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ORIGINAL ARTICLE

All Innovations are Equal, but Some More than Others: (Re)integrating Modification Processes to the Origins of Cumulative Culture

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Abstract The cumulative open-endedness of human cultures represents a major break with the social traditions of nonhuman species. As traditions are altered and the modifications retained along the cultural lineage, human populations are capable of producing complex traits that no individual could have figured out on its own. For cultures to produce increasingly complex traditions, improvements and modifications must be kept for the next generations to build upon. High-fidelity transmission would thus act as a ratchet, retaining modifications and allowing the historical buildup of complex traditions. Mechanisms acting against slippage are important, of course, but cultures also need to move forward for the ratchet to retain anything important. In this article, I argue that studies of modification-generating processes and the many ways they shape cumulative culture have been overlooked. Key to a better understanding of cultural modification processes is taking seriously that cultural traditions consist of complex, hierarchically structured recipes. Taking such structures seriously and assessing the different ways they can vary in cultural design space, a novel picture for the onset of cumulative cultural evolution emerges. I argue that a possible impediment for cumulative culture in nonhuman animals may in fact reside not so much in the fidelity of their social transmission but rather in the constraints, internal and external, on their capacity to modify complex, hierarchically structured cultural recipes.

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Introduction

The cumulative open-endedness of human cultures represents a major break with the social traditions found in nonhuman species (Heyes 1993; Tomasello et al. 1993; Tomasello 1994/2009, 1999; Boyd and Richerson 1996; Mesoudi et al. 2004; Richerson and Boyd 2005; Tennie et al. 2009; Mesoudi 2011; Lewis and Laland 2012; Dean et al. 2014). As traditions are altered and the modifications retained along the cultural lineage, human populations are capable of producing complex traits that no single individual could have figured out on its own. While it is common to point at humans' technological and scientific development as evidence of this process (Basalla 1988; Arthur 2009), similar claims advancing the idea that nonhuman animals also produce cumulative cultures are more controversial (see Dean et al. 2014 for a review).

A central issue in this debate consists in identifying the cognitive novelties that served as the key difference-makers between human cumulative cultures and nonhuman (and protohuman) noncumulative traditions. A popular candidate is modern humans' capacity to transmit culture through high-fidelity social learning (Heyes 1993; Tomasello et al. 1993; Tomasello 1994/2009, 1999; Boyd and Richerson 1996; Tennie et al. 2009; Lewis and Laland 2012; Dean et al. 2014). According to this mainstream view, for cultures to produce increasingly complex traditions, improvements and modifications must be retained for the next generations to build upon. High-fidelity social transmission is said to ensure that cultures do not slip back, which would force the reinvention of the same improvements over and over again. In this sense, high-fidelity social transmission acts as a ratchet retaining modifications and allowing the historical buildup of complex traditions (Tomasello et al. 1993; Tomasello 1999).

Mechanisms acting against slippage are important, of course, but cultures also need to move forward if the ratchet is to retain anything important at all: they need to derive novel innovations from existing traits. What I suggest here is a different, albeit complementary line of reasoning about the population-level conditions and evolutionary implications of cumulative culture. I argue that studies concerned with the evolutionary origins of cumulative culture have overlooked the importance of *modification*-generating processes and their role in patterning cumulative cultures. There are many ways that novel derived innovations can be produced, and, depending on the structure of the design space explored by the population, different kinds of modification mechanisms will lead populations to exhibit different evolutionary patterns. However, in the context of the onset of cumulative cultures, there is little work that takes seriously the population-level consequences of differences in innovative processes. I suggest that the little attention devoted to the differences in innovative processes has led to the misguided impression that nonhuman species are comparatively as innovative as humans, suggesting that an increased capability in retaining cultural novelties is the main, if not only, key difference-maker between species with noncumulative traditions and those with cumulative cultures.

In this article, I approach the generation of novel cultural traits out of existing traditions from a population-level perspective. Individuals do not produce cumulative cultures on their own: populations do so through the transgenerational aggregation of their members' capabilities and the structure of the network in which these members are embedded. Accordingly, the theoretical literature concerned with cumulative culture mainly focuses on the population-level effects of an increase in transmission fidelity, whether it is the product of novel social learning capabilities in individual organisms or the effect of specific sociodemographic structures, or both. In a similar vein, I examine how cultural traits are structured, what sorts of modifications they can undergo, and how these structures scale-up in constraining a cultural population's exploratory behaviors. I argue that the diverse way traditions can be cumulatively modified affect the exploratory behaviors of cultural populations, and in turn that the contingencies which make some cultural trait functional or not constrain just what can serve as a viable cumulative step. The conclusion I reach is that even if a population is endowed with members capable of innovating and transmitting their improvements with high-fidelity social transmission, with the wrong modification processes the structure of the design space can constrain the population to wallow in noncumulative traditions. I sketch a plausible evolutionary scenario to illustrate my argument. However, such scenario does not aim at pinpointing the key biological novelties that distinguish human from nonhuman innovative mechanisms, nor do I intend to offer a precise step-by-step lineage-based explanation of how human populations acquired the capacity to produce cumulative cultures. Rather, I am interested in how design spaces constrain which modification mechanisms can act as potent agents for cumulative culture, and how the study of the richness of cultural modification mechanisms and of cultural design spaces is a sine qua non for a science of cumulative cultural evolution.

(Re)integrating Modification Processes

The Ratchet Metaphor

Cultural evolutionists and students of animal traditions typically refer to human cultures as being cumulative (Heyes 1993; Boyd and Richerson 1996; Tomasello 1999; Mesoudi et al. 2004; Richerson and Boyd 2005; Tennie et al. 2009; Mesoudi 2011; Dean et al. 2014). Cumulative culture is a process better understood as a cultural form of descent with modification. Not only are individuals capable of altering the behaviors they learn from others (modification), but they can also transmit the new forms to others down the cultural lineage (descent). As modified traits are transmitted, further modifications can in turn be made and transmitted. With time and proper design spaces (see below), populations will build up complex cultural traits that no single individual could have figured out on its own. There are thus minimally two constitutive conditions for cumulative evolution:

(1) *Production of modifications*—There is a variation-generating mechanism that produces new traits by modifying existing traditions.
(2) *Inheritance of modifications*—It is not enough for modifications to be derived from existing traits, they must also be transmitted from one generation to the next. Modifications that are not transmitted will not serve as a basis for cumulative cultural evolution.

Tomasello (1994/2009, 1999) and others refer to the retention of modifications in socially transmitted behaviors as a "ratchet effect." The ratchet effect is a mechanical metaphor that stresses the role of social transmission to "lock in" novel modifications of socially transmitted traits in a population's cultural repertoire. Adherents of the ratchet metaphor family of explanations typically stress the high fidelity of human social transmission as the key condition to ensure that improvements of cultural traditions are transmitted as such to the following generations (Tomasello 1994/2009, 1999; Richerson and Boyd 2005; Tennie et al. 2009; Lewis and Laland 2012; Dean et al. 2014). Fidelity is a retention mechanism (Charbonneau 2014), acting against "slippage" as it ensures that the population does not need to reinvent the novel trait over and over again. Generation after generation, through faithful social transmission steadily retaining novel improvements, populations can develop complex cultural traits that no single individual could have devised alone during its own lifetime.

Early versions of this line of reasoning insist specifically on the uniqueness of the human lineage possessing specific kinds of social learning mechanisms—e.g., that humans can copy behaviors through imitation and teaching whereas chimpanzees can only emulate one another by learning that some end result is obtainable (Galef 1992; Tomasello et al. 1993; Tomasello 1994/2009, 1999). Recent evidence, however, suggests that nonhumans are also capable of imitating and teaching to some degree (e.g., Whiten et al. 2005; Horner et al. 2006). Accordingly, proponents of the ratchet effect now argue that it is a mixture of multiple, enhanced social learning mechanisms and cognitive capabilities (shared intentionality, motivation to conform, etc.; e.g., Tomasello 1994/2009; Tennie et al. 2009), as well as social factors (demography, connectedness of the population, etc.; e.g., Powell et al. 2009; Pradhan et al. 2012) that ensure high-fidelity social transmission (Dean et al. 2014 for a review). Nevertheless, the ratchet effect and the mechanisms acting against slippage remain the explanatory focus of studies on the differences between human cumulative cultures and nonhuman noncumulative traditions.

The Disqualification of Modification

The explanatory sufficiency of the factors that the ratchet metaphor picks out as key difference-makers logically depends on the fact that a population is already capable of producing improvements of cultural traditions, since without modifications there would not be much to slip back from. This has been amply recognized, and it is often repeated that the generation of modifications is also necessary for cumulative cultural change (e.g., Tomasello 1999; Tennie et al. 2009; Mesoudi et al. 2013; Dean et al. 2014). Surprisingly, in the context of the debate about the evolutionary origins of cumulative cultures, the different ways modifications are produced and how they generate cumulative culture have received little attention. Some work has been invested in building and analyzing evolutionary models that distinguish between different modification mechanisms and their differential impacts on cumulative culture (e.g., Lewis and Laland 2012). However, most theoretical work on the biological origins of cumulative culture assumes that modifications are introduced for free, typically by adopting a coarse-grained distinction between "cultural mutations" and "recombination." For instance, a recent state-of-the-art discussion's only comment on the population-level effects of cultural modification mechanisms was that they "generate cultural variation" (Mesoudi et al. 2013, p.197). It seems thus safe to say that, in the context of the origins of cumulative culture, modification mechanisms have generally been overshadowed by worries about transmission fidelity, and so has the rich evolutionary potential of their diversity.

This is not to say, however, that the inventiveness of human and nonhuman animal species has not been an object of serious investigation. Comparative innovation studies of nonhumans and humans are part of an increasingly growing field of empirical and theoretical research (e.g., Reader and Laland 2003; O'Brien and Shennan 2010). One key result of these studies is the discovery that many nonhuman species appear to be comparatively as inventive, as they exhibit rates of innovation close to those of humans. For instance, Whiten et al. (2001) document larger-than-expected cultural repertoires in chimpanzee populations, repertoires due to an accumulation process. Other work, such as Lefebvre et al. (1997) for instance, correlates high inventiveness in nonhuman animal species with an increase in brain size. However, what these results, among others, seem to have suggested to proponents of the ratchet metaphor is that the capacity to produce novel cultural variants is comparatively as widespread in non-cumulative-culture species as it is for modern humans, and thus, to explain why only we possess cumulative cultures, we ought to look elsewhere to find a good explanation. Part of the literature seem to endorse—more or less explicitly—this reasoning and, in a similar fashion, disqualify the generation of modifications as a key candidate difference-maker:

> The process of cumulative cultural evolution requires not only creative invention but also, and just as importantly, faithful social transmission .... Perhaps surprisingly, for many animal species *it is not the creative component*, but rather the stabilizing ratchet component, that is the difficult feat. (Tomasello 1999, p. 39; emphasis added)
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> [Cumulative culture] obviously relies both on inventiveness, for the cultural novelties, and on faithful transmission across generations to keep the novelties in place until other novelties come along. The claim in [Tomasello et al. 1993] was that *while inventiveness is fairly widespread* among primates, humans transmit cultural items across generations

> much more faithfully, and it is this faithful transmission (the ratchet) that explains why human culture *accumulates modifications* over time in a way that chimpanzee and other animal cultures do not. (Tennie et al. 2009, pp. 2405–6; emphasis added)
>
> Theoretical analysis provides support for the link between high-fidelity transmission mechanisms and cumulative culture: *irrespective of the rate of innovation*, cumulative culture cannot emerge without accurate transmission. (Dean et al. 2014, p. 286; emphasis added)

Although research on the innovative capacity of human and nonhuman species has arguably found comparably high rates of inventiveness, it is unclear whether nonhumans' capacity for inventiveness consists only of learning directly from the environment, with innovations then diffused and preserved by social learning as unchanging traditions, or if inventiveness also encompasses *alterations of existing social traditions*, thus satisfying the first condition of cumulative culture (see above). In other words, these studies typically do not contrast between innovations from scratch and modifications.

By innovation from scratch, I refer to what is usually understood as a form of behavioral plasticity obtained by an individual learning some behavior by interacting with its environment. For instance, a chimpanzee playing with rocks and nuts may learn how to crack the nuts through these ecological interactions. Such innovations can later be transmitted through social learning and if so, serve as seeds for cultural traditions. However, innovations from scratch do not necessarily depend on a species' capacity for social learning, as they can be produced whether or not a population is capable of maintaining cultural traditions.

In contrast, modifications rely on a species' capacity for social learning since they are alterations of existing traditions. For instance, a chimpanzee could realize that some rock materials are better than others at cracking nuts and thus improve upon the nut-cracking tradition initiated by another's innovation from scratch. An individual acquires a cultural trait from some other individual and alters that trait. Hence, modifications rely on the existence of cultural traditions, and thus on a capacity for social learning (Tomasello 1999). However, it is important to understand that modification processes need not be the same as social learning processes. Whereas social learning ensures the transgenerational transmission of traditions, modifications are *alterations* of the socially transmitted traits. They generate something new from something old. So there is no possibility of modification if the population is incapable of social learning. However, a population capable of social learning is not necessarily capable of improving upon a tradition, because it may lack the creative capacities necessary to alter traditions (see below). A modification process thus introduces novel but derived variants into a population's repertoire: a modification relies on a lineage relationship between an original, ancestral trait and the modified form produced from it.

The notion of inventiveness used to dismiss the role of innovative processes as key difference-makers between noncumulative nonhuman traditions and cumulative human traditions fails to pinpoint this distinction. Indeed, as far as I know, no empirical research shows that nonhuman species are capable of modifications but incapable of cumulative cultures, although they convincingly illustrate that there are plenty of innovations from scratch in nonhuman noncumulative cultures.

The lack of a distinction between these two forms of innovation is problematic for an argument that supports the disqualification of modification processes as a potential difference-maker. The error is to blend together rates of innovation from scratch with rates of modifications and infer that nonhuman species produce comparably as many derived traits as do humans. For instance, a species that was twice as inventive as humans would still be unable to produce cumulative culture if the only form of innovation it were capable of generating was innovations from scratch. With cumulation, it is the capacity to produce derived innovations that matters, not the rates of inventiveness per se. In fact, if the rates of nonhuman inventiveness are to be used at all to dismiss modification processes as potential difference-makers for cumulative culture, the disqualification ought to be based on comparing the relevant capacities: that of generating modifications, not innovations from scratch. Once we make it clear that there is an important difference between modifications of cultural lineages and possibly initiating novel traditions through innovations from scratch, it becomes obvious that there are only very scarce studies in the relevant literature that explicitly discuss modification processes *in contrast to* innovations from scratch (but see Enquist et al. 2011; Lewis and Laland 2012). In order to resolve this absence, we ought to clarify just what the mechanics of cultural modification consist of.

Modification and Transmission

Modification and Complex Recipes

A modified or derived trait is one that retains some of the properties of its ancestor but also differs in other respects. It must retain part of what the ancestor was made of so as to be genealogically related, but it must also differ in some respect if it is to serve as an alteration of the ancestral trait. Thus, for a tradition to undergo cumulative modifications, the transmitted trait must possess some structure that can

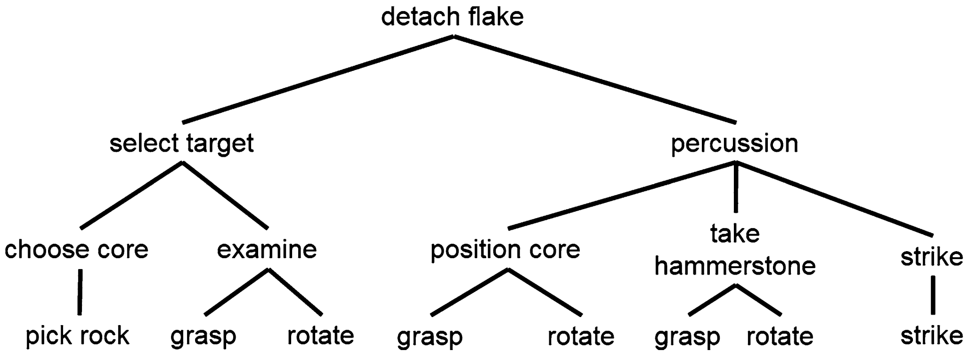

Fig. 1 The hierarchical structure of a recipe to detach a stone flake. Nodes represent goals and cognitive decisions, with the action component figuring at the lower level of the recipe's structure. An action-level modification would consist of altering the specific sequence of actions (e.g., throwing instead of striking) or of modifying some property of an action (e.g., changing the striking angle). Hierarchy-level modifications would alter the subgoals of the recipe and the dependencies between the subassemblies (e.g., adding a new subgoal). Adapted from Stout (2011), p.1052

be partly modified and partly retain ancestral qualities. By structure, I mean that the cultural trait can undergo transformations of some of its parts without the whole being disturbed.

There is a vast literature concerned with the structure of behaviors. One general point of consensus among cognitive psychologists, neuroscientists, linguists, paleoarchaeologists, anthropologists, primatologists, and artificial intelligence researchers is that behaviors are hierarchically organized (Lashley 1951; Chomsky 1957; Miller et al. 1960; Simon 1962; Schank and Abelson 1977; Greenfield 1991; Byrne and Russon 1998; Byrne 1999, 2002, 2003; Whiten 2002; Mesoudi and Whiten 2004; Botvinick 2008; Stout 2011; Guerra-Filho and Aloimonos 2012; Pastra and Aloimonos 2012). Cultural evolutionists have also noted this property for complex cultural traits and have studied some of the evolutionary implications of the hierarchical structure of cultural traits (Mesoudi and Whiten 2004; Mesoudi and O'Brien 2008b; Enquist et al. 2011; Querbes et al. 2014). In fact, there is a growing consensus to understand complex cultural traits in terms of cultural recipes (Mesoudi and O'Brien 2008b, 2009; O'Brien et al. 2010; Mesoudi 2011; Stout 2011; Querbes et al. 2014). The concept of recipe originates from paleoarchaeology, where it refers to the set of materials, actions, and instructions to be followed in order to produce some artifact (Neff 1992; Lyman and O'Brien 2003; Mesoudi and O'Brien 2008b, 2009; O'Brien et al. 2010; Stout 2011).

In more general terms, we can understand a cultural recipe to consist of the organization of decisions and actions leading to the satisfaction of some intended goal (Byrne and Russon 1998; Mesoudi and O'Brien 2008b; O'Brien et al. 2010; Stout 2011). Thus conceived, recipes are hierarchically organized, cognitively complex, programs of action. What shapes the hierarchical organization of a recipe is the functional dependencies between actions and subgoals. A recipe is thus structured by assemblies of actions serving to complete subgoals. Ultimately, these all lead to the fulfillment of some overall, intended goal, i.e., the intended end result (Moore 2007, 2010; Mesoudi and O'Brien 2008b; Stout 2011; Lombard and Haidle 2012). The hierarchical structure of a recipe is typically represented as a decision tree with each node standing for subgoals and the lower components representing the actions required to satisfy the subgoal (see Fig. 1).

Recipes are thus hybrid entities, as they consist of sets of decision processes and of specific actions (Mesoudi and O'Brien 2008b; O'Brien et al. 2010). They are transmissible through social learning as they are observable (see below). Moreover, their structure is amenable to modifications, either in the specific dependencies between the decisions and subgoals that characterize them, or in terms of the specific actions required to satisfy these goals, or both.[1]

Cultural recipes can assume different kinds of hierarchical structures. Starting at the more superficial level, a recipe can be organized as a string of action units (Heyes and Ray 2000; Heyes 2005; Mesoudi and O'Brien 2008b). In this case, the recipe consists of a linear sequence of actions, the completion of one action prompting the manifestation of the next. The successful enactment of a string of actions is dependent on the order of completion of the action units. Early actions tend to be preparatory for later actions in the sequence, such as a chimpanzee grabbing a rock to use it to hammer a nut. Changes in early actions will thus tend to have important downstream effects on the production of later actions and thus on the successful

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[1] As with most of the literature concerned with the evolution of cultural recipes, I will remain agnostic as to the precise way these recipes are mentally represented by the individuals, and will thus discuss cultural variation and modifications in terms of changes in the recipes themselves.

completion of the whole sequence. However, superfluous actions—nonfunctional, noninterfering actions—such as those used in research about overimitative processes in humans and nonhumans, will not behave this way (see Lyons et al. 2007).

Strings of actions have a minimal hierarchical structure, as they require only the repetition of the same cognitive decision: when action A_x is completed, do action A_{x+1}, and this until the whole sequence is completed. Variation in sequences of actions thus offers a limited range of potential modifications, as only the specific actions are open for variation. For instance, a sequence of actions will be modifiable by altering the specific order of the actions, through the addition or subtraction of specific actions, or by replacing some actions by others. It must be noted, however, that specific actions also have many properties that can vary relatively independently from the rest of the sequence. For instance, a chimpanzee hitting a nut with a rock can vary in the kind of grip used to hold the rock, hand preference (laterality), angle of percussion, force of impact, amplitude of strike, and so on.

Alternatively, a recipe can have a much more complex hierarchical structure by possessing many levels of inclusively nested action assemblies and subgoals, culminating in the whole behavior's structure and main goal (Greenfield 1991; Byrne and Russon 1998; Whiten 2002; Byrne 2003; Mesoudi and O'Brien 2008b; Moore 2010; O'Brien et al. 2010; Stout 2011). Whereas in the case of linear sequences of actions the recipe proceeds by the enactment of each action unit in the specified order, in the case of deeper hierarchically organized recipes, assemblies of closely interacting action units serve the completion of subgoals, so that a specific assembly can be repeated until the subgoal it serves is satisfied (or it can be skipped if the subgoal is already satisfied). Action assemblies are integrated sets of action units and subgoals which can themselves comprise subordinate and more-integrated sets of actions. Inversely, they can also be nested under superordinate levels of more-general goals. These "modules" will tend to act as independent units or string of actions in their own right (Byrne 2005; Moore 2010). For instance, in the case of a nut-cracking behavior, a chimpanzee can repeatedly use a rock to hammer a nut on an anvil—and realign the nut if it moves—until the nut is cracked opened (subgoal). This can be done without the individual having to reinitiate the whole sequence of actions from the beginning, e.g., going back to gather more nuts (Mesoudi and O'Brien 2008b; Stout 2011). Hierarchically complex recipes can undergo modifications of their specific action components, just as with strings of actions. However, complex recipes also offer potential modifications at the level of their decision nodes, such as changes in the functional dependencies of the assemblies, altering their order by rearranging, adding, replacing, or subtracting them, or by modifying the goals/decisions that structure them and adjusting the actions in the assembly to serve the new subgoals. Novel recipes can also be generated using already known assemblies of actions from other behaviors by combining and interfacing them into novel complex behaviors (Mesoudi and O'Brien 2008b).

Modification and Transmission

The capacity to transmit structured traits (or cultural recipes) seems to be in part what proponents of the ratchet effect originally had in mind when they claimed that human social learning is more faithful than that of nonhumans (Tomasello et al. 1993; Tomasello1999, 1994/2009). Because the capacity to modify traditions depends on the existence of structured traditions (in contrast to innovations from scratch, which are learned not from tradition but from interactions with the individual's environment), only social learning mechanisms capable of transmitting structured recipes will be able to sustain cumulative culture. Indeed, without the transmission of the structure of a recipe, there are no possibilities to pass on part of the ancestral trait together with the introduced alterations. Social learning mechanisms relying on social priming followed by trial-and-error reinvention of a trait (e.g., local enhancement, emulation, etc.; see Hoppitt and Laland 2013) will fail to produce cumulative culture, as such learning mechanisms do not attend to the cultural recipes but rather only retain their end results. A chimpanzee developing an improved nut-cracking technique by adding stones under a wooden anvil to stabilize it would not be able to transmit the novelty if the other individuals of its tribe learned to crack nuts by trying to reproduce the end result alone without attending to the cognitive and behavioral structure of the recipe (i.e., emulation learning). In such cases, while there may be a tradition of cracking nuts, the tradition will be one of the transmission of the end results but not of the cognitive/behavioral structure of the cultural recipe. A model's specific nut-cracking improvements will not form lineage relationships with any earlier versions of the recipe since the structure of the recipe itself is not transmitted, and later chimpanzees will not acquire any information regarding the structure of the novel technique, that of stabilizing the anvil, as they only attend to the end result and not to the means of obtaining it. Such a population would then slip back at every generational turnover, needing to reinvent their very own individual nut-cracking techniques anew (Tomasello et al. 1993; Tomasello 1999).

On the other hand, social learning mechanisms such as imitation and teaching will support cumulative culture as these processes ensure the transmission of the structure of cultural recipes, and thus of the potential modifications that can be derived on these structures from the original recipe for action. According to this perspective, imitation and teaching are more faithful than emulation learning because they transmit more of the information concerning the trait of interest, such as information about its functional structure, i.e., the structure of intentional decisions, subgoals, and the actions required to satisfy such goals. In contrast, emulation would only transmit information about the feasibility of the end result and prompt an individual to rediscover a solution to the problem. A chimpanzee imitating another's technique for cracking nuts by attending to its actions and their specific organization will learn the recipe for cracking nuts as well as the end result (that nuts can be cracked). The chimpanzee could then spend its time improving the tradition by adding novel steps to the recipe (e.g., using another rock as an anvil to stabilize the nut-cracking process), and, accordingly, the next generation would then be able to learn the improved technique and have the chance to produce further ameliorative modifications. In this specific sense, high-fidelity transmission (transmission of structured recipes) is required if a culture is to undergo cumulative evolution.

However, even among social learning mechanisms that are capable of transmitting complex cultural recipes, not all such processes can transmit the same kinds of structured recipes. For instance, the transmission of a chain of actions can be done through associative imitation (Heyes and Ray 2000; Conway and Christiansen 2001; Heyes 2005), or what Byrne and Russon (1998) termed "action-level imitation." As a sequence of action is observed, the learner is able to recognize the precise order of each action unit and learn to reproduce the very same sequence of actions by forming correlational associations between each step and its equivalent representations in the individual's motor repertoire. In contrast, learning a recipe with more intricate conditionals will focus not so much on the precise string of actions of a model but rather on recognizing the subroutines, their dependencies, and the subgoals they serve. Byrne and Russon 1998 refer to such a family of processes as "program-level" imitation. One possible mechanism to do so is string parsing, which consists in identifying the statistical regularities observed between strings of actions and their results (see Conway and Christiansen 2001; Byrne 2003; Botvinick 2008). Either form of learning will ensure that a recipe—its precise sequence for action-level imitation or its hierarchical organization and the necessary actions in "program-level" imitation—is transmitted. Modifications of these structures can then be passed on from one generation to the next, and incrementally lead to cumulative evolution.

Clarifying what a modified trait consists of shows that it is logically dependent on the transmission mechanisms available to the species. For a novel variant to count as a modification of another cultural trait, the functional structure of the original recipe must be transmitted (or reconstructed) in order to be modified down the lineage. Species relying strictly on action-level imitation processes will not be able to produce modifications in terms of the hierarchical structure of the learned recipe as the complex, cognitive hierarchical organization itself will not be attended to at all during social learning episodes. Specific changes in the directly observable actions may be retained, but any potential modifications in the functional structure of the recipe will be lost. Inversely, social learning mechanisms capable of transmitting the cognitive/behavioral structure of a complex recipe will be sensitive to both modifications in observable actions and changes in the higher-level, cognitive/functional organization of the complex recipe.

There is a philosophical point to be made here. By definition, differences in cultural recipes that fail to be transmitted because the population lacks the social learning mechanisms capable of transmitting these differences are not modifications. In other words, alterations in a recipe that are not attended by the social learning mechanism available to a population will fail, in principle, to be modifications at all since they are not even possibly transmissible. Going back to the anvil stabilization technique, the novel behavior should not be understood as a modification if nut-cracking techniques are transmitted by emulation learning alone. This is because the structure of the behavior is not transmitted at all, and thus the anvil-stabilization behavior simply cannot be derived from the original recipe since the recipe itself is not even transmitted. The stabilization technique can certainly be understood as being more efficient than what individual chimpanzees usually (on average) reinvent by themselves in similar scenarios (i.e., not stabilizing the anvil).

It would be a trivialization of the notion of modification to accept untransmissible differences in socially acquired behaviors as potential modifications. In fact, two specific behavioral expressions always differ in some respect (if only in time and location). To keep the concept of modification meaningful, we ought to count as relevant differences those that are *transmissible*, that is, transmissible by the specific population we are examining. The relevance of information here is not to be understood strictly as functional information but rather, as overimitation studies show, in terms of what is, in a given population, transmissible at all. An untransmitted modification is an alteration of a trait that fails to be transmitted but that could have been transmitted given the social learning mechanisms available to the population. Thus, talk of *transmissible modifications* is pleonastic. This point is often obscured by loose talk of modifications failing to be transmitted because the species lack social learning processes that can transmit information about the structure of the complex behavior.

The distinction between modifications at the level of the action components of a cultural recipe and modifications at the level of the cognitive/functional hierarchy does make sense of known differences between human and nonhuman cognition. There is compelling evidence that nonhuman great apes are capable of learning not just sequences of actions but also the functional/cognitive structure of complex recipes, and thus to invent from scratch and learn from others complex recipes with hierarchical structures (Byrne and Russon 1998; Byrne 2005). However, nonhuman great apes seem to be limited in their capacities to actively manipulate higher-order relationships such as those characterizing hierarchically structured recipes and to innovate by modifying these hierarchies (Holyoak and Thagard 1995; Penn et al. 2008). Modern humans, on the other hand, are experts at intentionally manipulating the functional hierarchies of complex behaviors (Gentner 2003). Some have linked this domain-general human capacity to the evolutionary acquisition of a generative language, which also manipulates hierarchical structures (Greenfield 1991; Moore 2010; Stout 2011; Steele et al. 2012 and the following papers). For instance, modern humans seem to be the only living species capable of recognizing, let alone producing, analogical inferences (Holyoak and Thagard 1995; Penn et al. 2008; de Beaune 2009). Reasoning through analogies requires one to understand, map, and reflectively manipulate high-order relational structures of two objects, processes, or domains, and produce from the mapping novel knowledge (or behaviors) (Gentner 1983; Holyoak 2012). The capacity to draw analogies can lead one to transpose a specific behavior, useful in one environment or behavioral domain, to another, thus generating a novel cultural variant (Bushnell et al. 2005). For instance, the observation that one can heat and cook meat with fire can lead one to infer that other materials can also be cooked, inciting the individual to explore the results of heating and cooking other substances, such as vegetables, clay, fat, ochre, ore, and so on. Other cognitive processes might participate in humans' capacity to manipulate increasingly abstract and/or complex hierarchies, such as an increase in working memory and planning (e.g., Lombard and Haidle 2012), reflexive thinking or deliberate practice (e.g., Rossano 2009), or more subtle capabilities of causal reasoning and executive control (e.g., Vaesen 2012). A thorough review of candidate mechanisms goes beyond the scope of this paper (but see, e.g., Greenfield 1991; Roux and Bril 2005; Botvinick 2008; Ambrose 2010; Wadley 2010).

Exploring Functional Landscapes

I now turn to a distinction between two kinds (or poles) of modifications processes—action-level and hierarchy-level modifications—and examine the different exploratory behaviors they give rise to at the level of the population. I then compare how these two types of modification processes are capable of exploring functional landscapes with different topographies. I suggest that depending on the ruggedness of functional landscapes, some modification processes are more capable of producing cumulative culture than others. Inversely, in the wrong landscape, a modification process may be unable to produce viable variants at all, thus stalling a population's cumulative culture process even if the population is capable of high-fidelity social learning.

Design Spaces and Functional Landscapes

An *action-level modification* consists in the alteration of an action unit in a recipe. Errors creeping in the imitation of a string of actions or of a specific action assembly could be one instance of this kind of modification, as one action could be misinterpreted for another (e.g., throw-rock instead of hammer-with-rock) or as some properties of the action could be confused with one another (e.g., hit rock on core at 45° of incidence instead of 50°). From a population-level perspective, this means that cumulative evolution and the spread of cultural variance are better explained in terms of differences at the level of the specific actions while leaving the hierarchy of the recipe the same. In contrast, a *hierarchy-level modification* will consist in the alteration of the cognitive dependencies between action assemblies in a hierarchically organized recipe. As discussed above, the capacity to produce increasingly abstract analogical reasoning, an increase in working memory and planning capabilities, or a more sophisticated form of causal reasoning can all serve to produce higher-level modifications of this sort.

Action-level and hierarchy-level modifications *should not* be understood strictly to pertain to strings of actions on the one side, and more complex hierarchical structures on the other, as deeper hierarchically structured recipes can also vary in specific actions. Of course, some changes will be hybrid, in that they will imply both action- and hierarchy-level modifications. So it is better to understand this distinction more as a matter of degree (the two kinds are poles on a continuum). For instance, a change in a low-level subgoal (technically, a hierarchy-level modification) could cascade down to a change in only one specific action or property of action. I will consider such modifications as being close to the action-level pole. In contrast, combining sophisticated techniques together, such as hafting a spear with a knapped point using some adhesive, heavily relies on changes in the hierarchical organization of superordinate goals and action assemblies, forcing an important reorganization of the specific actions required to complete the recipes (Wadley 2010).

Cultural design space is an abstraction that represents all imaginable cultural traits. For the present purpose, it is sufficient to understand such space as the set of all possible recipes, interrelated by accessibility relations and distances (Stadler et al. 2001; Charbonneau 2015). Each coordinate point in the space represents a possible recipe variant, defined by its specific sequence of actions, and two neighboring variants differ from one another only by one action or one action parameter.[2] A population undergoing cultural change can be represented by a cloud of points moving in design space, with each particle of the cloud representing a single individual, located at the coordinate of the variant it holds. A population moves through design space by producing derived traits (modifications) and transmitting them to the next generation.

In a cultural design space, single-action modifications will transform a specific behavioral variant into one of its immediate neighbors. Single-action modifications will thus tend to produce novel variants relatively close in design space to the original variant because the new variant will nevertheless share many other actions with its ancestor. Hierarchy-level modifications, on the other hand, will tend to produce larger changes as action assemblies consist of multiple actions units. The higher the modified assembly is situated in the recipe's functional hierarchy, the furthest the new variant is likely to be as more actions are likely to be altered together. This means that hierarchy-level modifications have a better capacity to "jump" over multiple one-action neighbors and land further away in design space than action-level modifications do, the latter restricting populations to gradually walk their way, one action at a time, in order to travel to the same derived variant.

Design space can be augmented by mapping functional landscapes, where functional recipes take higher values than less or dysfunctional recipes. Among all conceivable recipes, some will be more functional than others, meaning that the overall goal and the intermediate subgoals constituting a recipe's structure (1) can all be successfully enacted, (2) that the recipe has a clear, recognizable end result to those who employ it, (3) and that the recipe, when enacted properly, satisfies its main intentional goal. For instance, using a stone to produce hard-hammer percussion on the edges of a brittle material (e.g., chert) in order to shape a hand ax is a functional behavior. In contrast, trying to shape a similar hand ax but hitting one face instead of an edge will fail to produce conchoidal fractures on the core and will likely result in a crushed core. In a functional landscape, the former technique will be located higher on the landscape than the latter (in this example, much higher).

Generalized throughout design space, these conditions will generate a functional landscape that populations can explore. Functional landscapes can have many topographies. A smooth functional landscape is one where one-action neighbors tend to be relatively as functional as one another. These landscapes will obtain when a change in a single action has little effect on the functionality of the recipe (Fig. 2a). For instance, one can increase or decrease the angle of percussion when knapping a core without disrupting the whole process of fabrication (e.g., with a hard-hammer, one can detach flakes with blows between 0° and 90° of incidence; see Whittaker 1994). Exploring smooth landscapes can be a relatively easy task as small modifications (e.g., learning errors) may lead to novel, perhaps more efficient recipes for action.

However, not all modified recipes will be relatively as functional as their one-action neighbor. For instance, choosing the wrong kind of red ochre can disrupt the production of adhesives for hafting spears (Wadley et al. 2009), and hard-hammer knapping with blow angles >90° will tend to spoil the platform, if not just break the core (Whittaker 1994). When such small differences lead to important changes in functionality, we speak of a rugged functional landscape (Fig. 2b). Such functional landscapes imply that coming by a novel recipe is a difficult task as most alterations of existing behaviors will lead to less functional or even dysfunctional recipes, i.e., recipes unable to produce their intended end result (Kauffman et al. 2000; Acerbi et al. 2011, 2012; O'Brien and Bentley 2011; Derex et al. 2015). In rugged landscapes, functional recipes will tend to be isolated from one another by valleys of less functional or dysfunctional behaviors. Of course, functional landscapes can be somewhere in between these two extremes, with differences in ruggedness depending on the granularity at which we view the landscape (Kauffman 1993; Godfrey-Smith 2012). For instance, we could have functional peaks with their top relatively flat, making such landscapes look like mesas of functional techniques surrounded by a desert of dysfunctionality (Fig. 2c).

If we assume that individuals are sensitive to learning functional traits and do not learn dysfunctional ones (or

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[2] I choose to characterize design spaces in terms of differences in actions only, putting aside differences in the cognitive structure of complex recipes. Doing so gives us a commensurable characterization of cultural variation for species capable of hierarchical modifications and for those that are only capable of action-level modifications. Adding the cognitive/functional structures of recipes in such space will complicate the whole matter beyond the needs of the argument made here. Nevertheless, future work will have to deal with such complexity (e.g., see Lombard & Haidle 2012).

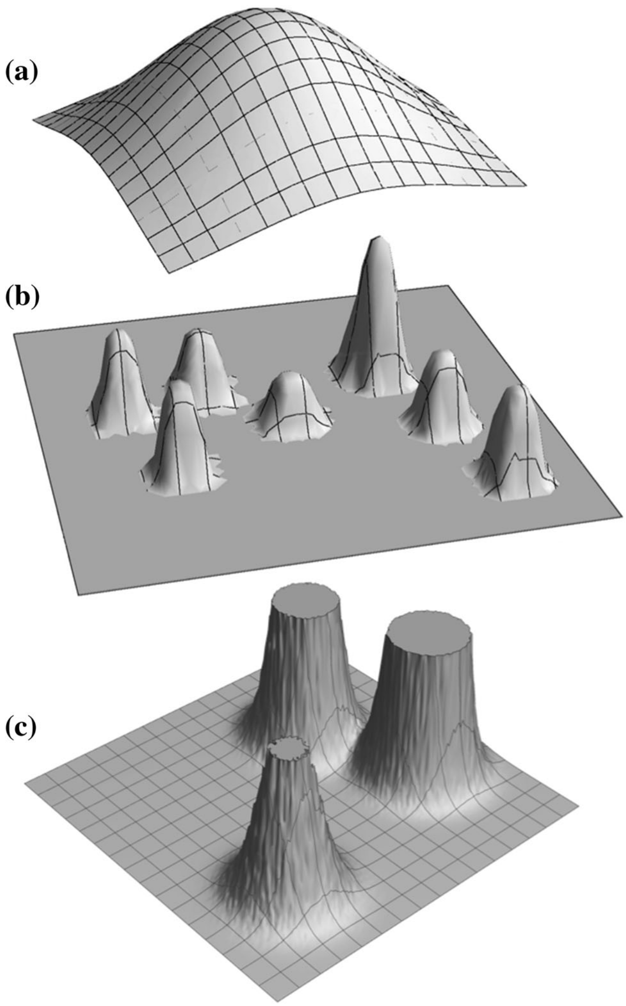

Fig. 2 Different action-specific functional landscapes, represented in three dimensions (functionality is represented on the z axis): **a** a smooth landscape, where neighboring variants have similar degrees of functionality; **b** a rugged landscape where neighboring variants have strong differences in functionality; **c** a rugged landscape with smooth plateaus

abandon the dysfunctional variant if it is obtained by some modification process), we can deal with the exploration of functional landscapes by cultural populations as if they were exploring fitness landscapes. This is usually assumed in the literature dealing with cultural fitness landscapes (e.g., see Kauffman et al. 2000; Mesoudi and O'Brien 2008a; Acerbi et al. 2011, 2012; Derex et al. 2015). However, we must be careful to understand that the two sorts of landscapes are not necessarily equivalent. Functional landscapes do not rest on the presupposition that different variants on the landscape are effectively competing with one another and thus that a population will tend to climb up functional peaks. For instance, discovering a new recipe for flint knapping does not mean that you abandon the old one. Moreover, the cultural fitness of a trait need not be influenced only by the functionality of the recipe. Other factors can affect the success of transmission of a tradition (e.g., esthetic values, interaction with social norms, etc.). However, in cases where the transmission of cultural traits is sensitive to their functionality (and only to their functionality), a population will explore a functional landscape by staying on functional peaks and avoiding dysfunctional valleys. In such context, we can understand dysfunctional recipes as having a fitness that is null. This is meant to capture the intuition that dysfunctional techniques will not be transmitted and thus will not serve as traditions that can undergo modifications. Dysfunctional recipes, in this respect, act like unviable organisms: they will not even have a chance at living and forming a lineage.

Exploring with the Wrong Tools

With these ideas in place, I argue that a population capable of high-fidelity transmission may be constrained to producing noncumulative traditions as the modification processes available to the population may be incapable of producing functional modifications. I then speculate that an analogous scenario may in fact characterize the onset of cumulative technological evolution in the human lineage and that the biological evolution of the right kind of creative processes may have been a key difference-maker between human cumulative cultures and nonhuman noncumulative traditions.

Imagine a population on a peak in a rugged functional landscape, such as the one represented in Fig. 2b. Suppose that the recipe has been invented from scratch by some individual, but that it spread in the population through a high-fidelity social learning mechanism. For simplicity, let us assume that it is a copying mechanism, a form of "program-level" imitation (see above), where little or no errors in transmission happen. We are now interested to see how differences in innovation processes will allow the population to explore this functional landscape, i.e., whether it will be capable of producing cumulative culture or not.

Suppose first that the population (let us call it Population A) was only capable of producing innovations from scratch, but not of modifying the recipes they learned from others. In such a situation, Population A would be unable to explore the design space further away than what individuals can invent on their own.[3] In our example, social learning will maintain the population on the peak (the innovation from scratch), but no cumulative culture will occur as there are no modification processes to move the population further into design space.

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[3] Tennie et al. (2009) refer to the set of functional recipes that are accessible through learning from the environment as that species' "zone of latent solutions."

Suppose now as a second scenario that our population (Population B) is also capable of innovations from scratch, but that in addition it is capable of producing action-level modifications. It may be incapable of producing hierarchical changes in the recipes, because, for instance, it lacks the appropriate cognitive mechanisms do to so. However, the population can modify single actions, perhaps by copying errors. However, given that Population B is situated on a peak in a rugged landscape, it will be unable to cumulate any cultural changes as all modifications it produces will tend to be less functional than the one it has already adopted, if not altogether dysfunctional. In this scenario, the population will be stalled on the peak, incapable of crossing the valleys of dysfunctional variants to the next functional peak.

Consider now a third population (Population C), situated on the same peak as the two previous populations. In addition to producing innovations from scratch and action-level modifications, Population C is also capable of producing changes in the hierarchical structures of its cultural recipes. Such modifications will allow a certain number of action units to vary so that the population can explore further away in design space. Even if we expect most trials at modifying a cultural recipe to land downhill, there is a possibility that the population can “jump” far enough to reach a new functional recipe (another peak). In this last scenario, our population is thus capable of cumulating cultural change where the other two populations failed.

Note that in all three scenarios, the populations possessed, by hypothesis, high-fidelity social learning. Nevertheless, Population A was unable to produce cumulative cultural change. This is because the population only possessed the capacity to generate new traditions from scratch but not to modify any existing traditions. In the two latter scenarios, the populations also possessed modification processes, thus satisfying the two conditions for cumulative culture (see above). In principle, the ratchet effect should follow, but for Population B, it didn’t. This absence of a cumulative process in Population B is not the effect of the population lacking a faithful enough social learning mechanism (by hypothesis we assumed it was a replicative mechanism). Rather, it is because the population was not equipped with the right tools to explore the constraining functional landscape in which it was located. In a different functional landscape, the situation for Population B could have been very different. For instance, if there existed ridges between functional peaks, meaning that there is a smooth path between two peaks, a population only capable of action-level modifications may have been able to traverse the ridge through cumulative culture.

What this shows is that the specific functional landscape, coupled with a specific modification process, may constrain a population to wallow in noncumulative traditions, even if the population is capable of high-fidelity transmission. Population C’s capacity for hierarchy-level modifications may not have allowed the population to jump far enough to reach a new functional recipe, as the closest peak may have been too far. But again, this is a question of the interaction between the modification capacities of a species and the structure of the design space it is exploring. The point I am making here is not to dismiss fidelity as a key condition for cumulative culture. Rather, I am claiming that modification processes and the specific functional landscape being explored by cultural populations are also potential difference-makers between cumulative and noncumulative cultural species. As indicated in the first section above, this alternative has not been taken seriously.

Admittedly, more work needs to be done to offer a more sophisticated characterization of a design space, taking the cognitive structure of the recipes into account. Moreover, it goes beyond the scope of this article to simulate specific models of modification processes and their relations to different functional landscapes. Nevertheless, the argument developed here gives us good reasons to start exploring these new possibilities.

We can already appreciate in a relatively intuitive manner the meaning of these results in terms of the evolutionary origins of cumulative culture in the human lineage. In the scenarios described above, we could see Populations A, B, and C as different moments in the evolution of our species. Population A may have had sophisticated traditions of complex, hierarchically structured recipes, complex traditions sustained by high-fidelity social learning. Nevertheless, it was incapable of producing modifications, so no cumulative culture occurred during its time on Earth. Later, the capacity to produce action-level modifications may have evolved, as in Population B. Population B may have inherited the sophisticated traditions of its Population A ancestors, but these recipes may have been too functionally fragile to sustain action-level modifications. The closest sustainable modified recipe may have been too cognitively demanding to come up with. As Population B evolved into Population C, it may have acquired richer cognitive capacities, such as the capacity to reflect upon and modify the hierarchical structure of cultural recipes. With these new capacities, Population C would have been able to modify the complex traditions it inherited from its ancestors and improve upon these recipes, producing the first instance of cumulative culture. A fourth Population D, with even more sophisticated modification processes, could then produce even farther leaps forward, thus accelerating the access of novel, more complex recipes. In this story, cumulative culture starts not when the species evolves faithful social transmission mechanisms, present since Population A. Rather, the key difference-maker is that of the acquisition of greater capacities for modifications.[4]

Although certainly speculative, is such a scenario far-fetched? Before concluding, I would like to briefly take a look back at the archeological record of the dawn of human technology and sketch a brief picture following the same line of reasoning.

The first traces of clear cumulative culture in our ancestors concern the transition from the Oldowan industry to the Acheulean industry, where Acheulean flaking techniques can be understood as sophistications of Oldowan flake detachment techniques (Moore 2007, 2010; Stout 2011). In fact, the transition between the Oldowan recipes and those of the Acheulean are characterized by the manipulation of the hierarchical structure of the recipes, notably by adding new high-level subgoals in the whole process and coopting *débitage* flaking into a preparatory shaping goal. Moreover, these changes are not obtainable by modifying the specific actions of the Oldowan flaking recipe. Indeed, the novelties of the Acheulean mainly concern changes in the subgoals, cognitive processes, and decisions required for the successful enactment of the derived techniques (Pelegrin 1993; Moore 2007, 2010; Stout 2011).

The Oldowan industry, although lasting for around 1.2 million years, remained relatively stable. In fact, it is still controversial whether there is any real intergroup variation during the Oldowan and, if so, whether it amounts to cumulative modifications or simply local adaptation through innovations from scratch (Stout et al. 2010). But what is perhaps even more important is that the Oldowan techniques are complex, hierarchically structured recipes, which demand for their transmission that one learn their complex hierarchical structure (Byrne 2004; Roux and Bril 2005; Stout 2011). This suggests that high-fidelity social learning was required to maintain Oldowan traditions. However, given the stasis of the Oldowan industry, it seems that the capacity for hierarchical modifications was the key difference-maker to get the population to the Acheulean recipes and to continue cumulating changes in their flint knapping techniques.

Admittedly, these latter considerations are highly theoretical and speculative. They only offer a plausible alternative scenario to the key differences between the cumulative cultures of humans and the apparently noncumulative traditions of nonhumans. More research on the cognitive evolution of the human lineage, how it results in changes in modification processes, and a finer grain of analysis to characterize design spaces and functional landscapes are required to clarify exactly what kind of scenarios of technological constraints may have shaped the origins of cumulative culture in our lineage. The functional landscape should also be carefully assessed through actualist studies, identifying which recipes can be successfully enacted, and which of their action-level and hierarchy-level variants produce functional dead ends. Nevertheless, we can now see that two populations with different sets of modification mechanisms can vary in their evolutionary patterns depending on the type of functional landscape they are exploring, and how the differences in their modification processes scale up at the level of the exploratory behaviors of the evolving cultural population.

Conclusion—All Innovations are Equal, but Some More than Others

In this article, I have argued that in order to produce and maintain cumulative culture, it is not enough for a population to be capable of innovating and transmitting the improvements with high fidelity. With the wrong modification processes, the structure of the cultural design space can constrain a population with high-fidelity transmission to wallowing in noncumulative traditions. This is not to deny the importance of retention mechanisms per se in shaping cumulative culture. Retention has an important role to play. Nevertheless, to show why high-fidelity transmission is not the sole key candidate difference-maker between human cumulative cultures and nonhuman noncumulative social traditions, I had to reject the more or less explicit disqualification of modification processes assumed by adherents of the ratchet metaphor. In order to do so, I took seriously the idea that not all modification processes

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[4] There are no reasons to assume that the cognitive capacity to produce modifications has in fact evolved as adaptions to serve such function. The underlying cognitive mechanisms may have evolved for other reasons, about which I will not speculate further here. Moreover, as a reviewer noticed, I have implicitly assumed that hierarchy-level modifications can only happen in one's mind, i.e., through some sort of cognitive process of mentally manipulating hierarchical structures. Indeed, there is always the possibility that a hierarchy-level modification happens by accident (as I have suggested for action-level modifications), either by discovering one "serendipitously" in one's own behavior or by observing another individual's accidental behavioral change. Intuitively, such form of accidental hierarchy-level change, although not impossible, strikes me as a relatively rare phenomenon as it likely requires a "large mistake" (but this is, ultimately, an empirical question, albeit a very interesting one). Nevertheless, I don't see this possibility as antagonistic to the way hierarchy-level modifications are defined, i.e., as a type of change in a complex recipe. Such accidental hierarchy-level modifications might allow a species with only action-level modification mechanisms to produce, once in a while, a hierarchy-level change and move forward in a rugged landscape. However, if early functional landscapes are highly rugged, creative cognitive processes capable of producing hierarchy-level modifications are likely to produce more systematically the cumulation of hierarchy-level changes, a cumulative process that is in turn more likely to be detected in the archaeological record than rarer, accidental hierarchy-level changes. I thank the anonymous reviewer for asking me to elaborate on this point.

will behave in the same way in terms of the exploratory behaviors they offer to a population, and this required a deeper theoretical analysis of just what a cultural modification consists of. I have argued that the differences in modification processes will produce different population-level exploratory behaviors, and that, depending on the structure of the region of cultural design space that a population explores and its local functional landscape, these population-level differences will have important impacts on the population's capacity to cumulate improvements in order to produce complex traits that no individual could have devised on its own.

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