Experimental and theoretical models of human cultural evolution

Marius Kempe and Alex Mesoudi*

The modern field of cultural evolution is now over 30 years old, and an extensive body of theory and data has been amassed. This article reviews models of cultural evolution, both experimental and theoretical, and surveys what they can tell us about cultural evolutionary processes. The models are grouped according to which of four broad questions they address: (1) How are cultural traits changed during transmission? (2) How and why do cultural traits accumulate over time? (3) What social learning biases do people use? and (4) What are the population-level consequences of different social learning biases? We conclude by highlighting gaps in the literature and promising future research directions, including the further integration of theoretical models and experimental data, the identification of the factors underlying cumulative cultural evolution, and the explanation of individual and cultural variation in social learning biases. © 2014 John Wiley & Sons, Ltd.

OVERVIEW

The main principle of the field of cultural evolution is that culture evolves in a Darwinian manner—that is, through a process of variation, competition, and inheritance, just as Darwin outlined in The Origin of Species.[1,2] Culture, in this usage, is taken to mean any information that is transmitted from one individual to another via social learning, rather than information that is transmitted genetically, or that is invented *de novo* by an individual independently and not transmitted.

The argument for this idea is relatively straightforward. Cultural traits, such as technological inventions, languages and linguistic features, religious and social customs, and so on, clearly vary (amongst each other), reproduce (from individual to individual), and compete (for memory or adoption). For example, there are around 6800 languages in the world, and approximately 5 million distinct patents have

*Correspondence to: a.a.mesoudi@durham.ac.uk

Department of Anthropology and Centre for the Coevolution of Biology and Culture, Durham University, Durham, UK

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been issued in the United States since its founding.[2] Languages are clearly learnt socially, while patents explicitly build on and cite earlier patents. Finally, competition takes place between cultural traits within these systems, such as the replacement of many irregular verbs with regular verbs in English since medieval times[3] and the replacement of certain stone tools with other types in the archeological record.[4]

Describing cultural change as 'Darwinian' implies no more than that culture exhibits these three properties (variation, competition, and inheritance), and makes no further claims regarding the relative importance of each of these, or the underlying mechanisms governing them. Consequently, while both cultural and biological change can be described as 'Darwinian', their details may be very different.[5] For example, while inheritance does not typically play a major role in driving genetic change, cultural inheritance/transmission may often be a major driver of macro-level cultural change in the absence of any competition/selection.[6,7] Similarly, while genetic variation arises through random mutation, new cultural variation may arise through nonrandom and intentional invention.[8] These differences do not invalidate a Darwinian model of cultural change, they merely require one that incorporates such differences.

Finally, modeling cultural change as an evolutionary process does not require that culture must always act to increase biological fitness, and indeed it may in some cases produce biologically maladaptive or neutral behaviors.[9]

The idea that culture evolves is in fact rather old; for example, Darwin mentions it in *The Descent of Man*.[10] Since then many prominent scholars in many fields have developed this idea, including William James,[11] Donald Campbell,[12] Richard Dawkins,[13] Karl Popper,[14] B.F. Skinner,[15] David Hull,[16] and Daniel Dennett.[17] The true beginning of the field, however, may be taken to be the books by Cavalli-Sforza and Feldman[18] and Boyd and Richerson,[19] who were the first to take the idea and develop it in a quantitative way, while simultaneously incorporating aspects of cultural evolution that differ from biological evolution such as those noted above. Since then a good deal of detailed work has been done, which has recently been surveyed accessibly by one of us.[5]

The aim of this article is to review the more specialized literature of models, both experimental and theoretical, which has accumulated since the founding books by Cavalli-Sforza and Feldman[18] and Boyd and Richerson.[19] The advantage of modeling is that it can shed light on complex phenomena by simplifying them, removing inessential features, and focusing solely on those features that the modeler suspects are important, or necessary to test a particular hypothesis. Mathematical models provide a way of running formal 'thought-experiments', by analyzing the consequences of a certain set of assumptions that are thought to hold in the real world, and provide a level of precision that is unattainable through purely verbal models. Laboratory experiments can also be used to model real-life instances of cultural evolution, allowing hypotheses to be tested under controlled conditions (again, removing all inessential features of reality) and allowing detailed records of behavior that are often not possible with real-life (e.g., archeological or ethnographic) data. Compared to mathematical models, experiments add some degree of external validity in that they measure the decision-making processes of real people, who, due to imperfections or biases in that decision making, may act in ways not captured or predicted by formal models. Thus modeling—both mathematical and experimental—is an important complement to observational research such as ethnographic field studies, historical and archeological research, and statistical data mining.

The review will be selective, rather than exhaustive, as the literature after 30 years is extensive. The review will focus exclusively on cultural evolution, rather than the interaction of cultural and biological evolution—itself an important and large topic with a varied literature known more specifically as gene–culture coevolution.[9,20] We also exclusively focus on humans, excluding the large and diverse literature on social learning in nonhuman animals.[21]

The review is structured around four important questions in cultural evolution that have recently received much research attention:

1. How are cultural traits changed during transmission?
2. How and why do cultural traits accumulate over time?
3. What social learning biases do individuals use?
4. What are the population-level consequences of different social learning biases?

HOW ARE CULTURAL TRAITS CHANGED DURING TRANSMISSION?

In this section, we discuss how cultural traits change during transmission generally, for example through remembering and perceiving. In the following section, we discuss how cultural traits increase or decrease in utility during transmission, leading to the phenomenon of cumulative cultural evolution.

It is well known that traits change simply through the process of learning, or copying, on the part of a naive individual. This process was first studied experimentally by Frederic Bartlett,[22] who pioneered the 'transmission chain' method. In this method, one individual is seeded with a cultural trait of some kind—for instance, a story or a picture—and then this individual transmits the trait to a second individual, who in turn transmits the trait to a third, and so on. The method can also be varied to have more than one individual in each link of the 'chain', so that a group of individuals in some way transmit a trait to another group of individuals. Finally, in this group setting, the 'turnover' of the chain can be altered so that instead of the entire group changing at every step, only one individual of the group is replaced by a new individual; this is known as the 'replacement' method and was first proposed by Gerard, Kluckhohn, and Rapoport.[23] The bulk of experiments pertaining to cultural evolution have been conducted with the transmission chain method and its variants.[24]

A large number of specific traits have been investigated with these methods, and different questions have been asked. The studies of Bartlett and his school[25–28] tended to use stories and drawings, and to frame open-ended research questions: What patterns can be found in the variation of the traits as they are passed along the chain? They also asked

how characteristics of the subject—for example, their cultural background or social status—affected the changes seen in the traits. Specific hypotheses, on the other hand, did not tend to be tested. The general conclusions were that, as they were transmitted, traits tended to lose detail and to increasingly resemble the individuals' preconceived notions. For example, in one of Bartlett's experiments,[22] an American Indian story called "The War of the Ghosts" was passed through a transmission chain made up of British participants, with the result that details such as the names of the warriors were lost, and unfamiliar elements such as the American Indian notion that something black comes out of a dying warrior's mouth was transformed into the more familiar Judao-Christian idea that his soul leaves his body.

However, the focus of these studies was on human psychology—memory—and not on cultural traits and their evolution. More recent studies have revisited this method with a view to understanding the details of cultural evolution. Thus, for example, Mesoudi, Whiten, and Dunbar[29] found that social information in stories was transmitted more accurately and lost less frequently than nonsocial information, in line with 'social brain' theories that posit that human cognition evolved primarily to deal with social information. Bangerter[30] found that gender stereotypes were superimposed on descriptions of scientific phenomena, with initially neutral descriptions of conception gradually transformed such that sperm cells were attributed activity and ova attributed passivity. Many similar experiments now give us a reasonable understanding of the variation in traits caused by the process of transmission.[24] These variations constitute examples of what is called 'cultural mutation' by some[18] or 'guided variation' by others[19] in the literature, where individuals change the traits that they receive from others in some non-random, biased manner, before the trait is passed on to another individual.

Researchers have also attempted to model these processes of change through transmission mathematically. The leading methodology here is the 'Bayesian' approach.[31–33] In this approach, individuals are thought of as possessing 'prior' biases (whether learned and/or innate) for certain characteristics of cultural traits (e.g., simplicity or learnability). They then observe 'data' from another individual composed of samples from a distribution of traits with varying characteristics. The models suppose that individuals combine these two sources of information in a manner that can be described by Bayes' theorem and create a 'posterior' distribution of trait characteristics which they present in turn to the next individual. This approach has had remarkable success in producing predictions qualitatively in accord with experimental results, even in experiments not originally designed to test the models (e.g., Beppu and Griffiths,[34] who created a Bayesian model which recreated the experimental results found by Jacobs and Campbell[35] that are discussed below).

While all of the aforementioned studies were carried out in a laboratory with a controlled experimental design, an important recent development has been the use of an 'open diffusion' method,[36,37] in which the individuals with whom the new trait is seeded are allowed to freely interact within a social group, and the transmission of the trait is observed. This technique allows researchers to document features of cultural transmission such as who chooses to transmit what to whom; for example, McGuigan and Cubillo[37] found that male children were more likely to transmit gossip than female children, and that both genders were more likely to transmit gossip than surprising factual information. The downside of this method is of course that some experimental control and precision is lost.

HOW AND WHY DO CULTURAL TRAITS ACCUMULATE OVER TIME?

Cumulative cultural evolution refers to the presence of traits that have been gradually modified and built upon over successive generations such that they are beyond the capabilities of a single individual to invent in a single lifetime.[38,39] Examples include the startling technological, scientific, artistic, and social achievements of humanity. Mathematical knowledge, for example, took thousands of years to accumulate,[40] with the Sumerians inventing written numerical notation around 2400 BC, Babylonians inventing simple arithmetical operations around 2000 BC, the Greeks contributing geometry in 300 BC, Arab scholars inventing algebra around 800 AD, and so on up to the present day. These accumulated traits can be distinguished from the cultural traits of other animals, such as nut-cracking in chimpanzees or the songs of certain species of birds, which do not appear to have accumulated over successive generations and could plausibly have been invented *de novo* by a single individual. The question here, then, is what factors allow and affect the accumulation of cultural traits in humans.[41]

Experimental work on cumulative culture using the transmission chain method was initiated by Caldwell and Millen.[42] In their experiments, individuals perform technological tasks that have a clear goal and measure of success, such as constructing a paper airplane to fly as far as possible, or building a tower using spaghetti and clay as high as possible. Each

participant completes this task as best they can, after which successive individuals in the chain perform the same task but are able to observe the previous individual's solution. The focus in these experiments is less on the nature of the cognitive processes involved in the task, and more on the degree to which successive individuals are able to improve on their predecessor's solution, and in the conditions which exacerbate or attenuate this improvement.

Caldwell and Millen[42] found that the quality of solutions improved as the tasks were transmitted through a chain, indicative of cumulative cultural change. In further studies[43] the same authors addressed whether particular mechanisms of social learning—imitation, emulation, or teaching—are necessary for accumulation. Imitation involves copying behaviors (here, the motor actions required to make the paper airplane), emulation involves copying end-products (here, the finished airplane design), while teaching involves the transmission of explicit advice (here, advice about how to make the paper airplane). Caldwell and Millen[43] found that each of these three mechanisms was sufficient, in contrast to previous claims that only imitation and teaching (and not emulation) can give rise to cumulative culture.[44] In a further study using the same task, meanwhile, it was found that allowing individuals to observe more than one model simultaneously did not increase the rate or degree of accumulation.[45]

This last result is intriguing because several mathematical models of cumulative culture have focused on the relationship between population size and the rate and degree of cumulative culture. That population size is an important factor in technological evolution in particular is suggested by both apparent links between increases in population sizes in the Upper Paleolithic and the concurrent appearance of so-called 'modern human behavior', including complex stone tools, decorations, cave art, and musical instruments,[46,47] and by the drastic loss of technologies in Tasmania after the area became an island 10,000 years ago and was therefore cut off from Australia.[48] These observations led to the construction of models in which changes in population size led to changes in the rate and/or degree of cultural accumulation in the population.[46–48] This effect occurs because in larger populations complex skills are less likely to be lost due to random transmission error, and rare beneficial modifications are more likely to be made. More recent models have increased the complexity of these models. Mesoudi[40] showed that an increasing cost of learning more, and more complicated, traits would produce S-shaped curves in the degree of complexity of over time, rather than a less realistic

exponential increase in complexity to infinity. Pradhan et al.[49] considered the effect of varying levels of interaction between members of the population, aiming specifically to explain the greater quantity of technologies found in chimpanzee populations compared to orangutan populations, and showed that this could be caused by the greater sociability of chimpanzees.

While chimpanzee populations may have *more* cultural traits than orangutans, neither species, nor any other primate species, appears to exhibit *cumulative* culture. The social and cognitive factors that may be responsible for this difference have also been explored experimentally. Dean et al.[50] had groups of capuchins, chimpanzees, and children solve a three-stage puzzle box to obtain rewards, with each solution predicated on the previous one(s). The children significantly outperformed the monkeys and chimpanzees on this minimally cumulative task, with verbal communication, imitation, and prosociality predicting the greater success in children. It is likely, therefore, that both sociocognitive (e.g., imitation fidelity) and socio demographic (e.g., population size/density) factors underlie the species differences in cumulative culture.

More recently three experimental studies have revisited the hypothesis that cumulative culture is facilitated by larger population sizes. Derex et al. found that simple and complex computer-designed traits (arrowheads and fishing nets) were maintained only in larger groups of 8 or 16 participants, and not in smaller groups of 2 or 4 participants. Muthukrishna et al.[52] found that complex symbol designs and difficult-to-tie knots were only maintained in transmission chains comprising five participants per generation, and not chains composed of a single participant in each chain. Similarly, Kempe and Mesoudi[53] found that jigsaw puzzles increased in completeness in three-per-generation transmission chains and not in one-per-generation chains. The negative finding of Caldwell and Millen,[45] therefore, may have been due to the particular task that they used, which may not benefit from social learning as much as the tasks employed in these subsequent studies.

WHAT SOCIAL LEARNING BIASES DO INDIVIDUALS USE?

'Social learning biases' here refers to the innate or learned rules which people use when copying other individuals[54]: rules specifying, for instance, what or from whom to learn. The use of the term 'bias' here is intended in a statistical sense, as indicating a deviation from 'unbiased', or undirected/random social transmission (rather than the normative sense of, say, 'racial bias'). While there has been a good

deal of theoretical work investigating what social learning biases natural selection may favor,[19,55] in the end there is clearly only one way to definitively establish what social learning biases people use: empirical observation and experiment. Accordingly, this section will focus on experimental work while the following section, dealing with the population-level consequences of given social learning biases, will focus on mathematical models, which allow such questions to be answered with suitable generality.

Here we will focus more on biases that concern from whom and what to copy, and less on biases concerning when to copy (e.g., depending on life-history variables[56]). This focus is appropriate because 'who' and 'what' questions are more directly relevant to understanding the population-level consequences of social learning biases, which is one of the primary aims of cultural evolutionary theory. Similarly, cultural evolutionary research is generally less concerned with the specific mechanism by which social learning takes place, such as imitation, emulation, teaching, and so on—as long as there is some mechanism to provide relatively faithful transmission, who and what is copied is more important at the population level than how it is copied. For this reason the majority of research in social psychology[57] and comparative psychology[58] is only tangentially relevant to this question.

Social learning biases relevant to cultural evolution can be divided into three categories using a convenient classification system by Richerson and Boyd[59]: 'content', 'model', and 'frequency-dependent' biases. Content biases occur when individuals pick a particular trait over others because of innate or learned preferences for a characteristic of that trait, such as its meaning, usefulness, or esthetics. Model biases occur when individuals adopt traits because of a characteristic of the person who knows the trait: for example, adopting a trait from prestigious or successful individuals.[60] Finally, frequency-dependent biases occur when individuals take up a trait because of the trait's relative popularity, or unpopularity, compared to other traits in their population; examples of this include conformity, which in cultural evolution is defined as adopting the most popular trait in a population with a probability greater than its proportion of occurrence in the population,[61] or anti-conformity, where the least popular trait is adopted with a probability greater than its proportion of occurrence.

While the transmission chain studies discussed in the previous section have been described as examples of content biases, content bias can also be seen to differ from cultural 'mutation' or the memorability of a cultural trait by the fact that individuals *choose* the relevant trait in some fashion. Using this definition,

there has been little work on content biases. One of the few studies is that of Wisdom et al.,[62] in which participants had to find the highest-scoring combination of 'items' in a virtual environment in which they could view other participants' items and scores. They found that content bias was an important element in participants' social learning strategies, with participants copying the highest-scoring items in addition to using model- and frequency-dependent biases.

There have been more studies examining model biases. A number of early studies from social psychology found strong effects of perceived expertise or status on people's judgements in domains such as esthetic judgements,[63] visual perceptions,[64] gambling,[65] and attitudes.[66] There has also been work specifically focused on children's learning, since a great deal of what we know is learned in childhood, with a good number of studies finding that children preferentially copy from older rather than younger models.[67–69] Cultural evolution researchers have extended and verified these early findings in light of recent theory and models. In an innovative experiment Wood et al.[70] found that children were biased more toward older models than self-professedly knowledgeable ones where these characteristics conflicted. Using adult participants, Mesoudi[71] conducted a study in which participants constructed virtual (computer-based) projectile points to conduct virtual hunts (with variable rewards) and were able during multiple rounds to view and possibly copy other individuals' points. This experiment found evidence for the presence of success bias but noted that the presence of the bias was heterogenous: rather than all individuals using it, some individuals used it very often and others barely at all. Using a similar paradigm, Atkisson et al.[72] found that individuals were more biased towards model characteristics, specifically the prestige of a model as indexed by the amount of time that other participants were said to have looked at the model's arrowhead designs, rather than trait characteristics, that is, the effectiveness of the arrowhead.

Finally, a number of studies have examined frequency-dependent biases, primarily conformity. The famous early studies of Sherif[73] and Asch,[74] which convincingly demonstrated that people may sometimes adopt the opinions of the majority, do not qualify as conformity under the cultural-evolutionary definition because it is not possible to tell whether people adopt the majority view with greater than proportionate probability.[19] Jacobs and Campbell[35] used Sherif's auto-kinetic task with the replacement method, described above, starting with confederates and ending with naive participants; they found that the 'conformity' to exaggerated majority judgements

was rapidly overwhelmed by people's trust in their individual perceptions. More recently, a series of experiments by McElreath and colleagues[75–77] utilized a virtual 'farming' task in which participants choose to 'harvest' one of two crops. Each crop has a stochastic payoff, and the optimal crop changes from time to time. Using variations on this design and model-fitting techniques, McElreath et al.[75,77] concluded that individuals use a complex mix of payoff-biased and conformist learning, while Efferson et al. found individual differences, with some individuals using the conformity bias and others ignoring frequency information. Finally, an experiment by Efferson et al.[78] using a variation on this design with Bolivian pastoralists found little evidence for either conformism or payoff-bias; this experiment is remarkable for its unusual (compared to other studies) participant group, an important step toward drawing conclusions valid for the entire human species.

WHAT ARE THE POPULATION-LEVEL CONSEQUENCES OF DIFFERENT SOCIAL LEARNING BIASES?

This question has been addressed through mathematical modeling since the books of Cavalli-Sforza and Feldman[18] and Boyd and Richerson[19] and thus represents probably the most studied aspect of cultural evolution. The mathematical tools used to address this question are those relating to dynamical systems, both deterministic and stochastic, with the majority of models falling into the class of Markov chains (i.e., processes that evolve probabilistically in a way that depends only on their current state), usually analyzed in discrete time-steps for ease of analysis.

Like in evolutionary biology,[79] cultural evolutionary researchers have realized the usefulness of constructing explicit neutral models in which individuals learn traits entirely 'at random', without the use of any particular social learning biases. Also like in evolutionary biology, there are a number of ways of conceptualising 'at random'. A series of 'random copying' models developed by Bentley et al.[80,81] assumes that individuals copy the trait of a random member of their population, finding that the resulting distribution of trait frequencies will follow a power law (i.e., a distribution in which the most popular trait types account for the majority of all trait copies, with successively less popular trait types accounting for smaller and smaller proportions of all trait copies), and noting similar distributions in traits such as the frequencies of baby names and dog breeds. This model has in fact even led to an advance in pure mathematics, where Eriksson et al.[82] proved 'Bentley's conjecture' that the

rate of turnover in this model is almost independent of the size of the population. Strimling et al.[83] have developed a variant of the model in which individuals may fail to learn a trait with some probability. Alternatively, Cavalli-Sforza and Feldman[18] modeled the 'random drift' of continuous, rather than discrete, traits, characterising the rate at which populations would vary if each individual made a slight (additive) error during the learning process.

The effects of specific biases can be seen against the background of the expectations generated by neutral models. Initial models of content, model, and frequency-dependent biases were analyzed by Boyd and Richerson,[19] partly with a view toward understanding their biological consequences. In particular, they found that conformist frequency-dependent bias leads to within-group homogeneity but between-group heterogeneity, a common phenomenon in humans.[61] They also identified the possibility of 'runaway' co-evolution between model preferences and trait values following model based (e.g., prestige) bias, which may explain exaggerated phenomena such as whole-body tattoos in certain societies. More recently, Strimling et al.[84] investigated the dynamics of content bias when the 'fitness' of a trait is partitioned into two components, 'diffusion' and 'retention', finding that the number of opportunities for learning was crucial in determining the evolutionary outcome, with traits with high 'retention' dominating only when individuals had a large number of opportunities for learning. Baldini[85] investigated model biases, such as success- or prestige-bias, comparing the dynamics of biases in which individuals averaged the success of all individuals with a certain trait with biases in which individuals imitated the single most successful individual. He found that although there were many situations in which each bias performed better than random copying, there were some situations in which each was worse than random copying: for the averaging bias, this occurred when the optimal trait had high frequency in the population, and for the most-successful bias when an on average suboptimal trait had a high variance in its outcomes. Mesoudi and Lycett[86] investigated the effect of conformist and anti-conformist frequency-dependent biases on the distribution of trait frequencies, showing that conformity leads to distributions in which a small number of traits dominate others in frequency, and anti-conformity to distributions in which traits of intermediate frequency are favored, both of which noticeably deviate from the power-law distribution noted above to result from random (unbiased) copying.

These models lead to quantitative predictions and, conversely, allow inference from statistical

data regarding a variety of traits. Researchers have also constructed and analyzed models specific to certain classes of traits. Starting from Boyd and Richerson,[19,87] there has been a vibrant literature showing how human cooperative tendencies may have arisen through a process of 'cultural group selection', that is, selection on groups differentiated by cultural traits (such as would be created by conformist bias, as noted above), and more recently researchers have applied the tools of evolutionary game theory to modeling cultural traits in situations where the utility of a certain trait depends on the traits adopted by other individuals, of which cooperation is a primary example.[88,89] Another set of processes of biological importance that have inspired cultural evolutionary models are the Neolithic and Industrial demographic transitions, where researchers have modeled the effects of technological and social change (e.g., the spread of contraception) on population sizes and compositions, both as individual traits[90] and in combination with other mediating traits.[91,92] Thus cultural evolutionary models provide both general explanatory schemes for cultural change and specific explanations for important biological and social phenomena.

DISCUSSION

Cultural evolution is now a burgeoning field, and much has been achieved. Much also remains to be done, and the preceding review suggests several directions for future research. In general, there can never be too much replication, integration between theoretical and experimental studies, ecological validity in experiments, and realism in theories. The creation of detailed models of cognition, such as the Bayesian models noted above, which can be validated experimentally represents a fruitful line of research which currently has only been applied to relatively low-level cognitive processes. More challenging will be to model the cognitive processes underlying creativity and innovation, or the acquisition of motor skills such as stone tool manufacture. With respect to cumulative culture, it is still unclear exactly what cognitive and social factors allow humans but not other species to accumulate beneficial cultural traits over time, and there is some contradictory evidence regarding the relationship between population size and cultural accumulation. Further experiments with more varied tasks and designs may resolve this apparent contradiction. The investigation of human social learning biases has shown that individuals show a good deal of heterogeneity in the biases they deploy, and that real-life social learning biases tend to be complicated and composed of mixtures of simple biases; future experiments may investigate these complexities. As well as individual differences, there may be meaningful cross-cultural variation in social learning biases. Social psychological studies suggest that people from Western countries are less likely to employ biases such as conformity than people from East Asian countries,[93] although as noted above the sense of conformity tested in such studies does not match that used in the cultural evolution literature. Future cultural evolution studies might more fully explore cross-cultural variation in social learning biases, and the factors that generate this variation.

In summary, theoretical models have led to a detailed understanding of cultural evolutionary dynamics, and future research should attempt to base modeling assumptions on empirically validated observations and describe the interplay between multiple, interlocking biases and processes.

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