Conservatism Versus Innovation: The Great Ape Story

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Commentary on Chapter 14: Conservatism Versus Innovation: The Great Ape Story

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Dictionary.com defines innovation as the “introduction of new things or methods” and it lists “tradition” as one of its antonyms. For those of us interested in ape behavior and cognition, this poses an interesting puzzle. Chimpanzees and orangutans are well known for their social traditions which persist over generations (Whiten et al., 1999; van Schaik et al., 2003) and yet, they have been traditionally considered some of the most innovative creatures in the planet. Can one be tradition-bound and yet a naturally-born innovator?

While some analyses suggest that this may indeed be possible, as evidenced by the correlation that exists between social learning and innovation across species (Reader & Laland, 2002), others have argued
that innovation is either not as common and robust as previously thought (Hrubesch, Preuschoft, & van Schaik, 2009) or it may easily be curtailed by social learning and social influence (Price, Lambeth, Schapiro, & Whiten, 2009; van de Waal, Borgeaud, & Whiten, 2013). The currently popular characterization of chimpanzees as conservative and conformists contrasts with the traditional notion of chimpanzees as flexible problem solvers and innovators.

The main goal of this chapter is to resolve this apparent contradiction at both the empirical and theoretical levels. To do so, I will review the evidence that has recently accumulated in problem solving and innovation on the one hand, and social learning and tradition on the other hand. Additionally, I will consider individual and contextual variables that may contribute to resolve the existing apparent contradiction. I will end the chapter with some reflections about the question of flexible cognition and cumulative culture.

**PROBLEM SOLVING AND INHIBITORY CONTROL**

Innovation is a crucial component of problem solving that can adopt different forms including applying an old solution to a new problem or producing a new solution to an old problem (Kummer & Goodall, 1985). Manrique, Voelter, and Call (2013) have argued that these two types of innovation may be quite different from a cognitive standpoint. Whereas using an old solution to a new problem requires transferring motor sequences and functional knowledge about object–object relations to a new situation, producing a new solution to an old problem also requires the inhibition of behaviors that were successful in the past. There is ample evidence that great apes display both types of innovation but I will primarily focus on the second type of innovation.

Inhibitory control has been documented in several primate species in a variety of contexts including object search, reaching, reversal learning, and even in temporal discounting. Amici, Aureli, and Call (2008) compared the performance of monkeys and great apes in a battery of five tasks that included all of these contexts. Results revealed two clusters of species with chimpanzees, orangutans, bonobos, and spider monkeys belonging to the high performance cluster and gorillas, capuchin monkeys, and long-tailed macaques forming the second low performance cluster. Interestingly, this distribution would not be predicted by phylogeny alone but it correlates well with some socio-ecological variables such as a social group’s likelihood to split and merge into multiple subgroups of different sizes and compositions over the course of multiple days (so-called fusion–fission dynamics). Interestingly, Aureli, Schaffner,
Boesch, Bearder, and Call (2008) had hypothesized that those species with high levels of fission–fusion dynamics (chimpanzees, orangutans, bonobos, and spider monkeys) should perform better in inhibitory control tasks than those species with low levels of fission–fusion dynamics (gorillas, capuchin monkeys, and long-tailed macaques).

Although most of the tasks used by Amici et al. (2008) only required relatively simple motor responses such as touching or pointing to one of two objects, one of the tasks (i.e., swing door) required a more complex reaching response. More specifically, subjects faced a panel with two square holes next to each other and covered by two transparent “doors” attached to the top part of each hole by a set of hinges that could only be opened by pushing them forward. A piece of banana was placed behind one of the doors so that directly reaching for the banana (and pushing the door forward in the process) invariably produced the undesirable outcome of displacing the banana away from the subject’s reach. To solve the task, subjects had to refrain from directly reaching for the banana and instead had to reach into the non-baited door to grab the banana from behind. Orangutans performed better than chimpanzees, gorillas, and 4-year-old children in this task. This task is reminiscent to some of the experiments that Köhler (1925) did with chimpanzees who were capable of taking indirect travel routes to a goal when the most direct route was blocked.

Puzzle boxes typically require even more complex manipulations than detour reaching (or traveling) tasks which in some cases even involve using tools. One particularly interesting case is when individuals have been using a solution for some time, with the possibility that it may have become fixated, and they must upgrade to a more efficient solution. Some studies have shown that apes are capable of sequentially innovating multiple solutions (Lehner, Burkart, & van Schaik, 2011; Manrique et al., 2012). For instance, Lehner et al. (2011) found that orangutans produced multiple solutions to extract liquid from a container and quickly abandoned those solutions that became ineffective after the conditions of the task were altered. Manrique et al. (2012) reported similar findings in all great ape species in a non-tool-using task.

Sequential innovation is not the sole purview of the great apes. Auersperg, von Bayern, Gajdon, Huber, and Kacelnik (2011) presented the so-called Multiple Access Box to New Caledonian crows and keas. Subjects could use four different methods (open a door, insert a stick, drop a ball, pull a string) to extract a piece of food placed inside the box. Once subjects became proficient with one of the methods, that method blocked and subjects had to find a new way to get the food with one of the remaining methods. Note that unlike the previous studies, subjects were prevented from entirely using a previously successful method, e.g., by completely removing the string from the box, which

IV. PUSHING THE BOUNDARIES OF CREATIVITY
might have eliminated some of the difficulties inherent to refraining from using a previously effective method if it was still available but no longer effective. In general, keas showed a preference for dropping the ball whereas crows preferred using the stick. Moreover, although one individual in each species discovered all methods, keas tended to discover more methods and do this faster than New Caledonian crows.

There are some studies, however, that have reported a failure to innovate in great apes. For instance, Hanus, Mendes, Tennie, and Call (2011) reported a case of innovation failure in chimpanzees probably caused by functional fixedness (Duncker, 1945). More specifically, Hanus et al. (2011) found that some chimpanzees that were unable to solve the floating peanut task (i.e., spitting water into a vertically-oriented tube to extract a peanut lying at the bottom of it) succeeded as soon as their familiar water dispensing device was replaced by a new one. Hanus et al. (2011) suggested that the familiar water dispensing device may have acquired a fixed function of supplying water that the new device lacked, thus hindering innovation for a new use of water.

Other studies that have reported individuals failing to abandon solutions that no longer worked have been interpreted as evidence of conservatism (Bonnie et al., 2012; Hrubesch et al., 2009). Bonnie et al. (2012) observed that chimpanzees continued to fish at an artificial termite mound after the food became gradually scarcer (fewer holes remained productive) over a period of several months. However, food was never completely exhausted because some holes continued to produce food for the entire period. In fact, there was a notable reduction in the use of the termite mound that precisely matched the amount of food available—something that strongly suggests that chimpanzees did abandon some of their original practices. Note that there was no alternative available when some of the holes became exhausted other than the other holes that remained productive. For an individual exploiting the still productive holes it may be a good idea (and nearly cost-free) to check those sources that were productive in the past in case they became productive again—as occurred in the second part of the study. If subjects had completely abandoned the occasional inspection of previously rewarded holes, they would have never been able to re-exploit them once they became productive again.

Hrubesch et al. (2009) also found persistence in chimpanzees in the face of failure. Namely, chimpanzees persisted in using sticks to get out-of-reach food from a platform instead of adopting a technique based on rattling the platform which produced more food than the stick technique. However, those individuals who persisted in using tools were also those who were the most efficient ones at using the tools. This means that they had less pressure to change to the new alternative. In fact, those chimpanzees who switched to rattling the platform were
mostly adult males, which some studies have characterized as less persistent than females at using tools for extended periods of time (Lonsdorf, 2005). When platform rattling was made ineffective, adult males who had used that technique continued to do so despite its low probability of success and their persistence was interpreted as conservatism. However, note that for those chimpanzees the option of changing to sticks may not have been a viable option, which is why they invented rattling in the first place. Moreover, trying that technique may not be an indication of conservatism but a case of probing as noted above. What would be needed is two techniques matched in difficulty so that one can assess whether individuals abandon one technique in favor of the other as soon as the latter provides a greater payoff. Would individuals adopt the technique offering the higher payoffs regardless of which of the two techniques they acquired first?

Another issue to consider is that suboptimal solutions (both in terms of motor efficiency and/or payoffs) may persist under an intermittent reinforcement regime but may disappear once the payoff becomes zero—although as we have seen they may occasionally reappear as a way of probing old solutions. In other words, it may be easy to mistake behavioral conservatism for responses under a partial reinforcement regime. This explanation is supported by data on reverse reward contingency tasks (RRC) in which subjects have to pick the smaller of two quantities to receive the larger quantity—a procedure similar to reversal learning. Several studies have shown that learning to suppress the choice of the larger quantity is slower when subjects receive non-zero quantities for incorrect choices than when they receive nothing (Silberberg & Fujita, 1995; Vlamings, Hare, & Call, 2010). In fact, one of the most effective correction procedures to train subjects to select the smallest quantity in RRC tasks consists of giving them no reward upon making the wrong choice (Silberberg & Fujita, 1995).

Although the zero payoff effect provides a good explanation for why apes were more likely to innovate when a solution becomes completely ineffective compared to when it still provides intermittent reinforcement, there are other studies showing that apes do upgrade to solutions better solution even under partial reinforcement conditions. For instance, Manrique and Call (2011) reported that chimpanzees, bonobos, and orangutans extracted juice from a box by dipping and licking a piece of electric cable (three copper filaments covered by plastic and held tightly together by a plastic shaft). Interestingly, all orangutans tested and one chimpanzee discovered the use of the cable as a straw to extract the liquid—a technique which was much more efficient than the dipping technique in terms of both speed and quantity of juice extracted.

In summary, the reviewed evidence suggests that ape conservatism in most problem solving tasks may be more apparent than real. Apes’
persistence may occur under partial reinforcement or because other options are not possible. Re-trying a previously successful solution as a way to probe whether conditions have changed is quite adaptive and it may represent an alternative explanation to conservatism. Furthermore, some studies have documented both innovation and even repeated innovation of more efficient solutions even though the existing ones produced non-zero payoffs. Future studies could investigate whether individuals trained to obtain food with one technique abandon it for another one matched in terms of difficulty but producing a higher payoff.

SOCIAL LEARNING AND SOCIAL TRADITIONS

It is well known that different wild populations of chimpanzees and orangutans display different behavioral repertoires that some authors consider cultural variants, mainly related to the use of tools to extract food. For instance, using stones to crack open nuts, sticks to fish for termites or ants, or leaves to extract liquids are present in some populations but not others despite the fact that the potential for the appearance and spread of those behaviors are available in multiple sites. Consequently, the behavioral tool repertoires of the different populations vary considerably, not just in terms of the type of tool or the resource exploited but also in the techniques used to exploit the resources. For instance, western chimpanzees in Goualougo and Tai display 22 and 21 types of tool use, respectively, whereas eastern chimpanzees in Budongo only use eight types of tools (Sanz & Morgan, 2007; Whiten et al., 1999). The contrast is even more striking between populations of eastern chimpanzees, since Gombe and Mahale chimpanzees display 22 and 16 tool types, respectively, many more than those found among the chimpanzees of Budongo forest.

But perhaps even more striking than the large differences between populations is that some of these populations seem extremely conservative in the tools that they use and the way they use them. Gruber, Muller, Strimling, Wrangham, and Zuberbühler (2009) conducted a field experiment that consisted of presenting chimpanzees with a log filled with honey. The honey could be extracted by inserting tools through a set of holes. Chimpanzees in Kanyawara used sticks to extract the honey, which is not surprising since they had been observed using sticks for similar tasks. In contrast, Sonso chimpanzees (who live only 180 km away from Kanyawara) used their fingers and leaves (but not sticks) to extract the honey—in fact leaf sponging is a technique that they commonly use to extract water from crevices in their natural

IV. PUSHING THE BOUNDARIES OF CREATIVITY
habitat. More importantly, when leaves became ineffective because the honey that remained was too deep inside the log, they completely failed to innovate a solution to continue exploiting this resource. They were unable to use sticks to extract the honey—a behavior that is quite widespread among other wild and captive chimpanzee populations. Even pre-inserting sticks into the holes filled with honey so that when chimpanzees would realize about their utility when they pull them out produced no positive results. Chimpanzees extracted the honey dipped tools, licked them, and then discarded them, or stripped the leaves from the sticks and inserted them into the hole while discarding the now leafless stick!

Mesoudi (2011) has argued that conservatism, like the one exemplified above, may be the reason why there is so little evidence of cumulative culture in nonhuman great apes or nonhuman animals more generally. Furthermore, Hrubesch et al. (2009, see also Whiten, Horner, & de Waal, 2005) have pointed out that both conservatism and social conformity may contribute to make cumulative culture in nonhuman animals a rare phenomenon.

The possibility that chimpanzees are behavioral conformists, i.e., once they have learned a technique and used it repeatedly they are incapable of abandoning when it becomes obsolete. This explanation, however, is seriously undermined by the studies reviewed in the previous section. Alternatively, it is conceivable that chimpanzees are conservative because they are social conformists—they are either unable to change what they have learned socially or unwilling to deviate from what others are doing. We explore these two possibilities next.

One hypothesis to explain the putative social conformity is that social learning leaves an indelible mark, much stronger and difficult to change than individual learning. In other words, socially acquired information is more resilient to change than individually acquired information. For instance, Price et al. (2009) found that subjects who learned to use a tool by observation had greater difficulty inventing a new technique compared to those individuals who learned the use of the tool individually. Marshall-Pescini and Whiten (2008) also suggested that chimpanzees became “stuck” on less efficient solutions that they learned socially. The authors confronted young chimpanzees with an artificial fruit that could be opened with a tool in two ways. One way was simpler (but less efficient) than the other. A human demonstrated first the simple method to the chimpanzees and three subjects learned it (two other chimpanzees learned this method on their own during a baseline period). Then the experimenter demonstrated the second more complex and efficient method but none of the chimpanzees adopted it, presumably as the authors argued because they became stuck on the first method they (socially) learned.

IV. PUSHING THE BOUNDARIES OF CREATIVITY
Although this evidence is suggestive, it is hard to attribute the fixation effect to social learning per se, given that two other chimpanzees who learned on their own also failed to benefit from the human demonstration (of the second technique). Moreover, it is unclear whether individuals actually learned socially in the first place given that two chimpanzees learned individually. An additional control group with additional exposure (and without demonstrations) could have helped tease apart these alternatives. Age might have also been an issue in this study because the median age of the chimpanzees tested was only 3 years and in fact, no chimpanzee younger than 3 years of age learned how to operate the apparatus. Nevertheless, it is still possible that social learning has a dampening effect on the probability of innovation, and that such an effect might contribute to explain why chimpanzees who learned socially failed to adopt more efficient techniques (Gruber, Muller, Reynolds, Wrangham, & Zuberbühler, 2011; Gruber et al., 2009). However, better data are needed to confirm this possibility. Also, note that Hrubesch et al. (2009) found the opposite effect, i.e., individually acquired behavior was immune to social influence even when the alternative solution was more profitable.

But as mentioned before, it is possible that individuals did not abandon their current technique because it was profitable enough. Even if social learning were to have the dampening effect once the behavior has been acquired and consolidated, this does not necessarily mean that when they acquire social information they do it in an inflexible manner. On the contrary, there is some evidence showing that chimpanzees are selective about the information that they adopt depending on the situational constraints. For instance, Horner and Whiten (2005) found that chimpanzees observing a human model using a sequence of actions (some needed to actually open and others completely unnecessary and ineffective) to open an artificial fruit copied the demonstrated techniques depending on whether the artificial fruit was clear or opaque. Chimpanzees who witnessed the actions on the opaque box were more likely to copy all the demonstrated actions, whereas chimpanzees witnessing the demonstration on the clear artificial fruit only copied those actions that were actually needed to open the box (they ignored unnecessary actions such as inserting a stick that had no causal effect because its path to the food was blocked by a barrier). Buttelmann, Carpenter, Call, and Tomasello (2008) also reported selectivity in copying the body part executing an action depending on the contextual constraints faced by a human demonstrator touching a box that produced music and lights. More specifically, enculturated chimpanzees who observed a human using an unusual body part to activate the box, used the same unusual body part more often when there was no physical constraint that it would have impeded the human to use a usual body part to

IV. PUSHING THE BOUNDARIES OF CREATIVITY
activate the box (e.g., activating a night light by touching it with the forehead rather than with the hand). These results suggest that chimpanzees are not completely tied to what they see when they are learning a new technique—but the data are not incompatible with the idea that chimpanzees become less flexible once they have already learned the technique by observation. In fact, it is an open question whether chimpanzees who learned to open an opaque artificial fruit compared to those who learned from the clear box would be equally likely to abandon their technique as soon as it became obsolete.

Another possible explanation for why chimpanzees may give priority to social compared to individual information is the influence that group majorities may have on individuals. That is, social learning per se is not the key, but majorities in general bias subjects’ behavior.

The effect of group majorities on the individual’s behavior is well documented in several domains in various species (Day, MacDonald, Brown, Laland, & Reader, 2001; Galef & Whiskin, 2008; Pike & Laland, 2010). Moreover, several studies have shown that after chimpanzees acquire a solution using social information and later on they discover an alternative solution individually, they typically revert back to the initial socially learned solution both in a token selection (Bonnie, Horner, Whiten, & de Waal, 2007) or a tool-using task (Whiten et al., 2005). Some authors have interpreted these findings as an indication of social conformity (Claidiere & Whiten, 2012; Whiten et al., 2005). However, Van Leeuwen and Haun (2013) pointed out that conformity in those studies is conceptualized as preserving the initial solution rather than abandoning it in favor of an alternative solution used by the majority of individuals. In fact, Van Leeuwen, Cronin, Schütte, Call, and Haun (2013) found that chimpanzees did not abandon their initial solution when confronted with a majority of individuals using an alternative but equally profitable solution. However, chimpanzees did abandon their original solution when they observed (and experienced) that a new solution provided a more profitable payoff. Similarly, Yamamoto, Humle, and Tanaka (2013) found that chimpanzees that learned a “straw-dipping” technique abandoned it for a “straw-sucking” one that was more efficient after observing conspecifics using it. These two studies corroborate previous findings reviewed in the previous section showing that chimpanzees are perfectly capable of abandoning techniques in favor of more efficient or profitable ones.

Another aspect that ties with the literature on problem solving is that regardless of the way that subjects learned to solve a task (either social or individual learning), it is clear that individuals try new things even when their current solution is already profitable. Dean, Kendal, Schapiro, Thierry, and Laland (2012) also observed that chimpanzees and capuchin monkeys continued exploring the properties of an
apparatus after they succeeded but unlike children they failed to acquire more complex (and profitable) solutions by observation. Thus, once a solution is found, chimpanzees seem to engage in either further exploration or a “testing-the-waters” approach that may reveal new possibilities. What is less clear and still a matter of debate is whether (and if yes, why) the newly discovered options are ultimately adopted by the individual. In any case, what this suggests is that social learning does not in general (although there may be some exceptions, e.g., Price et al., 2009) make the adoption of other strategies less likely.

In summary, the idea that social learning makes change more difficult is intriguing but the evidence supporting it is mixed, with some studies potentially showing a greater resilience for behavior learned via social influence while others show no such effect. The effect of the social environment, rather than the social learning mechanisms per se, is another tantalizing possibility but once again the evidence is rather mixed. The following section will attempt to throw some light onto these results.

**INDIVIDUAL AND CONTEXTUAL DIFFERENCES**

The two previous sections have revealed two important things. First, there is a set of mixed results with regard to the innovative tendencies of the great apes. Second, and perhaps more importantly, there seem to be a variety of factors that play a role in the observed differences. Next, I will briefly explore both individual attributes (personality, age, and species) and contextual variables (task, setting) that may be contribute to clarifying the relation between innovation and conservatism.

Recent years have witnessed an unprecedented research interest in the question of individual differences and personality in nonhuman animals. Boldness-shyness is one of the personality dimensions has been most intensively investigated. Typically, this dimension is assessed by presenting individuals with novel foods and/or novel objects and researchers measure the latency to taste or to approach those novel items. This test has revealed both species and individual differences. At the species level, bonobos are shier than chimpanzees and orangutans—a result that has been linked to the higher degree of tool use and varied foraging repertoire in chimpanzees and orangutans, compared to bonobos (Herrmann, Hare, Cissewski, & Tomasello, 2011). At the individual level, bolder chimpanzees perform better than shier chimpanzees in physical (but not social) cognition tasks (Herrmann, Call, Hare, Hernandez-Lloreda, & Tomasello, 2007). In contrast, no relation between those two variables was found for 2.5-year-old children.
Thus, bolder individuals are more likely to try new things and therefore they would be the prime candidates for innovation. However, the relationship between boldness and innovation may not be as straightforward as it may appear. Günther, Brust, Dersen, and Trillmich (2014) found that although shier cavies (Cavia aperea) are slower than bolder individuals to explore and learn an object discrimination task, they are faster than bolder individuals at reversal learning when the previously rewarded option is no longer rewarded. Thus, bolder individuals may be quicker to innovate but they are slower to abandon a previously profitable option, thus hindering their adoption of alternative solutions. This is important because it supports the idea that innovation and inhibitory control are related but may not be the same phenomenon. Additionally, it is tantalizing to link boldness and impulsivity even though these two constructs do not appear to be one and the same, at least not in humans (Cross, Copping, & Campbell, 2011).

Whereas the relation between boldness and innovation has received some empirical support, it is an open question whether one could also find personality traits that identify individuals that are more prone to adopt the behavior and products of the innovators once they have become familiar with them. Groups formed by a mixture of innovators and copiers would be capable of sustaining cultural evolution. The faithful adoption of others’ behavior or their products (without further innovation) could be facilitated by social learning itself (although this will depend on the task), or perhaps those individuals who rely on social learning are also less prone to innovate than those who are bolder and rely on individual learning. Herrmann et al. (2007) could have potentially discovered the relationship between boldness and social learning in chimpanzees. Unfortunately, the data on social learning showed a floor effect, meaning that the tasks (or the procedure) may not have been sensitive enough to detect social learning. Alternatively, this may mean that chimpanzees (which are bolder than 2.5-year-old children) tend to rely more on individual than social learning, especially when the tasks are not opaque—an issue that we will return to when we discuss the effect of task on performance.

Age, sex, and species are other attributes of the individual that may impact on innovation and conservatism. Manrique and Call (2015) found that task persistence in the face of failure was age dependent in the great apes. They found that the youngest and the oldest individuals included in the study were the most persistent ones whereas the middle aged subjects adapted quicker to the new conditions and modified their behavior accordingly. Marshall-Pescini and Whiten (2008) found that chimpanzees younger than 3 years of age failed to adopt any of the demonstrated methods. However, as Marshall-Pescini and Whiten (2008) pointed out, the chimpanzees they tested may have been too
young to benefit from demonstrations. With regard to sex differences, Hrubesch et al. (2009) found that adult male chimpanzees were mainly responsible for inventing a platform rattling technique, presumably because they were more efficient than with the alternative tool-using technique—something that fits with the idea that female chimpanzees are more prone than male chimpanzees to use tools for extended periods of time (Lonsdorf, 2005). There are also species differences in several tasks. For instance, Manrique, Voelter, and Call (2013) found that chimpanzees, bonobos, and gorillas invented one solution based on forcefully projecting the reward out of the apparatus while only one of the orangutans did. It is conceivable that banging actions are more prominent in the repertoire of African apes than in orangutans. In contrast, orangutans were more likely than chimpanzees and bonobos to discover the use of a piece of electric cable as a straw to drink from a container (Manrique & Call, 2011).

Contextual factors may also play an important role in explaining the observed differences between studies. One such factor is the type of task, more specifically, the nature of the relation between the elements of the task. Puzzle box tasks are grounded on physical (causal) relations between their object components and food delivery. For instance, a tool is used to displace a piece of food or some box “defense” needs to be removed before the subjects can access the food. In contrast, token tasks are grounded on an arbitrary relation between objects and food delivery. For instance, depositing a token inside a particular container or choosing one of two tokens is what determines the delivery of the reward. There is no physical rule governing the reward delivery but an arbitrary rule set by the experimenter. It is conceivable that these arbitrary rules are more opaque than those grounded on physical relations but once acquired they may be more easily transmitted faithfully down a chain of individuals. In fact, Horner and Whiten (2005) found that when the physical relations in a puzzle box were made opaque, chimpanzees were more likely to copy the behavior of a demonstrator including actions that were irrelevant to solve the task. This could explain why studies using tokens might be more likely to produce uniformity in groups compared with studies not based on tokens. An individual confronted with a task in which she cannot deploy her individual knowledge might be more likely to rely on the behavior of others (Hopper, Schapiro, Lambeth, & Brosnan, 2011). Note that tokens per se are not causing this effect because when individuals have acquired knowledge about tokens on their own they can become immune to the influence of social information (van Leeuwen et al., 2013).

The setting where the task takes place is another important consideration. Some authors have argued that innovation may be more likely to occur in the captive setting because it is a “safe” environment basically
devoid of dangerous creatures and stimuli—clearly a case that it is not true in the field. As a consequence, experimenting in the field, especially for young individuals, may be more costly than in the laboratory. In a similar vein, Lehner et al. (2011) pointed out that captive (or rehabilitant) orangutans were more prone to innovation than wild orangutans (Russon, Kuncoro, Ferisa, & Handayani, 2010) and suggested that innovation in captivity may have been associated with positive reinforcement (e.g., finding food rewards under novel containers). However, this should not be taken as an indication that innovation does not occur in the wild. On the contrary, innovation has been reported in the field, although it may not persist (Kummer & Goodall, 1985) and it still may be less prominent than in the laboratory. Unfortunately, with a few exceptions (Gruber et al., 2009; Matsuzawa, 1994) there has been comparatively little field experimentation in the area of ape innovation.

CONSERVATISM, SOCIAL CONFORMITY, AND CUMULATIVE CULTURE

Neither conservatism nor social conformity provides a compelling argument to explain the putative lack of cumulative culture among non-human apes. Conservatism is not present in every study and when it appears it depends on the return benefits and individual variables such as boldness, age, and species. In fact, most studies show non-conservatism in one way or another. Moreover, some studies show repeated innovation and even those that do not indicate that subjects can revert to alternative solutions not just when current solutions cease to produce benefits but also even when their current solutions continue to be rewarded. Those findings paired with data on inhibitory control and reversal learning suggest that apes in general should not be characterized as conservative. This conclusion fits with large scale studies that have shown that primates, and apes in particular, score high both on innovation and inhibitory control (Amici et al., 2008; MacLean et al., 2014; Reader & Laland, 2002).

Social conformity is an equally unsatisfactory explanation for the lack of cumulative culture since it is not observed in every study when complex tasks are involved. More robust is the evidence based on token tasks (or opaque puzzle boxes type tasks), but most of this evidence is based on reverting to the original solution rather than abandoning the original solution for another one that is equally beneficial. Additionally, some studies have shown that apes can abandon their current solutions for other more profitable ones even when social pressure would predict the opposite. Interestingly, the most compelling case for social conformity has been
reported in vervet monkeys, not apes. Van de Waal et al. (2013) observed that migrating vervet monkey males abandoned (not just reverted) their original preference for one type of corn and adopted the preference displayed by most members of the group where they had just immigrated.

Although this finding may qualify as a case of social conformity, which is one of the pillars of human culture, it is still hard to consider it as cumulative culture because the acquired technique is still rather simple—a choice between two types of food. Tennie, Call, and Tomasello (2009) have argued that one key aspect of cumulative culture is that the practice or product derived from it cannot entirely be invented by a single individual, no matter how innovative. In our culture, a computer, the wheel, or even a mundane paper clip are just some examples of massively concentrated knowledge distilled and accumulated over multiple generations which could not have been invented by a single individual. Social institutions would also represent cases of collective knowledge accumulated over multiple generations that could not be invented by one individual alone without a proper starting point. Incidentally, this complexity criterion would also disqualify dropping a token inside a container to obtain a food reward since individuals could learn this on their own.

Since neither conservatism nor social conformity appear to be a satisfactory explanation for the putative lack of cumulative culture in non-human animals, we must search elsewhere. I will provide a sketch of an answer here. Let’s begin our search by returning to the original conundrum that motivated the present chapter. Innovation and tradition are antonyms and yet, they work in conjunction, at least in humans, to create cumulative culture. Apes display both innovation and traditions but no cumulative culture. What else may be needed to develop cumulative culture? Technical sophistication is one aspect that has already been mentioned. But technical sophistication develops when the best solutions are preserved and for that to happen two things are necessary. First, subjects have to face a problem that requires new solutions, and second, individuals have to be able to benefit from the behavior of others. This means that social learning mechanisms such as imitative learning and teaching need to be in place so that observers/apprentices can copy the existing solutions which in turn they can further improve on their own. Note that once solutions reach a certain level of complexity or arbitrariness, imitative learning and instruction may be the only way to acquire them from and transmit them to others, respectively. This is particularly true for behaviors that are not supported on objects or artifacts but are both arbitrary and conventionalized among members of a particular group. For instance, think about the hand gesture consisting of extending the index and middle
fingers while keeping the thumb and the two other fingers retracted used to indicate “victory.” Individual invention would be highly unlikely to produce this exact same pattern and even more unlikely would be to associate this particular finger topography with its referent. Note that arbitrary conventions are often developed within human groups as a marker of group identity, and consequently, they should be things that could only be acquired and transmitted socially.

There is another consideration that may help explain cumulative culture in humans beyond social learning mechanisms. Humans like doing things with others and like others in their groups. The intrinsic motivation that compels humans to be and behave like others paired with our extended mental temporal horizon, that is, our ability to think about the past and into the distant future, has enabled humans to transfer knowledge not only to those present here and now but also to those that will be present in future generations. In a sense, humans have become knowledge “hoarders” for the benefit of future generations with traditional songs, libraries, and the internet as our knowledge repositories. This extended society encompassing past, present, and future generations bound together by a cumulative common knowledge has become one of the key features of humankind.

TWO DIRECTIONS FOR FUTURE RESEARCH

But let’s leave our species aside and return to nonhuman apes by putting on the table two important outstanding issues that will allow us to close the chapter. First, there is the relation between innovation and tradition. At the species level it seems that there is a good relation between the two (Reader & Laland, 2002), at least in primates and provided we take social learning as a proxy for tradition. Whether innovation and tradition are also related at the individual level or instead constitute two different factors is still an open and fascinating question. Recent analyses on physical cognition in apes have suggested that at the individual level things like learning, inhibitory control, and inference may be segregated not part of a single G factor (Herrmann & Call, 2012). Although Herrmann et al. (2007) also explored the relation between social learning and other aspects of cognition, we did not find a relation, although as I mentioned earlier, a floor effect may have prevented us from uncovering any relation. It is conceivable that the high social learning and innovation is a result of different individuals contributing to each of those two aspects or alternatively, they may also be also related at the individual level. Future studies are needed to elucidate this question. If the answer is that different individuals contribute it may help us reconcile the terms innovation and tradition antonyms;
they work together to produce cultural progress and when that progress is preserved along the lines that I suggested earlier, cumulative culture emerges.

The second point is the puzzling conservatism displayed by the Sonso chimpanzees. Does this represent a case of social conformity, cultural override, functional fixedness, or perhaps a combination of the three? I was extremely puzzled, and I still am, when I read that study. I would have thought that chimpanzees could have overcome their bias. Is this special about this population? Is this perhaps typical of wild populations? It is imperative to test other populations using the same methodology to find out whether this phenomenon is restricted to this population/behavior or whether it is something more general in the field. It is conceivable that this conservatism does not apply to other populations. After all, other populations adapt to artificial provisioning devices (van Lawick-Goodall, 1971) and respond well to field experiments of various sorts (Matsuzawa, 1994). However, the extent of their flexibility, especially compared to captive populations is unknown. It is conceivable that wild chimpanzees in general are not as conservative as suggested by this study. Field experimentation is therefore sorely needed to put lab and field results on an equal footing.

References


IV. PUSHING THE BOUNDARIES OF CREATIVITY


IV. PUSHING THE BOUNDARIES OF CREATIVITY
Commentary on Chapter 14: Conservatism Versus Innovation: The Great Ape Story

Can tradition and innovation go hand in hand? This is the question posited by Josep Call in his chapter on Conservatism Versus Innovation: The Great Ape Story. As someone who is interested in studying culture and human creativity, I am naturally drawn to the thesis of this paper. It is almost a known fact that certain characteristics of individuals, including being traditional or conservative, are negatively associated with creativity. When comparing the creativity of members from different cultures, a general belief is that a collectivist-orientated culture, where individuals are driven to maintain the harmonious state of a society and conform to the cultural norm, may have a more stifling effect on the development of creativity than an individualist-orientated culture, where individual autonomy and self-directed learning is encouraged. However, such a belief has been challenged by recent evidence making the relationship between tradition and creativity far more complex than once thought.

But let’s put aside the debate on whether or not tradition hampers the development of human creativity and focus on the thesis of this chapter, that is, to examine the relationship between tradition and innovation displayed in the nonhuman world. I want to emphasize that creativity and innovation are not synonymous. Creativity is defined as the ability to generate original and appropriate ideas in any domain and innovation is the successful implementation of creative ideas. Whereas creativity is often measured through open-ended tasks that independent raters can evaluate at a later date, innovation is assessed through problem solving, either by applying an old solution to a new problem or producing a new solution to an old problem. This chapter adopts the concept of innovation.

This chapter begins by posting an interesting puzzle that chimpanzees and orangutans (or apes) are conservative and conformist species. Nevertheless, they are also believed to be the most flexible problem solvers and innovators on Earth. In exploring this puzzle, the author first carefully examines the empirical evidence on animal problem solving, inhibitory control, and innovation across different ape species. His conclusions: conservatism and innovation are not necessarily contradicted by one another. They are both adaptive mechanisms that apes developed for pursuing a better payoff. In fact, there are mixed results
regarding apes’ conservatism, some of which suggest that apes are not as conservative as people have generally believed. The observed conservatism (e.g., persistently using existing tools or methods acquired either through social learning and individual exploration) can be explained by partial reinforcement. In other words, apes choose to stick to tradition when old solutions still work. When a solution becomes completely ineffective, apes are more likely to innovate. Therefore, depending on the payoff, apes are capable of choosing between repeating previously successful solutions and innovating new solutions when the old ones fail.

To further examine the relationship between apes’ conservatism and innovation, the author explored the evidence on social learning, social influence, and conformity, as well as their impact on innovation across different several subgroups of apes. Again, results are mixed. There are evidences that socially acquired information (by observing another individual’s successful solution) has a dampening effect on the probability of innovation, such that apes choose to abandon their own individually gained solution to conform to the majority. However, other studies have shown that apes are capable of abandoning techniques in favor of more efficient or profitable solutions regardless of how techniques are acquired (either through social observation or individual exploration). In other words, innovation can take place in the face of majority influence to pursue better outcomes.

So what influences apes’ likelihood to innovate or conform? The answer: it depends. Similar to humans, individual factors such as age, gender, personalities (e.g., boldness-shyness) and contextual variables (such as task and setting), can contribute to the likelihood and degree to which individuals or species conform or innovate.

To me, the most intriguing discussion of this chapter is on conservatism, social conformity, and cumulative culture. Apes preserve tradition through social learning and innovation, but have yet to develop cumulative culture. It is tempting to blame conservatism and social conformity on the lack of cumulative culture among apes. However, conservatism and social conformity were not present in all studies examined by Call’s chapter. Most importantly, human beings also display a great deal of conservatism and innovation to establish, preserve, and evolve their civilization.

Back to the initial question proposed by this chapter: “Can tradition and innovation go hand in hand?” Certainly the question can be examined by applying it to human beings. Preserving tradition and taking risky steps for innovation seem to be on two opposite ends of a spectrum, yet both are needed to make progress in any field. On one hand, it is important to actively acquire and master the existing knowledge, norms, and skills accumulated and passed on over generations; on the
other hand, it is also important to take an occasional “gamble” and shift away from tradition in order to make progress in a field.

There are two common approaches in psychology to examine the relationship between tradition and innovation/creativity of human beings. One is by studying the cognitive process and examining the relationship between fixation and creativity or insight problem solving. Fixation refers to knowledge about an existing paradigm. In fixation, knowledge or an obvious solution is automatically activated which leads to an inability to generate new solutions. Tradition takes the form of knowledge or skill fixation, which may undermine innovation and creativity. There seems to be overwhelming evidence from cognitive research that establishes a negative relationship between fixation and creativity.

Another approach is to study individual differences and to find some characteristics that promote creativity. These characteristics include personality traits (openness to experience, extraversion), gender, religious affiliation, and culture (collectivist versus individualist).

However, new evidence from both approaches suggests that the relationship between preserving tradition and innovation/creativity is more complex than people used to think. For example, recent evidence demonstrates that creativity can benefit from tasks that are highly structured (in a way rather fixed), especially for those individuals who have a higher personal need for structure (Rietzschel, Slijkhuis, & Van Yperen, 2014). This suggests that fixation and structure can sometimes help innovation when individuals use structured knowledge as a base for further exploration.

Similarly, closely examining the Confucian ideology and creativity, Niu (2013) claimed that the notion of tradition does not necessarily contradict with creativity, at least in the Chinese context. Compared to the Western conception of creativity, creativity in the Chinese context puts greater emphasis on the continuation between past, present, and future. Therefore, to be creative, a person should actively acquire knowledge accumulated in the past and practice certain skills to reach perfection. Some other scholars also examined the relationship between Confucianism and innovation within organizations and concluded that maintaining a harmonious relationship in fact could help innovation at the organizational level. For example, a study of Chinese employees in a business setting found that Zhongyong (the doctrine of mean), a core value of Confucianism prescribing the extent to which a person puts priority on traditional propriety and interpersonal harmoniousness by following the doctrine of mean (often viewed as an important characteristics of conservatism), was found to have a positive effect on organizational innovation, especially when employees realize the importance of innovation to the organization (Du, Ran, & Cao, 2014).
Evidence like the two listed above suggest that tradition does not necessarily hamper creativity at the individual and group levels. When making structure and tradition meaningful to individuals, this structure and tradition can even stimulate creativity and facilitate the process of innovation.

So what can we learn from the studies on conservatism and innovation in the animal world? Conservatism is not always apparent. Preserving tradition and striving for innovation are both important adaptive mechanisms that are not necessarily on opposite ends of a spectrum; rather, they can work hand in hand in facilitating cultural progress. The findings from animal research seem to echo what we have learned from research with human beings, and eventually help us better understand the progress of cultural evolution.

References