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Bonobos voluntarily share their own food with others

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Comparisons between chimpanzees and humans have led to the hypothesis that only humans voluntarily share their own food with others [1–4]. However, it is hard to draw conclusions because the food-sharing preferences of our more tolerant relative, the bonobo (*Pan paniscus*), have never been studied experimentally [5]. We gave unrelated bonobos the choice of either monopolizing food or actively sharing: we found that bonobos preferred to release a recipient from an adjacent room and feed together instead of eating all the food alone. Thus, food sharing in bonobos does not depend on kinship or harassment and suggests our own species' propensity for voluntary food sharing is not unique among the apes [6].

We tested pairs of unrelated bonobos (and in some cases non-group members) in a situation in which sharing requires forfeiting part of their own food. Seven subjects were tested before their morning meal (see Supplemental data available on-line with this issue). In a row of three adjacent rooms, food was placed in the center test room. We observed whether each subject allowed a recipient to enter the test room from one of the two adjacent rooms by helping them to open the door between the two rooms (see Figure 1 and the Supplemental movie). Both doors into the test room were locked by 'keys' (wooden pegs). The keys could only be removed by the subject and could not be removed by the recipient. Once the recipient was moved into one of the two adjacent rooms, food was placed in the test room and the subject was allowed to enter the test room. If bonobos are capable of voluntarily sharing food, they should choose to open the recipient's door before opening the door to the empty adjacent room and before eating all of the food in the test room. In contrast, a random pattern of door opening or any aggression following the release of the recipient would suggest subjects simply could not inhibit opening the doors.

After the sharing test, all subjects were tested on a different day in a solo control condition of five trials. The control was identical to the test except instead of the recipient, additional food was placed in one of the adjacent rooms (Figure 1). This tested: first, whether subjects, on their own, could eat the same amount of food provided in the test; and second, whether subjects could inhibit opening a door when something attractive was inside one of the rooms (for example, rather than quickly collecting the additional food and bringing it back to eat with the food in the test room). We predicted that subjects would eat all the food in the control and would not reflexively open the door to the adjacent food room even though they were attracted to the food inside.

In the test trials, the subjects had a significant preference to open the recipient's door instead of the door to the empty room (see Figure 1; mean trials opened first: recipient's door = 5.85 ± 1.47; empty door = 0.86 ± 0.4; T = 2, N = 7, p = 0.042, Wilcoxon test; this and all subsequent tests are two tailed; note: opening a door was *only* coded if uneaten fruit pieces were still remaining). Subjects opened the recipient's door first more frequently in both the first and second test sessions (five trials were administered on two different days; first test day: recipient's door = 2.71 ± 0.81; empty door: 0.29 ± 0.18; T = 1, N = 6, p = 0.045; second test day: recipient's door = 3.14 ± 0.7; empty door: 0.57 ± 0.3; T = 2, N = 7, p = 0.042, Wilcoxon test; there was also no significant difference between sessions, p > 0.7, Wilcoxon test). Within sessions, moreover, subjects opened the recipient's door first as often in the first two trials of both sessions (mean = 1.86 ± 0.55 trials) as they did in the last two trials of both sessions (mean = 2.42 ± 0.61 trials; p = 0.2, Wilcoxon test).

Finally, four of the seven subjects (three of whom were paired with a non-group member) had significant

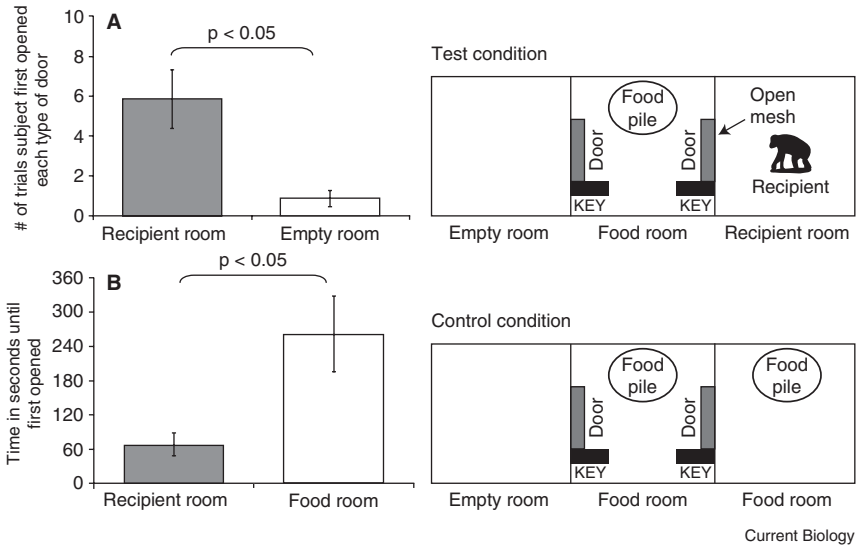

Figure 1. Results of the food-sharing trials.

(A) Mean (±SEM) number of trials where subjects opened the recipient's door first or the empty room first out of the ten test trials (subjects refrained from opening either door in 3.4 ± 1.26 trials out of 10). (B) Mean (±SEM) time in seconds before subjects opened the recipient's room in ten trials of the test condition and the extra food room in the five trials of the control condition. Subjects were only credited with opening the recipient room first if uneaten fruit pieces were remaining in the test room. Statistical comparisons were made with Wilcoxon tests, two tailed. Diagrams on the right represent the experimental set-up for the test and control condition carried out in the same row of three adjacent rooms. After the food pile, keys and recipient were in place the subject was let into the food room (recipient placement in one of the two adjacent rooms was counterbalanced within and between subjects). Subjects could open one, both or none of the keys into either of the adjacent rooms. All walls of the test rooms are made of vertical bars with 10 cm gaps, so subjects were easily visible to each other and could easily interact physically (see Supplemental movie S1).

individual preferences for opening the recipient's door first ($p < 0.05$, binomial probability). When released, recipients always obtained preferred fruit (mean of 8 ±1.06 pieces per trial when released and a mean 4 ± 1.06 pieces across all trials). Subjects released recipients to co-feed for the majority of the total feeding time during each trial and the recipient spent significantly more time co-feeding than they were excluded from feeding (proportion of feeding time: subject fed alone = 19.4% ± 0.06; recipient allowed to co-feed = 80.6% ± 0.06; N = 6, T = 3.5, $p < 0.03$). In addition, the proportion of feeding time that the subjects allowed the recipients to co-feed did not change between the first and last time a recipient was released within a session. Moreover, analysis of social behavior suggests that the sharing observed was not contingent upon social or communicative interactions before or during sharing (see Supplemental data). Finally, no form of aggression was ever observed.

In the solo control trials, subjects ate all the food and also preferred to open the door to the room baited with food first instead of the door to the empty room (food room = 4.14 ± 0.46, empty room = 0.71 ± 0.42; N = 7, T = 1, $p = 0.025$, Wilcoxon test). The frequency of opening the recipient's door in the test (reported above) and the door to the food room in the control did not differ (82.9% ± 0.09 of trials subjects opened the food room, $p > 0.3$, Wilcoxon test). Critically, however, subjects opened the recipient's door in the test condition significantly faster than the door to the food room in the control trials (mean seconds to open: recipient room = 68.8 ± 19.8 seconds, food room = 261.14 ± 66.5 seconds; N = 6, T = 1, $p = 0.046$, Wilcoxon test; see Figure 1). Finally, in a small supplemental control similar to [6], in which subjects could allow access to food they themselves did not have access to, both test subjects more often released a recipient into a room with food instead of an empty room (one had a significant preference; supplemental materials).

Overall, the observed sharing was not due to non-social factors including: satiation, as bonobos shared similarly in the first and last trials of each session; and a general inability to inhibit opening doors, since subjects did not randomly open doors in the test and resisted opening the door to the food room for several minutes in the control. Sharing was costly since subjects ate all the food in the solo condition but was not explained by social factors including: harassment, since recipients could not approach the food without the subject's help; kinship, since none of the subjects were related; and attempts by subjects to reciprocate previous favors, since subjects even shared with recipients who were non-group members. Therefore, subjects preferred to voluntarily open the recipient's door to allow them to share highly desirable food that they could have easily eaten alone — with no signs of aggression, frustration or change in the speed or rate of sharing across trials. This stable sharing pattern is particularly striking since in other non-sharing contexts bonobos are averse to food loss and adjust to minimize such losses [7,8]. Subjects may have shared in an attempt to receive favors in the future from the recipients or due to a more altruistic motivation (Supplemental data). Regardless, future research is needed to explore the precise mechanism(s) that motivate and maintain voluntary sharing in bonobos and other nonhumans [9,10].

Supplemental Data

Supplemental data are available at http://www.cell.com/current-biology/supplemental/S0960-9822(09)02201-5

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