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Report

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

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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 adult bonobos (n = 24) maintained high, juvenile levels of food-related tolerance. We also investigated the ontogeny of inhibition during tasks that simulated 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.

Results

Bonobos and chimpanzees differ in their morphology, physiology, behavior, and cognition, despite the two species having diverged relatively recently (2.5 to 0.85 million years ago) [1–4]. Their differences are thought to arise partly from shifts in developmental pathways. Relative to chimpanzees, bonobos have been shown to exhibit pedomorphism (retention of ancestrally juvenile traits into adulthood) in aspects of their cranial morphology [5]. Bonobos also appear to retain juvenile levels of play and nonconceptive sexual behavior into adulthood, characteristics that facilitate high interindividual 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: Interindividual Tolerance

In the first experiment, we examined interindividual 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], with distinctions in methodology as outlined in the Supplemental Experimental Procedures available online) to 15 pairs of chimpanzees and 12 pairs of bonobos of varying age (mean dyad age in years ± standard error of the mean [SEM]: bonobos 9.0 ± 1.1; chimpanzees 9.3 ± 0.8; independent samples t test, p = not significant [NS]).

Subjects were paired with similarly aged partners. Equal numbers of male-male, male-female, and female-female dyads were tested (details in Table S2). Each dyad received nine trials of a food-sharing task. There were three 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, i.e., both subjects obtained food, and (2) cofeeding, i.e., subjects fed from the same food source simultaneously. Play and sexual behavior were also coded in each trial (see Supplemental Experimental Procedures and Supplemental Results).

Chimpanzees showed a significant negative relationship between average dyad age and both measures of tolerance, sharing and cofeeding (linear regression, sharing: $r^2 = 0.31$, $p = 0.03$; cofeed: $r^2 = 0.46$, $p = 0.006$; Figure 1). In contrast, there was no correlation between dyad age and sharing or cofeeding in bonobos (sharing: $r^2 = 0.01$, p = NS; cofeed: $r^2 = 0.15$, 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 third molar at the time of testing [12]. We performed a 2 × 2 analysis of variance (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 honestly significant difference [HSD] $p < 0.05$), whereas 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, or between adult chimpanzees and adult bonobos (Tukey's HSD $p > 0.05$).

We performed a similar ANOVA for cofeeding and again found a significant effect of age category [$F(1,26) = 15.67$, $p = 0.001$]. Post hoc tests showed that juvenile chimpanzees cofed significantly more than adult chimpanzees (Tukey's HSD $p < 0.01$), whereas 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 cofeeding (Tukey's HSD $p > 0.05$), but adult bonobos cofed significantly more than adult chimpanzees (Tukey's HSD $p < 0.05$).

Thus, both the sharing and cofeeding measures demonstrated that whereas 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 Results). Given these results, we conducted two further experiments to test whether the more relaxed feeding style of bonobos is related to changes

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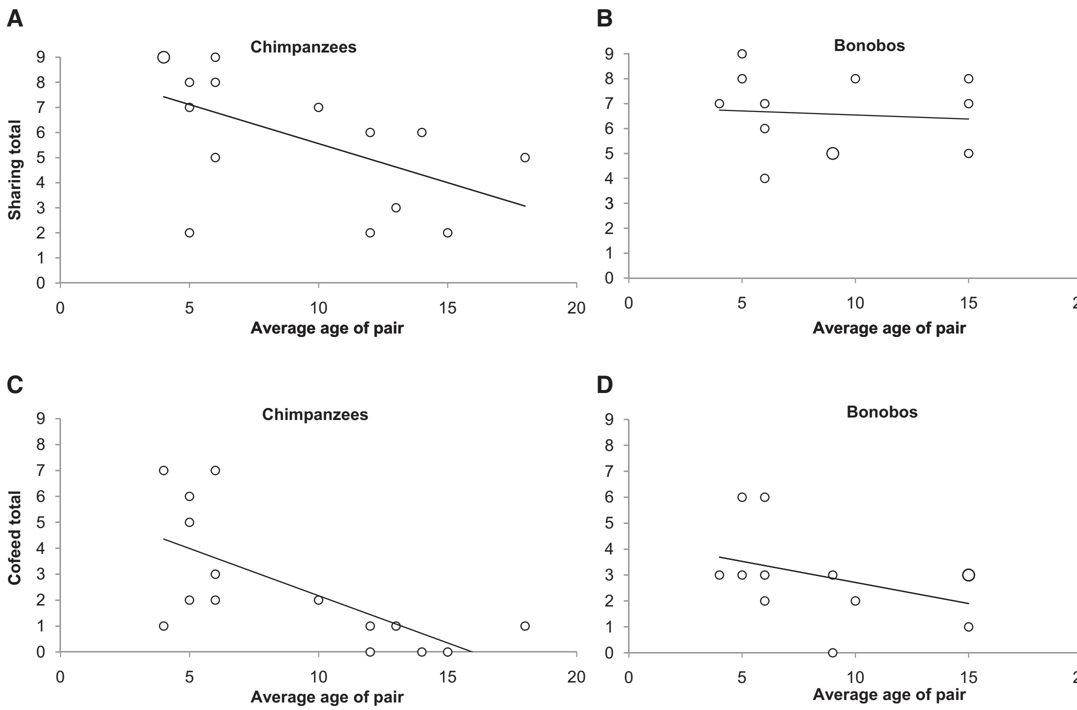

Figure 1. Experiment 1: Interindividual Tolerance in Feeding Behavior According to Species and Age

(A) Chimpanzees' average age of pair (dyad age) in relation to the number of trials (out of nine total) in which individuals shared food.
(B) Bonobos' dyad age in relation to the measure.
(C) Chimpanzees' dyad age in relation to the number of trials in which they cofed.
(D) Bonobos' dyad age in relation to this measure.
Small circles represent one dyad; large circles represent multiple dyads with the same behavioral score.

in the ontogeny of their inhibitory abilities in situations simulating feeding competition.

Experiment 2: Social Response Inhibition

In the second experiment, 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 both of 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 particular intolerant group members. We classify this as a social problem because subjects could use the identity or location of the experimenters as cues to the food location.

Table 1. Experiment 1: Performance across Species and Age Groups in the Interindividual Tolerance Test

	Sharing	Cofeeding
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)

Number of trials (out of nine total) in which individuals shared or cofed during the food-sharing task. Age groups are divided into juvenile and adult as described in the text. Means for each variable are listed with standard error of the mean in parentheses.

Bonobos exhibited a significant positive relationship between age and performance on the test (linear regression, $r^2 = 0.35$, $p = 0.006$; Figure 2), whereas the performance of chimpanzees did not correlate with age ($r^2 = 0.06$, p = NS; Figure 2). We also performed a 2 × 2 ANOVA with species and age category as factors, classifying subjects as either preweaning (2–4 years, n = 10 per species) or postweaning (5–7 years, n = 10 per species), based on the weaning age of 4–4.5 years 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 × age category interaction [$F(1,36) = 6.31$, $p = 0.02$]. Post hoc comparisons revealed that postweaning individuals of the two species performed at similar levels (Tukey's HSD $p > 0.05$) (Table 2). However, preweaning bonobos performed less skillfully than postweaning bonobos (Tukey's HSD $p < 0.01$) and preweaning chimpanzees (Tukey's HSD $p < 0.05$). In contrast, preweaning chimpanzees performed as well as postweaning 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; a second estimate of subject age (weight) revealed

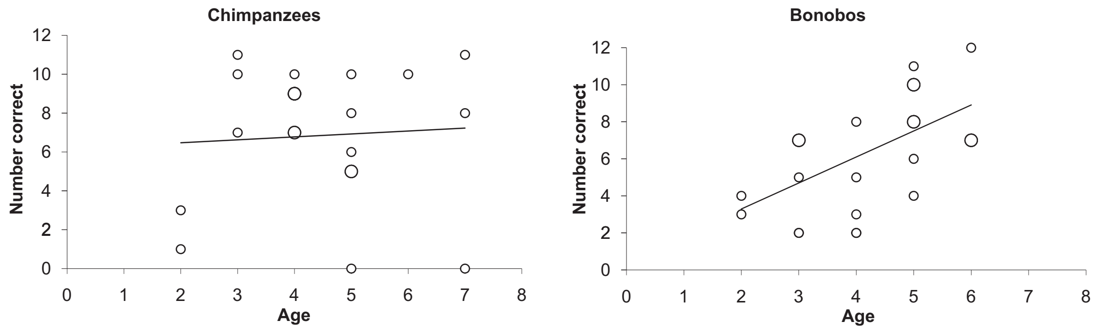

Figure 2. Experiment 2: Social Response Inhibition According to Species and Age

Relationship between each subject's age and its overall number of correct choices in the 12 social response inhibition test trials. Small circles represent the performance of a single subject; large circles represent multiple individuals with the same performance score.

the same pattern of results as above, and removal of outliers did not change the results (Supplemental Results).

However, this task appeared to be relatively simple, given that only the preweaning bonobos struggled. Because postweaning 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 the third experiment, we evaluated the ability of subjects to adjust to changes in the sharing behavior of two experimenters in a social reversal learning paradigm. Seventeen bonobos and 11 chimpanzees participated (mean age in years ± SEM: chimpanzees 9.8 ± 1.4; bonobos 10.2 ± 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 in which the experimenter hiding the reward was switched. The experimenter who reliably shared food in the introduction now always had no food, whereas 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 2 × 2 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 ten and last ten trials separately, because subjects can have difficulty with the reverse association at first and 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 ten 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 or a significant interaction. Chimpanzees performed somewhat better than bonobos on these first ten trials (Table 3).

In contrast, in the last ten trials of the reversal, bonobos showed a positive relationship between age and performance ($r^2 = 0.35$, $p = 0.01$), whereas chimpanzees did not ($r^2 = 0.004$, p = NS; Figure 3). An ANOVA of performance on the second ten 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 ten trials, there was no species difference in performance in these latter ten trials (Table 3). Instead, post hoc tests revealed that adult bonobos significantly outperformed juvenile bonobos on the last ten trials (Tukey's HSD $p < 0.05$), whereas 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, whereas 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

Table 2. Experiment 2: Performance across Species and Age Groups in the Social Response Inhibition Task

	Introduction	Test
Chimpanzees preweaning	2.80 (0.47)	7.40 (1.01)
Chimpanzees postweaning	3.20 (0.29)	6.30 (1.24)
Chimpanzees mean	3.00 (0.27)	6.85 (0.79)
Bonobos preweaning	3.20 (0.20)	4.60 (0.69)
Bonobos postweaning	3.30 (0.26)	8.30 (0.78)
Bonobos mean	3.25 (0.16)	6.45 (0.66)

Four introduction trials and 12 test trials were performed. Age groups are divided into pre- and postweaning as described in the text. Means for each variable are listed with standard error of the mean in parentheses.

Table 3. Experiment 3: Performance across Species and Age Groups in the Social Reversal Learning Task

	Last Trial Introduction	Reversal, First Ten Trials	Reversal, Last Ten 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)

"Last Trial Introduction" represents how many trials it took subjects to learn the introductory association to the criterion of 84% correct. For the reversal, performance separated into the first ten trials, last ten trials, and overall is shown. Age groups are divided into juvenile and adult as described in the text. Means for each variable are listed with standard error of the mean in parentheses.

trials relative to juvenile chimpanzees and relative to adults of both species. Furthermore, 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 Results). 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 test).

In sum, experiment 3 tested an older population 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 observed previously when adults of the two species were compared in a nonsocial 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. Interindividual tolerance in sharing food decreased with age in chimpanzees, whereas bonobos maintained juvenile levels of tolerance into adulthood. Infant bonobos were less capable of inhibiting themselves from begging for food than same-age chimpanzees were, with chimpanzees being 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 pedomorphic cranium suggests that common developmental mechanisms 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 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. Although 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: Interindividual Tolerance

Subjects in all three experiments were tested at the Tchimpounga Chimpanzee Sanctuary in the Republic of the Congo and the Lola ya Bonobo Sanctuary in the Democratic Republic of the Congo. (Table S1 provides a list of subjects' experimental participation. Note that the chimpanzees tested here were *Pan troglodytes troglodytes*, not *Pan troglodytes schweinfurthii* as previously tested [6].). For this experiment, we tested 30 chimpanzees (4–19 years) and 24 bonobos (4–23 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 for this and subsequent experiments were two-tailed. All tests were videotaped, with behavior scored from the video. See Supplemental Experimental Procedures for

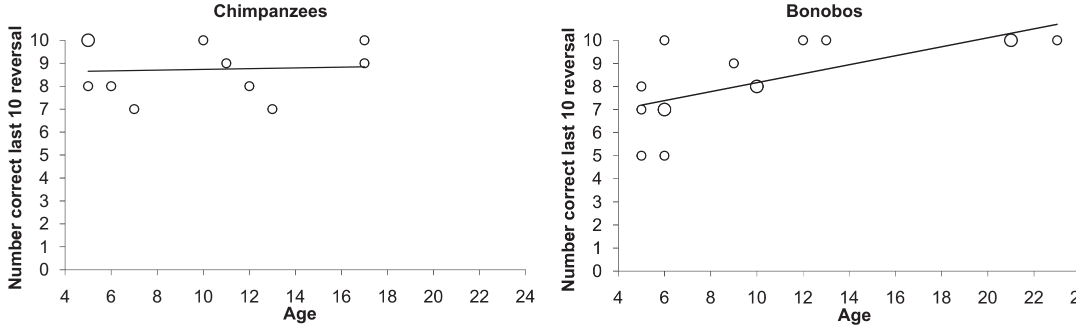

Figure 3. Experiment 3: Social Reversal Learning According to Species and Age

Number of correct choices that subjects made in the last ten trials of the social reversal learning test in relation to their age. Small circles represent the performance of a single subject; large circles represent multiple individuals with the same performance score.

additional methodological details and Supplemental Results for control analyses.

Experiment 2: Social Response Inhibition

Subjects in both species ranged in age from 2 to 7 years. We tested 6 female and 14 male bonobos 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 experimenters taking food in the trial reached toward the food container. Those individuals did so simultaneously in view of the subject, and 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, although all tests were also videotaped.

Experiment 3: Social Reversal Learning

Chimpanzee subjects' ages ranged from 5 to 17 years; bonobo subjects' ages ranged from 5 to 23 years. We tested 6 female and 11 male bonobos 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 experimenters appeared to take food from a container, but only one experimenter did so. The two experimenters presented their closed fists to the subject, so that the subject did not know who was holding food. The same experimenter held food for every trial of the introduction, and the other experimenter always held food in the reversal. The two experimenters always stood in the same position for a given subject's entire test session (with their locations counterbalanced 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 Supplemental Experimental Procedures and Supplemental Results.

Supplemental Information

Supplemental Information includes Supplemental Results, three tables, one figure, and Supplemental Experimental Procedures and can be found with this article online at doi:10.1016/j.cub.2009.11.070.

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