LETTERS

Conformity to cultural norms of tool use in chimpanzees

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Rich circumstantial evidence suggests that the extensive behavioural diversity recorded in wild great apes reflects a complexity of cultural variation unmatched by species other than our own[1–12]. However, the capacity for cultural transmission assumed by this interpretation has remained difficult to test rigorously in the field, where the scope for controlled experimentation is limited[13–16]. Here we show that experimentally introduced technologies will spread within different ape communities. Unobserved by group mates, we first trained a high-ranking female from each of two groups of captive chimpanzees to adopt one of two different tool-use techniques for obtaining food from the same 'Pan-pipe' apparatus, then re-introduced each female to her respective group. All but two of 32 chimpanzees mastered the new technique under the influence of their local expert, whereas none did so in a third population lacking an expert. Most chimpanzees adopted the method seeded in their group, and these traditions continued to diverge over time. A subset of chimpanzees that discovered the alternative method nevertheless went on to match the predominant approach of their companions, showing a conformity bias that is regarded as a hallmark of human culture[11].

Owing to logistical and ethical constraints on translocation and other field experiments, social learning in apes has been studied experimentally predominantly in captive populations. Over 30 such experiments in the past 15 years have provided evidence of imitation and other forms of social learning[17]. However, the extent to which the cultural interpretation of data from the wild is supported by this work remains contentious[14–15,18], principally because all of the controlled experiments have been restricted to one-to-one learning, typically relying on a human model. The extent to which the social learning documented is sufficient to sustain traditions has thus remained unclear.

Our experiment bridges the gap between population-level studies of wild apes and one-to-one social learning experiments by (1) extending the experimental approach to the group level, (2) focusing on ape-to-ape transmission, and (3) using a powerful 'two-action' methodology[17]. In this approach, individuals see a given task completed using one of two possible techniques, allowing the extent to which their own subsequent behaviour matches the demonstration to be systematically measured. We studied three groups of chimpanzees: a control group exposed to a new task with no expert present, and two experimental groups, each supplied with a familiar, conspecific expert trained to solve this new task in a different way. Unlike previous attempts to study traditions using a single experimental group[19–22], our three-group design allows us to measure the extent to which two quite different techniques are copied sufficiently well to become traditions, with the control condition identifying baseline levels of individual discovery.

We used a naturalistic foraging task that we called the 'Pan-pipes' (Fig. 1). Unseen by her group mates, a high-ranking adult female from each of two groups was first trained to recover food from a Pan-pipe apparatus exclusively using one of two new tool-use techniques: 'Lift' or 'Poke' (Fig. 1a, b). The rest of the group (each $n = 16$) was then allowed to watch their local expert (while their access to the Pan-pipes was prevented) over a seven-day observation

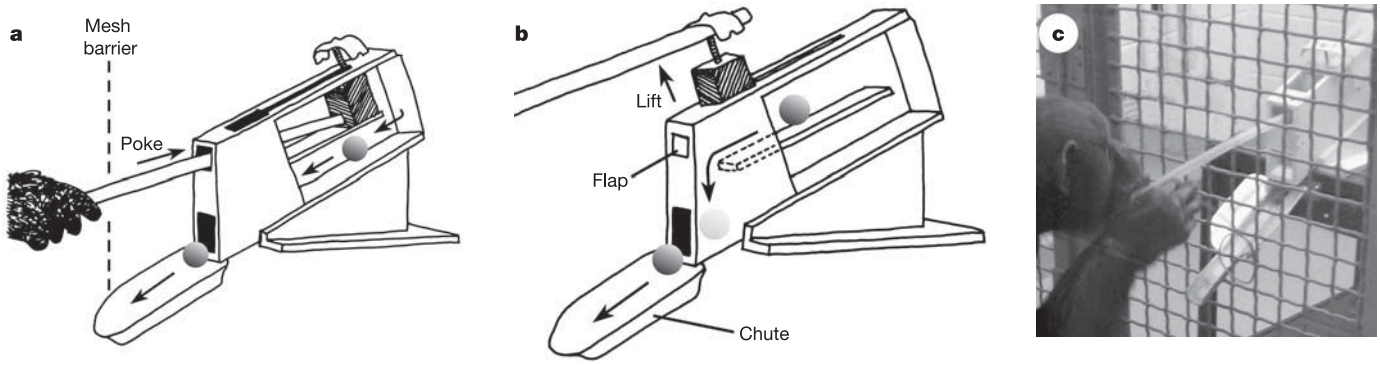

Figure 1 | Two techniques for gaining food from the 'Pan-pipes' apparatus. For each technique, the chimpanzee must insert a stick-tool through mesh caging to contact the apparatus and free a desirable food item that is trapped behind a blockage in the upper of two pipes. The food then rolls down a chute into the chimpanzees' enclosure. The Pan-pipes were 12 cm outside of the enclosure. **a**, In the Poke method, the stick-tool is inserted under the front flap, pushing the blockage back along the ramp so that the food is knocked off and rolls forward underneath. **b**, In the Lift method, the stick-tool is passed under hooks, allowing the blockage to be lifted and the food to roll forward. **c**, Chimpanzee GG performing the Poke method. A video of Pan-pipe operation can be found in the Supplementary Information.

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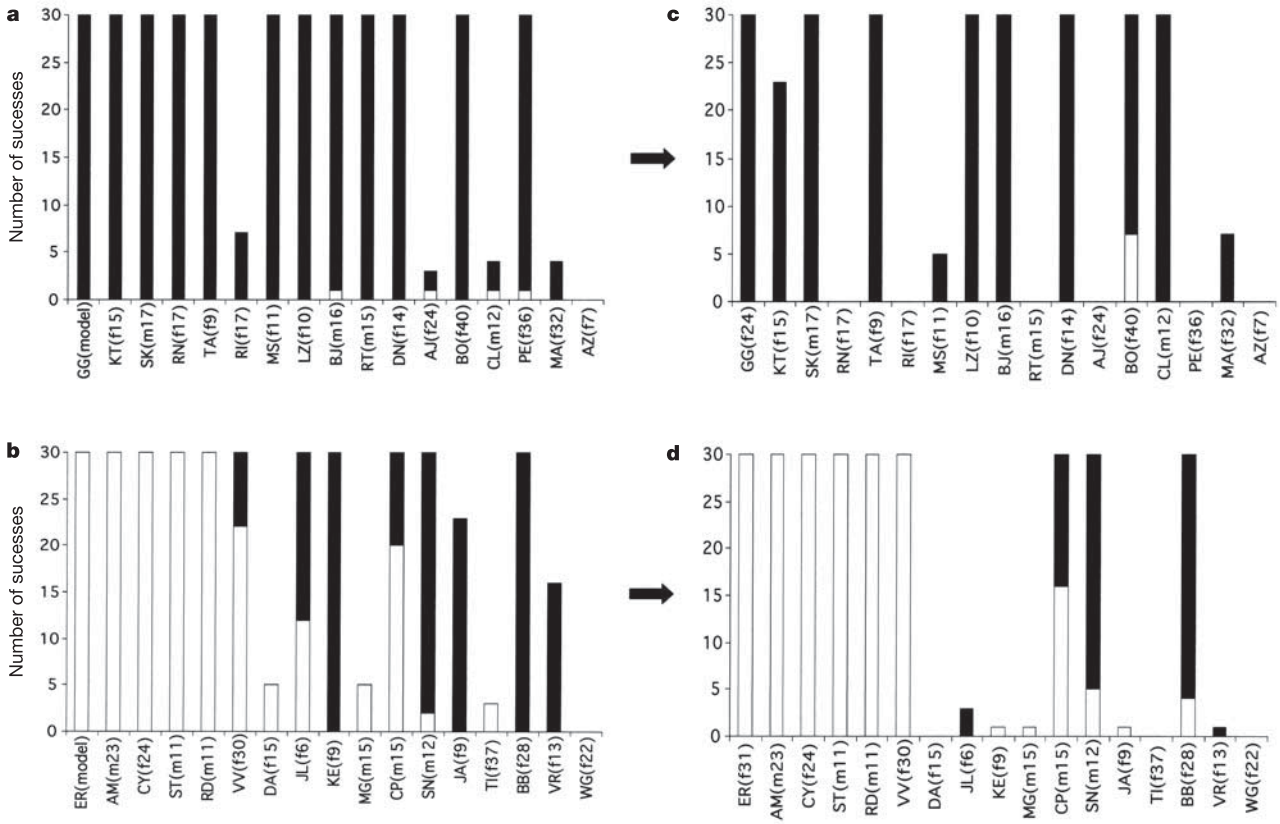

Figure 2 | Adoption of the Poke and Lift methods in two groups. a, Poke group at T1. **b**, Lift group at T1. **c**, Poke group at re-test (T2). **d**, Lift group at re-test (T2). Black bars indicate Poke; white bars indicate Lift. The ID code for each chimpanzee is given together with a gender code (m, male; f, female) and their age in years. Chimpanzees are arranged left to right in the order of their first success in gaining food, starting with the trained model for each group. Data show up to the first 30 successes of each chimpanzee in T1 and T2.

phase of 20-min daily sessions. In this phase, we counted how many demonstrations each chimpanzee paid attention to, which ranged from 8 to 205 per chimpanzee. The expert consistently used the method it had been trained on, and each success was watched by 1–10 chimpanzees (median 4). Both groups showed intense and extended interest in the expert's activities.

The task was then made accessible to all chimpanzees over a total period of 36 h, spread over 10 days (T1). In this phase, 15 chimpanzees in each group successfully used the tool to gain food. Median latency from gaining access to the task until the first success was 29 s (range 5–434 s) for the Poke group, and 52 s (range 2–477 s) for the Lift group. This contrasts with the behaviour of six control chimpanzees offered the task, first individually for 1 h, and then as a group for 4.5 h. All control chimpanzees manipulated the tool and food chute repeatedly, and two inserted the tool into the lower of the Panpipes, but none succeeded in gaining any food (Fisher Exact Test for success, experimental versus control animals, $P < 0.001$).

Preferential adoption of the Lift technique (%Lift = %Lift/(Lift + Poke) in up to the first 30 successes) was significantly greater in the Lift group (median 73.3%, interquartile range 3.3–100.0%) than in the Poke group (median 0.0%, interquartile range 0.0–1.7%) (2-tailed Mann-Whitney *U*-test, $n_1 = 15$, $n_2 = 15$, $Z = 3.31$, $P < 0.001$) (Fig. 2a, b). In the Poke group, all tool users adopted predominantly the Poke technique. In the Lift group, the first six chimpanzees to succeed adopted the Lift method predominantly. However, chimpanzee JL then discovered both the Poke and Lift techniques, and continued to use both of them (Fig. 2b). Two other chimpanzees in this group then acquired both methods, while two adopted only the Lift method and four only the Poke method.

These data suggest waning of the pattern introduced by the expert, at least in one group. However, when the apparatus was reintroduced two months later (T2) and data obtained for 23 chimpanzees that worked at the task, the statistically significant difference in the preferential adoption of the Lift method was maintained ($n_1 = 10$, $n_2 = 13$, $Z = 3.56$, $P < 0.001$). Indeed, all but one tool user in the Poke group now used Poke exclusively (Fig. 2c), and all but two in the Lift group used the Lift method, a majority of them exclusively (Fig. 2d). As expected with this naturalistic approach, overall activity at the task varied greatly, constrained by social dynamics and probably by individual characteristics such as motivation and learning capacity.

To our knowledge, these data provide the first robust experimental demonstration of the spread and maintenance of (1) alternative traditions in any primate, and (2) alternative tool-use techniques in any non-human animal. Additionally, the 'two alternatives' methodology shows that learning involves not merely the facilitation of an existing competence, but a capacity to acquire particular local variants of the technique, precisely as required if the behavioural variants identified in wild populations are indeed socially transmitted.

Additionally, we found evidence of a conformist bias, identified in numerous human studies as a powerful tendency to discount personal experience in favour of adopting perceived community norms[23–25]. As a substantial number of chimpanzees ($n = 14$) succeeded in gaining food using both methods at some point within T1, we were able to define conformity in this context as adoption of the group's norm despite being able to use both methods. Figure 2 suggests that the Poke method was the more conducive to our chimpanzees, so that with no conformity bias, those chimpanzees discovering both methods would be expected to converge on using Poke. Instead, for 13 chimpanzees that used both methods at T1 and also performed at T2, the median percentage of acts matching their

Table 1 | Grades of social conformity

Grade	Characteristics	Chimpanzees in present study
1. Short-latency conformity	After the discovery of an alternative method of task solution, there is nevertheless a rapid convergence on the norm of other group mates (in the present study, this effect was typically observed on the same day).	MS***, BJ***, BO***, PE***, CY***, RD***, VV***
2. Long-latency conformity ('incubation')	After discovery of an alternative method, convergence towards the norm of group mates develops only after an extended period (chimpanzees listed here are those that show an increased proportion of the method consistent with their group norm at the two-month re-test compared with T1).	CL, ST***, SN, CP***, KE, JA, BB**
3. Matching	The norm of group mates is adopted, with no performance of any alternatives. This category could be considered 'blind conformity' insofar as the method conforms to that witnessed, with apparent blindness to alternatives. However, it differs from conformity as defined in the categories above, in which matching occurs despite knowledge of alternative approaches. Thus, this category equates simply to high-fidelity social learning.	KT***, SK***, RN***, TA***, RI**, LZ***, RT***, DN***, MA**, AM***, DA*, MG***, TI*
4. Non-conformity ('contrariness')	A method for task solution contrary to the norm among group mates is exclusively (VR) or increasingly (JL) preferred.	VR, JL

Two forms of strong conformity (short- and long-latency), in which a chimpanzee adopts the group norm despite having discovered an alternative, successful method, are distinguished here from a weaker sense of conformity (matching) that corresponds to high-fidelity social learning. Chimpanzees from the Poke group are shown in bold. Uncorrected binomial and chi-squared statistics are used to indicate the strength of effect for each individual (see main text for group-level statistical tests). Chimpanzees listed in Grade 1 are those that showed a rapid return to their group norm after demonstrating both methods. Three asterisks, $P < 0.001$ (binomial test). All conformed during T1 except for chimpanzee BO (BO performed the alternative method, briefly, only at T2). Chimpanzees listed in Grade 2 showed a shift in bias towards their group norm only from T1 to T2. Two asterisks, $P < 0.05$; three asterisks, $P < 0.001$ (chi-squared test). Chimpanzees in Grade 3 showed an immediate bias to their group norm. Asterisk, $P < 0.05$ (one-tailed); two asterisks, $P < 0.05$ (binomial test); three asterisks, $P < 0.001$ (binomial test). AJ provided too little data to be classified. See Fig. 2 for age and sex of chimpanzees. Raw frequency data are provided in the Supplementary Information.

group norm was significantly higher at T2 than T1 (T1 median 75.0%, interquartile range 11.8–99.4%; T2 median 99.4%, interquartile range 28.7–100%; two-tailed Wilcoxon test, n-ties = 14, $T^+ = 14$, $P < 0.02$), and for eight of these chimpanzees, the increase was in Lift. A strong conformist bias had already been seen in six chimpanzees at T1, when each achieved over 36 successes but the percentage of contrary acts never exceeded 3% in either group (bias to group norm always $P < 0.001$, binomial test) (see Table 1).

These findings encourage us to outline a tentative taxonomy of conformist and allied effects (Table 1). Using this classification, we find that once we have accounted for those chimpanzees in our study that either (1) discover the alternative technique but subsequently show evidence of conformity, or (2) 'conform' in the more basic sense of adopting the local technique without discovering the alternative, only two 'non-conformist' chimpanzees remain, exclusively or increasingly performing the alternative technique. As many as 18 out of 30 of the successful chimpanzees we studied showed substantial conformity effects at the individual level (indicated by triple asterisks in Table 1).

Other aspects of the complex subject of conformity have recently become of interest to researchers studying a variety of taxa, from fish to humans[26–27]. Here we have shown a non-human species conforming to a group norm, despite possession of an alternative technique that represents the norm of another group. Conformity fits the assumption of an intrinsic motivation to copy others, guided by social bonds rather than material rewards such as food[5,28]. This has important implications for the transmission and evolution of culture, creating positive feedback that may amplify differences between the traditions of different groups[11,27]. The substantial variation in the tendency to conform indicated by our results is likely to have additional consequences for the shaping of cultural change.

Our findings also challenge the common assumption that social learning is a function of the juvenile period[29]. In contrast with data from wild chimpanzees suggesting an early sensitive period in which nut-cracking must be learned[16], and that young males are relatively delayed in the social learning of termite fishing[10], our results show that both sexes can show strong social learning and continue to do so into adulthood.

Finally, it has been argued that evidence for imitation in apes comes largely from individuals that are 'enculturated' by close interactions with humans, shaping their attention in non-natural ways, whereas other apes may lack the social learning necessary for culture[30]. Our data, from chimpanzees reared with conspecifics and lacking intense interactions with humans, demonstrate a clear capacity for the cultural transmission of alternative technologies among apes. These results suggest an ancient origin for the conformist cultural propensities so evident in humans.

METHODS

Subjects. Subjects were three separate populations of chimpanzees (*Pan troglodytes*) at the Field Station of the Yerkes Primate Center, median age 15 years (range 6–40 years old). Ages of individual chimpanzees in experimental groups are shown in Fig. 2, and ages and notes on the background of all chimpanzees are provided in the Supplementary Information, together with criteria for model choice. Of the 34 chimpanzees in the two experimental groups, at least 25 were known to be reared by their mothers in captivity; only one was reared in a human home and is thus probably human 'enculturated'[30].

Procedures. Details of experimental procedures are given in the Supplementary Information.

Coding. Details of recording and coding methods are given in the Supplementary Information. The principal tool techniques analysed here, Lift versus Poke, could be coded unambiguously because of the tool placement and effects on the Pan-pipe. Interobserver reliability for Poke versus Lift actions, based on coding 10 actions for each of 10 chimpanzees from video records, was 100%, and agreement on success (food delivery) was 94.2%.

Statistics. Owing to the open group context in which the chimpanzees were tested, some chimpanzees performed the task over a thousand times while the experimenter waited for the responses of those chimpanzees that performed least. For this reason, a cap of 30 was set on the number of initial responses by each chimpanzee that would be used to test the hypothesis that alternative traditions had arisen in the two groups at T1. Figure 2a, b summarizes these results. The analysis of conformity required a different approach, because this relied upon individuals recorded as performing both techniques, which some chimpanzees only did after they had achieved 30 successes. Accordingly, for the conformity analysis, total frequencies (tabulated in Supplementary Table S3) were used in the comparison between T1 and T2. Further details of statistical methods used are in the Supplementary Information.

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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