The reluctant innovator: orangutans and the phylogeny of creativity


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Young orangutans are highly neophobic, avoid independent exploration and show a preference for social learning. Accordingly, they acquire virtually all their learned skills through exploration that is socially induced. Adult exploration rates are also low. Comparisons strongly suggest that major innovations, i.e. behaviours that have originally been brought into the population through individual invention, are made where ecological opportunities to do so are propitious. Most populations nonetheless have large innovation repertoires, because innovations, once made, are retained well through social transmission. Wild orangutans are therefore not innovative. In striking contrast, zoo-living orangutans actively seek novelty and are highly exploratory and innovative, probably because of positive reinforcement, active encouragement by human role models, increased sociality and an expectation of safety. The explanation for this contrast most relevant to hominin evolution is that captive apes generally have a highly reduced cognitive load, in particular owing to the absence of predation risk, which strongly reduces the costs of exploration. If the orangutan results generalize to other great apes, this suggests that our ancestors could have become more curious once they had achieved near-immunity to predation on the eve of the explosive increase in creativity characterizing the Upper Palaeolithic Revolution.

1. Introduction

Modern human societies thrive on creativity, the disposition of individuals to systematically pursue the generation of novel ideas, products and procedures [1]. Crucially, creativity requires no external trigger such as novelty or an imminent problem that has to be solved but corresponds to an intrinsic interest in exploring and innovating. What are the historical origins of this disposition to be creative, which has led to an unprecedented rate of innovation? A convincing answer to this question is not merely of interest to behavioural biologists and comparative psychologists, but may also have direct applications in the modern world.

Traditionally, most interest in this question has come from palaeoanthropologists [2]. However, because the roots of creativity may precede the hominin lineage, the increasing interest of behavioural biologists [3,4] and primatologists [5,6] in animal innovation may help to complete the picture of the phylogenetic origins of human creativity. Because creativity is only one of the diverse processes that can lead to successful innovations, it is useful to examine the various circumstances under which any specific source of innovation can become prevalent. And because great apes are our closest living relatives, the study of the phylogeny of human innovation may be especially productive in this taxon. Here, we report on field and captive studies of orangutans in the light of these questions.

Innovation (as a behaviour pattern) refers to a solution to a novel problem, or a new solution to an old problem [7], or, more generally, to novel, learned behaviour patterns acquired by an individual [3,8]. If we define innovativeness as an individual’s capacity to innovate, innovativeness can be seen as an expression of problem-solving ability or behavioural flexibility or variability in space or time. Comparative studies have shown a correlation between brain size and problem-solving ability in birds [9,10] and primates [11,12], as well as between innovativeness or brain size and colonization success (an expression of flexibility) in birds [13], mammals [14] and lizards [15]. In birds, the variety of technical
innovations, rather than the tendency to add food types to the diet (arguably representing weaker innovations, more likely among dietary or habitat generalists) was correlated with brain size [16]. All these findings strongly suggest that larger-brained organisms are better at solving more (or more difficult) problems, and that humans, being far bigger-brained than any of their relatives, are likely to be even more so.

Although these correlations between innovation and problem-solving and brain size are suggestive, they do not necessarily imply that innovation or creativity is a major expression of intelligence in nature, let alone that it is its main function. Field-workers rarely witness innovations being made and rarely report that animals are truly curious (with rare exceptions: [17]). Moreover, there are major differences between wild and captive animals [18,19], discussed in detail in §4. The comparative results therefore do not imply that large brain size automatically implies high innovativeness in nature; animals in nature may deploy their intellectual abilities mainly for different purposes.

The aim of this paper is to examine the conditions favouring innovativeness in orangutans in order to draw conclusions about the human ancestral state. Similar patterns may apply to the other great apes as well, but because much critical information is still missing for them, our inferences for hominins must remain preliminary. Orangutans are semi-solidary arboreal apes, living on the Southeast Asian islands of Sumatra and Borneo. They are relatively and absolutely large-brained [20], are among the best primate problem-solvers [12,21] and have large innovation repertoires, especially in the subsistence and comfort domains [5,22,23].

After a brief terminological excursion, we will first describe skill acquisition in wild orangutans. A developmental approach is essential because innovations are by definition behaviours that do not have a strong genetic basis and thus do not arise reliably during development, but must instead be acquired and may therefore accumulate with age. We have done extensive studies of skill development in wild orangutans [24]. The data yield the paradoxical result that wild orangutans are novelty averse, rarely engage in independent exploration, and yet have extensive repertoires of learned skills, which qualify as innovations, which they acquire mostly through socially induced exploration. Wild orangutans, then, appear to avoid novelty and rarely explore. We then turn to the results of work on orangutans in zoos and rescue centres and find a striking contrast in novelty response and innovativeness. This so-called captivity effect or captivity bias [19] is also found in other primates, in particular great apes, and allows us to develop a hypothesis for the conditions that make an otherwise exploration-avoidant great ape into a highly exploratory, and thus innovative and even creative one. Finally, we apply this insight to hominin evolution.

## 2. Innovation and its sources

Innovations are novel, learned behaviour patterns acquired by an individual [3,8]. They are not part of the innate repertoire, nor are they predictably triggered by suitable environmental or social conditions. They therefore do not arise reliably in all maturing individuals of a population, but are instead invented only by a (generally small) subset of all the individuals exposed to the set of conditions in which it can arise.

The most obvious way to recognize innovations is to observe their origin, i.e. when an individual comes up with a behaviour that at that time is new for the population. Each particular innovation has a certain probability of appearing anew in suitable conditions in a given species. This probability can in principle be estimated through experiments [25,26]. Unfortunately, this procedure is rarely feasible, leading most researchers to operationalize the concept by resorting to opportunistic population-level criteria for innovation. The most commonly used measure is that it is novel for the population [3]. This operationalization has been very fruitful, but inevitably also introduced some ambiguity in measurement and interpretation. First, the criterion is necessarily imprecise since it obviously depends on the size of the population and the duration of study, and also assumes continuous observation. Fortunately, taking research effort into account makes this measure more reliable, as evident in the persistently obtained correlations with brain size or colonization success mentioned above. Second, this operationalization may have produced a focus on novelty-induced innovations, since they may be most common nowadays, as a result of anthropogenic disturbance. Despite these ambiguities, comparative studies have still yielded clear-cut results, as we saw above, probably because studies tend to rely on similar criteria for rarity [3], and novelty-induced innovations may be a good measure of overall behavioural flexibility.

Confusion has arisen because individuals may also acquire innovations, as defined above, using social learning. Social learning of innovations generally leads to a much higher probability of acquisition than independent exploration does; this probability increases as the mechanisms of social learning deployed become more precise. While relying on social learning, individuals can therefore accumulate a large innovation repertoire without ever making an innovation themselves. The great capacity for social learning in great apes [27] makes this a particularly common pathway of acquisition in this lineage, especially in the light of their known cultural repertoires, which are made up of innovations. Orangutans are an example: they are good social learners [28] and have large cultural repertoires [29]. Indeed, in principle, an individual could acquire a large repertoire of innovations without ever making a single innovation.

This approach has given rise to alternative ways of estimating a species’ innovation potential. First, one can examine a population’s repertoire of innovations using techniques similar to those developed for the recognition of cultural variation [5,8]. Innovations should be rare and will therefore often vary among populations that are otherwise comparable in their environmental conditions and genetic background. A second way is to focus on acquisition. If innovations are acquired through social learning, we must see indications: selective attention and/or socially induced practice [30,31]. Thus, innovations can also be seen as ‘learned skills,’ as opposed to routine skills that develop reliably in all individuals of the taxon without extensive social learning [32]. The set of learned skills is broader than the set of innovations as traditionally defined, but as we noted above, innovations are not qualitatively distinct from other behaviours (since there is continuous variation in the probability of independent appearance) and almost certainly not represented as qualitatively different by the individuals in the process of acquiring their behavioural repertoire during development. Nonetheless, it is clear that it is only possible to compare studies that use similar methods to estimate the innovation repertoire of a given species or population.

Perhaps because of the emphasis on novelty-induced innovations, and because the low probability of catching the
process of innovation in the act experimentally, the sources of independent innovation in nature—the focus of this paper—are relatively poorly known. While there has been some interest in the cognitive processes underlying innovation [6,33,34], there is remarkably little information on what might be called the natural history of innovation: the contexts in which innovations arise in nature. Here we offer a preliminary classification of these contexts. We can use it to identify the main contexts used by orangutans, and more generally to demarcate creativity relative to the other triggering conditions (table 1).

First, innovation may arise in response to novelty (some novel element in the environment: object, food item, context, organism, etc.), which usually involves some subsequent exploration (but note that novelty response and exploration are distinctly regulated motivations with distinct functions: [35]). Although this pathway has been the focus of much attention, it may actually be rather rare in long-lived and big-brained species where young individuals, who potentially encounter much novelty, avoid it, and by the time they are adult may no longer encounter much that is novel per se [16]. Thus, innovative responses to novelty may not be the most important source of innovations in species most comparable to hominins. Second, exploration may be elicited by the failure of pre-existing routines, which requires individuals to find new solutions to old problems and thus leads to innovation, as emphasized by the definition of Kummer & Goodall [7]. Thus, a particular technique may no longer work, e.g. because the substrate has changed or the right raw materials are no longer available for tools, and a new way is sought to solve the same problem. This paradigm has most commonly been used experimentally to assess individual innovativeness [36] or to ask whether individuals show cumulative innovations or ratcheting [37,38]. Arguably, failures of pre-existing routines have historically been rare for most species in natural conditions, although they often have increased recently owing to anthropogenic disturbance [39,40]. However, they may have become more common at one stage among our ancestors. Potts [41] links the origin of new hominin species and technological innovations to periods of high climate variability.

Third, innovations may simply happen by accident, as a result of the individual going through a routine activity that somehow goes wrong and produces a novel result. For this to happen, the individual must be able to recognize the result as worth retaining and remember the actions that led to it. It can therefore arise in the absence of exploration. This is a well-known pathway in hominins. Many of the innovations requiring fire, such as heat treatment of stone tools, ceramics or metallurgy, must have been discovered accidentally when the raw materials were exposed to a regular fire [42]. It is unclear to what extent such accidents are a major context of innovation in non-humans.

Fourth, innovation may arise as a result of exploration that was triggered because a clearly defined problem presented itself. For instance, an ape sees a bees’ nest and is attracted to the smell, or has learned from previous experience (e.g. because it encountered pieces of honey comb) that this resource is attractive. This well-defined problem elicits targeted exploration, which may occasionally lead to innovation, for instance the use of tools to perforate the nest and extract the honey. Such situations are potentially common, especially in the context of subsistence. Some forms of tool use may have arisen this way [43].

A fifth possibility is that a general lack of access to essential resources (food, shelter, water, mates) may lead to systematic exploration in search of these resources. Systematic exploration may be required because no targeted search is possible given that it is not clear which environmental problems can be solved. This pathway to innovation is captured in the adage ‘necessity is the mother of invention’. Whether this is regarded as creative depends on the weight attached to the spontaneous motivation of the exploration process. Possible instances include innovations made by low-ranking or juvenile individuals that cannot gain access to preferred resources [44–46] or by animals during times of food scarcity.

Table 1. The natural history of innovation in large-brained and long-lived species such as great apes: contexts in which novel behaviour patterns may arise.

<table>
<thead>
<tr>
<th>no.</th>
<th>eliciting factor</th>
<th>mechanism</th>
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<tbody>
<tr>
<td>(I) novelty-induced</td>
<td>novelty</td>
<td>little or no exploration needed; hence, can only explain simple innovations</td>
</tr>
<tr>
<td>(II) failure-induced</td>
<td>failure of specific pre-existing routine induces persistent exploration</td>
<td>individuals are required to find a new solution to an old problem, which induces persistent targeted exploration of well-defined problem space</td>
</tr>
<tr>
<td>(III) accidental</td>
<td>routine behaviour accidentally leads to innovation</td>
<td>routine behaviour in absence of novelty, concrete problem or exploration; merely requires recognizing the innovation and remembering the procedures</td>
</tr>
<tr>
<td>(IV) problem-recognition</td>
<td>recognizing a novel problem, e.g. the presence of familiar but inaccessible food items</td>
<td>recognition of the problem and goal-directed exploration and solving of a well-defined problem</td>
</tr>
<tr>
<td>(V) necessity-induced</td>
<td>systematic exploration driven by general need (absence of food, shelter, etc.)</td>
<td>extrinsically motivated exploration and innovation of undefined problem space</td>
</tr>
<tr>
<td>(VI) creative</td>
<td>systematic exploration in the absence of specific problem or novelty</td>
<td>intrinsically motivated exploration and innovation (curiosity), perhaps playful</td>
</tr>
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3. How wild orangutans acquire their innovations

A young, naive orangutan, for which the whole world is new, continuously encounters novel items. Although this could in principle lead to high rates of independent exploration of unfamiliar items, this is not the case. Field observations on orangutans have long suggested that they avoid novelty. We therefore decided to test this impression experimentally in our well-habituated study populations at Suaq Balimbing (Sumatra) and Tuanan (Borneo), both inhabiting swamp forests. Small platforms in the shape of ape nests were hoisted into the canopy within the height range of orangutan travel and provided with novel items, including novel foods. The results [52] showed that wild orangutans, both Sumatran and Bornean, pass the novel stimulus at a safe distance and avoid approaching novelty for several months (figure 1). In both the Sumatran and the Bornean site, only a single (adolescent) individual was ever recorded as contacting the novel items, despite their being available for nearly five and over eight months, respectively.

Instead of individual exploration, orangutan infants take all their cues from their mother, especially during their first few years of life. Peering at close range at the mother’s activities results in interest and subsequent practice [31]. Begging plays the same role in food selection [53]. Exploration during the pre-weaning years is therefore predominantly targeted at the resources already exploited by the mother. Accordingly, infants largely ‘inherit’ their mother’s diet, even if different females in the same area eat different diets [31], and populations in the same habitat on opposite sides of an impassable river show marked differences in their non-fruit diets [23]. After weaning, when maturing individuals begin to range more

[47,48]. There is no evidence for this in orangutans [43,49], nor in chimpanzees and bearded capuchin monkeys [43], although others have suggested it is important among chimpanzees and capuchin monkeys [47,48]. In the case of orangutans, populations with more bark feeding (which happens in response to food scarcity) have smaller innovation repertoires [50]. Thus, just because particular innovations would strongly improve fitness does not mean they are therefore made.

Finally, systematic exploration in the absence of obvious eliciting stimuli suggests some level of genuine curiosity: deliberate, intentional searching for a new behaviour pattern, in the absence of any recognized problem or general scarcity. Such intrinsically generated systematic exploration can be playful and spontaneous. Any innovations that arise in this way can be ascribed to creativity. Although creativity is always accompanied by exploration, in the case of humans this may be brief, as most of the creative process takes place in mental simulation. Although modern humans sometimes show this, its importance in human history is contested [51]. Moreover, in non-verbal species it may be difficult to demonstrate that systematic exploration is not triggered by some need.

Overall, then, we expect accidental innovations and those that arise in response to a newly recognized problem (entries III and IV in table 1) to be the most common pathways to innovation among large-brained, long-lived organisms such as great apes.
fall-back foods [54]. The rarity of spontaneous exploration also argues against context VI, true curiosity.

Additional comparisons among orangutans, chimpanzees and capuchins [43] strongly suggest that feeding innovations often concern the most nutritious and thus most favoured food sources. In fact, most of the cognitively more demanding feeding innovations mainly concern high-quality foods [40,43], with few exceptions [47], thus suggesting that opportunistically encountered, clearly defined problem situations triggered innovations (as per context IV in table 1). Moreover, their presence is predicted by a null-model that links the specific innovation to the opportunities for it to happen, based on the frequency of encounters between the animal and the appropriate context [43].

Along with the near-absence of exploration, these correlations suggest that the majority of innovations arise accidentally or opportunistically (contexts III and IV in table 1), at least when it comes to subsistence. For now, this conclusion must remain based on plausibility, as it is difficult to conduct the relevant experiments: examining exploration and innovation rates by individuals facing extreme scarcity or finding themselves in novel habitats (or both).

4. Orangutans in zoos and rescue centres

The same study that examined responses to novelty in wild orangutans was repeated with zoo animals using the same and very similar sets of novel items [52]. The contrast was striking (figure 1). Zoo orangutans approached novel objects with the same latency as familiar ones, i.e. within seconds rather than months. Thus, zoo orangutans showed no neophobia.

In other work, we attempted to use the same criteria for innovations as used in the work on wild orangutans [5]. Lehner et al. [55] found that zoo orangutans have far larger innovation repertoires in comparison with their wild counterparts, even though they had far fewer generations to assemble them. Rehabilitant orangutans (ex-captives that are being cared for by humans in the enriched conditions of rescue centres and are often trained for release into the wild) are very similar to zoo orangutans in their response to humans and their general lack of neophobia (L. Damerius 2015, unpublished data). Indeed, the innovation repertoires of rehabilitants when in natural habitats significantly exceed those of wild populations with comparable intensity of observations (figure 3, taken from data tabulated in [22]).

The large size of these innovation repertoires strongly suggests unusual innovation rates among zoo and rehabilitant orangutans. Zoo orangutans, when provided with the conditions in which orangutans in some wild populations show particular innovations, not only tended to independently reinvent these same innovations, but also quickly produced several additional variants not seen in nature [55]. Similarly, in a study of water use by rehabilitant orangutans kept on an island in a river, Russon et al. [6] found that they produced various innovations that never been seen in the wild and are highly unusual for a species that normally avoids deep and flowing water. These results suggest that this difference is not merely owing to reduced neophobia among the captive orangutans, but also to more thorough exploration of the kind akin to curiosity-driven creativity (context VI in table 1).

It is important to assess whether the orangutan pattern also holds for other primate species, in particular other great apes. Do they also show high levels of neophobia and low levels of independent exploration in the wild, but show much less neophobia and more exploration in captivity? If so, one can reasonably assume that our hominin ancestors showed similar predispositions too.

A generally more neophobic response to novel foods and novel objects in the wild compared with captivity is not restricted to orangutans, but has been reported for many non-human primates [56,57], a finding recently replicated for spotted hyaenas [58]. In fact, the only species systematically benefiting from approaching novel items may be vagrant species (which therefore often encounter novel situations and items) lacking opportunities to acquire social information, or species living in risk-free habitats. Keas (Nestor notabilis), for instance, are parrots living in high mountains in New Zealand in a predator-free habitat. They show true neophilia [17].

Wild chimpanzees are conservative and unwilling to taste novel foods [59], but many readily accept novel food in captivity [60], as in orangutans. When presented with novel food items, captive chimpanzees were even more hesitant compared with gorillas and orangutans, and more frequently observed their conspecifics handling the novel items [61]. Captive chimpanzee infants are neophobic towards novel foods and pay attention to their mothers before ingesting it [62], suggesting the same pattern in the wild.

Less information is available for exploration than novelty response, and whether captive individuals engage more in independent exploration compared with their wild counterparts, as has been shown for the orangutans [52]. However, the contrast between wild and captive individuals reported for orangutans holds for several species with regard to innovations. Reader & Laland [63] noted that innovations are relatively more common among zoo-living primates compared with the wild. Many primate species can learn to use or even make tools in captivity when they would never do anything like it in the wild [64], and this effect may be found also in non-primate species [19,65]. Captive individuals are better problem-solvers in many species of mammals [58,66,67] and birds [65,68].

5. Explaining the contrast

The unexpectedly large contrast between wild and captive orangutans, and presumably other great apes as well, could
reflect increased response to novelty, increased exploration, more effective exploration or some combination thereof. We will discuss variation in novelty response and exploration, and also compare the results reviewed above with those found in other species.

(a) Novelty response

Given the risk of responding to novelty, individuals should generally benefit from avoiding it, provided they can acquire the relevant information otherwise. Thus, for species and individuals with access to reliable social information it is adaptive to be neophobic (in the functional sense of the term). Indeed, species with long life expectancy, for which the risk of injury or even death are weighted more seriously, should with rare exceptions routinely rely on social information. The data on orangutans fit this prediction, but so does work on other primates. First, observations on infants closely following adults and paying special attention to adults’ activities are reported for many primate species in the wild, from lemurs [69] to macaques [70] to chimpanzees [71]. Similar observations are reported for other mammals [72] and birds [73,74], as well as for captive primates [75]. Second, experiments show that naive individuals lose their neophobia when accompanied or provisioned by others, who may or may not be more knowledgeable [76–78], a finding replicated among orangutans [62,79].

The widespread preference for social information suggests that the role of novelty response in producing innovations may well have been overestimated [80]. If individuals can rely on social information when immature, they do not need to respond to novelty. Thus, novelty response is unlikely to have been a major source of innovation among many non-human primates [4,34,52,81].

In captive orangutans, novelty response may well be a major source of innovation, showing that it can be elicited under the right circumstances. The reduction in neophobia seen in zoo-living orangutans is best explained by the presence of human keepers who act as trusted role models in the same way that parents or other conspecific caretakers do in nature [52]. In effect, then, the captive animals are still relying on social information. In addition, the absence of any negative reinforcement of responses to novelty of all kinds in zoo settings no doubt also contributes to the erosion of neophobic tendencies.

Nonetheless, novelty response alone is unlikely to explain the observed captivity effect, because of the major differences in how and how many animals explore, discussed next.

(b) Exploration tendency

Our data suggest that wild orangutans are loath to explore. This can be explained by the costs it entails. First, it may entail immediate risks, as when potentially poisonous or dangerous prey or substrates are explored. Second, exploration, especially when ultimately unsuccessful owing to limited cognitive abilities, entails an opportunity cost, in that it can waste time and energy. Third, and presumably most importantly, the attention devoted to exploration may compete with other vital activities, such as attention to predators or hostile conspecifics [82,83].

We can therefore develop predictions based on variation in the external (ecological) and internal (life history, niche, age, etc.) factors affecting this trade-off between predation risk and exploration, based on earlier work on the deployment of exploration [63] and social learning [84]. However, in many cases, it will be difficult to disentangle the effects of novelty response from those of exploration, because studies of exploration inevitably tend to involve at least some novel elements. The predictions that can be made end up being quite similar to those for novelty response. In general, animals should avoid exploration if they can, unless they cannot afford to because they lack vital skills or resources or unless the risk is so low that it is outweighed by the benefits of learning. Social information should be sought whenever possible, because relying on it is faster and more efficient.

The negligible rate of independent exploration among wild orangutans fits these predictions. The larger innovation repertoires and more complex innovations generally seen among orangutans living in zoos or rescue centres suggest greatly increased exploration relative to the wild. Zoo-living orangutans are well-known problem-solvers, including extensive use of tools [85], and can be coaxed into producing innovations that go well beyond the range observed in the wild [38]. Likewise, Russon [86,87] describes the persistence and patience with which recently reintroduced, ex-rehabilitant orangutans in Borneo try to establish effective feeding techniques.

(c) Captivity effect

Various explanations have been offered for the captivity effect [7,19,58,66]. One hypothesis emphasizes that humans may act as role models for the animals in captivity [22,52]. Another stresses that animals in captivity have more leisure time owing to the absence of predators and because they do not have to forage for their needs [88]. We interpret this ‘free-time’ hypothesis to imply that captivity provides individuals with the opportunity to give a task undivided attention for a prolonged period of time, both for independent exploration as well as for exploration triggered by human role models. In nature, animals have a higher cognitive load: they are continuously distracted by various tasks that need to be attended to and coordinated as well as plans that need monitoring. Among these tasks, predator vigilance is perhaps most important in many species. Because attention is a limited resource, vigilance interferes with the animals’ ability to give a particular task their prolonged, undivided attention [58,66,83].

Each species therefore should have an optimum time allocation to exploration, which will largely depend on its safety level. Species living at lower risk of predation should therefore be able to solve more problems or to solve the same problem faster than species with lower levels of safety and thus higher levels of necessary vigilance. Thus, all other things being equal, we may expect relatively more prolonged exploration, and thus innovation, in larger rather than smaller species, in arboreal rather than terrestrial species, or species with large groups rather than living solitary, and in species with sentinels rather than those lacking them. Although these predictions have not yet been tested systematically, some observations support them. For instance, keas do not just lack neophobia, they are also extremely exploratory [17], whereas a comparative study on over 60 parrot species revealed, among other results, that parrots on islands are generally less neophobic than their mainland counterparts [89].

Obviously, brain size should be linked to attention span as well: it does not pay to evolve extensive problem-solving abilities if these can never be used. Even if a species relies nearly
exclusively on social learning to acquire its skills, this still requires reasoning capacities and prolonged undivided attention because social learning involves many of the same basic cognitive abilities as asocial learning does [90, 91].

6. How about our ancestors?

It has often been noted (e.g. [92]) that the rate of change in human technology was remarkably slow, at least when assessed based on the visible parts of the palaeo-archaeological record (i.e. stone artefacts). This strongly suggests that for a long time hominins were very similar to great apes, although at some point in pre-history the rate of change picked up markedly. It also suggests that the ape strategy may also still be common in humans. Indeed, the default strategy of learning by human children remains copying if it is available, even if it is unreliable [93]. The same conclusion follows from a tournament organized by Rendell et al. [94], in which the aim was to acquire as much adaptive behaviour as possible in a complex environment. The most successful strategies focused quite heavily on social learning, and only switched to independent exploration when they could observe no useful innovations from others. The tournament was competitive, and social learning was only possible because agents inadvertently demonstrated the most effective techniques. Thus, if teaching were added, there would even be less incentive to engage in costly independent exploration.

Routine reliance on copying and avoidance of independent exploration (unless socially induced) may therefore have been the basic ancestral state in humans as well [51]. As with apes, then, the default human state is a preference for social learning. Innovations can nonetheless accumulate in a population over time because of the combination of various other pathways to innovation (table 1) and effective social transmission, especially when teaching is involved.

The number of innovations, in terms of both complexity and diversity of artefacts, gradually increased, but especially during the Upper Palaeolithic Revolution and even more clearly since the Neolithic [95]. One explanation for this increase is that it was merely an effect of increased population size. Thus, even if innovations continue to be produced by processes other than creativity, larger populations will show more and more complex innovations, which may create a positive feedback loop without any systematic exploration [51, 96]. However, an alternative, or non-exclusive additional possibility is that the reluctant explorer was turned into a curious and creative explorer under particularly safe conditions (table 1: necessity-induced [V] or creative [VI]).

The striking captivity effect in orangutans and other primates may help to explain whether the explosion in cultural complexity was owing to creativity or more passive processes. The disappearance of neophobia and the strong increase in exploration among captive orangutans allows creativity to blossom. This shift is analogous to becoming a top predator, which frees up the mind to explore. This may have happened gradually. Some technological innovation, such as the appearance of stone-tipped weapons or spear-throwers on the eve of the Upper Palaeolithic [97, 98], may finally have turned our ancestors into the top predators in their ecological communities, and so made them virtually immune to predation. The timing of this change corresponds to a major leap in the complexity and diversity of technology known as the Upper Palaeolithic Revolution. Even if it was more gradual than previously assumed [99], there was still a remarkable increase in the rate of cultural change, which has never slowed down since.

This scenario of reduced predation risk as the engine of creativity is plausible. For instance, when people experience the so-called flow and are at their most creative, they are totally oblivious to distractions in the environment [1]. Thus, these flow experiences are only possible when not under high predation pressure or other distracting concerns. However, although the absence of predation risk is a necessary condition for such concentrated creativity, it is not enough without there being clear incentives for the curious individuals to engage in systematic exploration. Individuals may have begun benefitting from trade based on the appearance of specialization, which in turn is linked to the number and complexity of learned skills needed in daily life. Alternatively, it is possible that at some stage, owing to the establishment of cooperative breeding [100], joint innovation became favoured [101].

Regardless of when exactly human creativity began to flourish, it seems safe to conclude that the virtual absence of creativity in wild orangutans and many other species indicates that our ancestors were not creative until relatively recently. In fact, the results provide some support for the alternative view that until quite recently the feedback between constant rates of accidental innovation and demography provides a plausible alternative to enhanced creativity for changes in human cultural complexity.

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