

Tolerance Allows Bonobos to Outperform Chimpanzees on a Cooperative Task

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Summary

To understand constraints on the evolution of cooperation, we compared the ability of bonobos and chimpanzees to cooperatively solve a food-retrieval problem. We addressed two hypotheses. The “emotional-reactivity hypothesis” predicts that bonobos will cooperate more successfully because tolerance levels are higher in bonobos. This prediction is inspired by studies of domesticated animals; such studies suggest that selection on emotional reactivity can influence the ability to solve social problems [1, 2]. In contrast, the “hunting hypothesis” predicts that chimpanzees will cooperate more successfully because only chimpanzees have been reported to cooperatively hunt in the wild [3–5]. We indexed emotional reactivity by measuring social tolerance while the animals were cofeeding and found that bonobos were more tolerant of cofeeding than chimpanzees. In addition, during cofeeding tests only bonobos exhibited socio-sexual behavior, and they played more. When presented with a task of retrieving food that was difficult to monopolize, bonobos and chimpanzees were equally cooperative. However, when the food reward was highly monopolizable, bonobos were more successful than chimpanzees at cooperating to retrieve it. These results support the emotional-reactivity hypothesis. Selection on temperament may in part explain the variance in cooperative ability across species, including hominoids.

Results and Discussion

In experiment 1, we compared social tolerance between bonobos and chimpanzees by measuring cofeeding within bonobo dyads in the same way it was previously assessed in chimpanzees [6]. Dyads were presented with a food platform that had two food dishes spread apart 2.7 m on either end. Food was baited in one of three ways: (1) dispersed-divisible: both food dishes were baited with approximately 0.25 kg of sliced fruit; (2) clumped-divisible: one food dish was empty, and

the other was baited with 0.5 kg of sliced fruit; or (3) clumped: one food dish was empty, and the other was baited with two pieces of fruit. Previous observations led us to predict that bonobos would cofeed more than chimpanzees (particularly when food was in one dish and easily monopolizable) and would actively reduce social tensions while feeding, especially through socio-sexual behavior and play ([7–14], but see [15]).

Bonobos were indeed more tolerant than chimpanzees. Figure 1 shows that when the three food conditions are considered together, bonobos cofed more often than chimpanzees: bonobos cofed in an average of 4.4 trials, versus 2.8 trials for chimpanzees [$t(24) = 3.38$, $p = 0.002$, independent t test; Figure 1]. This difference was especially pronounced in the four trials in which food was placed in a single dish (clumped-divisible and clumped conditions). In this context, bonobos cofed an average of 2.4 trials, whereas chimpanzees cofed in only one trial ($t(24) = 3.52$, $p < 0.001$, independent t test; Supplemental Data available online). Social behavior showed similar trends. During the cofeeding experiment, bonobos showed no aggression and exhibited significantly more socio-sexual behavior [$t(9) = 2.512$, $p < 0.017$, Welch independent t test] and play behavior [$t(9.144) = 2.330$, $p < 0.022$, Welch independent t test] than the chimpanzees (Figure 1). These differences cannot be explained by age because the estimated ages of the bonobos (mean 9.6 years) and chimpanzees (mean 11.6 years) did not differ significantly ($p > 0.2$, independent t test). Thus, regardless of age, chimpanzees showed little socio-sexual behavior, play, or aggression. Whereas bonobos interacted with ease, chimpanzees appeared to avoid each other.

In experiment 2, we tested cooperative ability by presenting a group of bonobos with a novel cooperative task previously presented to a group of chimpanzees by Melis and colleagues [6]. Sharable amounts of food were placed in both food dishes on the food platform (as in the dispersed-divisible condition of experiment 1). The food platform was then placed 1 m out of the subjects' reach. In order to bring the food platform within reach, the subjects had to cooperate by simultaneously pulling a rope (Figure 2; Supplemental Data). Importantly, in experiment 1, the two species did not differ in their tendency to cofeed when the food was dispersed and divisible (all bonobo and chimpanzee pairs tested cofed in both trials, except three chimpanzee pairs, two of which cofed in one trial each, Supplemental Data). Therefore, the emotional reactivity hypothesis predicts no difference between the two species' ability to spontaneously cooperate to obtain out-of-reach food that both species are equally capable of sharing by cofeeding. However, the hunting hypothesis predicts that chimpanzees should be more skilful at cooperating to obtain the food because only they have been reported to solve analogous problems in the wild by working together to obtain food that is otherwise unobtainable (i.e., via cooperative hunting).

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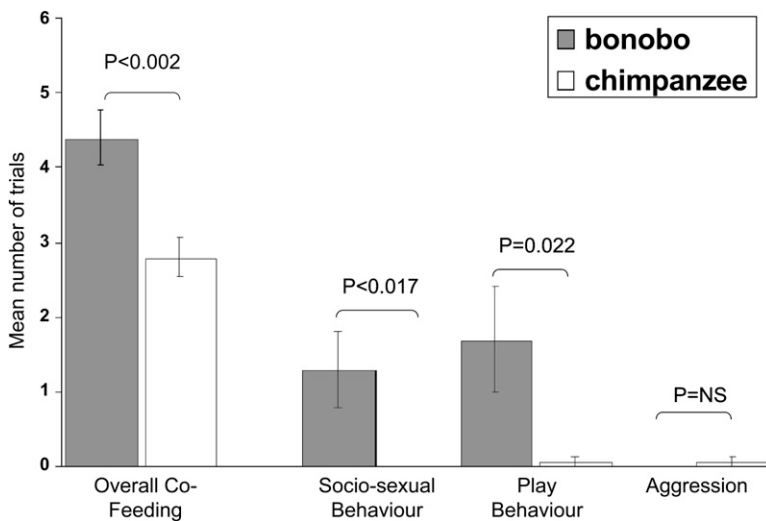


Figure 1. The Mean Number of Trials in which Ten Pairs of Bonobos and 16 Pairs of Chimpanzees Co-Fed and Engaged in Socio-Sexual, Play, and Aggressive Behavior in the Co-Feeding Test in Experiment 1

Error bars indicate standard error of the mean.

In support of the emotional-reactivity hypothesis, there was no difference between the species' ability to cooperate spontaneously to obtain divisible-dispersed food (mean success \pm SEM: bonobos = 1.5 ± 0.65 , chimpanzees = 2 ± 0.48 ; $p > 0.5$, independent t test; [Supplemental Data](#)). Overall, 50% of bonobo pairs (4/8) and 69% of chimpanzee pairs (11/16) spontaneously solved the task at least once within the six-trial test session.

To further test whether tolerance affects cooperative flexibility, we conducted a third experiment one year later to compare the cooperative ability of both species when they had to (a) work together to obtain sharable food, as in experiment 2, and (b) work together to obtain a highly monopolizable food reward. The emotional-reactivity hypothesis predicts that (1) both species will remain equally skilful at cooperating to obtain sharable food (divisible-dispersed) and (2) the bonobos will be more skilful at cooperating to obtain monopolizable

food (clumped) because they have higher levels of social tolerance in this context.

Results ([Figure 3](#)) support the emotional-reactivity hypothesis. First, five of six dyads of chimpanzees had far more experience solving this same cooperative problem because they had participated in additional experiments between the second and third experiments ([16]; A.M. et al., unpublished data). In contrast, the bonobos had no additional experience except a few warm-up trials (range 0–13 trials). Yet the bonobos, in replication of the findings of experiment 2, were again able to cooperate to obtain divisible and dispersed food (highly sharable) at the same level as the chimpanzees [$t(10) = 0.66$, $p =$ not significant, independent t test; [Supplemental Data](#)]. Moreover, the bonobos were more skilful than chimpanzees at retrieving clumped food that was highly monopolizable—regardless of their partner. This was the case both when we examined differential success

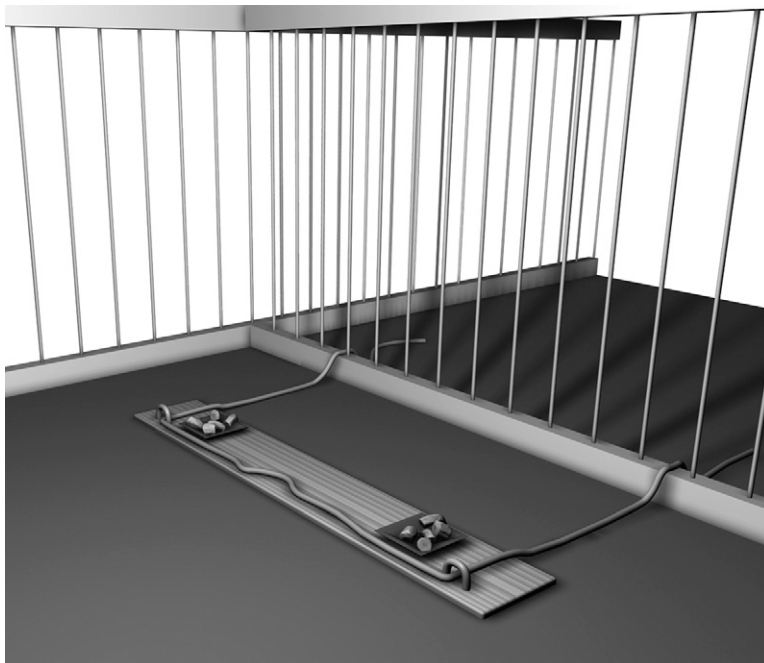


Figure 2. Experimental Setup

The figure shows the baited food platform, metal loops, threaded rope extended into the test room, room layout used in the two studies, and placement of the food platform. In experiment 3, a third food dish was placed in the middle of the platform. The cooperation apparatus, a methodological breakthrough developed by Hirata and Fuwa [20], consisted of a long flat food platform (17 cm \times 3.4 m) placed outside the subjects' testing room. Food could be placed on wooden dishes (17 cm \times 27 cm) on the ends of the food platform. A rope (7.6 m) could be placed through loops on top of and across the length of the platform, so that both ends of the rope extended from the platform through the metal bars into the testing room. Pulling only one end of the rope was ineffectual because the rope would come out of the loops attached to the platform. Thus, subjects could only obtain the food by pulling both ends of the rope simultaneously toward their room (or by pulling one end while holding the other one). Once the food platform was close enough to their room, they could reach through the metal bars and obtain the food. From Melis et al., 2006b [16]. Figure published with permission from AAAS.

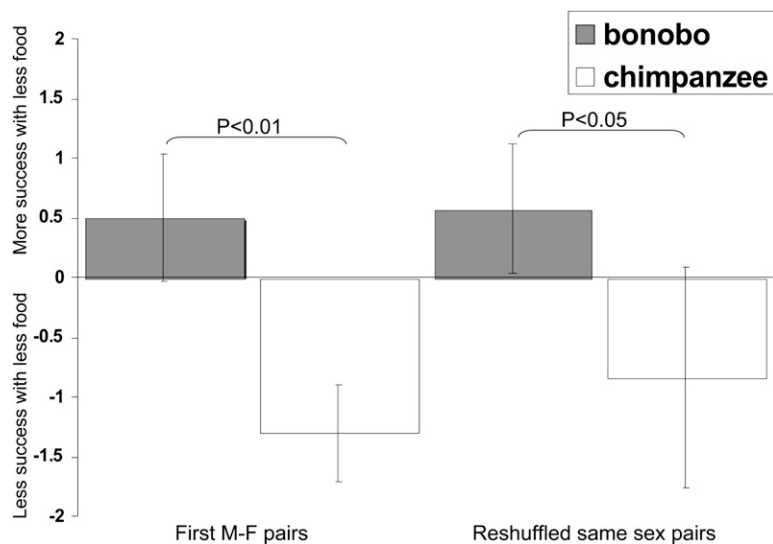


Figure 3. Species Difference in the Probability of Cooperation as a Function of Food Condition in Experiment 3

Histograms show the mean difference, calculated as difference scores, for the number of trials in which subjects cooperated in the dispersed-divisible condition (highly sharable) versus the clumped condition (highly monopolizable). Data are shown for (left) individuals with their original opposite-sex partner and (right) with their new same-sex partner. Error bars indicate standard error of the mean.

when subjects were initially paired with an opposite sex partner [$t(10) = 2.8$, $p < 0.01$, independent t test; [Supplemental Data](#)] and when we examined subjects that were re-paired with a same-sex partner in a second round [$t(10) = 1.9$, $p < 0.05$, independent t test; [Supplemental Data](#)]. Critically, in clumped-food trials in which dyads cooperated, a single chimpanzee partner monopolized the food more often than a single bonobo did [round 1: $t(8) = 4.5$, $p < 0.001$; round 2: $t(8) = 7$, $p < 0.001$]. When a pair had successfully cooperated to retrieve the food, one chimpanzee monopolized 93% (range 93%–100%) of the food pieces in both rounds, whereas no bonobo ever took more than 68% of the total food pieces retrieved by the pair (range 50%–68%). Again, there was no significant difference between the ages of the two groups tested (mean estimated age in round 1: bonobo, 7.9 and chimpanzee, 7.5. In round 2: bonobo, 7.1 and chimpanzee, 9; independent t test $p > 0.5$; [Supplemental Data](#)).

Discussion

This study provides the first experimental comparison of social tolerance and cooperation in chimpanzees and bonobos. As anticipated from observational studies, bonobos proved more tolerant while cofeeding than chimpanzees. When challenged to cooperate to obtain sharable food, bonobos and chimpanzees were equally successful. But in tests with monopolizable food, bonobos were more successful at cooperating than chimpanzees. This success translated across different partners; bonobos outperformed chimpanzees even when both groups were re-paired with a second, same-sex partner. All of the chimpanzee pairs tested were among the most tolerant dyads within their social group ([6]; [Supplemental Data](#)) and had performed as well as the bonobos in cooperating to obtain highly sharable food. Five of the pairs had even previously participated in experiments demonstrating that they understood exactly what was required to solve this same task ([16]; A.M. et al., unpublished data). In addition, the differences in performance between species were not due to differences in age, relations between the sexes, or experience. Finally, in

experiment 3 one chimpanzee in each pair tended to monopolize the entire clumped-food reward, whereas the bonobos did not, suggesting that cooperation between even the most tolerant chimpanzees is vulnerable to defection by unrewarded subordinates.

Thus, although the two species were equally successful at cooperating when food was sharable, when food was monopolizable, bonobos cooperated more often and more effectively (i.e., after successful cooperation, bonobos co-fed more). This result conflicts with the hunting hypothesis because, unlike chimpanzees, bonobos in the wild have not been reported to cooperate to obtain otherwise unobtainable food [5].

However, our results do support the emotional-reactivity hypothesis. This hypothesis suggests 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 [2, 17, 18]. The hypothesis was initially suggested by the finding that foxes that have been selected for reduced fear and aggression toward humans are more skilled at using human gestures to find food than foxes from a control population ([1, 18], and see [19] for a related example in chimpanzees). The hypothesis was subsequently supported by Melis et al. [6], who found that cooperation was constrained in chimpanzee dyads with low social tolerance. 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 ([16]; also see [20, 21]). 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 is high [6]. The current result further supports the emotional-reactivity hypothesis by demonstrating that bonobos, with their tolerance

levels relative to those of chimpanzees, can outperform even the most tolerant and experienced chimpanzees on a cooperative task when the reward of joint effort is monopolizable.

In summary, our results suggest that cooperation may fail as a result of social intolerance even when two individuals understand that they need another individual's help to solve a problem. A subordinate may avoid a dominant, or a dominant may 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 noncooperative interactions, such as direct competition over food and mates, potentially limit an individual's or species' behavioral flexibility in approaching novel social problems. Increased behavioral flexibility can result if selection acts on these social emotions so that 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 [2, 17].

Such selection could occur for reasons unrelated to cooperative ability. For example, selection for tameness appears to be responsible for enhanced abilities to use human gestures in domesticated foxes [1]. Analogously, Wrangham and Pilbeam [22] suggested that bonobos evolved from a chimpanzee-like ancestor primarily by selection against aggressiveness; if so, this may have paved the way for enhanced social tolerance and cooperative ability in this experimental setting. In the case of humans, our species' unique forms of cooperative behavior may likewise have been catalysed not merely by greater intelligence but also by increased social tolerance or prosociality [2, 17].

Further research is necessary to allow us to understand how increased tolerance in bonobos may result in flexible cooperation; it will be important to examine the bonobos' understanding of the collaborative nature of novel social tasks as in [16] and to examine their naturally occurring behavior. There is also the exciting possibility of replicating the current experiments with a larger sample of adults and juveniles so that the levels of cooperation between the different sexes and age classes can be more fully tested. Such testing might shed light on whether bonobos and chimpanzees differ substantially in male-male, male-female, and female-female relationships, as has been previously suggested (e.g., [11]). Such research will be crucial for determining whether differences in levels of hominoid prosociality are due to heritable differences in neurophysiology, as has been recently suggested (cf. [23, 24]). Further research on the differences between bonobos and chimpanzees offers an unprecedented opportunity to understand why these two sister species differ and how and why our own lineage became so divergent.

Experimental Procedures

In experiments 1 and 2, the performance of 20 bonobos living at Lola ya Bonobo Sanctuary in the Democratic Republic of Congo was compared to that of 32 chimpanzees previously studied at the Ngamba Chimpanzee Sanctuary in Uganda. Before this study, none of the apes had participated in an experiment requiring them to cooperate (see Supplemental Data for the age and sex of subjects in each dyad). Subjects were first tested as pairs for their

ability to co-feed. Each pair was tested in six trials (two trials with each of the three conditions described above). The food platform was placed against the metal bars of the subjects' test room. Once the platform was baited, subjects were released into the test room to retrieve the food. Subjects' behavior was coded for whether they both fed in each trial and whether they had playful, socio-sexual, or aggressive interactions (see Supplemental Data for operationalized definitions). Before experiment 2, subjects were individually introduced to the cooperation apparatus. Food was placed in the two food dishes so that the subjects could retrieve the food if they pulled both ends of a rope that was threaded through two loops attached to the food platform (pulling one end resulted in failure because the rope came unthreaded). Finally, in experiment 2 each dyad participated in only six cooperation test trials. Once the food tray was baited and out-of-reach, the rope was placed so that one individual could not reach both ends simultaneously, i.e., success required cooperation (Figure 2). When subjects were released, they had the opportunity to pull the rope simultaneously to successfully obtain the food. Failure resulted if only one end of the rope was pulled or if the tray was not retrieved within 5 min.

A subset of 12 bonobos and 12 chimpanzees compared in experiments 1 and 2 were again tested in experiment 3. Bonobo pairs were selected to match the age and sex of the most tolerant chimpanzee pairs from the previous Ngamba sample from experiments 1 and 2 (see Supplemental Data). Importantly, the Ngamba chimpanzees had gained additional experience while participating in similar experiment tasks previously ([16]; A.M. et al., unpublished data), whereas the bonobos, having only participated in experiment 1 a year before, remained naive. Therefore, after bonobos were given a very brief warm-up (see Supplemental Data), pairs of subjects were tested in two sessions of six trials. In the first session, as in experiment 1, food was highly sharable and placed in both dishes (the dispersed-divisible condition). In the second session, only four small pieces of food were placed in one center dish (clumped condition). Once the platform was baited, to avoid the bonobos' being distracted by humans operating the doors into the testing room, as in experiments 1 and 2, the rope ends were simply thrown within reach of subjects as they were waiting in the testing room (this new procedure was used with both species). Subjects were then given 1 min to obtain the food by pulling the rope. The procedure used in the second session was then repeated on a third day after each subject was paired with a new partner (from one of the twelve subjects who participated in the first session), and their ability to obtain the monopolizable food was tested. Therefore, each subject received 18 test trials (Supplemental Data). All pairs (except one chimpanzee pair) were male-female dyad in the first round, and all pairs in the second round were same-sex pairs.

Supplemental Data

Supplemental Data include Experimental Procedures and four tables and are available online at <http://www.current-biology.com/cgi/content/full/17/7/619/DC1/>.

Acknowledgments

We are grateful to both sanctuaries for hosting our research. At Lola ya Bonobo Sanctuary (www.friendsofbonobos.org), we are thankful to Claudine Andre, Dominique Morel, Crispin Kamate Mahamba, and Pierrot Mbonzo for their enthusiasm and support for our research in collaboration with the Ministry of Environment. In particular, we appreciate the hard work of the animal caregivers: John Claude Nzumbi, Stany Mokando, Claude Paluku, Amos Kisungu, Philippe Kunaka, N'dombe Luvualu, and Kadogo Manzambi. At Ngamba Island Chimpanzee Sanctuary (www.ngambaisland.org), we thank Lilly Ajarova, Debby Cox, Richard Ssunna, and the trustees for their help and support in collaboration with the Ugandan National Council for Science and Technology and the Uganda Wildlife Authority. In particular, we appreciate the hard work of the animal caregivers: McAnthony Gum, Paul Kibirege, Isaac Mujaasi, Lawrence Mugisha, Mandy Musumba, Gerald Muyingo, Amos Okello, Robert Okello, and Stany Nyandwi. The research of B.H. and A.P.M. is supported by a Sofja Kovalevskaja award received from The Alexander von Humboldt Foundation and the German Federal Ministry for Education

and Research. Finally, we thank two anonymous reviewers who provided valuable and constructive comments that led to a much improved paper.

Received: January 11, 2007

Revised: January 30, 2007

Accepted: February 1, 2007

Published online: March 8, 2007

References

1. Hare, B., Plyusnina, I., Ignacio, N., Schepina, O., Stepika, A., Wrangham, R., and Trut, L. (2005). Social cognitive evolution in captive foxes is a correlated by-product of experimental domestication. *Curr. Biol.* *15*, 226–230.
2. Hare, B., and Tomasello, M. (2005). Human-like social skills in dogs? *Trends Cogn. Scin* *9*, 439–444.
3. Mitani, J., and Watts, D. (2001). Why do chimpanzees hunt and share meat? *Anim. Behav.* *61*, 915–924.
4. Boesch, C., and Boesch-Achermann, H. (2000). *The Chimpanzees of the Tai Forest* (Oxford, UK: Oxford University Press).
5. Fruth, B., and Hohmann, G. (2002). How bonobos handle hunts and harvests: Why share food? In *Behavioral Diversity in Chimpanzees and Bonobos*. C. Boesch, G. Hohmann, and L. Marchant, eds. (Cambridge, UK: Cambridge University Press), pp. 231–243.
6. Melis, A., Hare, B., and Tomasello, M. (2006). Engineering cooperation in chimpanzees: Tolerance constraints on cooperation. *Anim. Behav.* *72*, 275–286.
7. Kuroda, S. (1980). Social behavior of the pygmy chimpanzees. *Primates* *21*, 181–197.
8. de Waal, F. (1989). Behavioral contrasts between bonobo and chimpanzee. In *Understanding Chimpanzees*, P. Marquardt, ed. (Cambridge, MA: Harvard University Press), pp. 154–175.
9. Enomoto, T. (1990). Social play and sexual behavior of the bonobo (*Pan paniscus*) with special reference to flexibility. *Primates* *31*, 469–480.
10. Kano, T. (1992). *The Last Ape: Pygmy Chimpanzee Behavior and Ecology* (Stanford, CA: Stanford University Press).
11. Furuichi, T., and Hobe, H. (1994). Variation in male relationships in bonobos and chimpanzees. *Behaviour* *130*, 211–228.
12. Parish, A. (1994). Female relationships in bonobos (*Pan paniscus*): Evidence for bonding, cooperation, and female dominance in a male-philopatric species. *Hum. Nat.* *7*, 61–96.
13. Doran, D., Jungers, W., Sugiyama, Y., Fleagle, J., and Heesy, C. (2002). Multivariate and phylogenetic approaches to understanding chimpanzee and bonobo behavioral diversity. In *Behavioral Diversity in Chimpanzees and Bonobos*, C. Boesch, G. Hohmann, and L. Marchant, eds. (Cambridge, UK: Cambridge University Press), pp. 14–34.
14. Hohmann, G., and Fruth, B. (2000). Use and function of genital contact among female bonobos. *Anim. Behav.* *60*, 107–120.
15. Stanford, C.B. (1999). The social behavior of chimpanzees and bonobos—empirical evidence and shifting assumptions. *Curr. Anthropol.* *39*, 399–420.
16. Melis, A., Hare, B., and Tomasello, M. (2006b). Chimpanzees recruit the best collaborators. *Science* *311*, 1297–1300.
17. Hare, B. (2007). From nonhuman to human mind: What changed and why? *Current Directions in Psychological Science*, in press.
18. Trut, L. (1999). Early canid domestication: the farm-fox experiment. *Am. Sci.* *87*, 160–169.
19. Hare, B., and Tomasello, M. (2004). Chimpanzees are more skilful in competitive than cooperative cognitive tasks. *Anim. Behav.* *68*, 571–581.
20. Hirata, S., and Fuwa, K. (2007). Chimpanzees learn to act with other individuals in a cooperative task. *Primates* *48*, 13–21.
21. de Waal, F., and Davis, J. (2003). Capuchin cognitive ecology: Cooperation based on projected returns. *Neuropsychologia* *41*, 221–228.
22. Wrangham, R., and Pilbeam, D. (2001). African apes as time machines. In *All Apes Great and Small* (New York: Klavier Academics/Plenum Press Publishers), pp. 5–17.
23. Hammock, E., and Young, L. (2005). Microsatellite instability generates diversity in brain and sociobehavioral traits. *Science* *308*, 1630–1634.
24. Semediferi, K., Armstrong, E., Schleicher, A., Zilles, K., and van Hoesen, G.W. (1998). Limbic frontal cortex in hominoids: A comparative study of area 13. *Am. J. Phys. Anthropol.* *106*, 129–155.