Bonobos Exhibit Delayed Development of Social Behavior and Cognition Relative to Chimpanzees

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Bonobos exhibit delayed development of social behavior and cognition relative to chimpanzees

Victoria Wobber[1]

Richard Wrangham[1]

Brian Hare[2]

[1]Department of Human Evolutionary Biology, Harvard University, 11 Divinity Ave, Cambridge MA 02138.

[2]Department of Evolutionary Anthropology and Center for Cognitive Neuroscience, Duke University, 125 Biological Sciences Drive, Durham NC 27708.

corresponding author: wobber@fas.harvard.edu

RUNNING HEAD: Delayed development in bonobos

Summary

Phenotypic changes between species can occur when evolution shapes development. Here, we tested whether differences in the social behavior and cognition of bonobos and chimpanzees derive from shifts in their ontogeny, looking at behaviors pertaining to feeding competition in particular. We found that as chimpanzees (n = 30) reached adulthood they became increasingly intolerant of sharing food, whereas as adults, bonobos (n = 24) maintained high, juvenile levels of food-related tolerance. We also investigated the ontogeny of inhibition during feeding competition. In two different tests, we found that bonobos (n = 30) exhibited developmental delays relative to chimpanzees (n = 29) in the acquisition of social inhibition, with these differences resulting in less skill among adult bonobos. The results suggest that these social and cognitive differences between two closely related species result from evolutionary changes in brain development.

Highlights

Chimpanzees decrease in inter-individual tolerance with age; bonobos do not.

Chimpanzees outperform same-age bonobos in tasks of social inhibitory control.

Species differences in behavior may correlate with changes in brain development.

The same developmental pathway may mediate the ontogeny of numerous traits.

Results and Discussion

Bonobos and chimpanzees differ extensively in their morphology, physiology, behavior, and cognition, despite the two species having diverged relatively recently (2.5 to 0.85 mya) [1-4]. Their differences are thought to arise partly from shifts in developmental pathways. Relative to chimpanzees, bonobos have been shown to exhibit paedomorphism (retention of ancestrally juvenile traits into adulthood) in aspects of their cranial morphology [5]. Bonobos also appear to retain juvenile levels of play and non-conceptive sexual behavior into adulthood, characteristics that facilitate high inter-individual tolerance among adults when sharing food or cooperation in solving social problems [6-11]. However, there has been no direct test of the hypothesis that certain aspects of behavior or cognition in adult bonobos represent developmentally delayed forms of the traits found in chimpanzees. We tested this hypothesis by comparing the skills of semi free-ranging infant, juvenile and adult bonobos and chimpanzees in three tasks related to feeding competition, given the prediction that this area in particular differs between the two species.

Experiment 1 Inter-individual tolerance

In our first experiment, we examined inter-individual tolerance in competition for food. To assess whether bonobos' high levels of tolerance are in part a result of developmental delay, we administered a dyadic food sharing task similar to that used previously [6, distinctions in methodology outlined in Supplemental Online Methods] to 15 pairs of chimpanzees and 12 pairs of bonobos of varying age (mean dyad age in years ($\pm$ SEM): bonobos = 9.0 ($\pm$1.1), chimpanzees = 9.3 ($\pm$0.8), independent samples t-test, p = NS).

Subjects were paired with similarly aged partners. Equal numbers of male-male, male-female, and female-female dyads were tested (details in Supplemental Table 2). Each dyad received 9 trials of a food sharing task. There were 3 trial types, varying the food configuration in terms of the degree to which food could be monopolized. For each trial two measures of tolerant feeding behavior were coded: 1) *sharing* – both subjects obtained food; 2) *co-feeding* – subjects fed from the same food source simultaneously. Play and sexual behavior were also coded in each trial (Supplemental Online Material).

Chimpanzees showed a significant negative relationship between average dyad age and both measures of tolerance, *sharing* and *co-feeding* (linear regression, *sharing*: $r^2 = 0.31$, $p = 0.03$; *co-feed*: $r^2 = 0.46$, $p = 0.006$; Figure 1). In contrast, in bonobos there was no correlation between dyad age and *sharing* or *co-feeding* (*sharing*: $r^2 = 0.01$, $p = NS$; *co-feed*: $r^2 = 0.15$, $p = NS$) (Figure 1).

To further probe the relationship between age and sharing we classified subjects as adults or juveniles. We defined adults as those possessing a 3rd molar at the time of testing [12]. We performed a 2x2 ANOVA of sharing with species and age category as factors, and found a significant effect of age category ($F(1,26) = 4.13$, $p = 0.05$). Post-hoc tests revealed that juvenile chimpanzees shared significantly more than adult chimpanzees (Tukey's HSD $p<0.05$), while there was no difference in sharing between age categories of bonobos (Tukey's HSD $p>0.05$) (Table 1). There was no significant difference in sharing between juvenile chimpanzees and juvenile bonobos, nor between adult chimpanzees and adult bonobos (Tukey's HSD $p>0.05$).

We performed a similar ANOVA for co-feeding, and again found a significant effect of age category ($F(1,26) = 15.67$, $p = 0.001$). Post-hoc tests showed that juvenile chimpanzees co-

fed significantly more than adult chimpanzees (Tukey's HSD p<0.01), while there was no significant difference between age categories in bonobos (Tukey's HSD p>0.05) (Table 1). There was no difference between species in juvenile levels of co-feeding (Tukey's HSD p>0.05), but adult bonobos co-fed significantly more than adult chimpanzees (Tukey's HSD p<0.05).

Thus, both the *sharing* and *co-feeding* measures demonstrated that while chimpanzees became less tolerant as they reached adulthood, bonobos retained juvenile levels of sharing as adults. As a result bonobos were more tolerant than chimpanzees as adults [cf. 6]. We also found that compared to chimpanzees, bonobos exhibited higher levels of play and sexual behavior, possibly facilitating their higher feeding tolerance (Supplemental Online Material). Given these results, we conducted two experiments to test whether the more relaxed feeding style of bonobos is related to changes in the ontogeny of their inhibitory abilities in situations simulating feeding competition.

Experiment 2 Social Response Inhibition

In Experiment 2 we evaluated the ability of 20 infant and juvenile bonobos and 20 infant and juvenile chimpanzees to inhibit a social response (mean subject age in years (±SEM): chimpanzees, 4.5 (±0.3); bonobos, 4.3 (±0.3), independent samples t-test, p = NS). In this task, a subject could beg for food from three human experimenters who stood shoulder-to-shoulder in front of him or her. Subjects were shown that only the outer two experimenters held a food reward. Subjects were successful if they chose these two experimenters (by touching their hands) without choosing the middle experimenter's (empty) hand, with 12 trials performed. This problem resembles what young apes can experience during competition over meat or attractive

plant foods where individuals must inhibit the desire to beg from or feed near certain intolerant group members. We classify it as a social problem because subjects could use the identity or location of the experimenters as cues to the food location.

Bonobos exhibited a significant positive relationship between age and performance on the test (linear regression, $r^2 = 0.35$, $p = 0.006$; Figure 2), while the performance of chimpanzees did not correlate with age ($r^2 = 0.06$, $p = NS$; Figure 2). We also performed a 2x2 ANOVA with species and age category as factors, classifying subjects as either pre-weaning (2-4 years, N=10 per species) or post-weaning (5-7 years, N=10 per species), based on the weaning age of 4-4.5 years old observed in wild chimpanzees and bonobos [10, 13]. There was no main effect of species or age category on test performance, but there was a significant species x age category interaction ($F(1,36) = 6.31$, $p = 0.02$). Post-hoc comparisons revealed that post-weaning individuals of the two species performed at similar levels (Tukey's HSD $p>0.05$) (Table 2). However, pre-weaning bonobos performed less skillfully than post-weaning bonobos (Tukey's HSD $p<0.01$), and pre-weaning chimpanzees (Tukey's HSD $p<0.05$). In contrast, pre-weaning chimpanzees performed as well as post-weaning chimpanzees (Tukey's HSD $p>0.05$) (Table 2).

Thus, our findings demonstrate a species difference in the ontogeny of inhibitory control in bonobos, with a delay in bonobo development relative to that of chimpanzees. Bonobos took longer to develop the same skill level shown even among the youngest chimpanzees tested. Controls revealed no evidence for significant species differences in motivation or attention, while a second estimate of subject age (weight) revealed the same pattern of results as above and removal of outliers did not change the results (Supplemental Online Material).

However, this task appeared to be relatively simple, given that only the pre-weaning bonobos struggled. Since post-weaning individuals of both species performed similarly, the two species could in theory develop social inhibitory control at different rates but have similar skills as adults. To test this, we presented a slightly older group of bonobos and chimpanzees with a social inhibitory task that was cognitively more demanding.

Experiment 3 Social Reversal Learning

In Experiment 3 we evaluated the ability of subjects to adjust to changes in the sharing behavior of two experimenters in a social reversal learning paradigm. 17 bonobos and 11 chimpanzees participated (mean age in years ($\pm$SEM): chimpanzees, 9.8 ($\pm$1.4); bonobos, 10.2 ($\pm$1.4), independent samples t-test, p = NS).

Subjects chose between two human experimenters, only one of whom held a concealed food reward, until they learned that one human consistently held the food (to the level of 84% correct, see [14]). After reaching this introductory learning criterion subjects immediately received 20 reversal trials where the experimenter hiding the reward was switched. The experimenter who reliably shared food in the introduction now always had no food while the other previously "stingy" experimenter would now always share [15]. After this switch, we recorded the number of trials in which subjects chose the newly generous experimenter.

As a control for whether the two species were equally engaged in the task, we first assessed performance on the introductory trials. The two species did not differ in the number of trials it took them to reach the 84% correct criterion (independent samples t-test p = NS, Table

3). In addition, linear regression analysis showed that the number of trials needed to reach the introductory criterion did not correlate with age in either species.

In the reversal trials bonobos showed a significant positive relationship between age and performance (linear regression, $r^2 = 0.29$, $p = 0.03$), but chimpanzees did not (linear regression, $r^2 = 0.001$, $p = NS$). We also performed a 2x2 ANOVA with species and age category as factors, dividing subjects into juveniles and adults (as in Experiment 1). This ANOVA revealed only a weak effect of species ($F(1,27) = 3.58$, $p = 0.07$), with there being a tendency for chimpanzees to outperform bonobos on the 20 trials of the reversal (Table 3).

We further examined performance in the reversal by looking at the first and last 10 trials separately, since subjects can have difficulty with the reverse association at first, then solve the inhibitory problem over the course of multiple trials. Regressions showed no correlation between age and performance in the first half of the test session in either species. An ANOVA of performance on the first 10 trials with species and age category as factors showed a near-significant effect of species ($F(1,27) = 3.82$, $p = 0.06$), but no effect of age category, nor a significant interaction. Chimpanzees performed somewhat better than bonobos on these first 10 trials (Table 3).

In contrast, in the last 10 trials of the reversal, bonobos showed a positive relationship between age and performance ($r^2 = 0.35$, $p = 0.01$) while chimpanzees did not ($r^2 = 0.004$, $p = NS$). An ANOVA of performance on the second 10 trials demonstrated a significant effect of age category ($F(1,27) = 4.85$, $p = 0.04$), but no significant effect of species or interaction. In contrast to the pattern in the first 10 trials, there was no species difference in performance on these latter 10 trials (Table 3). Instead, post-hoc tests revealed that adult bonobos significantly outperformed

juvenile bonobos on the last 10 trials (Tukey's HSD p<0.05), while there was no difference in performance between adult and juvenile chimpanzees (Tukey's HSD p>0.05) (Table 3).

Thus in the first ten trials of the reversal, bonobos of all ages struggled while chimpanzees of all ages performed well. In the latter half of the reversal, younger bonobos continued to have difficulty but adult bonobos adjusted and subsequently raised the species mean for these ten trials to within the range of the performance of the chimpanzees. In short, the juvenile bonobos were slower than the other individuals to adapt to the reversal, performing at a lower level in the latter reversal trials relative to juvenile chimpanzees and to adults of both species. Further, adult bonobos exhibited less social inhibitory control than adult chimpanzees, with a tendency to perform worse during the first ten trials and overall. Results were similar when using weight as a proxy for age or removing outlier individuals, and motivation levels did not differ between the two species or correlate with test performance (Supplemental Online Material). Subjects who had previously participated in Experiment 2 performed no differently from the novel subjects in their learning of the initial association or in the reversal (independent samples t-tests).

In sum, Experiment 3 tested an older sample with a relatively challenging cognitive task, and again revealed a developmental delay in bonobos relative to chimpanzees. Our evidence that the delay in the ontogeny of social inhibition in bonobos persists into adulthood resembles differences seen previously when adults of the two species were compared in a non-social inhibition task [16, though see 17].

Discussion

Our findings support the hypothesis that developmental delays play a role in producing differences in the social psychology underlying food competition in bonobos and chimpanzees. Inter-individual tolerance in sharing food decreased with age in chimpanzees while bonobos maintained juvenile levels of tolerance into adulthood. Infant bonobos were less capable of inhibiting themselves from begging for food than were same-age chimpanzees, with chimpanzees successful from the youngest age tested. In a social reversal learning task, juvenile and even adult bonobos were more inhibited by their previously learned social associations than chimpanzees, who again showed adult levels of performance even as juveniles. Thus in both tolerance and social inhibition, shifts in the ontogenetic patterns of behavior corresponded to distinctions between adults of the two species. Controls ruled out differences in motivation or comprehension of the tasks as plausible explanations of the observed species differences.

The association in bonobos of juvenile levels of tolerance, delayed development of social inhibition and a paedomorphic cranium suggests that common developmental mechanism might be responsible for the retention of juvenile traits into adulthood. By analogy, populations of mammals selected for reduced aggression tend to exhibit ontogenetic delays across numerous traits relative to their wild-type ancestors [18, 19]. A similar process could be responsible for our findings, for example if selection against aggression in bonobos led to delays in the ontogeny of multiple other traits [20, 21]. This idea does not imply that bonobos are juvenilized globally. Instead, it suggests that juvenilization has occurred in a set of traits that are strongly genetically linked.

Understanding the evolutionary processes by which ontogenetic changes occurred in bonobos may provide insight into our own species' evolution. Herrmann et al. [22] proposed that

the crucial cognitive adaptation of humans relative to other apes is the accelerated development of social skills in infants. While the genetic changes that produce such developmental shifts are not well understood, if we can determine the process by which the ontogeny of bonobos evolved, inferences can be made regarding analogous evolution in our own species.

Experimental Procedures

Experiment 1 Inter-individual tolerance

Subjects in all three experiments were tested at the Tchimpounga Chimpanzee Sanctuary in the Congo Republic and the Lola ya Bonobo Sanctuary in the Democratic Republic of Congo (Supplemental Table 1 provides a list of subjects' experimental participation. Note: the chimpanzees here were *Pan troglodytes troglodytes* not *Pan troglodytes schweinfurthii* as previously tested [6]). For this experiment we tested 30 chimpanzees (4 to 19 years) and 24 bonobos (4 to 23 years). In all trials subjects were released into the test room simultaneously, with food placed prior to their release. Each dyad was given three trials of each of three food configuration conditions, with one condition presented per day over the course of three separate days for a total of nine trials. All statistics were for this and the subsequent experiments two-tailed. All tests were videotaped, with behavior scored from this video. See the Supplemental Online Material for additional methodological details and control analyses.

Experiment 2 Response Inhibition

Subjects in both species ranged in age from 2 to 7 years, and there were 6 female and 14 male bonobos tested, and 8 female and 12 male chimpanzees. Subjects were given one test session, consisting of three types of trials: warm-up, introduction, and test trials. In the two warm-up

trials, all three experimenters held food to introduce the test paradigm and the potentially unfamiliar humans. These were followed by four introduction trials where only two adjacent experimenters held food. Finally, in the 12 test trials the two nonadjacent experimenters always held food while the center experimenter did not. The three human experimenters maintained their position relative to one another throughout the test. Only those individuals taking food in the trial reached towards the food container. Those individuals did so simultaneously in view of the subject, then all three experimenters raised their arms toward the subject simultaneously and closed their fists so that the food was not visible at the time of choice. Performance was scored live by the experimenters, though all tests were also videotaped.

Experiment 3 Reversal Learning

Chimpanzee subjects' ages ranged from 5 to 17 years and bonobo subjects' ages ranged from 5 to 23 years. There were 6 female and 11 male bonobos tested, and 7 female and 4 male chimpanzees. For this experiment, two experimenters again stood in front of the subjects, with the potential to be holding food. In the test trials, both individuals appeared to take food from a container, but only one individual did so. The two experimenters presented their closed fists to the subject, so that it did not know who was holding food. The same experimenter held food for every trial of the introduction, and in the reversal the other experimenter always held food. The two experimenters always stood in the same position for a given subject's entire test session (with their locations counter-balanced across subjects). Subjects were given a maximum of 40 introduction trials to reach the 84% correct criterion, otherwise their test session was aborted and their performance was not included as part of the results (this occurred for 6 individuals, supplemental to the 28 individuals presented here). Performance was scored live, in addition to

being videotaped. Prior to the test trials, we performed a baseline task to ensure that any preferences that subjects possessed for one of the two human experimenters did not impact results in the test. The methods and results of this baseline are discussed in the Supplemental Online Material.

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Figure 1 Feeding behavior according to species and age, experiment 1. a) Chimpanzees'

average age of pair (dyad age) in relation to the number of trials (out of 9 total) where

individuals shared food b) bonobos' dyad age in relation to this measure c) chimpanzees' dyad

age in relation to the number of trials where they co-fed and d) bonobos' dyad age in relation to

this measure. Small circles represent one dyad while large circles represent multiple dyads with

the same behavioral score.

Figure 2 Social inhibition according to species and age, experiment 2. The relationship

between each subject's age and its overall number of correct choices in the 12 social response

inhibition test trials. The small circles represent the performance of a single subject while the

large circles represent multiple individuals.

Figure 3 Social reversal learning according to species and age, experiment 3. The number of

correct choices that subjects made in the last 10 trials of the social reversal learning test in

relation to their age. The small circles represent the performance of a single subject while the

large circles represent multiple individuals.

Tables

Table 1. Performance across species and age groups in the tolerance test, experiment 1. The number of trials (out of 9 total) where individuals shared or co-fed during the food sharing task. Age groups are divided into juvenile and adult, as described in the manuscript. Means for each variable are listed with standard error in parentheses.

	Sharing	Co-feeding
Chimpanzee juveniles	7.12 (0.88)	4.12 (0.85)
Chimpanzee adults	4.43 (0.78)	0.71 (0.29)
Chimpanzee mean	**5.87 (0.68)**	**2.53 (0.65)**
Bonobo juveniles	6.83 (0.70)	3.83 (0.70)
Bonobo adults	6.33 (0.62)	2.00 (0.52)
Bonobo mean	**6.58 (0.45)**	**2.92 (0.50)**

Table 2. Performance across species and age groups in the social response inhibition task, experiment 2. There were 4 introduction trials and 12 test trials performed. Age groups are divided into pre- and post-weaning, as described in the manuscript. Means for each variable are listed with standard error in parentheses.

	Introduction	Test
Pre-weaning chimpanzees	2.80 (0.47)	7.40 (1.01)
Post-weaning chimpanzees	3.20 (0.29)	6.30 (1.24)
Chimpanzee mean	**3.00 (0.27)**	**6.85 (0.79)**
Pre-weaning bonobos	3.20 (0.20)	4.60 (0.69)
Post-weaning bonobos	3.30 (0.26)	8.30 (0.78)
Bonobo mean	**3.25 (0.16)**	**6.45 (0.66)**

Table 3. Performance across species and age groups in the social reversal learning task, experiment 3. The last trial of the introduction represents how many trials it took subjects to

learn the introductory association to the criterion of 84% correct. For the reversal, we report

performance overall and separated into the first and last ten trials. Age groups are divided into

juvenile and adult, as described in the manuscript. Means for each variable are listed with

standard error in parentheses.

	Last trial introduction	Reversal, first 10 trials	Reversal, last 10 trials	Reversal overall
Chimpanzee juveniles	17.40 (2.77)	8.40 (1.12)	8.60 (0.60)	17.00 (1.64)
Chimpanzee adults	25.00 (3.72)	9.00 (0.52)	8.83 (0.48)	17.83 (0.87)
Chimpanzee mean	**21.50 (2.57)**	**8.73 (0.56)**	**8.73 (0.36)**	**17.45 (0.85)**
Bonobo juveniles	22.56 (2.69)	6.89 (0.95)	7.00 (0.71)	13.89 (1.22)
Bonobo adults	16.38 (2.69)	6.75 (0.94)	9.38 (0.32)	16.12 (1.16)
Bonobo mean	**19.70 (2.00)**	**6.82 (0.65)**	**8.12 (0.49)**	**14.94 (0.86)**