Not by transmission alone – the role of invention in cultural evolution

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Abstract

Invention and social learning have together empowered our species to inhabit virtually every part of the world. For the past fifty years, however, social learning has been regarded as the fundamental driver for the emergence of tradition and culture. As a result, innovation has been relatively understudied, outside the human lineage. This has left basic questions unanswered, such as: What factors promote the creation of new ideas and practices? And what affects whether they are spread or lost? We review the existing literature, focusing on the following four levels of investigation: traits (what sorts of behaviours are easiest to invent?), individuals (what intrinsic and contextual factors make some individuals more likely to invent new things?), populations (what features of social relationships and societies promote the rise and spread of new inventions?), and ecological contexts. We aim to inspire new research agendas by summarizing what is known and highlighting theoretical and empirical gaps in our understanding of the innovative process. Understanding the origin of humans' noteworthy levels of creativity requires a well-developed theory of creativity and innovation as well as a large comparative data set investigating these processes in nonhuman species from a wide range of taxa.

Keywords: creativity, cultural evolution, individual differences, innovation, invention

1 Introduction

During times of rapid environmental change, the success of hominid populations has depended in no small part on the ability of its members to devise new fitness-enhancing behaviours that exploit the novel aspects of the environment, which are then socially transmitted and improved on by conspecifics (Laland, 2017). Although humans are probably an extreme case regarding their propensity to innovate, it is likely true that innovation (i.e. creation of new behavioural variants, followed by extensive social transmission) is a common feature of many species, and that we will not understand their evolutionary dynamics unless we attempt to document and model these processes. Cultural evolution requires the capacity for (a) invention, i.e. the creation of novel behaviours or artefacts; (b) diffusion, i.e. transmission of these traits between individuals; and (c) innovation, i.e. the ability to establish these traits as stable characteristics of a (sub)group. Most research on the dynamics of cultural evolution have focused on (b) and (c). Here we want to emphasize the importance of investigating invention as well, as a better understanding of the origins of behavioural variation is critical to the study of cultural evolution.

Prior research effort has been unequally distributed across psychological mechanisms, taxa, levels of analysis, and methodological approaches. After reviewing what is currently known and identifying major knowledge gaps, we propose a set of promising research directions (observational, experimental, and theoretical) that could transform our understanding of inventiveness in the natural world. We organize our discussion around the following key questions about the nature and evolution of creativity:

1.1 Key questions

- What kinds of inventions readily occur to individuals?

- What kinds of inventions are truly novel for a given species?

- What features of behaviours, contexts, individuals, and group-level properties increase the probability of a novel invention being generated? And does the interaction between these variables differ according to the type of behavioural trait being invented?

Inventions cannot become innovations without social learning. Although there is insufficient space to describe the state of the literature regarding the transmission and establishment processes in the main text, the ESM appendix describes many findings relevant to the two questions below and discusses some of the remaining gaps in the social learning and cultural evolution modelling literature that need to be filled:

- Which inventions become innovations, i.e. behaviours that spread and establish instead of vanishing from group repertoires?

- How does population structure affect information transmission and accumulation?

1.2 Definitions

Here, we define the terms we will use in discussing the three distinct processes central to the study of innovation: the creation, transmission, and establishment of novel behaviour. We define invention as the creation of novel behaviour. Researchers of nonhuman animals often call these inventions "innovations." Here we will use the term "innovation" as it is typically used in the human innovation literature, to refer to inventions that succeed in diffusing widely through a (sub)group. Invention has been defined quite differently by different camps of researchers, according to the research question they are addressing. Some researchers cast their definitional nets broadly, including any novel behaviour as an invention, while others impose additional restrictions, e.g., that the behaviour serve an obvious useful purpose, or impact the performer's fitness. Sometimes it is stipulated that the behaviour must be something that a typical member of the species would not do under similar circumstances (Ramsey et al., 2007); this parallels the stipulation in US patent law that a patentable invention could not be created by a "person having ordinary skill in the art." Typically a behaviour is not described as an invention if it is acquired via social learning.

There are many ways by which something new might come about. Sometimes novel behaviours are produced by accident, when individuals fortuitously perform old behaviours in new circumstances, thereby producing useful new outcomes. Sometimes novel behaviours are generated accidentally by a process of ineffectual social learning, in which an animal produces an inexact replica of the behaviour they are watching. Other inventions are produced via deliberate attempts to solve a problem, either via trial and error learning or insight learning (i.e. solving a problem without trial-and-error, via mental rearrangement or restructuring of elements in a problem, perhaps based on past experience with some elements of that problem, resulting in a solution); this is particularly important when old solutions fail in novel circumstances, such as the absence of some critical material. Any attempt to describe an evolutionary scenario that predicts which individuals will be more inventive than others is likely to be applicable to inventions generated by some, but not all, of these cognitive processes.

To evaluate the selective pressures that influence processes of invention, it makes sense to use a broad definition in which inventions are described as novel behaviours, i.e. behaviours produced by an individual who has never before seen this behaviour performed by other members of its group. This excludes behaviours that naturally occur at certain points in development for all individuals, given particular environmental circumstances. It also excludes new behaviours acquired via social learning. It does include (a) novel behaviours that are produced by processes other than insight learning, (b) behaviours that are creative but apparently useless or even costly, and (c) behaviours that are likely accidental the first time they are performed. Notably, we do not require inventions or innovations to be fitness-enhancing for individuals or groups.

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1.3   Levels of analysis

To fully understand the factors that influence whether novel behaviours arise, are transmitted and become established in populations, it is necessary to investigate how the processes of natural and cultural selection operate on variation at all of the following levels of analysis. Below, we present questions that need to be addressed by a comprehensive research program to study the selective forces involved in the dynamics of cultural evolution. We focus only on the invention aspects in the main text. This is due both to space restrictions and relative neglect of invention in the comparative literature. We briefly discuss the social transmission and establishment aspects (which have been well reviewed elsewhere in the cultural evolution literature, e.g. (Centola, 2018; Rendell et al., 2011; Rogers, 2003; Whiten, 2019)) in the ESM.

Behavioural traits   What characteristics of behaviours might make them easier to invent or to transmit?

Individual   What characteristics of individual animals might make them better at inventing new behaviours, or at transmitting them to others (either as a demonstrator or a learner)?

Network/group   What aspects of group structure enhance the probability that new behaviours will be invented and/or spread? These could be demographic properties, e.g., the proportion of individuals who were of a particular sex, or the age structure, or the distribution of particular personality types. They could also be some aspect of the social network (e.g., association patterns, or the patterning of affiliative, cooperative or aggressive behaviours).

Ecology/context   What aspects of the context in which individuals live, or in which behaviours are performed, influence the probability of a behaviour being invented, or being copied from a demonstrator?

2   Creation of novel behaviours

2.1   What characteristics of behavioural traits make them more likely to be invented, and how does this vary across species?

What can be invented by an organism? This question is critical, but it is very challenging to answer. Importantly, an idea or behaviour could be "invented" on multiple occasions at different times—or at the same time in different places (Merton, 1961). The frequency with which the same type of behaviour is re-invented might provide clues to how easy it is to invent.

The question of what can be invented has been addressed empirically and theoretically. Empirically, researchers have attempted to document the range of a species' inventions—called the count method—and have categorised these into broad domains (see for example:

capuchin monkeys (Perry et al., 2017); orangutans (van Schaik et al., 2006); chimpanzees (Nishida et al., 2009)). A second empirical method gives humans and other animals problems to solve, usually a puzzle box with a reward inside, and asks how individuals invent solutions to the tasks (e.g. Derex et al. 2019; Diquelou et al. 2016; Thornton and Samson 2012). Both methods allow researchers to compare individuals' and species' inventiveness, but the experimental approaches do not allow one to assess a species' general inventiveness, as the responses available to an individual are restricted by the task itself (Reader et al., 2016).

Several ideas have been proposed to address how species' differences in creativity may arise. Inventions sometimes arise by serendipity rather than due to cognitive processes, e.g., when individuals make mistakes in copying, or fortuitously perform a behaviour in a new context with desirable results (Reader et al., 2016). These kinds of inventions do not necessarily require insight learning, but they are no less new, are possibly useful, and may become transmitted to others. Alternatively, inventions may be an emergent consequence of traits such as persistence and neophilia, an hypothesis for which there is some empirical support from problem-solving experiments with several species of birds (Diquelou et al., 2016). In addition to noting that innovation may be an emergent property of these personality traits, Griffin (2016) points out that certain aspects of morphology enable more diverse ways of manipulating the environment, resulting in species differences in rates of invention.

At the time a novel behaviour is produced, the costs and benefits of the behaviour are likely unknown, particularly when the behaviour is being produced in a novel context. Some useless looking behaviours do occasionally end up being incorporated into individual and group repertoires, and some are incorporated into long-lasting traditions. Take, for example, the human traditions of eating toxic cassava or fugu fish. Both of these foods require complex and non-intuitive food processing in order to render them edible. The initial step of the tradition probably involved a risky, apparently unpleasant or even deadly novel behaviour, which would have looked like a stupid mistake to a researcher coding the behaviour of the inventor, if the researcher was doing a short-term study. These examples challenge the notion that researchers can or should pre-judge the functional utility of behaviours. Natural and cultural selection will take their course; novel behaviour is intrinsically interesting, as it is the source of the variation on which cultural evolution operates.

Recombination is essential to human invention (Arthur, 2009). Rather than having to assemble the entire solution de novo, human inventors combine multiple existing solutions in novel ways (Foster and Evans, 2019). The camera phone did not have to be built from scratch; inventors could put it together by modifying and combining well-understood technologies. Insofar as those existing solutions are highly modular—with well-defined ways of linking them together—the inventor's job becomes easier. We know very little about the possibility of invention by recombination among non-human animals, where it might take the form of combining known behaviours in new ways. There is, however, some promising experimental work in some bird species indicating ability to construct compound tools in the absence of trial-and-error learning, reinforcement or cueing, which are suggestive both of recursive capacities and an ability to perceive when novel tools are required to accomplish a

goal (see for example Bayern et al. 2018). In order to learn more about the abilities of wild animals to invent via recombination of existing behavioural elements requires documentation of individuals' behavioural repertoires at a granularity that is rarely achieved in current studies.

2.2   What characteristics of individuals make them more likely to invent?

This question has been addressed via theoretical models, literature reviews, experimental approaches, and observational approaches (both with captive and wild animals). Age, sex, personality, and position in the social network and in the dominance hierarchy have each been previously associated with differences in the propensity to invent. Below we summarize the current state of knowledge regarding empirical work, focusing primarily on the nonhuman (comparative) literature, and in the ESM we discuss how the theoretical literature could better incorporate such knowledge into our understanding of cultural evolution dynamics.

Age   There is disagreement regarding the effect of age on the probability of invention. In a review of the published primate literature, Reader and Laland (2001) concluded that adult primates invent more often than do immatures, with the exception of chimpanzees (*Pan troglodytes*), which exhibited the opposite pattern. Kummer and Goodall (1985) also claimed that invention in chimpanzees was more common in juveniles than in adults, though this claim was subsequently disputed by other chimpanzee researchers (Nishida et al., 2009). In a recent meta-analysis surveying published innovation literature in mammals and birds, Amici et al. (2019) also found that older individuals were more likely to invent, but there was no consistent methodology for defining inventions. The problem with the data contained within these literature reviews is that they are not reports from researchers explicitly measuring invention and innovation, and are susceptible to observer biases (such as for behaviours that look especially human-like or peculiar to the human eye); furthermore, larger literature reviews such as (Amici et al., 2019; Reader and Laland, 2001) do not always distinguish between invention or innovation defined as "success at solving a problem" versus "creativity." The former definition might be biased towards older (larger, stronger, more experienced) individuals and the latter towards younger individuals. It would be much more enlightening to conduct studies in which the data are collected using methods specifically designed to answer the research questions.

In only one observational study in the wild has there been a systematic attempt to record inventions during the data collection phase, as they arise in a population, rather than using data collected for other purposes. Perry et al. (2017) conducted a decade-long study of wild capuchin monkeys (*Cebus capucinus*) to measure rates of invention and innovation to determine the characteristics of especially inventive individuals. Older, more socially-central individuals were more likely to invent new forms of social interaction, and younger capuchins were more likely to invent new foraging-related behaviours and new ways of manipulating their environments, as well as new ways to manipulate their own bodies. Younger capuchins ex-

hibit a more diverse repertoire of actions performed in the context of trying to open *Luehea* fruits (Perry, 2020), though it is not entirely clear whether this age-related effect is due more to higher rates of invention in younger animals or experience-related pruning of inefficient techniques in older animals.

The data from experimental approaches to study inventions are, however, mixed. For example, juvenile red-fronted lemurs (*Eulemur rufifrons*) and chimpanzees (*Pan troglodytes*) were more likely to be the first to solve a two-action task (Schnoell and Fichtel, 2012), and to learn about new species of nuts to crack (Biro, 2011). But older meerkats (*Suricata suricatta*) and captive callitrichids (7 species, from the genera *Leontopithecus, Callithrix* and *Saguinus*) were more likely to solve a novel task (extracting food from a puzzle box), perhaps because of their greater dexterity (Thornton and Samson, 2012) and motor competence (Kendal et al., 2005). No significant age-related effects were observed in wild Barbary macaques (*Macaca sylvanus*) solving a novel experimental puzzle box task (Amici et al., 2020).

Depending on the species and type of task, then, either the enthusiasm of youth and/or the wisdom of age can lead to inventiveness. We recommend that in the future, separate evaluations are made of age-related changes in the following contributors to creativity: (a) attraction to novel objects or situations (neophilia, tendency to explore), (b) tenacity in problem solving, (c) creativity in finding solutions (e.g. number of options tried), and (d) physical strength and dexterity.

It may be the case that individuals of different ages not only differ in their learning efficacy, but actually learn differently. Gopnik et al. (2015) have argued that human children have learning strategies that are more flexible and exploratory than those of adults. As a result, children are better than adults at deducing unusual abstract causal principles from observations, whereas adults are less creative but more efficient in their learning strategies. Other researchers have made the claim that young children are proficient social learners before they have developed creative problem-solving skills, at least for tool use (Beck et al., 2011; Cutting et al., 2011). At any rate, as Fogarty et al. (2015) note, there are almost certainly age-related changes in particular types of learning skills that need to be taken into account, along with population structure, when developing models of cultural evolution. Agent-based models developed by Lehmann et al. (2013) to better understand the circumstances that favour the accumulation of modifications over time (cumulative cultural evolution, CCE) examined the co-evolution of life history stages with the timing of use of social learning and individual learning. They found that CCE is favoured when infants learn from non-parental adults (oblique social learning) and juveniles use a mixture of individual learning and learning from their peers (horizontal social learning).

Sex Predictions regarding the impact of sex on propensity to invent stem from differences in body size (and hence competitive ability and free time) as well as differences in knowledge as a consequence of sex-biased dispersal. As in the case for age, it is not clear whether females or males are more inventive, although one meta-analysis of published data on novel foraging tasks in 29 bird and mammal species found that the larger-bodied sex was more

likely to innovate (Amici et al., 2019) – a finding that supports the "Free Time/Excess Energy hypothesis" but not the "Bad Competitor hypothesis" (see section 2.3). Considering the different life histories of males and females, one might predict that the dispersing sex would need to invent more than do individuals of the sex that remain with kin in the birthplace, because the dispersing sex is more likely to encounter novel situations. When a disperser joins a new group, it may also need to learn behaviours from the new group members. It might also have to be inventive because it has less access to other individuals it might copy. The data are mixed regarding philopatric sex hypothesis. For example, female red-fronted lemurs (the stay-at-home sex) and male meerkats (the leaving-home sex) were both more likely to solve an experimental task (Schnoell and Fichtel, 2012; Thornton and Samson, 2012). While the primate literature suggests that males may be more inventive than are females (Reader and Laland, 2001), Perry et al. (2017) found no differences between male and female capuchins across a decade of observations. The potential role of sex differences in inventiveness and innovation more generally is still far from clear.

Dominance rank   The "necessity is the mother of invention" hypothesis predicts that low-ranking individuals should be more inventive, whereas the "free-time and energy" hypothesis predicts that high-ranking individuals, who have greater access to resources, will use their spare time to find new things to do (Amici et al., 2019). To date, meta-analyses of published literature on innovation in foraging tasks yield no evidence that dominance is a useful predictor of inventiveness across species (Amici et al., 2019). For example, low-ranking chimpanzees are sometimes more inventive than high-rankers (Reader and Laland, 2001), while the most dominant starlings (*Sturnus vulgaris*) participating in an experimental problem-solving task were the fastest to learn how to solve the task (Boogert et al., 2006). In wild capuchins (*Cebus capucinus*) and wild hyenas (*Crocuta crocuta*), invention seems unrelated to dominance rank (Benson-Amram and Holekamp, 2012; Perry et al., 2017).

Social network position   The position an individual occupies in its social network could foster opportunities for being inventive. There is a well-established relationship between network position (specifically, the spanning of "structural holes") and invention in the literature on human invention (Burt, 2004). Turning to the animal literature, better-connected great tits (*Parus major*) and baboons (*Papio ursinus*) were more likely to find and use novel foraging patches, relative to individuals with more limited social connections (Aplin et al., 2012; Carter et al., 2016). Proximity to conspecifics might prompt certain kinds of object exploration, due to stimulus enhancement or social facilitation; however a meta-analysis by Amici et al. (2019) including 20 species of birds and mammals did not find a convincing relationship between proximity to others and propensity to innovate, though the relationship was stronger in wild animals than in captive animals. Possibly the relationship between network position and inventiveness is contingent on behavioural domain: Perry et al. (2017) found that more social wild capuchins were more prone to invent new social interactions, while less

social individuals were slightly more likely to invent new foraging behaviours or ways of manipulating their own bodies. This suggests that the relationship between network position and inventiveness may vary not only by species but by behaviour type.

Personality Because methods for studying animal personality are now well developed and there is considerable evidence of a role for personality in a range of animal decision-making (Vazire et al., 2007), the time is ripe to conduct more rigorous investigation of the impact of personality traits on propensity to invent and to transmit innovations. Brosnan and Hopper (2014) discuss five psychological factors that may limit innovative capacities, either in the invention phase or the transmission phase, by inducing individuals to stick with what they already know rather than exploring more novel options: neophobia (i.e. aversion to novel objects or situations), conservatism (not wanting to try new things), conformity (behaving like the majority), functional fixedness (being disinclined to use familiar objects in novel ways), and the endowment effect (exhibiting a preference for objects/foods already in their possession instead of potentially more desirable objects not yet in their possession). Although the authors cite some evidence in favour of these ideas, the evidence is still scant and more comparative data are desirable. Stable inter-individual differences in proclivity to invent, as seen in foraging guppies, *Poecilia reticulata*, (Laland and Reader, 1999), support a role for personality traits in inventiveness. Starlings (*Sturnus vulgaris*) that were quickest to feed in a novel experimental environment were also generally the ones who solved the task more quickly, which might suggest that boldness or exploratory proclivity might promote invention (Boogert et al., 2006). Male grackles (*Quiscalus lugubris*) that were less afraid of novelty, more exploratory, and more persistent were more likely to succeed in opening a box containing food (Overington et al., 2011), and the main predictor of success for wild hyenas in obtaining food from a puzzle box was diversity of techniques tried, with the primary inhibitor being neophobia (Benson-Amram and Holekamp, 2012). Neophobia also seems to explain speed of problem-solving in raccoons (*Procyon lotor*): less neophobic and more persistent individuals were more likely to solve a puzzle-box task (Daniels et al., 2019), and horses (*Equus caballus*) that were more active, more tenacious, and better at inhibition control were better able to feed from a novel feeder (Esch et al., 2019). Amici et al's (2019) meta-analysis of 38 studies of foraging tasks in 20 species of birds and mammals showed that individuals that are more explorative, neophilic and (to a lesser, non-significant extent) persistent are more prone to innovate; exploration more strongly predicted innovation in captive rather than wild animals.

The literature on humans is broadly consistent with the provisional findings from the comparative literature, with plenty of speculation as to the types of personality traits likely to promote invention and innovation. Sternberg (2006), in summarizing his life work in this area, speculates that all of the following traits may play a role in promoting innovation: willingness to overcome obstacles (which might be akin to perseverance), willingness to take sensible risks, tolerance of ambiguity, and tendency to seek opposition (which might be seen as contrariness or as anti-conformity). Simonton (1999) emphasizes some overlapping traits,

including independence, anti-conformity, openness, "behavioural and cognitive flexibility and boldness"; because he views human creativity as a Darwinian process in which successful inventions arrive through variation and selective retention (Campbell, 1960) — a point of view that goes back to William James (1880) — Simonton emphasizes the role of these traits in "the production of ideas both numerous and diverse."

Mood in humans can affect creativity. As a transient emotional state, mood is not the same as personality, but some personality types might be more prone to particular moods. People with more positive moods were more creative than those with neutral moods (Baas et al., 2008) and, in general, individuals with an emphasis on promotion focus (sensitivity to positive outcomes) rather than prevention focus (sensitivity to negative outcomes) were more creative. Importantly, although emotions are increasingly studied in non-human animals, the role of this possible contributor to inventiveness has not yet been carefully examined.

It would also be useful to examine the relationship between age, learning strategy and personality traits, as it seems probable that natural selection would have favoured both (a) within-species shifts in personality traits or attitudes relevant to learning strategies across different life history stages, and (b) different timing of these shifts across species that vary widely in their life history strategies (Perry, 2020). For example, younger capuchin monkeys (*Cebus capucinus*) are less neophobic and more playful, creative, curious, opportunistic, and active than older monkeys, and also more prone to attend to foraging conspecifics (Perry, 2020); these traits have obvious implications for propensity to invent and/or copy novel behaviours. However, it is possible that a species exhibiting a faster life history, smaller relative brain size and less alloparenting would be less extreme than capuchins in these age-related tendencies; further empirical research will be necessary to examine these ideas.

2.3   What are the circumstances that make inventions more likely?

As described above, it is not clear whether inventiveness is more likely due to (a) necessity (e.g. individuals that have little access to resources because they are subordinate in the dominance hierarchy, and/or too young to compete effectively), (b) access to opportunities (e.g., higher encounter rates with particular resources may promote attempts to exploit these resources (Koops et al., 2014) such as with new forms of tool use) and/or (c) having free time (Kummer and Goodall, 1985). All of these possibilities have received mixed support. Amici et al (Amici et al., 2019) attempt to distinguish the "Bad Competitor" hypothesis (which they equate with the "necessity is the mother of invention" hypothesis, assuming that smaller, lower-ranking individuals in poor body condition will be more inventive) and the "Excess of Energy" hypothesis (which assumes that individuals who are higher ranking, in better body condition, and of the larger sex, will be more inventive because they will need to spend less time foraging and can thus assume higher risk foraging strategies). Their analysis did not convincingly support either hypothesis, as there were no clear differences related to rank or body condition. Furthermore, older animals were more prone to innovate in their meta-analysis, and the authors predicted that younger individuals would be more innovative in

both the "Bad Competitor" hypothesis and the "Excess of Energy" hypothesis. The finding that the larger-bodied sex was more innovative seemed to support the "Excess Energy" hypothesis; however, the assumption that the larger sex will need to spend less time foraging seems debatable, as (a) the larger sex may have a higher metabolic rate or (b) have a reproductive strategy requiring more time spent in social competition relative to the smaller sex. It would be worth testing these hypotheses using more consistent methods in future work, and measuring invention, body weight, competitive ability, and activity budgets more explicitly in a way that permits greater cross-study consistency, as the variables used in this meta-analysis were, of course, measured for different research agendas. It would be particularly desirable to measure "free time" independently from "excess energy" and competitive ability, as these variables are not necessarily correlated. Dominants, by definition, will have higher competitive ability, but they may have less free time as a consequence of devoting more time to servicing social relationships, compared to a low-ranking peripheral group member. And alpha males may require extreme amounts of energy to maintain their bodies in good fighting condition to defend their positions.

3   What are the gaps in our knowledge regarding invention?

We have identified three major questions regarding propensity to invent that warrant further investigation: (a) What kinds of inventions readily occur to individuals? (b) What kinds of behaviours are truly novel for a given species? and (c) What features of behaviours and individuals increase the probability of a novel behaviour being generated?

To answer these questions, it is essential to ground research on animal invention in solid natural history. Until now, most empirical research on inventions has suffered from one of two flaws:

1. Observational work on behavioural novelty has been based on retroactive interpretation of data collected for other purposes, which means that it is subject to human memory and research biases about which behaviours are noticed and interpreted as novel.

2. Data have come from experimental studies in which a novel task is presented to the animals by a researcher, who has explicitly designed the task to be abnormal enough for that species that it can definitely be assumed to be novel to the animal; often the participants have to be trained to engage in the task. Invention in these experimental studies is often defined as being good at solving the task in the way the human researcher intended it to be solved. Such approaches, though they have their uses, do not permit the research subjects to express their full range of creativity.

How could this field move forward? Perhaps the greatest obstacle to research on inventions generally is the problem of determining rates of invention, and of determining what could have been invented but has not been. Systematically cataloguing the building blocks

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of species' creative intelligence (i.e., the behaviours that could be combined in order to create inventions) would help address the issue of what is "invent-able". Lack of systematically collected data on inventions also hampers our understanding of how species differ in their creative abilities generally, and how often or infrequently particular creative products are independently invented.

Convincing answers to our "major" questions are most likely to come from amassing longitudinal data sets in which we record not only the fine details of species-typical behaviour, but also any novel behaviours observed, using systematic methods. It is essential that we do this for large numbers of individuals, social groups, and species. The only naturalistic study of invention that has attempted such systematic documentation of entire repertoires of inventions is a study of ten white-faced capuchins groups (Perry et al., 2017). In this long-term study, a large staff of observers previously trained to identify all elements of the species-typical repertoire was trained to report in detail any behaviour not seen previously, in any behavioural domain, over a period of ten years. An observer with 26 years of experience collecting data on the study population inspected each observation, terming it an invention only if (a) it had not been seen previously in that individual or social group during the lifetime of the putative innovator during the entire 10-year period (i.e. was absent in the previous 5-10 years), and (b) if the behaviour was absent in the repertoires of at least some groups.

By collecting such data, along with association patterns and gaze directions, it should be possible to infer with a reasonable degree of accuracy what behaviours are new, and what behaviours are either socially learned or readily invented independently. Long-term studies afford the advantage of having detailed data about the kinship, age, association patterns, personalities and relationship histories of the individuals, enabling researchers to answer questions about the qualities of individuals that promote creativity. These studies can also gather consistent data about competitive ability and activity budgets, allowing them to adjudicate between the "necessity" and "excess of energy" hypotheses.

One of the challenges of defining new behaviours is deciding how finely to parse the behavioural sequences witnessed. All behaviours (both novel and non-novel) are constructed from the basic "building blocks" of motor patterns that are standard parts of a species-typical repertoire; the novelty comes into play in deciding on how to apply these behaviours to specific contexts, and how to combine these behaviours into sequences. If the coding of the data is fine-grained enough (including recording of all motor actions and the objects and contexts that they are applied to), it should be possible to make more rigorously objective decisions about what is novel than has been typical of past studies of innovation. One of the frustrations of trying to answer the question of what affects the invent-ability of behaviours is that we cannot accurately imagine the whole universe of "idea space" or "behaviour space" for behaviours that have not yet been invented but could (in theory) be invented. However, we can answer the question of what kinds of behaviours are likely to be invented (and what properties of individuals make them more likely to invent certain kinds of behaviours), by documenting all the behaviours that have been witnessed. We can then assess their "invent-ability" by noting how often these behaviours appear in individual and group behavioural

repertoires, while taking into account the amount of time the appropriate contexts for displaying these behaviours occurs. This approach could also be taken to ask the more specific questions of (a) given that a specific motor behaviour has been performed in one context, what is the likelihood that it will be performed in another context, and (b) given that an individual has performed part one of a (plausible) behavioural sequence, what is the probability that it will then proceed to perform step two and step three? These data can be used to inform modelling approaches.

Techniques used to represent the structure of invention space in human technological invention (Foster et al., 2019) could be profitably employed to represent species' behavioural repertoire and to quantify the novelty of particular behaviours. For example, behaviours could be characterized by the presence or absence of different building-blocks and the novelty of particular behaviours quantified by the (Hamming) distance from typical behaviours (Foster et al., 2013), which might distinguish incremental refinement of existing behaviours from more radical recombination (Foster and Evans, 2019). Or the invention space could be represented by a network where behavioural building blocks are linked when they are observed in combination; the novelty of particular behaviours is then characterized by its structural position, e.g., whether it combines building blocks that have not been combined before, whether it introduces a new building block, or whether it combines building blocks from distinct behavioural clusters (Foster et al., 2015). Similar network-based techniques could also be used to represent the way that distinct individuals combine specific behaviours in different contexts (paralleling the representation of scientists combining particular chemicals and methods to study certain diseases (Shi et al., 2015)). These rich representations can serve as input to models predicting the probability of behaviours being combined, or transferred across contexts, by particular individuals.

4 Conclusions and future directions

In order to deduce general principles about factors selecting for invention, it is necessary to collect data from multiple species, and to investigate variation in the attributes of behaviours, individuals, groups, and species. Thus far comparative data, particularly of the naturalistic variety, in which the animals themselves determine the problems to be solved, are scant and collected via such a diversity of methodologies that it is difficult to combine them meaningfully into a single comparative analysis. Available studies, primarily targeted at investigating which characteristics of inventors promote innovative tendencies, yield different answers both within and between species. We hope that clearer results will be obtained when the scientific community has obtained more data, using more stringent definitions and methodologies such as those described here, and considered variation in relevant characteristics at the level of the behavioural domain, individual, dyad and group, preferably integrating these levels of analysis. The roles of age, personality, and social network structure in determining inventiveness are particularly understudied, both empirically and theoretically (see ESM). The few

models of cultural evolution that do take age/life history into account seem to indicate that learning strategies shift over time, and that it is thus critical to incorporate age structure into these models. Perhaps the biggest gap in our knowledge regards whether individuals "prefer" to learn certain inventions compared to others (i.e. whether and how the particular characteristics of inventions affect their subsequent transmission, as in Rogers 2003).

Although field (and captive) experiments will always play an important role in understanding certain aspects of cultural evolution (especially learning mechanisms), they cannot substitute for careful collection of natural history data on behavioural variation of wild animals making behavioural choices in their natural environments. Longitudinal field studies – particularly those employing consistent data recording methods across decades – have a particularly important role to play in documenting how behavioural repertoires for individuals and groups change over time, in accordance with natural aging processes, changes in group composition, and ecological changes. Such studies will provide opportunities to ground truth models of cultural evolution that make predictions regarding the rates at which inventions will rise and spread under different assumptions regarding the social network structure and demographic characteristics of groups (e.g. number of models and characteristics of models (e.g. age, expertise, personality, rank, sex)).

Although much progress has been made in recent years in theoretical models of the invention and transmission of behaviours (Lewis and Laland, 2012; Smolla and Akçay, 2019), most cultural evolution models still assume invention to be a random process like genetic mutation, instead of incorporating variation at the level of the trait, individual, dyad, and group structure. Furthermore, these simple models typically treat invention as incremental rather than combinatorial. In this review, we focus more on the invention part of these models, but social transmission is of course critical to establishing and maintaining inventions in behavioural repertoires (see ESM). We know that different individuals differ in their rate in invention, and in the kind of inventions they create, and that the positioning of individuals within a social network will differentially impact the probability that inventions will spread, becoming innovations. It would also be important to develop models of invention and social learning having fixed or evolving structures.

Empirical data should guide parameterization of models regarding the likelihood of particular kinds of behaviours being invented (e.g. based on similarity to other behaviours in the repertoire, or on particular kinds of behaviours and contexts being combined). Three difficult (though not insurmountable) methodological challenges slow empirical work on invention and its role in cultural evolution: (1) Documenting behavioural repertoires (both individual and group) and how they change over time; (2) Documenting invention rates, and in particular distinguishing between independent inventions and socially learned adoptions of traits; (3) Documenting what proportion of "invention space" – i.e. combinations of behavioural elements and objects in routinely encountered ecological settings – is occupied by a particular individual or species. Solutions to these challenges will greatly speed progress at the intersection of theoretical and empirical research on cultural evolution.

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Competing interests

The authors declare that they have no competing interests.

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Electronic Supplementary Material

ESM 1.   Supplemental text to the main article

Inventions become innovations through their transmission via social learning. Here, we provide additional relevant findings regarding the state of the literature on the transmission and establishment processes to supplement the main text, which focuses on the invention phase.

Historically, research on understanding the spread of inventions through groups has focused on the characteristics of the individuals involved in transmission and maintenance of inventions, either from the point of view of the learner, the model, or the relationship between them (Rogers, 2003). Perhaps surprisingly, this empirical information has not been adopted into many theoretical models of the transmission of inventions through groups. In addition, there are gaps in our understanding of how the personality composition and age structure of a group affects the generation and subsequent transmission of inventions to make them innovations. Perhaps the biggest gap in our knowledge regards whether individuals "prefer" to learn certain inventions compared to others (i.e., whether and how the particular characteristics of inventions affect their subsequent transmission, as in Rogers 2003). However, there are additional gaps in our knowledge of the transmission and establishment process, some of which we describe below.

How does network structure affect how quickly and reliably innovations are transmitted?

Much research has been conducted on the factors affecting transmission within a dyad. However, empirical studies that look at how new behaviours or information spread along a network as a function of the distribution of individual traits remain rare. Likewise, most theoretical models assume that new behaviours appear at random, akin to mutations, whereas we know that different classes of individuals might invent at different rates as discussed in section 2.2 of the main text. The location of such individuals in a network, as well as the correlation between individual traits over a network, will affect whether, and how, newly invented behaviours spread in a population. Questions such as these remain largely unstudied, which limits our understanding of how diversity of individual traits and their distribution over the social network affects the dynamics of innovation and cultural evolution.

For the description of how traits diffuse through a social group or population, higher order structure and characteristics become important, not least because individuals in a population often interact more with some individuals than with others. The heterogeneity of interactions

is often captured as a network, where nodes represent individuals and edges between pairs of nodes represent whether or not the individuals interact or how frequently they do so. The network structure can have substantial effects on the speed at which a novel trait spreads throughout a population and how many individuals it will reach.

How exactly network characteristics affect the spread of novel traits depends on the type of trait (e.g., behavioural domain), which in turn influences the mode of transmission. That is, some traits are easily transmitted, such as internet memes or simple behaviours, and spread in an infectious disease-like manner (simple contagion). Other traits, which are less easily transmitted, for example, an elaborate food extraction technique, follow a so called complex contagion dynamic, where a single exposure to the trait is not sufficient to acquire it (Rogers, 2003). In the case of simple contagion, information may spread more rapidly through dense, as compared to sparse networks. This is because in denser networks, individuals interact more with each other, which increases opportunities to observe others (Lehmann et al., 2013). For example, information was shared more rapidly on the denser Digg social network site compared to the less dense Twitter social network site (Lerman and Ghosh, 2010). Additionally, highly clustered networks are predicted to impede information flow, as information gets "trapped" in local clusters (Weng et al., 2013).

However, if transmission follows complex contagion dynamics, an individual's probability of adopting novel traits is higher if she receives social reinforcement from multiple neighbours. Here, clustering is beneficial. This was shown in a study on the adoption of health behaviour, which found that new behaviours were more readily and more widely adopted in clustered networks than in random networks (Centola, 2010).

In addition to overall structural properties of the network, regularities within the network structure may promote or constrain information flow. For example, individuals may preferentially associate with others who share similar phenotypes, resulting in positive assortment or "homophily" at the structural level. Homophily may preclude some individuals from obtaining social information because particular individuals are more likely than others to generate information (Carter et al., 2015) and these individuals may not associate with naïve individuals (Weng et al., 2013). Conversely, negative assortment ("heterophily") may facilitate the transfer of information between information generators and non-generators. Thus, the propagation of information through a social network could be limited or enhanced by positive or negative assortment of information-generating phenotypes, respectively. A similar mechanism plays out in human social networks; because advantaged individuals are often more likely to adopt a new behaviour, and because they tend to associate preferentially with other advantaged individuals, network diffusion can be a powerful driver of inequality as beneficial behaviours spread through already advantaged networks (DiMaggio and Garip, 2012). This mechanism can be quite subtle, however; an experimental study in human social networks has shown that homophily promoted the adoption of a novel health behaviour in an online network (Centola, 2011). This might be because humans are more likely to be influenced by others who have similar traits to themselves—a version of directed social learning—and limited homophily across a mixture of characteristics (as in Centola 2011) facilitates directed

social learning.

These results show that variation in natural networks can be used to determine which social network structures promote or retard information flow, while the individuals that make up the network remain relatively constant. This kind of modelling would allow us to predict transmission of innovations in real populations of humans and non-human animals.

How does the age composition of groups and populations affect the spread and accumulation of innovations?

Age is a critical variable that affects how much individuals learn socially vs. asocially, and whom individuals learn from. Despite this, there has been relatively little empirical or theoretical work on how age variation in a population affects the spread and maintenance of innovations in populations. One class of theoretical models (Aoki et al., 2012; Lehmann et al., 2013) has considered the evolution of when and how long individuals learn socially and individually, and the consequences of these strategies for the accumulation of culture across generations. Their results show that the efficiency of different kinds of learning, as well as the trade-off between investing time into learning or inventing new behaviours vs. exploiting these behaviours, determine whether a learning schedule can evolve that can sustain new innovations in a population across generations. Another class of models (e.g. Fogarty et al. (2013) investigates the spread or decline of socially learned behaviours in age-structured populations with age-dependent learning rates. Fogarty et al. (2013) use this approach to understand the impact of social learning on fitness-changing behaviours (e.g., obtaining more education and having fewer children). They find that if such behaviours are transmitted between unrelated individuals (as opposed to just from parents to offspring), they can cause rapid demographic transitions where the age-structure of the population rapidly changes. The mathematical machinery of these models allows one to take into account the reciprocal feedbacks between the demographic structure of a population and the traits that change them. These feedbacks between the age structure and innovations can have profound effects on the spread and maintenance of cumulative culture. Another recent agent-based model on cumulative (but demographically neutral) culture, by Acerbi et al. (2012), allows individuals to display different learning rates as well as bias in whom they learn from. In that model, populations accumulate more cultural traits or modifications if individuals live longer (as they have more learning opportunities), but become more conservative, in the sense of having lower rate of cultural change. Interestingly, biasing social learning towards older individuals, even if they are more conservative, results in a rate of cultural change that is similar to or even higher than that expected when individuals meet at random. This is because older, more experienced individuals are better cultural models than young ones. These disparate modelling approaches all show that the age-structure of the group, and how different aged individuals learn from others, can profoundly affect the spread and maintenance of cultural traits. At the same time, this topic remains underexplored; for instance, we do not yet know how assortment in age in complex networks affects the spread of innovations, or how

age-dependent invention propensities interact with the demographic structure to determine long-term dynamics of cumulative culture.

ESM 2.   Gaps in the theoretical literature

There is a profound lack of theory on the effects of complex individual differences in the transmission of new traits

While there is strong evidence for inter-individual differences in motivation, capacity, and opportunity for cultural learning (for a review see Mesoudi et al. 2016), previous theoretical work has largely avoided addressing individual differences in individual and social learning. Some studies have varied the propensity for individual and social learning or let individuals compete with different social learning strategies (e.g. Rendell et al. 2010; Smolla et al. 2015). However, there is more to individual variation than simply learning propensity. Future models should more strongly focus on explicitly incorporating age structure, sex, dominance, kinship, and personality as possible factors influencing attention and cultural learning. This will make models more complex, but this complexity is needed to better understand how individual differences and preferences affect the diffusion of innovations.

There is a lack of models that simulate the natural process of invention and transmission of inventions

New inventions do not appear randomly from the space of all possible inventions. Instead, there is expected to be structure in the space of inventions. Inventions that are close to existing behaviours are easier to create and transmit, relative to those that are very different from existing behaviours (Foster et al., 2019). Furthermore, some behaviours might be easier to combine to give rise to new behaviours than others. Models of cultural evolution have paid very little attention to these factors so far, mostly treating the space of possible inventions as unstructured. Among the few exceptions is a paper by Lewis and Laland (2012), in which the authors distinguish between inventing completely new traits or tools, combining existing ones, or modifying them. This model abstracts away from individual, dyad, and network-level dynamics, and only considers the long-term dynamics of cumulative culture in a population. A more recent paper by Smolla and Akçay (Smolla and Akçay, 2019) considers a simplified structure to the space of cultural traits, where each trait (or proficiency level) builds on a single precursor. This framework can be extended to allow individuals to combine existing traits, or for a single trait to give rise to multiple "descendant" traits. By varying the probabilities of such events, as done by Lewis and Laland (2012), and the structure of the population, as done by Smolla and Akçay (2019) we can address how cumulative culture evolves in different innovation spaces.

Another interesting direction is to develop models of social and individual learning in invention spaces with fixed or evolving structures. Foster et al. (2019) provide a possible foun-

dation for this approach. That paper systematizes several measures of novelty for patents, based on different representations of the space of existing knowledge and different models of the inventive process. The authors show that these novelty measures are correlated with, for example, the variance in the success of the patent, with more novel patents having higher variance. Such techniques for representing invention spaces and modelling inventive processes can be built into individual and social learning models to determine the probabilities of inventing new behaviours and the ease with which they are transmitted socially.