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The importance of thinking about the future in culture and cumulative cultural evolution

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Thinking about possibilities plays a critical role in the choices humans make throughout their lives. Despite this, the influence of individuals' ability to consider what is possible on culture has been largely overlooked. We propose that the ability to reason about future possibilities or prospective cognition, has consequences for cultural change, possibly facilitating the process of cumulative cultural evolution. In particular, by considering potential future costs and benefits of specific behaviours, prospective cognition may lead to a more flexible use of cultural behaviours. In species with limited planning abilities, this may lead to the development of cultures that promote behaviours with future benefits, circumventing this limitation. Here, we examine these ideas from a comparative perspective, considering the relationship between human and nonhuman assessments of future possibilities and their cultural capacity to invent new solutions and improve them over time. Given the methodological difficulties of assessing prospective cognition across species, we focus on planning, for which we have the most data in other species. Elucidating the role of prospective cognition in culture will help us understand the variability in when and how we see culture expressed, informing ongoing debates, such as that surrounding which social learning mechanisms underlie culture.

This article is part of the theme issue 'Thinking about possibilities: mechanisms, ontogeny, functions and phylogeny'.

1. Introduction

The human species is remarkably adaptable. We thrive even in inhospitable terrestrial environments and our numbers have burgeoned across the globe since *Homo sapiens* evolved from our early hominid predecessors. These extraordinary human achievements are often attributed to the collective knowledge preserved in our cultures, or group typical behaviours generated by learning from others (social learning), and our ability to improve shared traits over time without requiring each generation to re-learn from the start (cumulative cultural evolution; [see 1–4] and table 1 for definitions). While many animals are said to exhibit these cultures or behavioural traditions), there are fewer clear cases of cumulative cultural evolution in nonhumans (discussed in [5]). Why humans experienced unapparelled cultural expansion and cultural improvement across their history is the source of much deliberation. One useful way to answer this question is to take a comparative approach that focuses on similarities and differences between humans' and other animals' socio-cognitive abilities.

Significant effort has focused on explaining what cognitive mechanisms underpin and support culture and cumulative cultural evolution. Many prerequisites have been proposed, including invention, creativity, copying error leading to variation, attraction to memorable traits and a plethora of social learning mechanisms. Others have been proposed for cumulative cultural evolution specifically,

Table 1. Table of important terms and their definitions.

term	definition
social learning	learning from the behaviour of others or their products; mechanisms include social facilitation, local enhancement, imitation and emulation, among others [4]
culture	group typical behaviour afforded by social learning [2]
cumulative cultural evolution	cultural modifications representing improvements, whereby traits typically become more complex or efficient across generations, that go beyond what an individual alone can invent [5]
planning	advance thinking about the action course needed to achieve an immediate goal
future planning	advance thinking about the action course needed to achieve a future goal
prospective cognition	future-orientated cognition that includes planning, simulation, prediction and intention [6]

including the predominantly human propensities to imitate, teach, cooperate and read others' minds (reviewed in [3]), as well as our advanced technical reasoning [7]. However, one potential mechanism that has received significantly less attention is prospection. Prospection is the ability to represent future possibilities and includes a range of future-oriented thought processes which can be grouped under the term 'prospective cognition' ([6]; table 1 and subsequent section for additional detail). We find the lack of attention surrounding the role of prospective cognition in culture and cumulative cultural evolution curious as they seem interconnected. At the very least, many described cultural behaviours involve actions to achieve a future goal, such as transporting certain tools to a place where they are useful or using multiple tools in sequence. We thus propose that a fuller understanding of the context in which we should expect cultural behaviour and, especially, cultural improvement, should include an understanding of that species' prospective cognition.

In particular, we propose that prospective cognition may aid culture in two specific contexts: first, it may support the development (invention) of certain types of cultures that are focused on behaviours with future benefit, such as food preservation techniques or, in humans, the development of habits that promote long-term wellbeing (healthy habits, saving money). Second, it may allow for a more flexible implementation of cultural behaviour, as individuals can take into account how behaviours may or may not be beneficial in the future (figure 1). These may be useful in facilitating cumulative cultural evolution as groups incorporate habits and behaviours that benefit them into cultures (e.g. cultural norms of what to eat: avoiding certain, toxic, foods and seeking out others such as medicinal plants), and then those beneficial cultures are selected and developed upon (modern medicines). This latter proposal makes a corollary prediction that species with prospective cognition may be able to flexibly implement cultural behaviour based on future needs (i.e. understanding the goal and deciding whether or not to work towards it).

By contrast, we argue that cultural behaviour may also act as a stand in for those without prospective cognition, promoting behaviour that will benefit the organism in the future (through the observation and social learning of successful group mates' behaviours), without the organism needing to understand or make predictions about the future. That is, organisms may develop cultural behaviours that benefit their futures, either by simply learning from others, a successful strategy as individuals often perform the best performing behaviours in their repertoires [8] and so beneficial behaviours are selected for, or because some subset of the population is able to plan for the future and so establishes a beneficial culture (or a mix of both).

Although these proposals differ markedly in the relationship between cultural processes and prospection, they make the same prediction—that knowing what forms of prospective cognition a species has will predict in what contexts we may find certain kinds of cultural behaviours and, conversely, that knowing a species has a particular form of cultural behaviour may suggest that we should look for underlying forms of prospective cognition. However, they differ on some of the specifics. On the one hand, the former predicts more flexible, goal-directed behaviour focused on solving future needs, whereas the latter suggests a less comprehensive approach, potentially with less well-adapted responses because they are more heavily reliant on chance. That being said, it may not be possible to discriminate the two without knowing enough about a species' prospective cognition to make specific predictions about how it might manifest in a given situation. In both cases, however, incorporating a focus on future-oriented thinking is useful in predicting which species should be studied, in which cases prospective cognition is shaping culture and in which culture is substituting for prospective cognition, providing a better understanding of how cultural behaviour differs among species.

2. Thinking about possibilities in time

Thinking about possibilities is contextualized by our perceptions of time. As humans, we are not trapped in the present; rather, we think back upon past opportunities and speculate about the future. This ability to think about future possibilities has presumably conferred adaptive advantages: by thinking about possible future events, humans—or any species that does so—can engage in planning and potentially mold their actions to gain control over those events [9]. Research on this ability has grown substantially over the past few decades owing to its important function. One consequence of this growth has been the emergence of numerous terms whose relations with one another can be difficult to track. Here, we adopt an organizational framework proposed by Szpunar and colleagues [6], broadly defining prospective cognition as the ability to represent future possibilities. According to this framework, prospective cognition encompasses several modes of future-oriented thought including planning (pre-empted steps to meet a goal), prediction (estimated likelihoods), simulation (mental representations of the future), and intention (mental act of goal setting) [6]. Each of these modes can include content that is episodic (relating to a

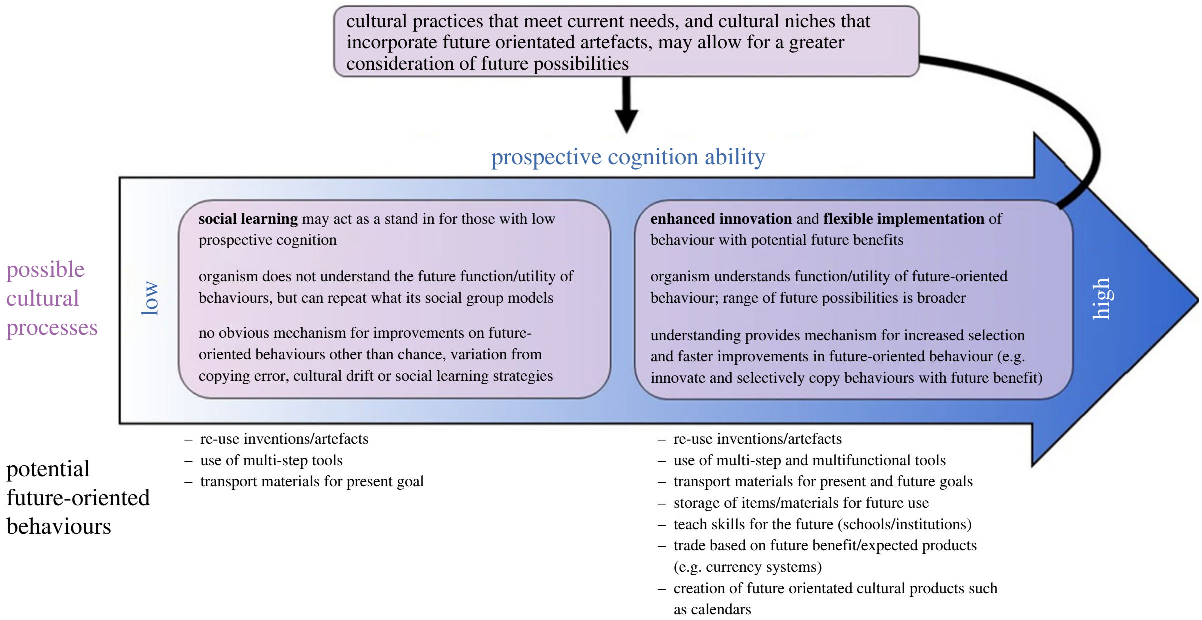

Figure 1. Schematic of the hypothesized relationship between prospective cognition, culture and cumulative cultural evolution.

specific personal experience), semantic (relating to general knowledge of the environment) or a mixture of both. Simulation, for instance, can involve constructing a projection of oneself at a specific future event (episodic simulation) or a representation of a future state of the world (semantic simulation).

Because of its relative prevalence in experimental tasks across species (discussed below), we will mainly focus on what planning offers culture by studying it from a comparative and developmental perspective. We will review what is known about planning for a future goal (that is, *future planning*), as well as planning how to complete a sequence of actions for a more immediate goal (*planning* in general). Finally, though our primary interest is in cognition, it is important to note that animals (including humans) do not have to actually *understand* the future benefits conferred by their behaviours. While it is easy to infer that future-oriented traits emerged because of such an understanding, with animals behaving *as if* they understand potential future gains, these traits could have been selected through a range of other proximate mechanisms (as discussed more in subsequent sections).

3. The ontogeny of human prospection

Infants appear largely stuck in the present when born. As they get older, they begin to exhibit behaviours that suggest an expansion of their temporal world into the past and future. A large body of research indicates that this temporal expansion is marked by protracted developmental improvements in their ability to not only remember the past, but to also represent, mentally simulate, and plan for future possibilities [10–12]. Here, we take a closer look at the development of prospective cognition in humans (see [6]). Since the human literature on planning is extensive, we focus largely on children's developing ability to plan for future, rather than immediate, goals (e.g. packing a toy to play with during a trip scheduled for tomorrow). We also limit our discussion to future planning studies that have used tasks of episodic foresight, while acknowledging the breadth of other important work on this topic (see [13] for a review).

Episodic foresight is the ability to mentally project one's self into the future in order to pre-experience possible situations or scenarios [14]. It is considered the future counterpart to episodic memory as it involves mentally simulating the 'what, where, and when' details of a personal future event [15]. Since language limitations make it difficult to assess this ability via verbal report in young children, many studies have instead assessed behaviours that suggest a consideration or anticipation of possible future events. The behavioural tasks used by these studies share similarities with those used to examine future planning behaviour in non-human animals, providing valuable data for a comparative perspective.

The most common assessments of episodic foresight in young children are versions of Tulving's 'spoon tests', in which, in the original, a girl pre-emptively clings to a spoon that will be needed to eat her dessert the next day [16]. These tests establish an anticipated need or goal, and then assess whether children successfully select an object that will meet that future need or goal. In one such study, Suddendorf *et al.* [17] showed 3- and 4-year-olds a locked box containing a sticker. After appearing to break the key needed to open the box, the experimenter brought the child to another room for a 15 min delay. Upon being told they would be returning to the original room, children were asked to choose one of four keys to bring with them. Only 4-year-olds selected the correct key at an above-chance level, suggesting they were anticipating the future to open the box. Similar approaches have shown increases in future-oriented behaviour between the ages of 3 and 5 years, including studies examining children's ability to select objects that meet a future physiological state [18] or play a future game [19]. Together, this work converges to support an emergence of future-oriented behaviour between the ages of 3 and 5 years old.

A debated question is the extent to which the reviewed findings reflect the development of future planning and/or episodic foresight in young children. One concern with spoon tests is that performance may be more reflective of developmental differences in memory (e.g. choosing the key that will open the box in the future requires remembering which key opens the box). Though there is some support for age-related improvements being driven by memory [20], other work has found that age effects remain even when memory is high across age groups [21]. Additional concerns surround the extent to which these tasks can be solved without considering the future at all (e.g. through simple associations; [12]). While methodological limitations make it impossible to fully address these concerns, creative paradigms have attempted to mitigate interpretive difficulties by placing additional demands on processes inherent to planning and/or episodic foresight (e.g. temporal reasoning, novel generation and self-projection; e.g. [22–24]). Performance on these more complex tasks is sometimes lower than that observed in simpler versions but is largely consistent with the presence of future-oriented behaviour by 5 years of age. This developmental pattern is also supported by a handful of studies that have assessed episodic foresight using more direct verbal methods with young children (e.g. asking the child to describe 'yesterday' and 'tomorrow' events [25,26].

The reviewed work indicates there is an emergence of—and improvements in—behaviours consistent with future planning and episodic foresight between the ages of 3 and 5 years. While spoon tests are typically not used with older children given their ceiling performance, developmental improvements in language make it easier to collect verbal reports of mental content. Using this approach, studies have shown protracted age-related improvements in children's ability to report possible future events that are personal, specific, and episodically rich between 5- to 9-year-olds and adults [27], as well as across childhood and into adolescence [28,29]. Altogether, this rich literature documents the emergence of behaviour consistent with future planning and other forms of prospective cognition between the ages of 3 and 5 years, as well as continued improvements in prospective cognition across childhood and into adolescence (e.g. [9,11,30]). While the majority of this human work has considered the advantages of future thinking from the perspective of the individual (e.g. improved decision making or spatial navigation; see [31]), we speculate that these advantages extend to one's social group, perhaps allowing for more flexible implementation of cultural behaviour (see below for further discussion).

4. The phylogeny of prospection

Since the turn of the ninteenth century, philosophers and psychologists have deliberated the question of whether other animals are mentally bound to the immediate present. Today, though the debate continues, there is some consensus that animals behave in ways that benefit their futures (think of food caching birds or beavers constructing dams). The current debate centres more around whether these acts are primarily owing to associative learning or fixed action patterns rather than planning. This has implications for what they understand about their futures, including whether (and which) animals are not tied to their perceptual present and which capacities they share with humans [32].

Various approaches have been taken to study future planning in animals, typically focusing on whether they can appropriately pick the right object (food, tool) or location depending on what happened in the past or what they (presumably) expect to happen in the future. Female chimpanzees of the Tai forest, for example, preferentially select sleeping sites close to short lived, high-calorie fruit sources over sleeping sites bearing other fruits [33] and cuttlefish eat a smaller amount of a less-preferred food when they know they will get a better option later [34]. Western scrub jays also remember when they cache food, where it is located and what food they stored [35], which allows them to selectively retrieve preferred but perishable food after short delays but skip retrieving spoiled food after longer delays. With respect to tool choice, early studies on animal planning adapted the spoon task [16] for comparative use, testing orangutans', chimpanzees' and bonobos' abilities to select and save a functional tool that would be useful later to retrieve an out-of-reach reward from a larger array of available tools [36,37]. Much like children, the apes saved functional tools for future use (for up to 14 h), leading the authors to conclude that human future planning probably evolved from precursors shared with an ape common ancestor. This may be too narrow a scope, however; appropriate tool selections according to future needs are not limited to the great apes. For example, Goffin cockatoos (*Cacatua goffiniana*) also demonstrate flexible selection of tools for an anticipated, better-paying task, which required forgoing an immediately available reward [38].

Given the current debate over whether tool selection is because of knowing its usefulness and value in the *present* moment, recent tasks have begun to include two tool-apparatus combinations, requiring subjects to choose between two valuable items. In these tasks, New Caledonian crows (*Corvus moneduloides*) inhibit selection of a previously useful, rewarding tool and instead opt for the now correct tool needed for a future task [39], suggesting they understand when the item is useful, rather than simply recognizing *that* it is useful. Such behaviour begins to rule out past tool-reward associations as the reason individuals prefer a tool, strengthening the case for future planning. The current phylogenetic distribution of future planning behaviour suggests that this ability is so important that it has been selected in a variety of different ecological contexts. In particular, we see it in species that cache, use tools, and/or have complex social dynamics, although there is a disproportionate amount of research effort devoted to the study of primates and corvids, so it is too early to rule out other potentially relevant factors.

One challenge to interpreting these data relative to planning is that we do not know the degree to which these species understand the future, or whether they have simply learned these future-oriented behaviours through trial-and-error based experience. Behavioural tests rely upon many abilities, which can make it difficult to disentangle underpinning mechanisms [40]. Studies with children indicate the important role of past reinforcement/practice in these tasks, emphasizing how critical it is to consider the role experience plays when interpreting results. For instance, 4-year-olds can correctly choose which of two tools is needed for a future task when they have used the correct tool in the past, but fail to do so when they have used both tools in the past, suggesting their tool choice may be based more on associative learning than a consideration of the future [41].

Of course, regardless of the degree to which they understand it, the fact that other species act *as if* they understand the future suggests that it is sufficiently useful that there has been selection for behaviours that fill this role. As we discussed earlier, one benefit of considering culture in relation to prospective cognition is that it might help us understand some of the variability in the expression of cultures, if, for instance, prospective cognition allows individuals to flexibly determine which patterns of behaviour to copy and in what contexts. This probably does require at least some ability to consider the future. However, it is not essential; we may find situations in which animals and humans act in ways that will benefit them in the future even if they do not have an understanding of the future *per se*, something we discuss in more detail below.

5. The impact of planning on the development of culture and cumulative cultural evolution

One key advantage of prospective cognition, we have proposed, is that it allows individuals to flexibly copy who, what, and when they want to meet future goals. Indeed, humans are quite good at this. We develop traditions surrounding storage, shelter, and institutions, equipping ourselves—and future generations—for what is to come. Many human cultural artefacts and technologies required forethought and future planning, suggesting that prospective cognition may have enabled the development of some cultural products [42]. Our question, then, is the degree to which other species' cultures show evidence of future planning.

Much work in animals has focused on tool behaviours, which allows us to explore how other species solve problems that, in humans, benefit from advanced planning [43]. Among the primates, chimpanzees, are a particularly good model for several reasons. First, they show more than 39 cultural behaviours in the wild [44], of which 30 involve tools [45]. In addition, they manufacture tools, use tool sets of multiple tools in sequence to achieve a goal, and transport tools to the location at which they are needed. These three factors (tool manufacture/sequenced tool use/transporting tools and their re-use) appear to require at least forethought and planning, suggesting that prospective cognition could also play a role in animal cultures and, perhaps, their cultural complexity. We consider each of these factors in turn.

The first, tool manufacture, is postulated to require forethought or a degree of future planning [43]. That is, individuals must find, fashion and even transport items (the third factor) before goal attainment, suggesting that they must, to some degree, plan by representing conditions not perceptually available to them in the moment. Although tool use is rare among animals for a variety of reasons unrelated to planning (lack of ecological necessity, lack of available tools, lack of any number of cognitive abilities), this postulated role of future planning seems to us a key one (see [46] for an in-depth discussion of animal tool behaviours). Indeed, detachment from the immediate by planning can spur novel, complex technological inventions and modifications that are essential to cultural evolution, and, along with cultural flexibility, are a potential benefit of prospective cognition.

Considering an example, chimpanzees' tool manufacture and modification is suggestive of a degree of planned actions. They can both innovate and socially learn to combine tools to lengthen them to gain items that are otherwise unreachable [47], generalizing this behaviour to novel contexts [48], and they can detach tool sections to create functioning probes and straws [49,50]. In the wild, the flimsy stems and twigs used by these primates in the Republic of Congo to fish for insects are modified by fraying the ends to make the so-called 'brush tipped probes', an innovation that improves tool efficiency [51,52]. This latter behaviour occurs almost exclusively prior to interaction with the nest [51,52], suggesting that it may be intentional [53]. Though tool use is present in a number of species, typically corvids and primates, tool modifications to attain goals, such as the ones described here, are much rarer; to the extent that this is accomplished without prospective cognition, it may suggest that these species also will not be as flexible in choosing which cultural aspects to copy at which times (social learning strategies that dictate who, when and what to copy are present in diverse taxa; see [54]), but the extent to which prospective cognition promotes enhanced selectivity in some animals is yet to be considered. Indeed, if this hypothesis is accurate, we would predict that tool manufacture will covary with flexibility of copying (from whom, in what contexts), presumably owing to the degree of prospective cognitive involved.

It seems likely that the second factor, sequenced tool use, also involves planning. In tool kits, specific tools, often made out of different materials, are used in sequence, during extractive foraging bouts. In the Goualougo triangle, apes often use multiple tools in sequence, for instance pounding food sources with stout branches before selecting less robust twigs and stems to probe for honey and insects from nests [51,52,55]. When nests are elevated, a perforating twig, instead of stout sticks and branches, is used to open the termite tunnels on the outer surface nests. The specificity in their tool use in sequenced actions, with different tools for different functions, suggests that they have not simply extrapolated the use of one tool to several different tasks. Further, the chimpanzees in this area adjust the hierarchical order of their tool sequences according to external conditions [55], displaying some flexibility in behavioural steps. Highly flexible and complex tool extraction sequences have similarly been observed in chimpanzees extracting honey from subterranean tests in Loango, Gabon [56]. If tool choice and order are determined prior to engaging in the tool use behaviour, this suggests to us a degree of flexibility that may indicate they are deploying their group's culture in the contexts in which it is to their benefit.

Complicating this picture, we cannot rule out the role of trial and error driven by immediate goals (e.g. if tool A does not work try tool B or C) rather than planning in the development of sequential tool use. Indeed, a recent detailed analysis of termite fishing behaviours in young chimpanzees documented the onset of easier actions (probing to collect termites using existing or manual openings) prior to more difficult ones (puncturing nests open) that required more physical strength [57]. Because the physical constraints mean that each behaviour was learned separately before combining the two actions into a behavioural sequence, this could be an example of behavioural chaining rather than planning. However, infants and juveniles, despite lacking the physical strength for success, still *attempted* to puncture holes in subterranean nests, making it difficult to tease apart planning versus sequential tool use by trial and error. In addition, as we discuss below, it could be that they learn a functional sequence of behaviour with no understanding of how it aids success, which would be an example of a cultural behaviour (if social learning is involved) substituting for prospective cognition. Unfortunately, this difficulty highlights the challenge facing any researcher exploring prospective cognition, whether or not in the context of culture; especially with observational studies, it can be very difficult to determine why subjects choose an order or what previous experiences they may have had that taught them via trial and error rather than an understanding of the future benefits of their actions (indeed, the same can be said of cultural learning).

Finally, the third factor, the transportation and reuse of tools according to potential risk, location and need, strongly suggests the influence of thinking about future benefits on a cultural behaviour. For instance, chimpanzees cracking nuts routinely reuse and transport hammers and anvils to where they are needed [58]. Furthermore, at this site's outdoor laboratory, chimpanzees were observed to preferentially transport nuts and stone tools when competition for resources was high, moving away from the provisioning site and potential competitors [59], suggesting that they understood both what tool they needed *and* the consequences of not bringing their own. Conservation of tools for future use occurs in other contexts and locations as well; chimpanzees in the Goualougo triangle keep their stout pounding and puncturing tools but discard their flimsier tools used to collect insect prey and honey [43]. Unfortunately, again, while these findings suggest anticipation of future use outside immediate contexts (future planning), we cannot rule out alternative explanations, such as saving tools because they are favoured or transporting a tool because it is perceived as valuable.

The larger question, of course, is how prospective cognition is linked to these cultural behaviours. To the extent that future planning is involved (which, as we detail above, is still open for debate), a conjunction between future planning and culture may contribute to the overall complexity and flexibility of these behaviours. For instance, perhaps these tool use behaviours are flexible because the chimpanzees understand how they are linked to their desired future outcomes. If so, this could suggest that, as in humans, future planning, and potentially other forms of prospective cognition, can open the door to new forms of cultures in animals that possess the necessary causal cognition to, first, create functioning tools or, more broadly, any complex behaviour or artefact, and second, understand well enough the causal power of different acts or artefacts to allow selective transmission in the first place. This is easily testable; if true, animals displaying relatively complex cultures (such as the invention and social transmission of tool modification or sequenced actions) should also show elements of prospective cognition (such as future planning) and vice versa, that animals which show future planning should also evince more complex cultures and/or more flexible deployment of cultural variants. More specifically, we postulate that future planning is especially important in two ways. First, future planning can help generate new or more complex behaviours as a spur for initial innovation and modification. Second, future planning could aid in the selectivity needed at the stage of social transmission, prioritizing behaviours that pay in the future (selective social learning strategies such as 'copy in proportion to future payoffs': [42, p. 226]).

Further, consideration needs to be given to the potential limitations or constraints in future planning and what it means, if anything, for the extent of cultural capacities. For example, does the fact that children plan more steps ahead than their primate relatives [60,61] allow them to better recognize the future benefits of others' behaviour? That is, with extended projection of one's future and future planning, individuals may be in a better position to recognize observed behaviours that are not presently useful but could be later on, enabling onlookers to prioritize learning of acts that are deemed valuable to their future success. In this sense, prospective cognition may enable users to pay greater attention to, and preferentially copy, certain behaviours they foresee experiencing because of the benefits that they can predict. If no such solution is witnessed for a predicted scenario, this projection could also prompt individuals to pre-emptively invent new solutions, and modify, or recombine, old behaviours. This may provide more time and/or motivation for behavioural refinement than can occur when inventions are confined to relatively short periods around immediate conditions. Taken together, they could lead to new, cumulative improvements that become cultural (new inventions and dissemination thereof according to traits' predicted values). Such enhanced recognition of behaviours that *could* pay off might help explain differential use of pay-off-biased social learning strategies between the species, in which children's switching to observed behaviour is predicted by the payoffs gained by others, whereas chimpanzees' is by the value of rewards they themselves received [62].

Another question is whether planning for *multiple* plausible futures facilitates cultural improvement by adapting innovations to alternative circumstances, or improves social learning by encouraging the learning of numerous strategies that could prove useful in different variations of future events. We know that primates can predict outcomes based on past knowledge (e.g. [63–65]), but less is known about whether they plan behaviours based on multiple, possible outcomes. Recent findings suggest that 3- to 4-year-old children plan for more than one future event by pre-emptively placing each hand under two potential exits for a single reward, whereas other apes had difficulty with the same task ([66–68] but see [69]). Planning for potential, upcoming variations of future events may prove useful in improving cultural traits and artefacts by adapting them to function in numerous scenarios, as is the case for multifunctional or adaptable tools (e.g. universal socket wrenches and Swiss army knifes); a potentially important driver of cumulative cultural evolution. Whether humans are indeed better equipped for simulating multiple futures requires further empirical evidence, as does the degree to which our shared knowledge improves consideration of future possibilities because we can learn from others' experiences [40].

Lastly, there may be other cognitive abilities that influence prospective cognition. For instance, while animals can inhibit, or delay gratification, for fairly long periods of time [70], seemingly essential for any behaviour that involves future planning, their inhibitory ability can be surprisingly inflexible, with animals struggling to inhibit previously learned outcomes in order to learn new, better, ones [71–73]. This is a significant constraint on evolving cultural complexity, which, in humans, often involves solutions or behaviours of ever-increasing complexity, as in cultural 'ratcheting' [74]. It may also constrain animals' ability to use future planning to recognize potentially beneficial innovations or prioritize different behaviours in different contexts. Similarly, differences in the forms and/or strength of causal reasoning across species may limit problem solving and constrain the content of plans, in turn impacting the developmental space for cultural traits. As discussed by Seed & Laland [40], while some primates and corvids share with humans the recognition of relevant tool properties (e.g. their length), they fair less well with understanding deeper causal relationships, such as the properties that are perceptually opaque (e.g. gravity) that help humans construct general theories of hidden causation. These general theories of causation and the ability to reason about opaque forces, with our enhanced ability to simulate conditions not yet incurred (generate novelty: [40]), may partially explain why humans remain outliers in their innovativeness, again highlighting the importance of prospective cognition for cultural innovation and improvement.

Of course, this is not to suggest that prospection is always required for successful inventions. As noted by Mesoudi [75], human foresight is often inaccurate and human culture has still done very well through processes including serendipitous discoveries and learning through blind trial and error. Indeed, this last point reiterates our earlier one, that in some cases culture may stand in for prospective cognition when cultural changes are driven by processes that involve no future-oriented cognition but nonetheless result in outcomes that benefit the organism in the long run. On the one hand, of course, this seems contradictory to our earlier argument, given that the path from culture to prospective cognition runs in a different direction. However, in either case prospective cognition and culture are related. Indeed, if, as we argued earlier, prospection supports culture both through planning for the future goals and flexible deployment of cultural behaviours, we might expect to see a de-coupling of cultural behaviours that support future benefits and flexibility when culture is standing in for planning (figure 1). In addition, given that cultural behaviours which benefit the future arose because they are selected for other reasons, drift or pure luck, and happen to provide future benefit, there is a limit on the breadth and complexity that we would expect. Specifically, prospective cognition opens the door to a new level of novelty afforded by planning for future scenarios, through simulating conditions beyond the present or those that are directly perceptually available. Without this ability, and the necessary causal reasoning (discussed above), inventions can only progress so far before their complexity and efficiency plateau, rendering selective social learning of successful behaviours insufficient as it, alone, cannot modify behaviour [76].

6. The impact of culture on the development of prospective cognition

While we have made a case that prospective cognition influences the degree to which animals innovate and flexibly deploy cultural behaviours, the reverse may be true as well, with culture influencing how, when and in what contexts prospective cognition develops. At the most basic, of course, culture allows the time and space to develop future goals. Routine tasks, such as planning routes to work, involve many cumulative inventions across generations that yielded pathways, trains, buses and cars. In many cases, the advent of these cultural products (e.g. agriculture and institutions that trade in consumables) alleviate present motivations, such as the need to forage or to cultivate produce. With basic needs met, a shift towards prospective cognition and the pursuit of goals in the distant future can occur, spurring modes of future thought [42]. Social learning also allows users to learn from the experiences of others, which in turn may improve the accuracy and breadth of prospective cognition as individuals can prepare for events they themselves have not experienced, but have gained knowledge of through interacting with others. This opens additional possibilities to consider the future, which will probably open even more possibilities, creating a continuously increasing opportunity. More specifically, the content of one's culture, at least in humans, should impact the content and expression of prospective cognition, including the extent to which the future is prioritized over past or present times. Indeed, the few studies that have examined this idea suggest that culture has important consequences for modes of prospective cognition. Human cultures differ in the content and emotional valence of memories of the past and imagination of the future [77,78], as well as in the level of specificity of the information they provide [79]. Asian and Asian American college students, for example, are less likely to imagine future events from a third-person or observer perspective than European American students [80]. Culture also influences orientation towards the past or future [81] and how we perceive time can influence how we prioritize our goals. For instance, differences between European Canadians and Chinese/Chinese Canadians' temporal focus (thinking about the past or future) explains whether they attached more monetary value to past versus future events [82].

These effects of culture on prospective cognition are evident from an early age. Indeed, culture is so strong that parents' or others' culturally mediated future projections for children can influence their developmental course; in some cases, cultural differences in expectations about the timing of infant milestones may impact when they occur. For example, Jamaican mothers projected that their offspring would sit at a younger age than English and Indian mothers expected, and the ages children met some motor stages closely matched these cultural mediated expectations [83]. This may also be the case for behaviours related to prospective cognition; Chinese children delay gratification longer than British children, possibly owing to cultural differences in parental expectations of impulse control and willpower [84]. Similarly, Carlson *et al*. [85] found that delay-of-gratification in preschool children has increased, with children in the 2000s waiting approximately 2 min longer than children in the 1960s (irrespective of age, sex, geography and sampling effects). The authors speculated that gains may be owing to increases in symbolic thought and changes to culture (cultural evolution) such as to our technologies, preschool education and public attention to executive function skills. These findings suggest that culturally determined expectations on cognition related to prospection can have direct consequences on their development in young children.

All of these examples, of course, regard humans. While the power of culture to impact cognition is impressive, it remains to be seen whether similar effects are evident in other species. Perhaps humans are uniquely susceptible to cultural influences, but the fact that group culture can influence animal tool use (e.g. the types of materials chimpanzees choose to crack open nuts or the tools they use to extract honey; [86,87]) suggests that similarly strong pressures, at least in theory, could exist in other species. Thus, the question for other species becomes two-fold; how is prospective cognition influencing the development and flexible deployment of culture, and how is culture, in turn, influencing the ways in which prospective cognition develops.

7. Future directions

Once heralded as a distinguishing feature of humans, comparative studies are providing provocative examples of prospective cognition in the broader animal kingdom, a feature that may be important for understanding another former bastion of human uniqueness, culture. While we argue that this relationship is important for understanding how culture manifests, there are other implications. For instance, this perspective could contribute to the ongoing discussion around which social learning mechanisms underlie culture. Indeed, rather than suggesting that some mechanisms are capable of supporting culture and others are not, we would argue that they do it in different ways. Specifically, species with prospective cognition may be able to more flexibly implement culture, suggesting that they may benefit from emulation (recreating others' end-states or goals) or imitation (action/intention copying), in which they understand the goals of the target and can decide whether or not to copy the behaviour based on their own future needs. Similarly, perhaps prospective cognition plays a role in human over-imitation, by augmenting over-imitation when the future value or reason for a behaviour is opaque, leading individuals to blindly copy irrelevant behaviours because they could eventually be useful to them (over-imitation). Conversely, species that lack prospective cognition may be unable to consider how a behaviour will affect their future needs and so culture may be transmitted via different processes, such as stimulus/local enhancement or different social learning strategies (e.g. copy successful individuals rather than traits with future benefit). If it is the case that both prospective cognition and imitation/emulation require similar higher-level cognitive abilities, it may be difficult to separate whether one enhances the other or whether they co-occur given sufficient cognitive development, but thinking in this way may nonetheless help us make predictions about species' abilities.

Related to this first idea, we predict that, if prospective cognition is important for the flexible adoption of cultural traits (owing to the capacity to innovate and recognize an observed behaviour's future value to oneself) species evidencing these forms of cultures should display prospective cognition and vice versa. A good starting point is determining whether the phylogenetic spread of prospective cognition aligns with complex (e.g. cumulative culture) or flexible cultures (e.g. species that preferentially copy traits in context when they will have future benefit). A secondary question is what modes of prospective cognition, present to what extent, could facilitate cultural change. For example, if mental time travel to the future (an ability to mentally project into one's personal future) promotes cumulative culture in humans, does the episodic-like memory (which possibly engages the same mental time travel system) argued to be present in some animals (see [88] for a review) facilitate forms of culture somewhere in between cumulative and simple traditions?

One challenge to our current knowledge base about prospective cognition is a dearth of studies that are truly direct comparisons between humans and other species. In particular, most human tasks are verbal, whereas, by definition, those with non-humans are not. This changes the nature of the task, but not in predictable ways, given that it is not always clear if we are making the task easier for humans by giving them instructions and training, or easier for the non-humans in our attempt to avoid penalizing them [89]. There are two ways to address this challenge. First, comparisons between verbal and nonverbal tests in humans can validate that the non-verbal task is testing the same capacity, thereby helping with interpretation of the non-human results. Moreover, of course, we need to test humans, too, using non-verbal studies (e.g. [90]). This will help clarify the degree to which non-human prospective cognition is, or is not, similar to that in humans and foster greater cross-fertilizations between groups with different epistemic backgrounds.

A second issue with many of the verbal tasks used in the literature is that they do not necessarily translate well to other cultures and languages. Indeed, the widespread over-reliance on western, educated, industrialized, rich and democratic samples (WEIRD; [91]) poses a significant challenge to the external validity of our conclusions concerning prospective cognition in humans. As we discuss above, we know that cultural background influences how at least some aspects of prospective cognition develop. Thus, it is essential that we extend these studies beyond WEIRD samples. Moreover, using variability across human populations would also afford one more avenue through which we might begin to examine the predictions our proposal outlines.

One thing human cultures have in common is their extreme adaptability and complexity. It seems likely that our prospective cognition tendencies contribute in some way to this cultural flexibility and change—as well as explain some of the variability among us. We argue that prospective cognition is essential in understanding how culture influences innovations and the ability to flexibly use culture to our advantage, but this relationship is symbiotic, with culture shaping prospective cognition and, potentially, even taking the place of it in some circumstances. To what extent, however, is this relationship unique to humans? The answer to this question will help us understand how this connection evolved and the contexts in which we can expect different manifestations of this relationship, ultimately helping us better understand how and why culture came to be such a dominant force for humanity.

Data accessibility. This article has no additional data.

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All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

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