



Prospection and natural selection

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Prospection refers to thinking about the future, a capacity that has become the subject of increasing research in recent years. Here we first distinguish basic prospection, such as associative learning, from more complex prospection commonly observed in humans, such as episodic foresight, the ability to imagine diverse future situations and organize current actions accordingly. We review recent studies on complex prospection in various contexts, such as decision-making, planning, deliberate practice, information gathering, and social coordination. Prospection appears to play many important roles in human survival and reproduction. Foreseeing threats and opportunities before they arise, for instance, drives attempts at avoiding future harm and obtaining future benefits, and recognizing the future utility of a solution turns it into an innovation, motivating refinement and dissemination. Although we do not know about the original contexts in which complex prospection evolved, it is increasingly clear through research on the emergence of these capacities in childhood and on related disorders in various clinical conditions, that limitations in prospection can have profound functional consequences.

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Introduction

The future matters. Present actions can influence the chances of survival and reproduction, and thus natural selection has produced mechanisms that increase the likelihood of future benefits and decrease the likelihood of future harm (e.g. [1,2]). Most species are attuned to important long-term regularities such as fluctuations of light, temperature and food availability that are tied to daily and annual cycles. Perhaps most conspicuously, as cold winter months approach some species prepare for food scarcity by hoarding. Organisms that adapt effectively to recurrent fluctuations outbreed those that do not.

Even *Escherichia coli* bacteria, when travelling through human digestive tracts, switch on genes for maltose digestion ahead of reaching the maltose-rich section [3]. However, many significant environmental features do not change cyclically. Contingencies change; sometimes very rapidly. Thus, natural selection has also favoured mechanisms that enable animals to adjust their behaviour to new, local regularities. Animals can learn; and thus predict.

Here we were asked to discuss prospection, defined as ‘thinking about the future’, and its relationship to survival. We will first discuss fundamentals common to many species, before considering the fitness consequences of the human capacity to consider diverse and remote future possibilities (for a recent review of studies on the neurocognitive mechanisms see [4]).

Basic prospection

Associative learning

Some adaptive flexibility can be achieved by a capacity for developmental parameter-setting during critical periods, and other types of individual learning. In fact, all associative learning may be regarded as future-oriented mechanisms that enable individuals to track local regularities and adapt their behaviour so as to increase the chances of future rewards and avoidance of punishments [5]. Animals equipped with a capacity for positive and negative states (e.g. pleasure and pain) may prospectively guide actions by learning about their immediate antecedents: when the learned antecedents recur, the animal can predict imminent reward or punishment, and drive action before these become manifest.

It may be questioned whether such learning really involves any representation of the future situation and hence should be classified as prospection. Early theorists such as Thorndike suggested that organisms simply learn associations between stimulus and response, leaving the reinforcer as mere catalyst [6]. However, it later became evident that the reinforcer can be part of the associative network, and its evaluation can change [7]. Animals not only learn that certain actions are rewarding in particular circumstances, but that those actions also lead to specific kinds of outcomes. In other words, instrumental actions can be goal-directed and considered a form of prospection. When expectations are not met, animals often change their behaviours accordingly. For instance, primates reject to work for a less-preferred food once they see another individual receiving a preferred food for the same work [8], or once they have noticed that the experimenter is not rewarding them as well as they could [9••]. In other

words, the animals demonstrate ‘disappointment’ when they do not get what they expect.

In their influential approach, Rescorla and Wagner modelled Pavlovian learning on the basis of such a mismatch between the animal’s expectation and the reality that unfolds, for when expectations are met there is little for the animal to learn [10]. From this perspective, prospection is not only guided by what the animal knows, it also plays a critical role in learning itself (see **Box 1** for a relevant discussion in the context of navigation). Recent work conceptualizes the disjunction between expectation and experience as also playing an important role in more complex prospection, and in neural and cognitive processing more broadly, although many important open questions remain about the ability of such ‘predictive processing’ accounts to effectively integrate observations at various levels of analysis [11–13,14**,15,16].

Complex prospection

Associative learning enables prediction of what happens next. Aside from rare cases such as taste aversion [17], learning tends to build on immediate antecedents and expectations tend to be about instant consequences. Contiguity between events is critical for associative learning, and even a hiatus of minutes, let alone hours or days, typically makes learning of associations between events impossible. Furthermore, these expectations appear to be fixed to specific pairings and so do not lend themselves to more complex prospection, such as consideration of multiple, mutually exclusive possibilities that may occur. A human hunter may prepare a trap for several potential exits his prey may try to take from its hideout. By contrast, even our closest animal relatives, great apes, appear to struggle preparing for two simple alternatives (see **Box 2**).

Perhaps uniquely, humans can consider many, even remote alternative future scenarios, and embed them into larger narratives [18]. Even if we have never experienced the situation before, we know that one career choice has different consequences than another, or that following the suggestion to play a game involving crossing a street blindfolded is a bad idea. People think about future events often and tend to do so with optimism [19,20] (though there are cultural differences [21,22]). Even though we are often not quite accurate in what we predict, we endlessly entertain options and evaluate them in terms of, for instance, their likelihood and potential consequences, and these thoughts guide our actions [23]. This capacity to flexibly travel in our minds into the future and organize current actions accordingly may be referred to as ‘episodic foresight’ [24] (we prefer this label over the phrase ‘episodic future thinking’ partly because its counterpart is ‘episodic memory’ and not ‘episodic past thinking’). We maintain that episodic foresight has given our ancestors a tremendous adaptive advantage over creatures with more limited prospection,

Box 1 Navigation and prospection.

Animals often seek situations that harbour rewards or lead to safety by navigating based on representations of space [88,89]. Mantled howler monkeys, for instance, traverse the canopy in ways that enhance the quantity of mature fruits they can gather [90]. The underlying neurocognitive machinery of such navigation in mammals is critically dependent on the hippocampus [91], featuring a complex network of place-, grid-, border- and head-direction-cells that code spatial representations [92]. A recent computational model suggests that the hippocampus may support navigation by generating *predictions* about spatial movement [93]. Compatible with this notion, single place cell recordings in rats have identified sequences that seem to indicate simulation of future movement [94] (but see [95,96]), although debate continues about the nature and complexity of the events that nonhuman animals might be able to represent [97,98]. In fact, a key function of the hippocampus may be to guide exploratory behaviours to facilitate learning about the environment, achieved by the active maintenance of relevant memory traces [99]. Recent evidence suggests that the prefrontal cortex (PFC) is involved in influencing this type of hippocampal maintenance of relevant memories in a context-dependent manner [100,101]. The results of recent lesion studies have also been taken to suggest that a network involving the vmPFC and hippocampus is necessary for more complex prospection in humans [102].

Box 2 Preparing for mutually exclusive possibilities.

The future is uncertain and, being aware of this, humans frequently make backup plans. For instance, people may prepare what they are going to do if they pass or fail the exam, if the weather is going to be good or bad, or if the love interest does or does not say ‘yes’. Contingency plans can be devised to address multiple possibilities and can involve very complex strategies. To examine the emergence of the simplest, fundamental capacity to foresee mutually exclusive outcomes of an event, Redshaw and Suddendorf devised a minimalist paradigm involving the drop of a desirable object into an upside down Y-shaped tube and giving subjects an opportunity to catch it (left panel) [87**]. Chimpanzees, orang-utans and two-year-old human children prepared by placing one hand under one of the two exits, and therefore ended up catching the reward only some of the time. Older children were more successful: by age four, most children spontaneously and consistently covered both exits from trial one onwards, assuring themselves the reward. They hence demonstrated a capacity to prepare for at least two mutually exclusive versions of an imminent future event. Some younger children, and even one chimpanzee, covered two exits on some trials, but then reverted to a one-handed response, suggesting a lack of insight. In a recent follow-up study, young children and chimpanzees showed a similar pattern of responses when presented with a situation involving two parallel tubes and an experimenter who simply dropped the target into one of them (right panel) [103] (Figure 1).

as it enabled them to prepare for dangers and to seize opportunities before they manifested. We now describe recent research on three broad aspects of complex prospection.

Considering possibilities

Options can be evaluated and compared [25] based on mental simulations of these events as if they were currently happening [26,27]. The feelings that are evoked during these simulations are referred to as affective

forecasts [28], and play an important role in motivating future-directed behaviour [29,30]. For instance, affective information derived from simulations can influence decision-making in the context of intertemporal choices where future and present rewards must be weighed up [31,32]. Relatedly, recent evidence suggests imagining goal-related episodic future events can attenuate delay discounting [33], reduce calorie consumption in overweight people [34] and reduce aspects of alcohol demand [35,36] (also see [37,38]). Relatedly, a mentally simulated future danger may evoke feelings associated with an emotional fear or anxiety response instead, and this may provide the motivational currency to spur appropriate defensive behaviour in the here-and-now [39,40].

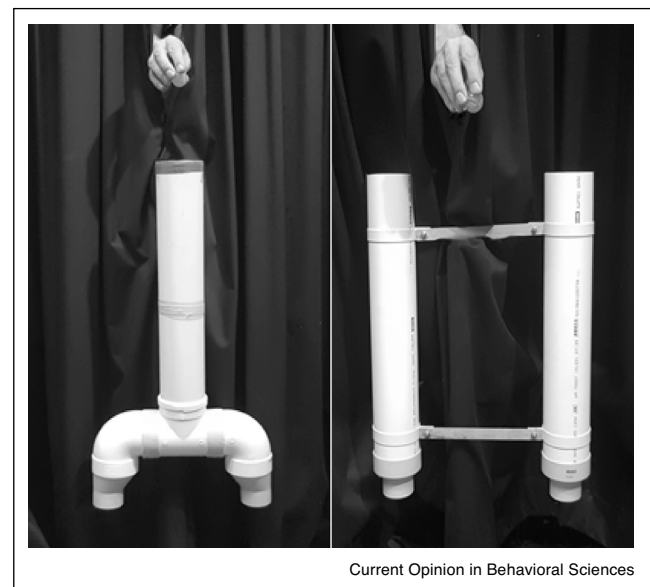
Mental simulations of the future can thus also support the encoding of options [41–43], for example intentions to be deployed at a later time (i.e. so-called ‘prospective memory’) [44–46]. Another critical advantage of the capacity to encode possibilities is that this allows one’s mental model of a future scenario to be updated in the light of new information before action is taken. This may help explain why humans prospect so frequently, and often involuntarily [47–49], and why mental simulations of the future tend to cluster around personal goals [49–52]. In a dynamic world, episodic foresight is most effective if it involves repeated mental trial and error, monitoring and reflection, so that solutions to anticipated future scenarios can be fine-tuned and adjusted to avoid dangers and capitalize on opportunities. To date, however, episodic foresight has mainly been studied with single time point measures in more static contexts.

Social exchange

Language enables humans to refine their foresight through others’ experiences, predictions and reflections. We ask questions and give each other advice about what to expect [53]. Humans have a fundamental urge to exchange mental scenarios and insights [18,54]. Such exchanges often concern functionally relevant information, such as about potential future threats [55**]. Through exchange of experiences, reflections and plans, we humans have been able to coordinate our cooperative activities in ever-more powerful ways [18], and researchers are beginning to separately examine personal and collective future thinking (e.g. [56,57]). Communication about future scenarios can lead us to abandon, amend or solidify plans or intentions, or to create new ones in light of the acquired information. The regularity of such exchanges suggests that there may have existed selective pressures on those who failed to collaborate [58], as well as on the inability to distinguish co-operators from defectors, and information that could help from information that misleads [59].

We argue that complex prospection is a quintessential human survival mechanism [60,61], and that humans all

Figure 1



The apparatus used to assess preparation for two possible event outcomes, either caused by a hidden mechanism (**left panel** [87**]) or by an experimenter rapidly dropping the target into one of the parallel tubes (**right panel** [103]).

incessantly benefit from the foresight of others, allowing us to deal with problems before they arise and to shape the future to our design. Consider tools, upon which much of this prudent preparation depends. Humans innovate. We can imagine the functionality and aesthetics of the things we make before we make them, or we may try a small-scale version before investing into a large project. Regardless of whether we have creatively figured out a solution to a problem or merely stumbled upon it by accident, what turns the solution into ‘innovation’ is the recognition that it has future utility (i.e. prospection) [62]. Once we realize a tool has future utility, we are motivated to retain the solution so we can use it again, to spend time improving it, and to share it with our friends (or sell it). Whereas many species use tools and some even make them, only humans seem to keep them, refine them, and share them. Our solutions become better as tool kits and options accumulate and spread through a population. We can all benefit when people with better or complementary sets of skills improve existing technologies, even if such efforts are ultimately driven by the innovator’s own anticipated material benefit. These processes have enabled us to establish ever more powerful toolsets that have allowed us to dominate the planet.

Shaping one’s future self

We can not only shape the world by design, but even our own future capacities. Through deliberate practice — repeated actions driven by the goal to improve future capacities — we can intentionally acquire skills. This has

been studied primarily in the context of elite expertise [63], but is equally critical to how we all acquire more basic skills, such as tying shoelaces [64]. Similarly, we deliberately seek information that we consider will be useful to future situations, or cultivate metacognitive strategies to overcome our own mental shortcomings (e.g. by setting ourselves reminders to deal with our forgetfulness). Metacognition and episodic foresight are inextricably intertwined: one must be aware of one's current limitations in order to identify the appropriate route towards improvement [65,66,67*]. Together, these strategies enable us to become knowledgeable and proficient in areas we select, and the fact that people can make vastly different choices about what matters goes some way to explaining why humans are so tremendously diverse in their expertise [18].

Humans acquire deliberate practice, information search and reminder setting capacities gradually in childhood [68,69]. As these capacities emerge, adults may begin to prompt young children to pursue certain types of expertise over others. However, even without instruction or other external prompts, we can autocue practice based on our own simulations [70]. Humans regularly spend thousands of hours practicing skills that they or others believe to be worthwhile improving, and much of this is critical to our survival and reproductive success.

The costs of complex prospection

The capacity to think ahead also comes with tremendous costs. Learning to prudently prospect is resource intensive and competence develops only gradually [70,71]. Worse still, we often fail to foresee significant events and our predictions are often wrong. Even when we foresee roughly correct outcomes, we are often inaccurate in terms of specifics [28]. For instance, we tend to mispredict the extent to which future events will have an impact on the way we will feel [72]. This has costs to our wellbeing, as does the fact that we repeatedly think about future problems that we can do little about [47,73]. Prospection confronts us with unwelcome facts such as our own mortality [74] and with problems that may appear insurmountable. Although the ability to anticipate and prepare for future threats is probably a key adaptive component of threat management in humans [40,75–77], it can bring to mind profound and persistent concerns. The current generation, for instance, is increasingly becoming aware about the diverse global, long-term consequences of our collective behaviour that individually we have little power to correct.

There is also a growing recognition that prospection plays a critical role in a range of common and severe psychiatric conditions, from anxiety disorders and depression to schizophrenia and suicidal tendencies [78–86]. But even the well-adjusted are often struggling to enjoy the here and now, as their minds are busy worrying about the

future and trying to plot their way to happiness. As John Lennon sang: 'Life is what happens while you are busy making other plans'. The study of prospection is only still in its infancy and we foresee increasing research efforts as people recognize its profound roles and diverse consequences for our success individually and as a species.

Conflict of interest statement

Nothing declared.

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