feeding ecologies. We compared a group of bonobos and chimpanzees in two foraging tasks that were both administered in identical ways to both species. The first task was based on the task used with the callitrichids just described, whereas the second was similar in that it was a choice task but it measured whether subjects preferred to choose a safe or risky payoff. Based on the behavioral ecological data described for bonobos and chimpanzees, we predicted that chimpanzees would be more patient and risk-prone than bonobos in these experiments. Our rationale for these predictions hinged on the fact that bonobos have access to larger feeding patches and high levels of high-quality fall-back food (e.g., herbs) and thus likely evolved in a similar environment where they infrequently gained by taking risks while foraging. Meanwhile, chimpanzees, which must deal with scarcity more frequently and even often participate in the riskiest forms of foraging (i.e., monkey hunting), likely evolved in an environment where they often gained by taking risks while foraging. In support of the ecological prediction, we first found that, when we gave both species the choice of having two pieces of food now or six pieces of food later, chimpanzees maintained their preference for the larger reward with up to a two-minute delay whereas bonobos began to lose their preference after a one-minute delay was introduced (Figure 3). From this differential temporal discounting rate it was concluded that chimpanzees are willing to assign higher value to future foraging payoffs than bonobos (Rosati et al. 2007). In a second task, we compared the two species' risk preferences. Subjects made a series of choices between a fixed option that always yielded four pieces of food when chosen or a variable option that on some trials yielded one food piece but on other trials yielded seven pieces. Although the variable option had two potential payoffs at either extreme, the two food amounts varied with

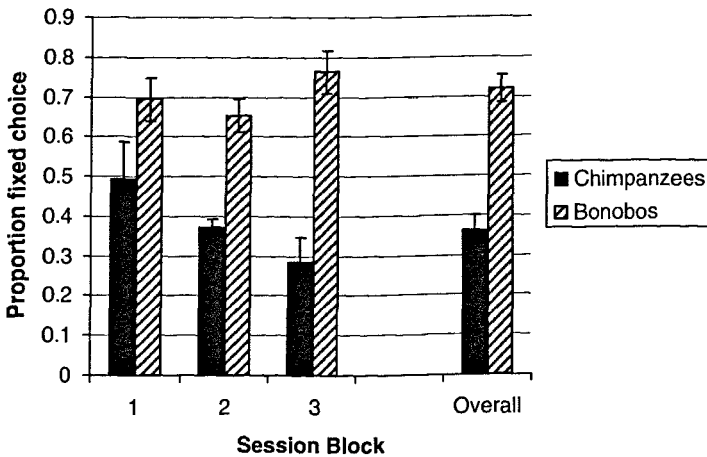


Fig. 3 Patterns of risk preferences in apes across session blocks. Error bars represent standard error. Overall, chimpanzees were significantly risk-seeking, whereas bonobos were significantly risk-averse. Chimpanzees became slightly more risk-seeking as sessions progressed

equal probability. Therefore, the expected values of the two options were equivalent in that a preference for or against either option indicated a sensitivity to risk. Again in support of our predicted species differences, bonobos were risk averse, developing a strong preference for the fixed option, whereas chimpanzees were risk-prone, developing a strong preference for the variable options (Heilbronner et al. 2008).

Taken together, these experimental comparisons between the foraging psychologies of chimpanzees and bonobos suggest that they have very different feeding preferences that map directly onto the differences observed in their feeding ecology. These findings then provide further support to the hypothesis that a variety of differences in bonobo and chimpanzee behavior may have been shaped by the unique challenges their feeding ecologies presented them over evolutionary time. Having established the link between the psychology and feeding ecology of these species, in the next section I discuss a set of test designed to examine whether the differing levels of intra-group competition observed in these two species may have also left a signal in their social psychology.

4 Social Emotions Constrain Primate Cooperation

One of the benefits of living in a social group is that individuals can solve problems with joint action among group mates that any individual alone would be unable to solve. For example, group-living primates often mob predators that are much larger than any individual in the group (e.g., Cheney and Seyfarth 2007). However, while group-living primates frequently act together to defend themselves, their kin or their group mates from predators, non-relatives, or non-group members, the majority of primates in general restrict their cooperative behavior to a few agonistic contexts (Harcourt and de Waal 1992). While naturally occurring cooperation is largely restricted to certain contexts in primates, there is variance among species in their potential to act together in a novel way to solve a novel problem. It has commonly been proposed that there are constraints on cooperative problem solving in primates (Povinelli and O'Neill 2000; Stevens and Hauser 2003; Tomasello et al. 2005), but most recently it has become apparent that species differences in flexible cooperation may in part be a result of constraints created by dominance style. For example, Petit et al. (1992) presented rhesus macaques, with strict dominance hierarchies, and tonkean macaques, with more relaxed hierarchies, with a problem that required joint action to solve it. Sharable amounts of food were placed under heavy rocks that no one monkey could move alone. To obtain the food, at least two monkeys needed to push the stone simultaneously. The more egalitarian tonkean macaques were more successful at producing joint action to retrieve the food than the rhesus, which almost never were able to retrieve the food (only one highly tolerant pair). While the tolerant tonkeans could interact around the stone together, rhesus macaques were simply too inhibited to ever approach the stone while another rhesus was trying to manipulate it. Rhesus macaques could not produce the solution to a novel cooperative problem simply because dominants could not inhibit

their aggression towards other group mates that could have potentially helped them solve the problem.

The “emotional reactivity hypothesis” posits that changes in social emotions that accompany changes in social systems and allow species to interact more or less prosocially can dramatically alter social problem-solving skills across species (Hare and Tomasello 2005). The hypothesis led to the prediction that chimpanzees and bonobos with differing emotional reactions to sharing would also differ in how flexibly they could cooperate to obtain food (Hare et al. 2007). Specifically, the hypothesis predicts that, while both species will be skilled at cooperating in novel tasks, the flexibility of chimpanzee cooperation will be more constrained by intolerance between potential partners than in bonobos, since they do not always share food. Indeed, in support of the prediction, it was found that cooperation was constrained in chimpanzee dyads with low social tolerance (Melis et al. 2006a). Removal of such constraints allowed chimpanzees to show relatively sophisticated cooperation. First, highly tolerant pairs who co-fed tended to spontaneously solve the cooperative food-retrieval task. Second, when these same pairs were tested for whether they understood the role of their partner in solving the cooperative task, they spontaneously recruited a conspecific if they needed help in retrieving the food tray. Third, these same pairs preferentially recruited a more skilful partner over a less skilful partner in the same task (Melis et al. 2006b; also see Hirata and Fuwa 2007). Therefore, although chimpanzees can exhibit sophisticated collaborative skills (i.e., flexible recruitment, coordinated and synchronized efforts, etc.), these abilities are not revealed unless tolerance levels between partners are high (Melis et al. 2006a).

To further understand constraints on the evolution of cooperation, Hare et al. (2007) compared the ability of a group of age- and sex-matched bonobos and chimpanzees to cooperatively solve a food-retrieval problem. First, we indexed emotional reactivity by measuring social tolerance while co-feeding in both bonobos and chimpanzees. Dyads were presented with a food platform that had two food dishes spread 2.7 m apart on either end. Food was baited in one of three ways, varying the degree to which it could potentially be monopolized by one individual: two feeding sites with lots of food, one feeding site with lots of food, or one feeding site with two pieces of food. Based on previous observations we predicted that bonobos would co-feed more than chimpanzees (particularly when food was in one dish and easily monopolized) and would actively reduce social tensions while feeding, especially through socio-sexual behavior and play (Kuroda 1980; de Waal 1989; Enomoto 1990; Kano 1992; Furuichi and Ihobe 1994; Parish 1994; Doran et al. 2002; Hohmann and Fruth 2000, but see Stanford 1998). Our comparison revealed that bonobos were more tolerant of co-feeding than chimpanzees. In addition, during co-feeding tests, only bonobos exhibited socio-sexual behavior, and they played more. Thus, regardless of age, chimpanzees showed little socio-sexual behavior or play. Whereas bonobos interacted with ease, chimpanzees appeared to avoid each other.

After confirming experimentally that bonobos are more tolerant of co-feeding as predicted, we conducted a second experiment in which we tested the cooperative ability of bonobos and chimpanzees by presenting them with an instrumental task that required two individuals to simultaneously pull two separate rope ends to obtain

out-of-reach food. First, we placed the long food platform out of reach of the testing room, baited it with food, and then threaded a rope through two metal loops at either end of the platform. One end of the rope was then placed within reach of each test room. Pulling only one end of the rope was ineffectual, since the rope would come unthreaded from the loops attached to the platform. Thus, subjects could only obtain the food by pulling both ends of the rope simultaneously towards their room. If two subjects did pull both rope ends, they could pull the tray within reach and obtain the food on the platform. Using this method, we compared the ability of both species to 1) work together to obtain sharable food and 2) work together to obtain a highly monopolizable food reward.

Results support the emotional reactivity hypothesis (Fig. 4). First, the chimpanzees had far more experience solving this same cooperative problem than the bonobos, having participated in previous experiments using this same task (i.e., Melis et al. 2006a,b). In contrast, the bonobos were completely naïve to the task before being tested for this comparison. Yet the bonobos were able to cooperate to obtain highly sharable food at the same level as the chimpanzees and were more skilful than chimpanzees when retrieving highly monopolizable food, regardless of their partner. This was the case when examining differential success both when subjects were initially paired with an opposite sex partner and again when subjects in a second round were repaired with a same-sex partner. The findings support the idea that one route by which social problem-solving can evolve is through selection on emotional systems, such as those controlling the expression of fear and aggression (Hare and Tomasello 2005; Hare et al. 2007). Such flexibility is likely an incidental by-product of selection for social systems and the emotions that allow for them that are adapted for dealing with different levels of feeding competition. Therefore, both bonobos and tonkean macaques more readily show cooperative behaviors than their close, but more despotic relatives.

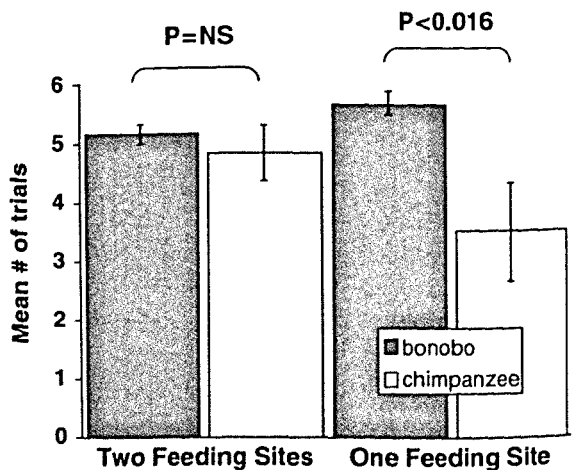


Fig. 4 The mean number (+/- SEM) of trials that pairs of subjects from each species successfully obtained the food platform using cooperation when there were either two feeding dishes or only one

5 Summary and Future Comparisons

Our two closest relatives, the bonobo and chimpanzee, have psychologies that differ in ways that will allow for insights into our own species' evolution. Bonobos live in richer forest and have less intragroup competition over food than chimpanzees. As a result, it has been observed that bonobos in the wild and in captivity are more tolerant in food-sharing contexts than chimpanzees. Based on these differences it has been proposed that 1) each species' psychology will differ, having evolved in response to their differing ecologies and 2) among these psychological differences, it is temperamental differences (levels of emotional reactivity) that are most pronounced and may result in the two species approaching social problems in different ways. First, consistent with the observation that bonobos live in richer environments, bonobos value future food payoffs less than chimpanzees while also avoiding risky foraging decisions that chimpanzees prefer. Second, consistent with lower levels of intergroup competition, it was found that bonobos are capable of more flexible cooperative behavior than chimpanzees if the joint problem requires high levels of tolerance.

Both of these species' differences in foraging preferences and cooperative flexibility support the first proposal above that each species' psychology will differ as a result of their ecology; however, only the finding that tolerance constrains cooperation provides a direct test of the hypothesis that it is temperamental differences that, in part, regulate species differences in problem solving. In this case, we found that cooperation failed in chimpanzees due to social intolerance, even when the two chimpanzees being tested understood that they needed another individual's help to reach their goal. A subordinate might avoid a dominant or a dominant might fail to inhibit her tendency to monopolize a reward. In this way, certain social emotions (elicited during interactions with another animate being) that are normally adaptive in non-cooperative interactions, such as in direct competition over food and mates, potentially limit an individual's or species' behavioural flexibility in approaching novel social problems. Increased behavioral flexibility can result if selection acts on these social emotions so they no longer constrain cooperative interactions. Finally, cognitive evolution can result, if the cognitive ability responsible for the revealed flexibility then itself becomes the target of selection (Hare et al. 2005; Hare 2007).

Therefore, it will be important to consider how the human temperament may be different from other apes and may be in part responsible for human forms of problem-solving (Hare, 2007). However, much more research will be needed if we are to understand the importance of temperamental variables in shaping problem-solving skills. This research will require broad-scale comparisons across a range of species, including non-primates (e.g., Seed et al. 2008; Fidler et al. 2007). In the case of our closest relatives, we will need to compare the emotional reactivity of bonobos and chimpanzees across a range of domains. For example, while we do not have direct evidence yet, future research may reveal that the differing foraging preferences we have found in bonobos and chimpanzees are also regulated by differences in their emotional reactivity. For example, perhaps bonobos in general are more risk averse across a variety of domains due to differences in their emotions'

response to uncertainty. An initial comparison of bonobo, chimpanzee and human children in their response to novelty seems to support this possibility (Herrman et al., in preparation).

The future of any such research program involving bonobos and chimpanzees will depend on the large, semi-captive populations of these apes in sanctuaries in Africa. It is only in such sanctuaries that powerful comparisons between bonobos and chimpanzees can be made, because it is only there that there is the necessary sample size. In the two sanctuaries with which we work, there are almost 60 bonobos and 140 chimpanzees. These sanctuaries provide an unmatched resource not only because of the presence of dozens of young infants of both species that grow up in highly enriched and natural environments (sanctuary apes live together in large social groups in massive tracts of tropical rainforest), but also because they can be tested in a setting similar to a conventional laboratory (indoor enclosures) for a fraction of the cost. By continuing to develop African sanctuaries as world-class resources for researchers, we can look forward to knowing what changed and why during our species' evolution, while simultaneously contributing to the welfare and conservation of the remaining captive and wild populations of our two closest relatives living in their African homes.

Acknowledgments My thanks to Vanessa Woods for providing helpful comments on an earlier version of this manuscript. This research is supported in part by the Humboldt Foundation and the German Federal Ministry for Education and Research.

References

- Boesch C, Boesch-Achermann H. (2000) The chimpanzees of the Tai forest. Oxford: Oxford University Press.
- Boesch B., Hohmann G, Marchant L. (2002) Behavioral Diversity of Chimpanzees and Bonobos, Cambridge, Cambridge University Press.
- Cheney D, Seyfarth R (2007) Baboon metaphysics. Chicago, Chicago University Press.
- de Waal F, Lanting F (1997) Bonobo: the forgotten ape. Berkeley, University of California Press.
- de Waal FBM, Davis JM (2003) Capuchin cognitive ecology: cooperation based on projected returns. *Neuropsychologia* 41:221–228.
- de Waal F (1989) Behavioral contrasts between bonobo and chimpanzee. In: Marquardt p (ed) Understanding chimpanzees. Cambridge, Harvard University Press, pp. 154–175.
- Doran D, Jungers W, Sugiyama Y, Fleagle J, Heesy C (2002) Multivariate and phylogenetic approaches to understanding chimpanzee and bonobo behavioral diversity. In: Boesch C, Hohmann G, Marchant L (eds) Behavioral diversity in chimpanzees and bonobos, Cambridge, Cambridge University Press, pp. 14–34.
- Enomoto T (1990) Social play and sexual behavior of the bonobo (*Pan paniscus*) with special reference to flexibility. *Primates* 31:469–480.
- Fidler A, Oers K, Drent P, Kuhn S, Mueller J, Kempanaers B (2007) Drd4 gene polymorphisms are associated with personality variation in a passerine bird. *Proc Biol Sci* 274:1685–1681.
- Fruth B, Hohmann G (2002) How bonobos handle hunts and harvests: why share food? In: Boesch C, Hohmann G, Marchant L (eds) Behavioral diversity in chimpanzees and bonobos, Cambridge, Cambridge University Press, pp. 231–243.

- Furuichi T (1997). Agonistic Interactions and Matrifocal Dominance Rank of Wild Bonobos (*Pan paniscus*) at Wamba. *Int J Primatol* 18, 855–875.
- Furuichi T, Ihobe H (1994) Variation in male relationships in bonobos and chimpanzees. *Behaviour* 130:211–228.
- Goodall J (1986) *The chimpanzees of Gombe: patterns of behaviour*. Cambridge, MA, Harvard University Press.
- Harcourt A, de Waal F (1992) *Coalitions and alliances in humans and other animals*. Oxford, Oxford University Press.
- Hare B (2007) From nonhuman to human mind: what changed and why. *Curr Directions Psychol Sci* 16:60–64.
- Hare B, Tomasello M (2005) Human-like social skills in dogs? *Trends Cogn Sci* 9:439–444.
- Hare B, Plyusnina I, Ignacio N, Schepina O, Stepika A, Wrangham R, Trut L (2005) Social cognitive evolution in captive foxes is a correlated by-product of experimental domestication. *Curr Biol* 15:226–230.
- Hare B, Melis A, Woods V, Hastings S, Wrangham R (2007) Tolerance allows bonobos to outperform chimpanzees in a cooperative task. *Curr Biol* 17:619–623.
- Heilbronner S, Rosati A, Stevens J, Hare B, Hauser M (2008) A fruit in the hand or two in the bush? Ecological pressures select for divergent risk preferences in chimpanzees and bonobos. *Biol Lett* 4:246–249.
- Hirata S, Fuwa K (2007) Chimpanzees learn to act with other individuals in a cooperative task. *Primates* 48: 13–21.
- Hohmann G, Fruth B (2000) Use and function of genital contact among female bonobos. *Anim Behav* 60:107–120.
- Hohmann G, Fruth B (2003) Culture in bonobos? Between-species and within-species variation in behavior. *Curr Anthropol* 44:563–609.
- Jensen K, Hare B, Call J, Tomasello M (2006) Are chimpanzees spiteful or altruistic when sharing food? *Proc Royal Soc B* 273:1013–1021.
- Kano T (1989) The sexual behavior of pygmy chimpanzees. In: Heltne PG, Marquardt LA (eds) *Understanding chimpanzees*. Cambridge, Harvard University Press, pp. 176–183.
- Kano T (1992) *The last ape: pygmy chimpanzee behavior and ecology*. Stanford, CA, Stanford University Press.
- Kuroda S (1980) Social behavior of the pygmy chimpanzees. *Primates* 21:181–197.
- Malenky R, Wrangham R (1994) A quantitative comparison of terrestrial herbaceous food consumption by *Pan paniscus* in the Lomako Forest, Zaire, and *Pan troglodytes* in Kibale forest, Uganda. *Am J Primatol* 32:1–12.
- Melis A, Hare B, Tomasello M (2006a) Engineering chimpanzee cooperation: social tolerance constrains cooperation. *Anim Behav* 72:275–286.
- Melis A, Hare B, Tomasello M (2006b) Chimpanzees recruit the best collaborators. *Science* 311:1297–1300.
- Paoli T, Palagi E, Borgognini Tarli SM (2006) Reevaluation of dominance hierarchy in bonobos (*Pan paniscus*). *Am J Phys Anthropol* 130:116–122.
- Parish A (1994) Female relationships in bonobos (*Pan paniscus*): evidence for bonding, cooperation, and female dominance in a male-philopatric species. *Human Nature* 7:61–96.
- Petit O, Desportes C, Thierry B (1992) Differential probability of coproduction in two species of macaque (*Macaca tonkeana*, *M. mulatta*). *Ethology* 90:107–120.
- Povinelli DJ, O'Neill, DK (2000) Do chimpanzees use their gestures to instruct each other? In: Baron-Cohen S, Tager-Flusberg H, Cohen DJ (eds) *Understanding other minds. Perspectives from developmental cognitive neuroscience*. Oxford University Press pp. 459–487.
- Rosati A, Stevens J, Hauser M (2006) The effect of handling time on temporal discounting in two New World primates. *Anim Behav* 71:1379–1387.
- Rosati A, Stevens J, Hare B, Hauser H (2007) The origins of human patience. *Curr Biol* 17:1–6.
- Ruvolo M (1997) Molecular phylogeny of the hominoids: inferences from multiple independent DNA sequence data sets. *Mol Biol Evol* 14:248–265.

- Stanford CB (1998) The social behavior of chimpanzees and bonobos: empirical evidence and shifting assumptions. *Curr Anthropol* 39:399–407.
- Stanford CB (1999) The social behavior of chimpanzees and bonobos - empirical evidence and shifting assumptions. *Curr Anthropol* 39:399–420.
- Seed A, Clayton N, Emery N (2008) Cooperative problem solving in rooks (*Corvus frugilegus*). *Proc Biol Sci* 275:1421–1429.
- Stevens J, Hauser M (2004) Why be nice? Psychological constraints on the Evolution of cooperation. *Trends Cogn Sci* 8, 60.
- Stevens J, Hallinan EV, Hauser MD (2005) The ecology and evolution of patience in two new world primates. *Biol Lett* 1:223–226.
- Stevens J, Vervaecke H, de Vries H, van Elsacker L (2006) Social structures in *Pan paniscus*: testing the female bonding hypothesis. *Primates* 47:210–217.
- Tomasello M, Call J (1997) *Primate cognition*. Cambridge, Oxford University Press.
- Tomasello M, Carpenter M, Call J, Behne T, Moll H (2005) Understanding and sharing intentions: The origins of cultural cognition. *Behav Brain Sci* 28: 675–691.
- Verwaecke H, De Vries H, van Elsacker L (1999) An experimental evaluation of the Consistency of competitive ability and agonistic dominance in different social contexts in captive bonobos. *Behaviour* 136:423–442.
- Verwaecke H, De Vries, van Elsacker L (2000) Function and distribution of coalitions in captive bonobos (*Pan paniscus*). *Primates* 41:249–265.
- White FJ (1992) Pygmy chimpanzee social organization: variation with party size and between study sites. *Am J Primatol* 26:203–214.
- White FJ, Wrangham RW (1988) Feeding competition and patch size in the chimpanzee species *Pan paniscus* and *Pan troglodytes*. *Behaviour* 105, 148–164.
- Wilson ML, Britton NF, Franks NR (2002). Chimpanzees and the mathematics of battle. *Proc Royal Soc London* 269:1107–1112.
- Wrangham RW, Peterson D (1996) *Demonic males: apes and the origins of violence*. Boston, MA, Houghton Mifflin.
- Wrangham RW (1986) Ecology and social relationships in two species of chimpanzee. In Rubenstein DI, Wrangham RW (eds), *Ecological Aspects of Social Evolution in Birds and Mammals*. Princeton NJ: Princeton University Press, pp 354–378.
- Wrangham RW (2000) Why are male chimpanzees more gregarious than mothers? Ascrumble competition hypothesis. In: Kappeler P (ed) *Primate Males*. Cambridge, Cambridge University Press, pp. 248–258.
- Wrangham R, Pilbeam D (2001) African apes as time machines. In: All Apes Great and Small. Birutė M.F. Galdikas, Nancy Erickson Briggs, Lori K. Sheeran, Gary L. Shapiro, Jane Goodall (eds) New York, Kluwer Academic/Plenum, pp. 5–18.
- Won Y, Hey J (2005) Divergent populations genetics of chimpanzees. *J Mol Biol Evol* 22:297–307.