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Report

Majority-Biased Transmission in Chimpanzees and Human Children, but Not Orangutans

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Summary

Cultural transmission is a key component of human evolution. Two of humans' closest living relatives, chimpanzees and orangutans, have also been argued to transmit behavioral traditions across generations culturally [1–3], but how much the process might resemble the human process is still in large part unknown. One key phenomenon of human cultural transmission is majority-biased transmission: the increased likelihood for learners to end up not with the most frequent behavior but rather with the behavior demonstrated by most individuals. Here we show that chimpanzees and human children as young as 2 years of age, but not orangutans, are more likely to copy an action performed by three individuals, once each, than an action performed by one individual three times. The tendency to acquire the behaviors of the majority has been posited as key to the transmission of relatively safe, reliable, and productive behavioral strategies [4–7] but has not previously been demonstrated in primates.

Results and Discussion

In many animal species, individuals learn socially from conspecifics and so carry the potential to "transmit" behaviors and strategies across generations [8]. Perhaps most strongly, chimpanzees and orangutans, each of which have behavioral repertoires that differ among different populations, have been argued to transmit behaviors culturally [1, 3, 6]. In comparison to other great apes, humans seem to transmit many more types of behaviors, and the behavioral differences between populations appear to exceed those observed in other animal species [9]. Much of the prior research attempting to account for these differences has focused on interspecies differences in the transmitted content—what is learned [10–12].

An equally important aspect of social learning is who learns from whom [13–15]: the social dynamics of social learning determine, for example, how quickly a behavior might spread within and between populations and how stably it might be retained subsequently [4]. Of particular importance in this regard is what we propose to call majority-biased transmission: the increased likelihood of naïve observers to acquire the behavior of the majority. In other words, if, due to any combination of underlying mechanisms, an individual is more likely to acquire the behavior displayed by the majority than other equifinal alternative behaviors, we refer to it as majority-biased transmission.

The majority response is an aggregate response based on the individual learning efforts of the entire group and therefore likely safer, more reliable, and more productive than any single response [4, 16]. If social learning is adaptive, natural selection should favor majority-biased transmission, as long as it does not completely block transmission of rare, high-quality variants [5–7]. Moreover, majority-biased transmission serves an important function in the structure of cultural diversity: in both species, chimpanzees [17] and humans [18, 19], individuals migrate across group boundaries. Hence, in both species, differences between groups should level out over time. Majority-biased transmission, in theory at least, can prevent the homogenization of cross-cultural differences [4]. Because immigrants into the group acquire the majority strategy with a greater probability than available alternatives, group-specific behavioral variants are preserved, even when there are high rates of migration [4, 16]. To stabilize group differences over time, the probability with which a naive individual will adopt the majority strategy must at least match the size of the majority within the population. If the probability to acquire the majority strategy exceeds the size of the majority within the population, it is referred to as conformist transmission [16, 20, 21]. Experimentally, conformist transmission has as of yet only been demonstrated in shoaling fish [22, 23].

Prior studies with primates demonstrated that observers, out of two available alternatives to open an artificial fruit, preferentially adopted the strategy that was dominant in their group [24–30]. In these studies, the behavior performed by the majority of individuals is almost certainly also the one that observers saw first and most often. So, we do not know whether the observing individuals acquired the behavior that they observed first, most frequently, or the behavior of the majority.

Study 1

In the present study, we investigated majority-biased transmission in human children, chimpanzees, and orangutans. To investigate whether individuals acquire the strategy of the majority specifically, and not the most frequently demonstrated strategy, we independently manipulated the number of demonstrators while keeping the number of demonstrations constant across strategies. Sixteen two-year-old human children (*Homo sapiens*), 15 chimpanzees (Pan *troglodytes*), and 12 Bornean orangutans (*Pongo pygmaeus*) participated in this study.

We constructed a box with three differently colored subsections (Figure 1). In the top of each section was a hole. If a ball was dropped in one of the holes, an electronic food-dispenser released a reward out of the bottom of the box. We controlled which subset of holes had active triggers. Participants, who had never interacted with the box, observed four familiar conspecific peers interacting with the box one after the other. These demonstrators were previously trained to strongly prefer one of the box's colored sections. One demonstrator (the minority) dropped a ball into one of the three colored sections three times in a row, receiving one piece of food for

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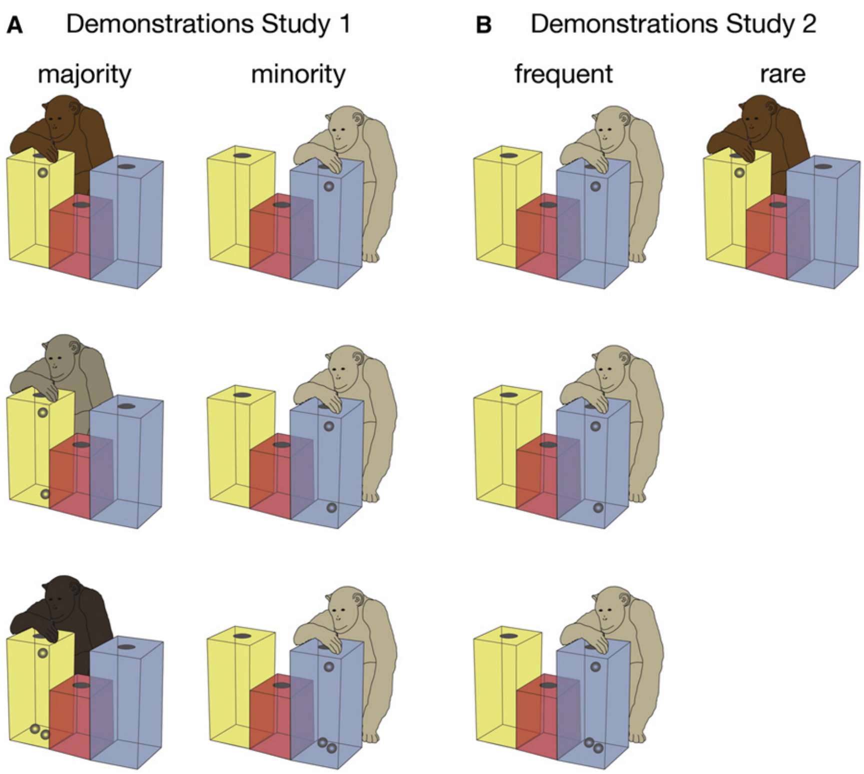

Figure 1. Structure of Peer Demonstrations in Study 1 and Study 2

(A) Demonstrations of different response options in study 1. One option is demonstrated by three different individuals, once each (majority). One option is demonstrated by one individual three times (minority). One option is never demonstrated. The real boxes were opaque, not transparent as indicated here. Every observer saw these two types of demonstrations by conspecific peers in counterbalanced order.

(B) Demonstrations of different response options in study 2. One option is demonstrated by one individual three times (frequent). A second option is demonstrated by one individual once (rare). One option is never demonstrated. The real boxes were opaque, not transparent as indicated here. Every observer saw two demonstrations by conspecific peers in counterbalanced order.

each dropped ball. The three other demonstrators (the majority), one after the other, all used the same colored section (different from the minority) once each, receiving one reward each (Figure 1A). The number of demonstrations was identical across the two demonstrated solutions (three demonstrations each), but one was demonstrated by a larger number of individuals than the other (3 versus 1 peers). The third option was never demonstrated. Which colored sections were demonstrated and the order of majority versus minority demonstrations were counterbalanced across subjects. After a successful demonstration, the models were beckoned aside, to a location where they could watch the observer but could not interfere. After a 5 min waiting period, the observer was then allowed access to the box, and the experimenter handed the observer a ball. After the observers had dropped a ball in the box, they were handed a second and then a third ball. Lost balls were replenished until either the participant had placed three balls in the box or 5 min had passed. Six chimpanzees did not respond within the allotted time. Observers received a reward for every ball they dropped in the box. All responses were recorded on video and coded both in situ and post hoc. Each response was coded as either copying the majority (majority response), the minority (minority response), or neither (other response).

To compare number of choices between response options, we used a Monte-Carlo approach. We simulated individuals to match our original subjects with regard to the number of choices they made, randomly (with replacement) putting balls into the available options. We then calculated the test-statistic (Ts) as the sum of the squared differences between the total numbers of balls per option and the mean number of balls per option. The p value was then estimated as the proportion of simulations revealing a test statistic at least as large as the original one. Usually we used 1,000 simulations, but when the p value was close to 0.05 we used 10,000 to estimate it more accurately. Chimpanzees did not respond randomly across options (Ts = 165; $p < 0.001$; majority: 72%, minority: 0%, other: 28%; see Figure 2A). We used the same Monte Carlo approach for pairwise comparisons between only two choice options. Here we considered only the balls that were actually dropped in the two relevant options as the number of choices to be simulated and considered only the two options to be compared as available. All p values of pairwise comparisons throughout the manuscript are Bonferroni-Holm corrected for multiple comparisons. Chimpanzees gave more majority responses than minority responses (Ts = 162; $p < 0.01$), more majority responses than other responses (Ts = 60.5; $p < 0.01$), and more other responses than minority responses (Ts = 24.5; $p < 0.01$). As measured by their most common response, out of the nine chimpanzees that responded, seven gave mainly majority responses (Figure 3A).

Children did also not respond randomly (Ts = 242; $p < 0.001$; majority: 56.3%, minority: 33.3%, other: 10.4%; see Figure 2A). They gave more majority responses than minority responses (Ts = 60.5; $p < 0.05$), more majority responses than other responses (Ts = 242; $p < 0.01$), and more minority responses than other responses (Ts = 60.5; $p < 0.01$). As measured by their most common response, 9 out of 16 children gave mainly majority responses (Figure 3A).

Orangutans responded randomly across the three response options (Ts = 2; p = 0.91; majority: 36.1%, minority: 33.3%, other: 30.6%; see Figures 2A and 3A).

Study 2

In a second study, we investigated whether individuals would also take frequency information into account when the number of demonstrators was stable. In contrast to study 1, we manipulated the number of demonstrations while keeping the number of demonstrators constant across strategies.

Fourteen 2-year-old human children (*Homo sapiens*), 14 chimpanzees (*Pan troglodytes*), and 14 Bornean orangutans (*Pongo pygmaeus*) participated in study 2. All participants had not previously participated in study 1 but were sampled from the same populations.

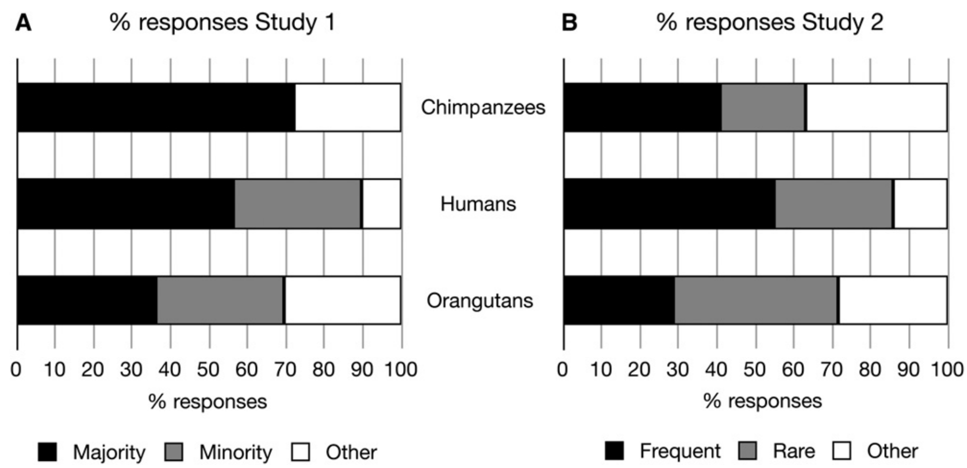

Figure 2. Percent Responses following Different Demonstrations in Study 1 and Study 2

(A) Percentage of given responses in either of the three response categories (majority, minority, or other), separately for the three tested great ape species in study 1.

(B) Percentage of given responses in either of the three response categories (frequent, rare, or other), separately for the three tested great ape species in study 2.

The setup of study 2 was identical to study 1, and the procedure was similar, with one crucial difference: study 2 had two demonstrators only. One demonstrator (frequent demo) dropped three balls into one of the three colored sections, receiving one piece of food for each ball. The second demonstrator (rare demo) dropped one ball into an alternative section of the box, receiving one piece in return. The number of demonstrators was identical (one demonstrator each), but one section was demonstrated more often than the other (three versus one demonstrations, see Figure 1B). The third option was never demonstrated. Each response was coded as either copying the frequently demonstrated strategy (frequent response), the infrequently demonstrated strategy (rare response), or neither (other response).

Chimpanzees distributed their balls randomly across the three response options (Ts = 14; $p = 0.56$; frequent: 40.7%, rare: 22.2%, other: 37%; see Figures 2B and 3B).

Children did not distribute their balls randomly across options (Ts = 146; $p < 0.01$; frequent: 54.8%, rare: 31%, other: 14.3%; see Figure 2B). Children gave more frequent responses than rare responses (Ts = 50; $p < 0.05$), more frequent responses than other responses (Ts = 144.5; $p < 0.01$), and no more rare responses than other responses (Ts = 24.5; $p = 0.10$). As measured by their most common response, 8 out of 14 children gave mainly frequent responses (Figure 3B).

Orangutans distributed their balls randomly across the three response options (Ts = 24; $p = 0.48$; frequent: 28.6%, rare: 42.9%, other: 28.6%; see Figures 2B and 3B).

Taking the results of the two studies together, chimpanzees seemed to consider the number of demonstrators more strongly than the number of demonstrations when deciding which information to extract from their social environment. Children considered both. Orangutans considered neither.

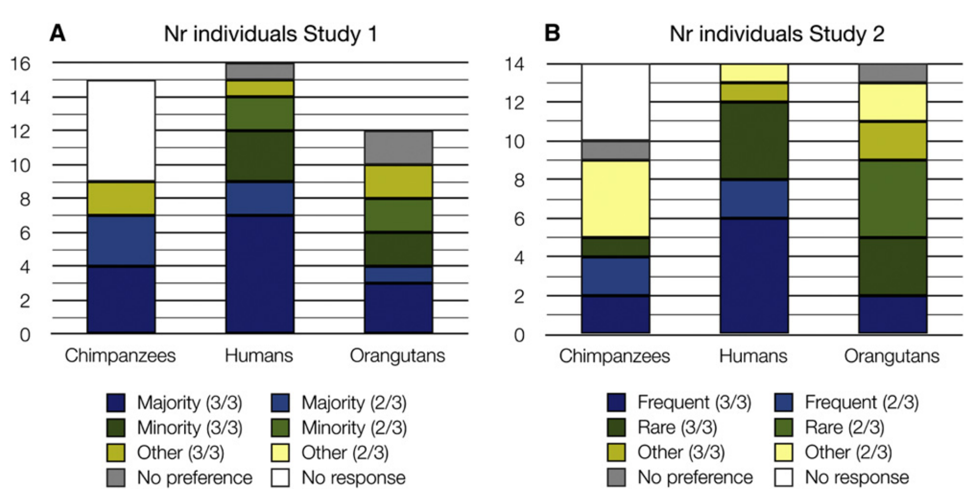

Figure 3. Number of Individuals following the Different Demonstrations in Study 1 and Study 2

(A) Number of individuals in study 1 that either mainly respond following one of the three response options (majority, minority, or other), or respond without indicating a specific preference.

(B) Number of individuals in study 2 that either mainly respond following one of the three response options (frequent, rare, or other) or respond without indicating a specific preference. Color shades in both panels indicate whether an individual gave three of three (dark shade) or two of three (light shade) possible responses following the same strategy.

The fact that human children, already at two years of age, and chimpanzees both tend to acquire the preference of the majority when attempting to learn a new skill, supports theoretical accounts of human evolution arguing for the prevalence of majority-biased transmission in social learning [31] and suggests at least a partial explanation for the stability of group-specific behavioral differences across neighboring groups in both species [4].

Although the majority seems to affect social learning in both human children and chimpanzees, several intriguing questions remain. For example, because the majority by definition encompasses most individuals in the group, several different social learning biases might underlie the transmission pattern reported here, such as the preference to copy what most individuals do, what the most prestigious individuals do [32], what individuals do that are similar to the observer [33], what the most skilled individuals do [34], or any combination thereof. The relative importance of these different factors might of course vary across species and ages, resulting in majority-biased transmission based on varying, equifinal compositions of underlying mechanisms.

Alternatively, the majority-biased transmission observed in study 1 could also be caused by naïve individuals copying one demonstrator at random. Future studies should vary the relative size of the two demonstrator groups: if the probability with which naive individuals acquire the majority behavior changes linearly in response to a change of the relative size of the larger group, random copying is likely. If, in response to a change of the relative size of the larger group, the proportion with which naive individuals acquire the majority behavior changes not linearly but in categorical steps when crossing certain relevant thresholds (majority (>50%) versus plurality (most common but <50%) versus minority (not most common) [35]), random copying is unlikely.

In our study, only chimpanzees show majority-biased transmission to an extent that could stabilize traits within a population across time. Based on our results, we cannot explain the larger effect in chimpanzees relative to human children, but we hope it will inspire future investigation.

Finally, it is significant that both human children and chimpanzees were more likely to acquire the majority behavior, but orangutans were not. Interestingly, in contrast to both humans and chimpanzees, Bornean orangutans (the species studied here) live in an individual fission-fusion social structure [36], largely excluding options for social learning from (groups of) other individuals beyond the mother infant dyad. Hence, the natural social structure of a species might explain, at least in part, which cues individuals pay attention to when learning from others.

Focusing on the social dynamics of social learning [13, 15] allows the investigation of previously unconsidered similarities and differences across species and exposes the social nature of cultural transmission and cross-cultural variability.

Experimental Procedures

Participants

Study 1

Sixteen 2-year-old human children (*Homo sapiens*) (10 females, 6 males; mean age = 2 years 3 months (2;3 years); SD = 2;2 months; range = 2–2;6 years), 15 chimpanzees (*Pan troglodytes*) (10 females, 5 males; mean age = 11 years; SD = 5 years; range = 4;6–21 years), and 12 Bornean orangutans (*Pongo pygmaeus*) (6 females, 6 males; mean age = 9 years; SD = 2 years; range = 6;6–12 years) participated in this study.

Study 2

Fourteen 2-year-old human children (*Homo sapiens*) (8 females, 6 males; mean age = 2;3 years; SD = 2;3 months; range = 2;1–2;6 years), 14 chimpanzees (*Pan troglodytes*) (10 females, 4 males; mean age = 12;6 years; SD = 4;4 years; range = 8–19;6 years), and 14 Bornean orangutans (*Pongo pygmaeus*) (5 females, 9 males; mean age = 7 years; SD = 1;4 years; range = 5;6–9;6 years) participated in study 2. All participants had not previously participated in study 1 but were sampled from the same populations.

All children were recruited from kindergartens in Leipzig, Germany, were native German speakers of normal ability range, and came from mixed socioeconomic backgrounds. All chimpanzees were housed at the Tchimpounga Chimpanzee Sanctuary, Republic of Congo. All orangutans were housed at the Orangutan Care Centre and Quarantine, Kalimantan, Indonesia. The presented study was noninvasive and strictly adhered to the legal requirements of the countries in which it was conducted. The study was approved by an internal ethics committee at the Max Planck Institute for Evolutionary Anthropology. Animal husbandry and research complied with the PASA Primate Veterinary Healthcare Manual and the policies of Tchimpounga Chimpanzee Sanctuary and the Orangutan Care Centre and Quarantine. Apes voluntarily participated in the study and were never food or water deprived.

Materials and Procedure

The Box

The box was attached to the outside of the steel mesh of an observation room in the case of the chimpanzees and orangutans and placed on the ground in the case of human children. Rewards were peanuts for chimpanzees and orangutans and chocolate drops for human children.

Training

During training, only one of the colored sections released food. Conspecific demonstrators were trained to strongly prefer one of the three colored sections of the box. Demonstrators were considered to have adopted a strong preference and met the criterion to perform as a demonstrator once they used this assigned color in 10/12 consecutive trials.

Exclusion Criteria

Demonstrations during which the observer was not facing in the direction of the demonstration were repeated. Trials in which one of the models would not accurately demonstrate the trained strategy were excluded and replaced by a new session with a new observer (study 1: chimpanzees, 1; humans, 10; orangutans, 0; study 2: chimpanzees, 10; humans, 2; orangutans, 0).

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