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The spread of a novel behavior in wild chimpanzees: New insights into the ape cultural mind

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For years, the animal culture debate has been dominated by the puzzling absence of direct evidence for social transmission of behavioral innovations in the flagship species of animal culture, the common chimpanzee. Although social learning of novel behaviors has been documented in captivity, critics argue that these findings lack ecological validity and therefore may not be relevant for understanding the evolution of culture. For the wild, it is possible that group-specific behavioral differences emerge because group members respond individually to unspecified environmental differences, rather than learning from each other. In a recent paper, we used social network analyses in wild chimpanzees (*Pan troglodytes schweinfurthii*) to provide direct evidence for social transmission of a behavioral innovation, moss-sponging, to extract water from a tree hole. Here, we discuss the implications of our findings and how our new methodological approach could help future studies of social learning and culture in wild apes.

Observations of tool use and tool making in wild chimpanzees have been documented since the 1950s.[1] These studies have had an enormous scientific impact and triggered an important debate on the nature and evolution of human culture.[2] Yet, the notion of culture in wild chimpanzees has continued to attract critique, mainly because field researchers have been unable to provide direct evidence that the behaviors they observed had been socially learnt. One difficulty has been that key behaviors, such as nut-cracking in Western chimpanzees, have originated in the distant past, sometimes several millennia ago.[3] As a result, it has never been possible to document the genesis and spread of a novel behavior in any wild chimpanzee community. In a recent study, we have been able to address this shortcoming by documenting the spread of 2 novel behaviors, moss-sponging and leaf-sponge re-use, in a group of wild chimpanzees in Budongo Forest, Uganda.[4] The behavior first appeared in response to a novel context, a waterhole within the root system of a large tree rich in minerals including sodium – an increasingly limited resource for Budongo chimpanzees due to the disappearance of other traditional sources.[5]

In our study, we were able to document, over the course of 6 days, the tool use behavior of 30 chimpanzees, who exploited the site in November 2011.[4] Using a novel analysis tool, Network-Based Diffusion Analysis (NBDA), we were able to directly test the predictions of 2 hypotheses, acquisition of novel behavior due to social or individual learning. Our results supported the first hypothesis, that is, that social learning was responsible for the spread of at least one behavior.[6-7] In contrast to previous studies, our models included a dynamic dimension, which enabled us to precisely take into account the interaction histories of all individuals involved, that is, whether they acquired the novel behavior as a consequence of observing other group members. The crucial advantage of our dynamic models is that they are not based on the assumption that social interactions are temporally

invariant, which captures the complexity of real-life empirical data in important ways. In the wild, social interactions are based on numerous, often ephemeral, contacts between individuals that hold information much beyond simple long-term aggregation data used by the static social network models used so far. In our opinion, NBDA offers significant potential for future studies of animal behavior. In the following we focus on the question of chimpanzee culture and outline 3 domains in which we anticipate particular progress.

Chimpanzee cultures change gradually over time

One pervasive view of chimpanzee culture is that behavioral traditions remain static once they have been established in a group. For example, surveys of long-term chimpanzee study sites have shown that behavioral innovations generally tend to be rare,[8-9] which has been interpreted as 'cultural conservatism'.[10] However, in recent years various new chimpanzee study sites have been established, including in highly degraded and human-dominated habitats, and data collected in these sites suggest that chimpanzee behavior may be more flexible than generally thought.[11] For our study group, the Sonso community of Budongo Forest, Uganda, we have been able to show that new behaviors can sometimes also appear in long-term field sites. This has been made possible due to the availability of long-term behavioral records that enable baseline comparisons. Our study also illustrates that behavioral change is likely to happen gradually, with modifications added to pre-existing behavior, rather than due to sudden emergence of radically novel behaviors. In our case, chimpanzees have been observed for decades to engage in leaf-sponging behavior to extract fluids from cavities. This is done by folding a bunch of leaves in the mouth to fabricate a sponge, typically in order to extract water from treeholes.[12-13] In utilizing a novel material (moss instead of leaves), moss-sponging can be interpreted as a modification of the existing leaf-sponging behavior. The second observed innovation, leaf-sponge re-use, where individuals re-utilize a leaf-sponge already made and left behind by another chimpanzee, is probably also a modification of leaf-sponging. The notion of gradual change is further supported by field experiments showing that wild chimpanzees appear particularly reticent to adopt behaviors that are too different from their existing repertoire, with novel solutions usually found within the broad range of existing patterns.[14] One possibility is that these limitations in behavioral flexibility are due to profound underlying cognitive limits, particularly in terms of the metarepresentational abilities available to chimpanzees.[15]

Why do innovations spread unevenly?

Data from several long term field sites indicate that behavioral innovations usually fail to spread throughout the group,[9,16] and understanding the reasons for this is of primary concern.[17] Our recent study can contribute to this discussion in the following way. Firstly, studies in captivity have highlighted the importance of a model's social rank for the transmission of novel behaviors, the so-called 'prestige effect'.[18-19] In our study, moss-sponging spread rapidly and all our models were dominant relative to the observing novices. In contrast, for leaf-sponge re-use we only found limited evidence for social learning. In this case, interestingly, the behavior was primarily demonstrated by subordinate individuals. More work is required to understand these patterns, but one approach will be in monitoring whether and how the 2 novel behaviors are maintained within the community.

Secondly, our study demonstrates that certain ecological conditions can trigger behavioral innovations that can subsequently spread throughout a group. In the case of leaf-sponge re-use, the behavior emerged in different individuals, most likely due to individual learning. The discovery of a new waterhole rich in minerals attracted a large number of chimpanzees, who engaged in leaf-sponging, which resulted in a high density of discarded leaf-sponges. We suspect that this significant change in the environment caused the emergence of leaf-sponge re-use. However, our study also suggests that, in at least some cases, social transmission can greatly speed up the spread of a novel behavior pattern through animal groups, as in the case of moss-sponging. In general, our study suggests that changes in the ecological conditions generate opportunities for individuals to invent novel behaviors, which then requires relevant models to display the behavior to others for it to spread throughout and be maintained within a community.[20]

How do chimpanzee cultures relate to human cultures?

Our findings demonstrate that chimpanzee cultural behavior, similar to human cultures, can be transmitted through social learning, suggesting shared common ancestry. By extension, our findings also suggest that australopithecines and early hominins already had the capacity to acquire some of their knowledge through cultural means. Nevertheless, there has been a long lasting debate about the social learning processes that underlie cultural learning and whether they are the same in the 2 species.[21] While it is unquestionable that modern humans rely on teaching and imitation to transmit culture,[22] it is less obvious whether this was also true for early hominins, for instance *Homo habilis* or *H.erectus*, or whether they employed other social learning processes, such as emulation.[23] As such, chimpanzees may be a valuable model in understanding how early hominin culture was transmitted.

Secondly, our study demonstrates how research on animal behavior can help to understand how basic cultural achievements may have been transmitted cumulatively during the first stages of human evolution, leading, for example, to the emergence of hand-axes.[24] In our chimpanzees, innovations were based on modifications of existing behavior, which may have lead to modifications of the underlying mental representation.[25-26] Elsewhere we have argued that chimpanzee culture should be analyzed beyond the surface behavioral patterns and include the study of how community-specific mental representations are formed by observing others. In our view, the precise category of social learning process utilized in behavioral acquisition is then less critical than the fact that animals are likely to create novel mental representations when observing others in carrying novel behaviors.

Understanding how chimpanzees handle novel ideas, cultural or not, may tell us more about both how our ancestors learnt from each other and how their achievements gradually changed into modern human cultures.

Disclosure of Potential Conflicts of Interest

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