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Great Apes Do Not Learn Novel Tool Use Easily: Conservatism, Functional Fixedness, or Cultural Influence?

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Abstract Animal culture has been of interest for decades but the concept remains controversial. Many researchers feel that animal behavior should not be granted the label "culture" because the latter includes more than "simple" behavioral variation. In recent years, the study of animal culture has been concerned mainly with social learning mechanisms, often claimed to be human specific, which led to the uniqueness of human culture. In addition, failure to innovate novel cultural behavior as often as humans is usually explained by psychological mechanisms presented as more parsimonious, such as conservatism or functional fixedness. However, it is unclear how cognitively complex these mechanisms are in the first place. Here, I analyze recent data obtained with wild chimpanzees (*Pan troglodytes schweinfurthii*) and wild-born orangutans (*Pongo abelii*) using the honey-trap experiment, in which individuals must devise a solution to reach inaccessible honey. I compare behavior of apes that developed a tool-based solution in the task with those that did not, and test whether conservatism and functional fixedness can explain individual variation in ape behavior. I find evidence of conservatism, with apes relying on their existing knowledge, and evidence of functional fixedness, with this knowledge potentially preventing them from innovating. However, the apes showed large intraspecific variability. I discuss the two mechanisms through a representational perspective to tackle their cognitive complexity. Understanding how conservatism and functional fixedness interact with ape cultural knowledge to limit innovation of novel tool use appears necessary to understand the full extent of ape cultures and how they compare to human cultures.

Keywords Animal culture · Conservatism · Functional fixedness · Great apes · Mental representations

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Introduction

Ape cultures have been of interest for decades (Goodall 1986; Hohmann and Fruth 2003; van Schaik *et al*. 2003a; Whiten *et al*. 1999). However, there has been controversy over whether to use or not the label "culture" to describe the well documented geographical behavioral differences between communities of the same species or subspecies (Fragaszy and Perry 2003; Galef 1992; for a review, see Laland and Galef 2009). Most commentators agree to a view of culture based on the definition of tradition provided by Fragaszy and Perry (2003, p. xiii): "a distinctive behavior pattern shared by two or more individuals in a social unit, which persists over time and that new practitioners acquire in part through socially aided learning," with culture itself being "the possession of multiple traditions, spanning different domains of behaviour" (Whiten and van Schaik 2007, p. 605), a definition I apply here. Yet, animal cultures have remained controversial, particularly because of the scarcity of situations that provide direct evidence of social transmission for animal presumed cultural behavior (Laland and Janik 2006). With the development of novel statistical tools (Hoppitt *et al.* 2010), it has now been possible to show convincingly that some of these behaviors are indeed transmitted through social learning processes in humpback whale (*Megaptera novaeangliae*: Allen *et al*. 2013), eastern chimpanzees (*Pan troglodytes schweinfurthii*: Hobaiter *et al*. 2014), and great tits (*Parus major*: Aplin *et al*. 2015). However, it is unclear whether these data allow us to describe this regional variation as cultural. While they may convince many biologists, it is not as clear that they will convince anthropologists (Hill 2009; Perry 2009) or psychologists (Tomasello 2009). Although providing evidence that behavior believed to be cultural is indeed transmitted through social learning is an important step in our understanding of animal cultures, the fact that wild animals learn cultural behavior socially is not surprising given the extended body of knowledge gathered on animal social learning (Heyes and Galef 1996). However, these data cannot address the question of whether other animals experience their cultural knowledge in the same way as humans do: a set of values or norms that they are willing to defend and stand for (Hill 2009; Perry 2009).

Beyond the behavioral level, a different approach is to explore the transmission of mental representations of cultural behavior (Gruber *et al.* 2015), that is, to focus on how representations of behavior, rather than behavior themselves, are being transmitted. For instance, a representation such as "stick-to-get-honey" (I am copying here the format of a simple representation chosen by Sperber 2000, p. 118) may exist in the mind of a chimpanzee fishing for honey and be re-created in the mind of another individual watching the first one (Gruber *et al*. 2015). This approach can also be applied to analyze particular psychological mechanisms that may be involved in the cultural process. Recent approaches to animal cultures try to understand which psychological mechanisms explain the limited abilities of animals to innovate novel cultural behavior. In particular, conformity, conservatism, and functional fixedness may play a role (Brosnan and Hopper 2014).

Conformity is defined as the alignment of one's attitude with a majority position (Asch 1956) and has been the focus of much recent work in the animal culture debate (Claidière and Whiten 2012; van Leeuwen and Haun 2013). Conformity at the representational level has to do with comparing one's own mental representations of techniques with the representations of others, a process allowing human groups to compare their cultural repertoires (Gruber and Zuberbühler 2012). Considering apes' limited mindreading abilities (Call and Tomasello 2008), it is, however, unclear whether they can truly engage in this kind of conformity (van Leeuwen *et al.* 2015).

Conservatism, at the behavioral level, is proposed when "mastery of a skill inhibits further exploration, and hence adoption of alternative techniques even if these are more efficient" (Hrubesch *et al.* 2009, p. 209). This definition highlights the fact that behavioral conservatism ("being stuck to a given technique") can be a potential hypothesis to explain limitations on innovation only if a preferred and well-known technique already exists. In addition, this definition does not tackle the issue of whether animals represent their techniques mentally, that is, whether they build and access mental images of their techniques. At the representational level, conservatism may imply that individuals are able to mentally compare representations of potential techniques and to choose to remain with the one already known as opposed to the novel one. For instance, chimpanzees may represent a known leaf-based technique to access a reward and prefer it over a less known stick-based technique (Gruber *et al.* 2015).

Functional fixedness is the "disinclination to use familiar objects in novel ways" (Brosnan and Hopper 2014, p. 2). Subjects thus experience difficulties in reaching the solution to a problem because their previous knowledge (for instance, of an object's conventional function) prevents them from "seeing" the novel use that can be made of this object (Defeyter and German 2003; Duncker 1945; German and Defeyter 2000). Functional fixedness has recently been proposed to explain the poor performance of captive chimpanzees to reach a food reward using water (Hanus *et al.* 2011). In these experiments, chimpanzees that had had an extensive knowledge of a water dispenser to drink and potentially spit on visitors in everyday life could not use it during the experimental task to obtain a food reward. Functional fixedness, at the representational level, concerns the understanding of the different uses that can be made of the same tool (Defeyter and German 2003). In this case, an animal may represent a tool within its usual usage, its fixed function, e.g., a leaf-sponge in the context of sponging water. During the process of functional fixedness, this representation of the function of the tool will hinder the use of the sponge for a different purpose.

In conformity, conservatism and functional fixedness, existing mental representations of formerly acquired knowledge will thus prevent apes from exploring their environment to find new solutions. Conformity and conservatism have more to do with a general representation of the strategy to be used (for instance, the stick is part of a general sequence that leads to the reward, and the representation encompasses the whole sequence rather than individual parts) while functional fixedness is rather about a specific representation of the function attached to a tool in particular, such as "stick-to-get-honey." While these mechanisms may hinder individuals' abilities to innovate, it is currently unclear whether they are cognitively complex and to what extent they rely on a representational perspective in animals displaying cultural behavior, in particular in great apes (Gruber *et al.* 2015).

To answer these questions, I explore and reanalyze here two previously published datasets obtained with wild eastern chimpanzees and wild-born captive orangutans (*Pongo abelii*) (Gruber *et al.* 2009, 2011, 2012b). Their results in an ecologically inspired cognitive task —the honey-trap experiment, a set-up where apes must figure a way to recover inaccessible honey from a hole drilled into a natural log— can help to test how wild apes categorise their tools as meaningful objects in their environment.

The goal of these experiments was to explore *what* made the chimpanzees and orangutans use particular tools, and similarly, not use other tools. As such, they can help assessing the different mechanisms proposed to explain limitations in tool use in animals. While conformity can be shown in certain experimental settings (Whiten *et al.* 2007), it was not applicable for these two datasets because all orangutans and most chimpanzees were tested in an individual setting and could not conform to the behavior of other apes. I therefore focus on conservatism and functional fixedness.

Because both the chimpanzees and the orangutans were exposed to the same task and under similar conditions despite the chimpanzee data having been collected in the wild and the orangutan data in a sanctuary, it is possible to apply the same analytical framework to the two datasets. In addition, the two groups tested had different knowledge of tools. For the chimpanzees tested, stick-tool use represented a novel solution to a novel problem to all individuals tested, while leaf-sponge was a potential existing solution to apply to a novel context. For the orangutans, stick-tool use represented an existing solution to an existing problem for some of the orangutans, whereas it would be a novel solution to a novel problem for others.

The datasets explore different aspects of how conservatism and functional fixedness act on great apes, particularly as the honey-trap task was novel for all the chimpanzees tested, but not for all the orangutans, some of which came from communities where they had likely seen honey being extracted from holes with tools. Previously acquired cultural knowledge prevented at least some individuals from developing novel behavior in the two studies, suggesting that their behavior can be connected to certain aspects of these two psychological mechanisms. These results therefore allow me to predict that a combination of conservatism and functional fixedness will explain some of the ape behavior. However, the heterogeneity of the results also suggests that other parameters may come in play. Here, I perform new qualitative and quantitative analyses of the existing datasets to assess whether the results obtained by chimpanzees and orangutans in the honey-trap experiments can be explained by conservatism or functional fixedness. I aim to determine which specific aspects of the results conservatism or functional fixedness may explain, in particular with respect to the limited success of the apes in adopting new techniques or adapting old ones to new tasks in the experiments.

Material and Methods

Study Sites and Subjects

I carried out the chimpanzee study in the Budongo Forest Reserve in western Uganda, at the edge of the western Rift Valley along Lake Albert (latitude 1°37′–2°00′N; longitude: 31°22′–31°46′E). The reserve is 793 km^2, consisting of moist, semideciduous tropical grassland and 428 km^2 of forest (Plumptre and Reynolds 1996). A total of 40 chimpanzees (mean age: 18.28 yr, range: 6–49; 24 females) participated in the experiments analyzed here. I conducted the orangutan study at the Batu Mbelin Quarantine Centre, Sibolangit, North Sumatra (3°19′42″N; 98°34′51″E), where confiscated wild-born orangutans are rehabilitated before they are released into undisturbed Sumatran forests (Gruber *et al.* 2012b). The orangutans are first housed individually in 2 × 2 × 2.5 m cages (isolation phase), which all include at least one suspended tire that can be used for nesting. Individuals can interact with other individuals housed next to them. When ready to join large social groups, they are transferred to 6 × 6 × 6 m cages that include various items (suspended tires, ropes, metallic platforms) for the socialization phase. In both phases, they are fed a variety of natural fruits that they will potentially later encounter in the forest once released. A total of 20 orangutans (mean age: 4.75 yr, range: 3–8.5; 8 females) participated in the experiments analyzed here.

Chimpanzee Dataset

During 2009–2015 I studied the tool use behavior of a wild community of chimpanzees (*Pan troglodytes schweinfurthii*) inhabiting the Budongo Forest in Western Uganda through the use of field experiments (Gruber *et al.* 2009, 2011; Gruber and Zuberbühler, 2012). The Sonso chimpanzees are noted for their limited cultural repertoire, mainly based on leaf-using behavior, but from which stick use is entirely absent (Reynolds 2005; Whiten *et al.* 1999). They use sticks only while building nests and sometimes during play, or as a play invitation gesture in juveniles (Hobaiter and Byrne 2011), but never during food acquisition, including while raiding natural bee nests (Gruber and Zuberbühler 2012; Reynolds 2005). In addition, this pattern, documented over 25 yr in Sonso, may not be restricted to the Sonso community as other chimpanzee communities in the Budongo Forest did not use sticks when they engaged in the same field experiments (Gruber *et al.* 2012a). Between 2009 and 2013, the honey-trap experiment consisted of presenting inaccessible but visible honey inside a hole of a given standardized size (4 × 5 × 16 cm; Gruber *et al.* 2009). Some chimpanzees first encountered a nonobligatory tool condition in which the honey could be reached directly with the fingers (Gruber *et al.* 2009). The data are not shown here because this condition was not given to the tested orangutans and to most chimpanzees. Nevertheless, the behavior of the chimpanzees that participated in the two conditions did not differ between these conditions and generally not from the other chimpanzees that engaged only in the obligatory condition. Chimpanzees in other wild communities acquire naturally honey from wild bee nests with the help of wooden tools manufactured from branches collected nearby (Whiten *et al.* 1999). However, there is no record from wild chimpanzees other than from the Sonso community manufacturing leaf-sponges to collect honey in natural settings. I observed the typical stick-use tool pattern during experiments with a control community, the Kanyawara community of Kibale Forest, Uganda, located 180 km from Budongo Forest. Members of this community use sticks to get honey from natural bee nests and also displayed this behavior during the experiment; in addition they dipped their fingers in the hole in an attempt to get the experimentally provided honey (Gruber *et al.* 2009). In contrast, none of the 40 Sonso chimpanzees that took part in the honey-trap experiment manufactured a stick to collect the honey during the experiments despite multiple encounters (Table I). All individuals that engaged in the experiment tried to finger-dip to obtain the honey, while a subgroup of individuals also adapted a behavior normally used to collect water, “leaf-sponging,” to recover the reward. This technique, considered universal among chimpanzees, consists of folding and chewing leaves in one’s mouth to collect water from tree holes and rivers (Hobaiter *et al.* 2014; Whiten *et al.* 1999).

Although initially only four chimpanzees used leaves to collect honey, more chimpanzees started displaying the behavior over the course of the 5 yr so that by 2013 10 individuals had employed this technique to solve the task (Table I). The two techniques do not appear to differ in the efficiency with which apes obtained honey, as the most proficient leaf-sponger (in Sonso) and stick-user (in Kanyawara) did not differ in the time they needed to empty the honey trap (Gruber *et al*. 2011). They are, however, both much more efficient than using one's hand, allowing one to empty the honey-trap completely, whereas using one's hand only allows one to recover drops of honey on the sides of the hole. By 2013, all 40 chimpanzees had spent more than 20 s engaging with the hole, the mean time needed by the Kanyawara chimpanzees before starting to manufacture a stick tool to collect honey during the experiments. This showed that it was not because of a lack of time or interaction with the device that the Sonso chimpanzees did not employ stick tools to recover the honey (Gruber *et al*. 2011). More surprisingly, during the course of the experiments, I exposed the Sonso chimpanzees to the stick-tool solution directly: they could remove and reinsert freely a stick placed in the honey trap. Despite extracting the stick, none of the 20 individuals that engaged in this condition ever reinserted it in the hole, failing to develop stick-tool use (Gruber *et al*. 2011). In some cases, individuals recovered the stick from the hole and licked the honey from the stick, but then discarded it before attempting unsuccessfully to recover the honey with their fingers. This suggests that the Sonso chimpanzees did not understand that the stick could be used as a tool.

Orangutan Dataset

I adapted the honey-trap experiment to test the cultural knowledge and the physical cognition of wild-born Sumatran orangutans (*Pongo abelii*). Although political instability prevented me from running the experiment in the wild in the Aceh province of Sumatra, Indonesia, where orangutans make use of tools during feeding acquisition contexts (van Schaik *et al*. 2003a), it was possible to expose recently rescued individuals to a modified honey-trap experiment in a quarantine center located in Sibolangit, North Sumatra (Gruber *et al*. 2012b). The goal of this center is to rescue young Sumatran orangutan orphans from the pet trade. The geographic location of the orphans at the time of rescue, and precise genetic identification for some of them (Krützen *et al*. 2011), allowed me to allocate them to tool-using (the swamp orangutans) and non-tool-using (the Langkat orangutans) populations.

Working in a sanctuary also allowed me to run an additional control compared to the previous experiments run in the wild in the form of a raking task, where subjects had to rake food with a stick from outside the enclosure toward them. This way, it was possible to test whether orangutans could demonstrate a behavior that they could have learned only at the sanctuary, through practice effects. More generally, the purpose of this task was to test whether differences in genetics between the two populations could explain potential differences in tool use, for example, one population being more inclined to use tools than the other (Laland and Janik 2006). The orangutans always engaged first in the honey-dipping task. This was to avoid an order effect, that is, the possibility that using a stick to rake food outside the enclosure may trigger naive orangutans to find the stick solution by insight during the honey-dipping task, as opposed to them relying on their cultural knowledge. When exposed to the honey-trap experiment, the orangutans behaved similarly to the chimpanzees: orangutans from tool-using areas were significantly more likely to extract honey with a stick than

Table I Summary of the encounters of the Sonso chimpanzees where they engaged actively with the honey-trap experiments in the obligatory setting (hole: 4 × 5 × 16 cm) over the 2009–2013 period

Non-leaf-spongers (30 individuals)					Leaf-spongers (10 individuals)				
ID	Sex	Age first	Duration(s)	Encounters	ID	Sex	Age first	Duration(s)	Encounters
AN	F	19	30	1	KC	M	6	392	1
HL	F	8	133	2	HT[a]	F	31	114	2
KE[a]	F	11	132	2	*JT*	F	10	319	2
KM[a]	F	10	50	1	*RE*[a]	F	12	127	4
KR[a]	F	7	276	6	RS	F	12	1224	4
KT	M	16	44	2	HW[a]	M	16	924	14
KU[a]	F	30	289	2	KA[a]	F	11	968	7
KW[a]	F	28	179	7	KS[a]	M	6	261	2
KY[a]	F	26	443	3	NT[a]	F	6	4040	12
KZ[a]	M	14	308	6	PS	M	11	26	2
ML	F	34	45	1					
MN	F	6	45	1					
MS[a]	M	18	1212	9			Age first	Duration	Encounters
NB[a]	F	47	2397	14	*Non-leaf-spongers*				
NK[a]	M	18	27	2	Mean		20.3	278.8	3.7
NR	F	13	441	7	Median		17	125.5	2
OK[a]	F	14	66	2	Max		49	2397	14
SB	F	29	382	3	Min		6	25	1
SE	F	38	45	1					
SM	M	16	45	1	*Leaf-spongers*				
SQ[a]	M	19	338	11	Mean		12.1	839.5	5
TK	M	49	267	2	Median		11	355.5	3
VR	F	12	358	2	Max		31	4040	14
WL	F	29	102	1	Min		6		1
ZD	M	8	33	1					
ZF	M	18	25	2					
ZG	M	12	119	3					
ZK[a]	M	6	118	2					
ZL[a]	M	14	382	10					
ZM	F	41	33	4					

Age first = age of first encounter with the apparatus; Duration = time spent engaging with the apparatus without developing the stick use behavior.

[a] Individuals that engaged in experiments where a stick was plugged into the honey. *Italic:* Individuals that died or emigrated over the course of the experiments.

orangutans from non-tool-using areas, mirroring the results obtained with wild chimpanzees. In contrast, their behavior did not differ in the raking task, showing that genetic differences could not explain differences in tool use. There was also substantial variation even within genetic groups, with some individuals being successful in the two tasks (double success; Table II) and others succeeding only in either the honey-dipping task or in the raking task

Table II Results of a selection of wild-born captive orangutans that engaged in the honey-trap experiment and a raking task

Individual	Sex	Age	Honey-dip effective time (s)	Tool/time raking (s)	
Double success					
EG	M	4.5	51	H	5
FR	M	4	227	S	3
JU	M	3.5	159	S	5
LU	F	4.5	147	S	5
ON	M	4	450	H	2
PK	M	4.5	225	H	14
PU	F	4.5	29	H	5
UD	M	8	29	S	10
Average		4.69	164.63		6.13
SD		1.39	140.92		3.94
Rake success					
BO	M	5.5	721	S	2
JB	F	4	528	H	3
LB	F	3	138	S	8
RK	M	4.5	137	S	2
TO	M	5.5	765	S	3
BA	M	4.5	370	S	18
Average		4.50	443.17		6.00
SD		0.87	251.72		5.74
Honey-dip success					
BW	F	4.5	171	n.a	n.a
MK	M	5	520	H	n.a
SC	F	5	776	H	n.a
WD	F	3.5	340	H	n.a
MA	F	8.5	215	H	n.a
MV	M	4	139	S	n.a
Average		5.08	360.17		
SD		1.77	246.84		

The age, sex, and performances of the individuals are given for individuals that succeeded in the honey-dipping task and the raking task (double success) or only in one of the tasks. Effective time (in seconds) was defined in the original study as "time of direct interaction or less than 1 m away" from the honey-dipping apparatus. We defined time raking (in seconds) in this study as the time spent by the orangutans before they successfully retrieved the reward using one of two tools: a stick (S) or a hook (H). We chose this definition rather than time to the first raking movement to avoid potential false positives of orangutans waving the potential tool toward the reward without using it *as* a tool. Five double-success individuals are excluded from this table because they faced different honey-dipping and raking tasks than the other individuals because of housing conditions. The 11 individuals that failed in both experiments are not represented. SD = standard deviation.

(single success). Finally, I excluded the individuals that did not succeed in any of the tasks ($N = 11$) and five double-success individuals that encountered a different setting to test their raking knowledge. These individuals are not represented in Table II.

Data Analysis

Taking into account the definitions presented in the introduction, I considered there was evidence of conservatism when individuals displayed behavior that they were known to use already in their normal daily life. A critical component of most definitions of conservatism is that individuals fail to explore novel solutions as long as their existing solution is giving at least some benefit (Brosnan and Hopper 2014). For instance, using one's hand to access the honey could lead individuals to obtain some drops of honey that remained on the sides of the hole. This could lead them to persist in using this technique, rather than developing a novel tool use method, even though using one's hand only became rapidly unsuccessful. Such behavior would qualify as conservatism (Brosnan and Hopper 2014). Another possible type of conservatism could consist of using a technique based on a known technology, e.g., the leaf technology, or a known technique, e.g., leaf-sponging, rather than exploring novel solutions based on a different technology, e.g., the stick technology. Such conservatism may be more in line with a general lack of knowledge or of ability to use this novel technology.

For functional fixedness, the focus was put on how apes used particular tools of a known function, e.g., a leaf-sponge to sponge water, in a novel context or a novel task, e.g., using a leaf-sponge to collect honey in the experimental setting. To study functional fixedness, I compared the time needed for double-success or single-success orangutans to select the stick as a tool in the two tasks (honey-dipping and raking task) with Mann–Whitney tests. I also used a Mann–Whitney test to compare the duration chimpanzee leaf-spongers and non-leaf-spongers engaged with the honey-trap experiment. Because they had different numbers of encounters with the log, I used a mean rate per individual calculated as the total duration spent engaging with the log during the experiment divided by the number of interactions of the individual with the log. In both cases, I used two-tailed nonparametric tests with exact P-value because of the low sample size, using SPSS 21.0.

Ethical Note

Uganda Wildlife Authority (UWA) and Ugandan National Council for Science and Technology (UNCST) gave permission to conduct the chimpanzee research. The Ethics Committees at the School of Psychology, University of St Andrews and the University of Neuchâtel gave ethical approval. The orangutan research complied with the laws of the Republic of Indonesia. The Indonesian Ministry of Research and Technology (Ristek) and the veterinary staff at Batu Mbelin Quarantine Centre reviewed and approved the research protocol.

Results

Chimpanzee Data

At both Sonso and Kanyawara, chimpanzees initially tried to rely only on their hands to obtain honey. This was a possible technique in the nonobligatory-tool condition, in which the honey could be reached directly with the fingers, but not in the obligatory-tool condition, in which the honey was too deep to reach using fingers only. For 10 of 40 chimpanzees in Sonso, the solution was to adapt a behavior normally used to fetch water, leaf-sponging, to acquire honey. For three of these individuals (KC, HT, and PS), this occurred after watching another individual manufacturing a leaf-sponge the first time it engaged with the log. The seven other individuals appear to have been independent innovators, either the first time (RE, RS, and HW) or the second time (KA, KS, and JT) they engaged with the log (excluding NT, who manufactured a sponge at her sixth interaction). Of these 10 individuals, after the innovation, three individuals did not remanufacture a sponge in their subsequent interactions with the log (RE, HT, and PS). Among the others, only HW and NT reused the leaf-sponging technique in several consecutive trials (HW: two trials, NT: three trials). These trials all occurred on consecutive days. In contrast, none of the 10 leaf-spongers manufactured a sponge in the immediate subsequent trial after a leaf-sponging trial when several weeks separated these two trials. For instance, chimpanzees could stop manufacturing a sponge for one (KA) or two (RS) trials and rely on their hands during these trials only before manufacturing again a leaf-sponge at the next trial.

Most of the tested Sonso chimpanzees, however, did not manufacture a tool and 30 of 40 attempted to recover the honey only by relying on their hands. Although some of them spent much time engaging with the hole (mean: 278.8s, range: 25–2397s, Table I), the non-leaf-spongers engaged significantly less with the log than the leaf-spongers (Mann–Whitney test, $Z = -2.03$, $P = 0.042$, $N_{\text{non-leaf-spongers}} = 30$ and $N_{\text{leaf-spongers}} = 10$). Interestingly, none of the 14 non-leaf-spongers (Table I) that encountered a stick inserted in the hole and could directly experience extracting this stick from the hole developed the stick-use behavior, despite having no successful technique to extract the honey. In this respect, their results are similar to the six leaf-spongers that also encountered the stick plugged into the honey and did not subsequently develop the stick-use behavior.

Orangutan Data

Twelve of 36 (single success, *ca.* 33%) orangutans succeeded in one task but failed in the other task, 13 (double success, *ca.* 36%) solved both tasks, and 11 (*ca.* 31%) solved neither task. An individual that did not succeed in recovering the honey could nevertheless be successful in raking food (six cases); but even more surprisingly, an individual that had just succeeded in recovering honey could fail the food raking task (six cases; not due to a lack of motivation as the videos showed clear attempts to get the food reward, which was one of the subject's preferred fruits; Table II).

In the honey-dipping task, the eight double-success individuals did not take on average more time than the single-success honey-dippers before selecting the stick as a tool (Mann–Whitney test, $Z = -1.551$, $P = 0.142$, $N_{\text{honey-dippers}} = 6$ and $\mathrm{N}_{\text{double-success}} =$

8; Table II). In the raking task, the single-success rakers and the double-success individuals did not differ in the time they took to select a tool as an option to rake (Mann–Whitney test, $Z = –0.790$, $P = 0.491$, $N_{\text{rakers}} = 6$ and $N_{\text{double-success}} = 8$; Table II). Four out of eight double-success individuals (50%) selected a stick rather than a hook to complete the task, while five out of six single-success rakers (*ca.* 83%) selected a stick rather than a hook. In contrast, four honey-dippers (but unsuccessful rakers) out of five selected a hook (80%; Table II).

Discussion

Conservatism and Functional Fixedness in Wild Ape Behavior

Chimpanzee Data All the chimpanzees that engaged with the experiment, whether in Sonso or Kanyawara, relied on the same initial technique: using their fingers to try to reach the honey. Great apes are reportedly conservative (Hrubesch *et al.* 2009; Lehner *et al.* 2011; Marshall-Pescini and Whiten 2008; *cf.* Manrique *et al.* 2013) and this may explain in part the results of the study: the Sonso chimpanzees did not adopt the novel stick-use behavior because their existing technique already provided them with a means to get the honey. Here, the results sort the tested chimpanzees into two groups that I discuss separately. Thirty chimpanzees relied only on their hands to try to access the honey. In addition to using their hands, 10 chimpanzees developed an alternative technique, the manufacture of a leaf-sponge, adapting a behavior that they use normally to fetch water.

Regarding conservatism, on the one hand, the non-leaf-spongers persisted in using a technique that was not successful in obtaining honey. In this respect, it is unclear whether they qualify for the usual definition of conservatism (a failure to adopt a behavioral alternative over a known behavior in the same task context; Hrubesch *et al.* 2009) because an individual should persist in a given technique only if this one can bring some reward (Brosnan and Hopper 2014). Here it could be argued that the non-leaf-spongers were nevertheless successful in getting a few drops of honey, but the fact that they engaged significantly less with the device than the leaf-spongers denotes either a loss in motivation or the development of frustration while attempting to get the honey. Nevertheless, it is hard to talk about a potential conservatism for the absence of a technique, particularly because the use of hands appears to be a baseline for any chimpanzee engaging with the honey-trap experiment, including the ones that used sticks in other sites (Gruber *et al.* 2009).

On the other hand, the case for conservatism may be supported for the 10 leaf-spongers, if one considers that the chimpanzees used the technique they normally use to fetch water. They may thus have selected the technique they knew (leaf-sponging) to solve the novel experimental task. Because leaf-sponges are as efficient as sticks to get honey, it is possible that conservatism may have been acting on these 10 chimpanzees. However, this explanation requires a cognitive investigation of the kind of transfer that occurred between the two tasks (natural and experimental). We need to understand why chimpanzees would consider the two tasks similar enough to use the same tool, when they did not mistake honey for water. Behavioral observations indeed showed that chimpanzees collected and tasted the honeycombs displayed as visible cues beforehand, and also experienced the physical properties of the honey while interacting with it; for example, they tried to get rid of the sticky honey remaining on their fingers by rubbing them against the log. These 10 chimpanzees did not appear to experience difficulty in transferring their knowledge of leaf-sponges to collect water to the task of getting honey. Some individuals manufactured leaf-sponges to get honey on the very first day they were exposed to the honey-trap experiments. However, it remains to be explained what made these chimpanzees select leaf-sponges as a useful tool to get honey in the first place.

Regarding functional fixedness, sticks do not have a fixed function in the Sonso community, with the exception of being dragged during display or play (Gruber *et al.* 2011). In particular, they are never used as tools (Gruber *et al.* 2009; Reynolds 2005). Sticks do constitute a basic material to build nests, but the vegetation is then mostly bent rather than detached from its original support. As a consequence, sticks do not appear to have a set function in the Sonso chimpanzee mind, in contrast to leaves, which are regularly used as tools in various contexts (drinking, hygiene, sexual solicitation). Indeed, females sometimes actively prevent their offspring from engaging with sticks (Gruber *pers. obs.*). One may potentially see functional fixedness in the lack of attribution of a function to sticks but this may perhaps be more adequately described as a "learnt irrelevance," where the formation of a novel association between two stimuli (in this case, the honey and the stick) can be greatly retarded if the individual has experienced the presentation of those stimuli independently from each other in its past (Mackintosh 1974). However, this redefinition of the concept appears to drift away from the original definition of functional fixedness (Defeyter and German 2003). Nevertheless the "lack of tool function" may in some ways have prevented the Sonso chimpanzees from developing the stick-use behavior.

Although functional fixedness may explain the difficulty of the Sonso chimpanzees to learn stick use, it cannot explain the use of leaf-sponges in this task, unless the concept of leaf-sponges is broadened to collect any kind of liquid. This, however, goes against the well documented natural cultural behavior of all chimpanzee communities observed so far, which have never been observed using leaf-sponges in a context other than water-fetching (Whiten *et al.* 1999). The results of the 10 chimpanzees that adapted the use of leaf-sponges to the honey-trap experiment suggest that the latter are not functionally fixed to "fetching water." As leaves are used as tools in a broad range of contexts, they may be represented as potential tools for many different activities, and their "natural function" may be that of a tool, but this hypothesis would need to be weighed against the other major use of leaves as a feeding resource (Gruber *et al.* 2012a), opening the possibility that different kinds of leaves acquire different functions ("foods" or "tools") in the course of ontogeny.

Orangutan Data The results of the orangutans that succeeded in at least one of the tasks can be used to assess the conservatism and functional fixedness hypotheses. First, the results found for the exclusive honey-dippers and rakers taken together may support the idea that orangutans may not be so good at transferring knowledge between tasks, a general behavioral trend suggested by captive studies across all great apes (Martin-Ordas *et al.* 2008). The orangutan data offer an alternative picture to the chimpanzee data, as none of the tested individuals used a different strategy to recover the food reward. For instance, none of the orangutans used the alternative "leaf-sponge" strategy, despite being provisioned with “leafy-sticks” like the chimpanzees. This may relate to the fact that orangutans are not known to manufacture sponges in the wild (van Schaik *et al*. 2009) or potentially that the modification of the tool, e.g., leaf removal, was too complex for the tested individuals.

Regarding conservatism, the 13 double-success individuals relied on the same technique (stick use) to solve the two tasks. One may thus argue that conservatism allowed these 13 individuals to succeed in both tasks, transferring their knowledge of sticks as tools from the honey-dipping task to the raking task. However, the fact that six other individuals succeeded in the honey-dipping task but did not succeed in the subsequent raking task makes it unlikely that the choice of using a stick in the second experiment is directly caused by using the behavior in the first task. In other words, it is unlikely that the fact of obtaining a reward in the first experiment led the orangutans to choose to use the same technique in the second experiment. In particular, if this had been the case, the choice of tools in the second experiment should have reflected this. The eight double-success individuals should have chosen to continue with a stick to obtain the piece of fruit, but their choice in this task was random (50% of hook choice). Although the hooks were all the same used as sticks in the original study (Gruber *et al.* 2012b), it is interesting to note that the great majority of single honey-dippers (80%) chose the hook, albeit unsuccessfully, in the raking task. This may suggest that they were opting for a different technique in the second task, under the form of the use of a different tool sustaining a potentially different function, which connects their results to functional fixedness. In this respect, although the results of these 6 single-success orangutans do not offer support for conservatism because they did not try to use the same tool or technique on a different substrate as the chimpanzees did, they may support the functional fixedness perspective.

Regarding functional fixedness, while conservatism may explain the behavior of the 13 double-success individuals, I directly tested whether functional fixedness could in addition explain the multiple uses of sticks by eight of them (Table II). For the double-success individuals, honey-dipping, being the first task, could indeed functionally fix the stick. If these eight orangutans experienced functional fixedness during the raking task, a delay to select a stick as the right tool to rake the food could be expected, considering that they had just successfully used a stick to fish for honey (German and Defeyter 2000). One prediction of this hypothesis is thus that the double-success individuals should have taken more time than the six single-success rakers to use sticks as a means to rake the food. However, this was not the case, as they did not spend more time selecting the stick as a potential tool for the raking task compared with the single-success rakers.

In sum, although functional fixedness did not affect the performances of at least 8 of the 13 individual orangutans in the raking task, it may nevertheless explain why 12 orangutans could not transfer their knowledge from one task to the other from a representational point of view. For the six honey-dippers, their existing knowledge was that the stick could be used to fish for honey (this knowledge had been acquired previously to arriving at the center). For the six rakers, their existing knowledge was that the stick was to be used to bring food closer to oneself (Gruber *et al*. 2012b). In both cases, the function of the stick was *that of a tool*. However, they would appear as two separate functions, as these 12 individuals could not transfer this function to the other task. It is unclear why functional fixedness, which has been defined as a universal in humans (German and Barrett 2005), would not affect all tested individuals, particularly considering that the single- and double-success individuals originated indistinctively from all geographical areas in Sumatra, thus excluding potential genetic explanations for this difference (Gruber *et al.* 2012b). Combined with the chimpanzee results, this suggests that one major aspect to take into consideration when attempting to analyze the results from these two datasets is the large intraspecific variation found between subjects.

Other Factors Influencing the Innovation Process and the Building of Cultural Representations: from Cultural Ontogeny to Individual Differences in Personality and Motivation

A key feature across the reported studies is the observed variation between individuals. It is simply impossible to explain the behavior of one species, or one subgroup, based on either functional fixedness or conservatism. One potential factor to be taken into account is the age of the participants. For the chimpanzees, all the leaf-spongers but one (HT) were juveniles or subadults at the time they adapted the behavior to the novel task. HT herself did so after observing her then-subadult son HW. This finding supports the idea of a critical period in chimpanzee learning, allowing both plasticity to learn but also flexibility in one's behavior (Matsuzawa 1999). However, this period of plasticity may be longer than the 5 yr suggested by Matsuzawa and colleagues, at least in the case of leaf-sponges (up to 12 yr old in this dataset). In contrast, considering that most adults failed to adapt the leaf-sponging behavior to the novel experimental task, it is likely that functional fixedness had then set the function of leaf-sponges to "fetching water" and to no other possible substrate.

Regarding the orangutan data, the great majority of individuals tested was younger than the age at which functional fixedness usually occurs in human children, who experience functional fixedness only from *ca.* 6 yr of age (German and Defeyter 2000). In particular, only one single-success individual was older than 6 yr old (mean age for the single-success individuals: 4.79 yr, $N = 12$, Table II), suggesting that functional fixedness could occur earlier in orangutans than in humans. However, considering that the mean age of the eight individuals that did not display functional fixedness was 4.68 yr ($N = 8$), it remains to be explained why an age-class effect does not appear to exist in orangutan functional fixedness, as in the human case (German and Barrett 2005).

Another possible factor that can explain the different performances between individuals is a difference in motivation. However, the use of a tempting reward such as honey, which is much favoured and consumed in all documented wild chimpanzee communities observed so far (Sanz and Morgan 2009) and is also a prized food in Sumatran orangutans (van Schaik *et al.* 2003b), makes it unlikely that the tested individuals had different levels of motivation to reach it. For instance, all individuals that possessed a technique, e.g., leaf-sponging or stick use, to collect the honey always consumed the honey entirely if undisturbed. Nevertheless, it cannot be excluded that individuals that did not develop a technique to get the honey became frustrated and experienced a lack of motivation in subsequent trials. In effect, the non-leaf-sponging chimpanzees spent less time on average than the leaf-spongers. However, this could also be a consequence of not having a successful technique to collect the honey and giving up earlier, rather than a lack of motivation. This situation does not apply to the orangutans that were tested only once. In addition to these individual parameters, other ecological parameters have to be taken into account when analyzing an individual's motivation in a cognitive task. Elsewhere, I have argued that the Sonso chimpanzees may not have developed the stick-using behavior because their current diet, mainly based on figs, buffers against ecological pressures such as food scarcity that may lead individuals to develop novel tool use (Gruber 2013; Gruber *et al.* 2012a). Therefore, their motivation could depend on ecological variation. More generally, it will be necessary to evaluate how environmental factors influence whether individuals will develop or copy novel behavior eventually.

Finally, a last idiosyncratic parameter that must be taken into account is the personality of the tested individuals and potential differences in their cognitive abilities. It is now well documented that chimpanzee personalities correlate with their ability to succeed in problem-solving tasks (Hopper *et al.* 2014; Massen *et al.* 2013), and that primate personalities also determine those individuals that will be most likely to socially learn (Carter *et al.* 2014). No data were collected in the two studies that would allow the isolation of particular personality traits, e.g., exploratory tendencies, or astute cognitive abilities in any of the participants. Whether they correlate with the characterization of individuals as conservative or subject to functional fixedness therefore remains to be investigated. In particular it will be necessary to develop tools to assess behaviorally whether some individuals are generally more likely to succeed in some tasks (Amici *et al.* 2012). Interestingly, 7 of 10 leaf-spongers appear to have adapted the leaf-sponging behavior present in their repertoire to the honey-trap experiment independently from each other, suggesting that chimpanzees may use behavior already part of their cultural knowledge in novel contexts (Yamamoto *et al.* 2008). These individuals thus were able to inhibit their baseline response in this context (using their hand) to adapt a behavior that they used habitually in a close context. The cognitive abilities of chimpanzees allow them to delay the obtention of a reward if they know they can get a larger one (Beran *et al.* 2013). A possibility is thus that the individuals that developed the leaf-sponging behavior were more patient than the others, and could eventually develop a technique that allowed them to maximize their gain.

Representations, Metarepresentations and the Scope of Conservatism and Functional Fixedness

While conservatism and functional fixedness are often presented as suited to explain animal behavior in a parsimonious way (Brosnan and Hopper 2014), it is currently unclear how cognitively complex these two mechanisms in fact are. Beyond the behavioral level, conservatism and functional fixedness can be analyzed at the representational level. This requires a deeper cognitive description of the phenomena at stake in apes to compare them with the human phenomena while taking into account the potential limits of great apes when accessing the representations of their knowledge (Gruber *et al.* 2015). As cognitive beings, great apes, much like other animals, constantly build mental representations of their environment. Previous work in captivity on symbolic capacities in chimpanzees has shown that they are able to sort objects as foods or tools, suggesting that this is within the extent of their cognitive capacities (Savage-Rumbaugh *et al.* 1978). Building a representation is not itself cognitively complicated and can readily be obtained by simple associationist mechanisms;

however, the real complexity lies in how animals are able to access their representations, which may require more complex cognitive mechanisms such as metarepresentations (Gruber *et al*. 2015). In the case of functional fixedness or conservatism, research must uncover whether the representations of the technique, or of the function of a given tool, directly hinder great ape innovative abilities. Defining conservatism as an attentional bias toward familiar and known objects at the expense of others will nevertheless imply that animals build representations of said objects that occupy their attention. In other words, conservatism may consist of an animal accessing a representation of a given technique in a known context. Similarly, functional fixedness may consist of an animal accessing a representation of the function of a given object. This process may or may not be a conscious one. The representation, in turn, can prevent the animal from exploring the use of novel objects because it is readily activated in the animal's mind if the context appears close enough to the one that triggered the building of this representation in the animal's mind in the first place.

The adaptation of leaf-sponge behavior to the honey-trap experiment by 10 Sonso chimpanzees suggests that these 10 individuals could assess that leaf-sponges were potentially adequate tools for the task at hand. The simple fact that they manufactured these tools after the discovery of the honey log shows that they had to represent leaf-sponges as potential tools before making them. Whether this is evidence of conservatism or innovative abilities, however, can be debated. On the one hand, they displayed innovative abilities by adapting the use of a known object to a novel context (Reader and Laland 2003). On the other hand, none of the Sonso chimpanzees adopted the stick-use behavior, potentially because it was too far from their known repertoire, and therefore displayed a kind of conservatism directly connected to their cultural knowledge. In particular, the cultural knowledge of the Sonso chimpanzees, by not including sticks as potential tools, may prevent them from acquiring the knowledge that sticks can in fact be used *as* tools: they may fail to conceptualize that there is a second option. In contrast, other communities with the stick knowledge may have a different set of representations, which allows them to use the sticks in this context. For instance, the Goualougou chimpanzees make multiple use of a variety of stick tools to gather honey (Sanz and Morgan 2009), suggesting that they can attribute different functions, or potentially the more general one of "tools," to the sticks in the context of honey fishing. In humans, functional fixedness may also be acquired through the filter of the culture to which an individual is exposed (Defeyter and German 2003; German and Defeyter 2000). Through this filter, they will observe and learn some practices, and not others. It will therefore be necessary to explore how ape cultural knowledge can lead to functional fixedness of given parts of their environment. Here, the orangutan data suggest that not all individuals experienced functional fixedness in the task, contrary to what has been described in humans as a universal phenomenon (German and Barrett 2005). The reasons why only some individuals in both studies display functional fixedness will need to be investigated, taking into account individual characteristics as well as their cultural background.

Beyond Social Learning Mechanisms: A Complementary Approach to the Animal Culture Debate

I have here argued that conservatism and functional fixedness, two psychological mechanisms often relied on to explain limitations in ape innovative behavior

(Brosnan and Hopper 2014), must be analyzed through a representational perspective to fully understand their implications in wild and captive ape behavior. Further research will decipher whether the two phenomena are linked, for instance, whether functional fixedness may potentially be formed through a general tendency to conservatism in great apes. More generally, it will be necessary to conduct studies to understand the relationship between the representations of cultural knowledge and mechanisms such as conservatism and functional fixedness to characterize how these mechanisms interact in the building of one's culture both in humans and other animals.

The representational approach proposed here may also bring a complementary perspective to current debates on animal culture. In recent years, criticisms of the concept have changed. They no longer deny that some kind of social learning is at work in the building of behavioral differences between communities of the same species (Laland and Galef 2009). However, anthropologists have pointed out that there is a clear difference between what they and biologists understand as culture (Hill 2009; Perry 2009). The debates on animal culture at both the behavioral and cognitive levels have been concerned with comparing "sets of behaviors" in animals, apes in particular, with sets of "beliefs" or "mental representations" in humans. While the external, observable "behavioral side" of nonhuman animal culture —the documented group-specific behavioral patterns— is now uncontroversial, the "cognitive side" of culture —the identification of the cognitive mechanisms that allow animals to acquire these behavioral patterns and the representational format under which they are transmitted— has become the forefront of the debate over recent decades. Imitation and teaching have been presented as hallmarks of human culture, with the presumed cultural behavior of monkeys and apes arguably relying on different social learning mechanisms (Galef 1992, 2009; Tomasello 1990, 2009). Based on these claims, there has been substantial effort over the last 20 yr to determine the precise transmission mechanisms relied on during the transmission of tool use in apes. Several social learning mechanisms have been identified during chimpanzee cultural transmission, including what may qualify as imitation, although with a lower degree of fidelity when compared with humans (Hobaiter and Byrne 2010; Whiten *et al.* 2009). The claim that imitation on its own may explain the exceptional human cultural abilities has thus weakened over the last decade, particularly as imitation is not necessary for accurate replication of behavior even in humans (Caldwell and Millen 2009; *cf.* Derex *et al.* 2013). In contrast, evidence for teaching in cultural animals, in particular wild apes, remains scarce (Boesch 1991), and could represent a true difference between humans and their closest relatives. Nevertheless, evidence of teaching, at least in a functional sense, has been found in other species, most prominently meerkats (*Suricata suricatta*) and ants (*Temnothorax albipennis*) (Thornton and Raihani 2010). Critically, these species do not exhibit behavioral variation that would qualify as cultural. Similarly, claims that teaching is critically important in the spread of cultural knowledge has been questioned even in humans (Henrich 2004; *cf.* Morgan *et al.* 2015).

It can be argued that this specific attitude toward a set of beliefs is a feature of human culture and that it may not be required in other forms of culture, which can then be defined simply as group-specific typical behavior patterns transmitted by social learning (Fragaszy and Perry 2003). An additional conceptual problem with using potential evidence of imitation and teaching as evidence of culture in other animals is that it builds a circular argument. If imitation and teaching are fundamental to —and part of the definition of—

culture, then any behavioral transmission that does not involve teaching and imitation cannot be culture. However, for such reasoning to be valid, it must then be supported by other evidence than simply the fact that these social learning mechanisms are particularly effective at transmitting culture in a given species, humans. Nevertheless, if one wants to truly compare human and ape cultures and decipher whether the two are evolutionarily connected, it remains necessary to identify how similar they truly are. In other words, chimpanzees may display behavior that qualifies as cultural because it is socially transmitted, but this may very different from what humans experience and only result from simpler associative mechanisms (Shettleworth 2010).

To counter this problem, it may therefore be more appropriate to define culture without reference to the underlying social learning mechanisms and empirically assess which of these mechanisms are responsible in different species for the observed behavioral variation. Under such a paradigm, culture can rely on different transmission mechanisms, and a species transmitting behavioral traditions between different generations while relying on social learning mechanisms other than imitation and teaching would still display traditions or culture (Franz and Matthews 2010). The representational approach described here supports the hypothesis that the unit of transmission between individuals may not be the behavior itself, but its mental representation in the mind of the individual that displays the behavior (Sperber 1996). In such a framework, imitation and teaching may still be put forward to explain the exceptional cultural abilities of humans, but as very efficient means of transmission of the cultural representations between individuals, allowing transporting the representations from minds to minds (Gruber *et al.* 2015) rather than as social learning mechanisms that specifically and qualitatively make culture different in humans when compared to other species (Derex *et al.* 2013; Morgan *et al.* 2015; Tennie *et al.* 2009). Such an approach, which will also benefit from frameworks and theories developed outside the domain of psychology and zoology, for instance in neuroscience and philosophy of mind, may be ultimately needed to understand how similar and different animal and human cultures are.

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