Cognitive culture: theoretical and empirical insights into social learning strategies

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Research into social learning (learning from others) has expanded significantly in recent years, not least because of productive interactions between theoretical and empirical approaches. This has been coupled with a new emphasis on learning strategies, which places social learning within a cognitive decision-making framework. Understanding when, how and why individuals learn from others is a significant challenge, but one that is critical to numerous fields in multiple academic disciplines, including the study of social cognition.

The strategic nature of copying

Social learning, defined as learning that is influenced by observation of or interaction with another individual, or its products [1], and frequently contrasted with asocial learning (e.g. trial and error), is a potentially cheap way of acquiring valuable information. However, copying comes with pitfalls [2] – the acquired information might be outdated, misleading or inappropriate. Nevertheless, social learning is widespread in animals [3,4] and reaches a zenith in the unique cumulative culture of humans. Understanding how to take advantage of social information, while managing the risks associated with its use, has become a focus for research on social learning strategies [5–7], which explores how natural selection has shaped learning strategies in humans and other animals.

Research on this topic has expanded rapidly in recent years, in part by building on a more detailed understanding of social learning and teaching mechanisms (Box 1). However, the expansion has primarily been fuelled by a strong link between theory and empirical work, as well as the often surprising parallels between the social decision-making of humans and that of other animals (Box 2). Thus, the field has moved beyond asking which psychological mechanisms individuals use to copy each other toward an exploration of the cognitive decision-making framework that individuals use to balance the competing demands of accuracy and economy in knowledge gain [8]. The marriage between the economics of information use and evolutionary theory has generated a rich research program that spans multiple disciplines, including biology, psychology, anthropology, archaeology, economics, computer science

and robotics. Researchers are now starting to gain an understanding of the functional rules that underlie the decision to copy others, and are beginning to appreciate that the rules deployed at the individual level profoundly affect the dynamics of cultural evolution over larger temporal and social scales.

Theoretical insights

Research into social learning strategies is supported by a rich and interdisciplinary theoretical background (Box 3) [5–18], with active ongoing debates, such as on the importance of conformity [5,16,17,19–21], whether the decision to copy is more dependent on the content of the acquired information or the social context [5,22,23], and whether, and under what circumstances, social learning can lead to maladaptive information transmission [2,5,13,24].

An important starting point was a simple thought experiment that became one of the most productive ideas to date related to the evolution of social learning, known as Rogers' paradox [10]. Anthropologist Alan Rogers constructed a simple mathematical model to explore how best to learn in a changing environment. The analysis suggested, somewhat surprisingly, that social learning does not increase mean population fitness, because its efficacy is highly frequency-dependent. Copying is advantageous at low frequency because social learners acquire their information primarily from asocial learners who have directly sampled the environment, but avoid the costs of asocial learning. However, copying becomes disadvantageous as it increases in frequency, because social learners find themselves increasingly copying other copiers. The information acquired is then rendered outdated by environmental change, giving a fitness advantage to asocial learning when the latter is rare. At equilibrium, both social and asocial learners persist with the same average fitness. Rogers'

Glossary

Conformist bias: positive frequency-dependent social learning for which the probability of acquiring a trait increases disproportionately with the number of demonstrators performing it.
Cultural drift: random, or unbiased, copying in which individuals acquire variants according to the frequency at which they are practiced.
Social learning strategy: evolved psychological rule specifying under what circumstances an individual learns from others and/or from whom they learn.

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Box 1. Social learning and teaching processes

A large amount of research has focused on determining the psychological mechanisms underlying social learning in animals. This was initially driven by the question of which non-human animals are capable of imitation, a process assumed to involve sophisticated cognition, requiring an observer to extract the motor program for an action from the experience of observing another individual perform that action [74]. The recognition of alternative processes through which animals could come to acquire similar behaviour following social interaction, not all of which implied complex mechanisms, eventually spawned a number of classifications of different social learning processes that can result in the transmission of behaviour between individuals [1,75]. Simpler mechanisms, such as local and stimulus enhancement (see Table I) were usually seen as explanations that should be ruled out before imitation could be inferred [76]. This enabled researchers to devise the two-action test, a laboratory procedure for inferring imitation [77]. The two-action method requires experimental subjects to solve a task with two alternative solutions, with half observing one solution and the other half the alternative; if subjects disproportionately use the method that they observed, this is taken as evidence of imitation.

In recent years, interest has shifted away from the question of 'do animals imitate?' towards the more general question of 'how do animals (including humans) copy others?' [78–81]. This approach includes recreation of the movements of objects in the environment,

copying the goals of observed behaviour, learning about the affordance of objects and imitation at a number of levels of copying fidelity [78,79]. Other researchers aim to elucidate the neural mechanisms and developmental processes underpinning imitation [80,81]. Collectively, this work has revealed an extensive repertoire of copying processes, all of which are probably exhibited by humans, but only some of which are observed in other species. Advances in both experimental and statistical methods [3,82,83] mean that specific learning processes can now be identified, which will potentially facilitate mapping of the taxonomic distribution of these processes.

Historically, teaching has been viewed as a contributor of additional and separate mechanisms to the list of social learning processes. However, recent findings on simple forms of teaching in ants, bees, pied babblers and meerkats [84] have led to the detection of correspondences between teaching and social learning processes. Social learning mechanisms relate primarily to psychological processes in the observer (pupil), whereas teaching processes relate specifically to activities of the demonstrator (tutor). Accordingly, alternative forms of teaching can be viewed as special cases of established social learning processes, in which the demonstrator actively facilitates information transmission. For instance, while many species, including ants, teach through local enhancement, humans might be unique in teaching through imitation.

Table I. A classification of social learning mechanisms.

Social learning mechanism	Definition
Stimulus enhancement	A demonstrator exposes an observer to a single stimulus, which leads to a change in the probability that the observer will respond to stimuli of that type
Local enhancement	A demonstrator attracts an observer to a specific location, which can lead to the observer learning about objects at that location
Observational conditioning	The behaviour of the demonstrator exposes an observer to a relationship between stimuli, enabling the observer to form an association between them
Social enhancement of food preferences	Exposure to a demonstrator carrying cues associated with a particular diet causes the observer to become more likely to consume that diet
Response facilitation	A demonstrator performing an act increases the probability that an animal that sees it will do the same. This can result in the observer learning about the context in which to perform the act and the consequences of doing so
Social facilitation	Social facilitation occurs when the mere presence of a demonstrator affects the observer's behaviour, which can influence the observer's learning
Contextual imitation	Observing a demonstrator performing an action in a specific context directly causes an observer to learn to perform that action in the same context
Production imitation	Observing a demonstrator performing a novel action, or action sequence, that is not in its own repertoire causes an observer to be more likely to perform that action or sequence
Observational R-S learning	Observation of a demonstrator exposes the observer to a relationship between a response and a reinforcer, causing the observer to form an association between them
Emulation	Observation of a demonstrator interacting with objects in its environment causes an observer becomes more likely to perform any actions that bring about a similar effect on those objects

Note that these definitions relate to psychological processes in the observer. The presence or absence of active demonstration or teaching (behaviour whose function is to facilitate learning in others) can be regarded as orthogonal to mechanisms in the observer. Hence, it is possible to categorize instances of teaching as, for example, teaching through local enhancement. For the original sources of these definitions, see Hoppitt and Laland [3] and Hoppitt *et al.* [84].

finding, although not paradoxical in any strict sense, was viewed as counterintuitive because culture, and thus social learning, is widely thought to be the basis of human population growth [25], which implies an increase in absolute fitness. More recently, spatially explicit models have exacerbated this challenge by suggesting that with certain kinds of population structure and realistic patterns of ecological change, social learning could drive asocial learning to extinction, with disastrous consequences for fitness when environments change [12,13].

This thought experiment vastly simplifies the choices available to individuals. Several studies have shown that a way out of this 'paradox' is through the selective use of asocial and social learning [5,12,14,15,18,26]. For example, a strategy termed critical social learning, which uses social

learning initially but switches to asocial learning if it fails to acquire an adaptive behaviour, outcompetes pure social learners and, under most circumstances, asocial learners, while also increasing fitness across a broad range of conditions [12,15]. However, there are also relatively narrow circumstances in which pure social learning outcompetes both individual learning and conditional strategies, while also increasing fitness [12]. The conditions for this exist when individual learning is challenging (e.g. very costly in time) but there are a range of viable alternatives available to copy, any of which might produce a reasonably effective, if not globally optimal, solution. Interestingly, these conditions seem to fit well to some examples of human cultural evolution that are best described by the kind of drift dynamics expected under unbiased (or random) copying,

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Box 2. Functional parallels in the social learning of humans and non-human animals

Experimental studies in non-human animals have explored both when animals copy and from whom they do so, and revealed surprising parallels with the social learning of humans [85]. Although the social learning mechanisms used can vary across species (Box 1), this does not mean we cannot learn a lot about the functional consequences of various strategies from comparative studies.

Studies of sticklebacks (*Pungitius* spp.) have revealed evidence that these fish disproportionately copy when uncertain [86], when the demonstrator receives a higher payoff than they do [87,88] and when asocial learning would be costly [89,90]. Sticklebacks are disproportionately more likely to use social information that conflicts with their own experience as the number of demonstrators increases, which provides evidence of conformist bias in this species [91]. It has also been found that small fish are sensitive to a range of attributes in their tutors, including age [92], size [93], boldness [94] and familiarity [95], and adjust their social information use with reproductive state, with gravid females much more likely to use social information than other individuals [90].

A similar set of studies investigated the contexts that promote the social enhancement of food preferences in rats (*Rattus norvegicus*) and provide evidence of the use of various strategies, including copy if dissatisfied, copy when uncertain, and copy in a stable environment [96]. As yet, however, there is no evidence that rats copy selectively with respect to demonstrator age, familiarity, relatedness or success [96]. By contrast, chimpanzees (*Pan troglodytes*) disproportionately adopt the behaviour of the oldest and highest-ranking of two demonstrators [97], and vervet monkeys (*Chlorocebus aethiops*) preferentially copy dominant female models over dominant males (females are the philopatric sex in this species) [98].

These studies imply that even relatively simple animals are capable of flexibly using a range of social learning strategies. Although there is clearly scope for further comparative experiments, it is apparent from existing research that strategic learning behaviour has evolved in a range of taxa, with strikingly similar context-specific patterns of copying to those observed in humans clearly evident [58,59,61]. This suggests that the evolution of copying behaviour is best regarded as a convergent response to specific selection pressures, and might not be well predicted by the relatedness of a species to humans.

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such as choice of pet breeds, baby names and aesthetic craft production [27].

One challenge for the developing field is that the potential diversity of strategies is huge, and only a small number of plausible strategies have been subject to formal analyses. Nonetheless, many of these have received theoretical support, backed up in several cases by empirical evidence from humans or other animals (Figure 1). Strategies relate

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Box 3. Modelling social learning from individuals to populations

A variety of theoretical approaches has been used to model the evolution of social learning strategies, commonly known as cultural evolution, gene–culture co-evolution and dual inheritance theory [5,9,10,14,16,18–21]. Typically, models are based on systems of recursions that track the frequencies of cultural and genetic variants in a population, often with fitness defined by the match between a behavioural phenotype and the environment. These systems range from those containing only two possible discrete behavioural variants through to traits that vary continuously along one or more dimensions, with evolutionarily stable strategy (ESS) and population-genetic analyses applied to these models [15,18,21].
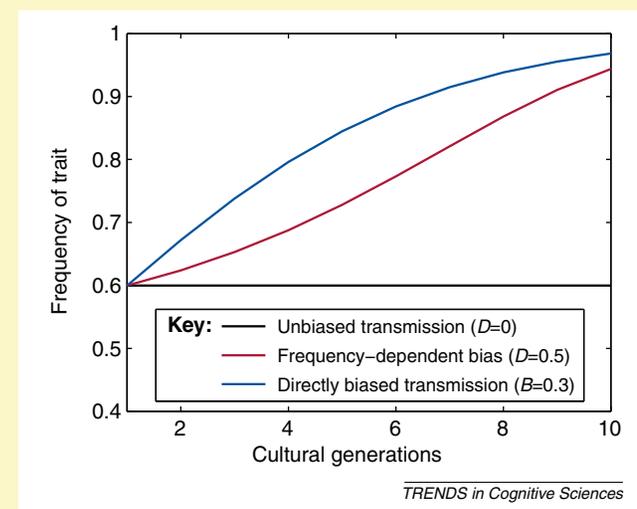
Other approaches include multi-armed bandits (in which a number of discrete choices with different expected payoffs are available to players [8,11,32]), reaction-diffusion models (in which differential equations describe the change in frequency of cultural traits over time and incorporate individual learning biases [17]) and information-cascade games (in which individuals choose from a limited set of options after receiving private information and observing the decisions of previous actors [50,52]), all of which have been influential in identifying adaptive social learning strategies. The complexities of tracking genetic and cultural parameters over time, and the need to incorporate increasingly complex learning strategies, have led to greater use of simulation modelling in recent years [12–14,19,26], which has enabled researchers to build models that are spatially explicit [12] and to separately track knowledge and behaviour [32].

Here we illustrate the methods using a classic model of unbiased, directly biased and frequency-dependent biased cultural transmission, introduced by Boyd and Richerson [5]. Consider a cultural trait with two alternative variants, denoted c and d, acquired through social learning. The model tracks the spread of c in the population; the proportion of the population with c is denoted by p. Each individual in the population is exposed to three randomly selected cultural role models: thus, the probability of having i role models with trait c, given p, is $M(i|p) = \binom{3}{i} p^i (1-p)^{3-i}$. To model cultural transmission with frequency-dependent bias, the strength of which is D, expressions for the probability that an individual acquires c when i role models have c are given in Table I (note that when D=0, then transmission is unbiased). This gives a recursion for the frequency of c in the population: $p' = p + Dp(1-p)(2p-1)$. A direct learning bias can be modelled by assuming that some feature of trait c renders it inherently more likely to be copied. B is the strength of this direct bias and the recursion expression is $p' = p + Bp(1-p)$. These equations can be used to compare the fate of trait c over time under different transmission biases, and show that the different individual-level learning strategies produce different outcomes at the population level (Figure I).
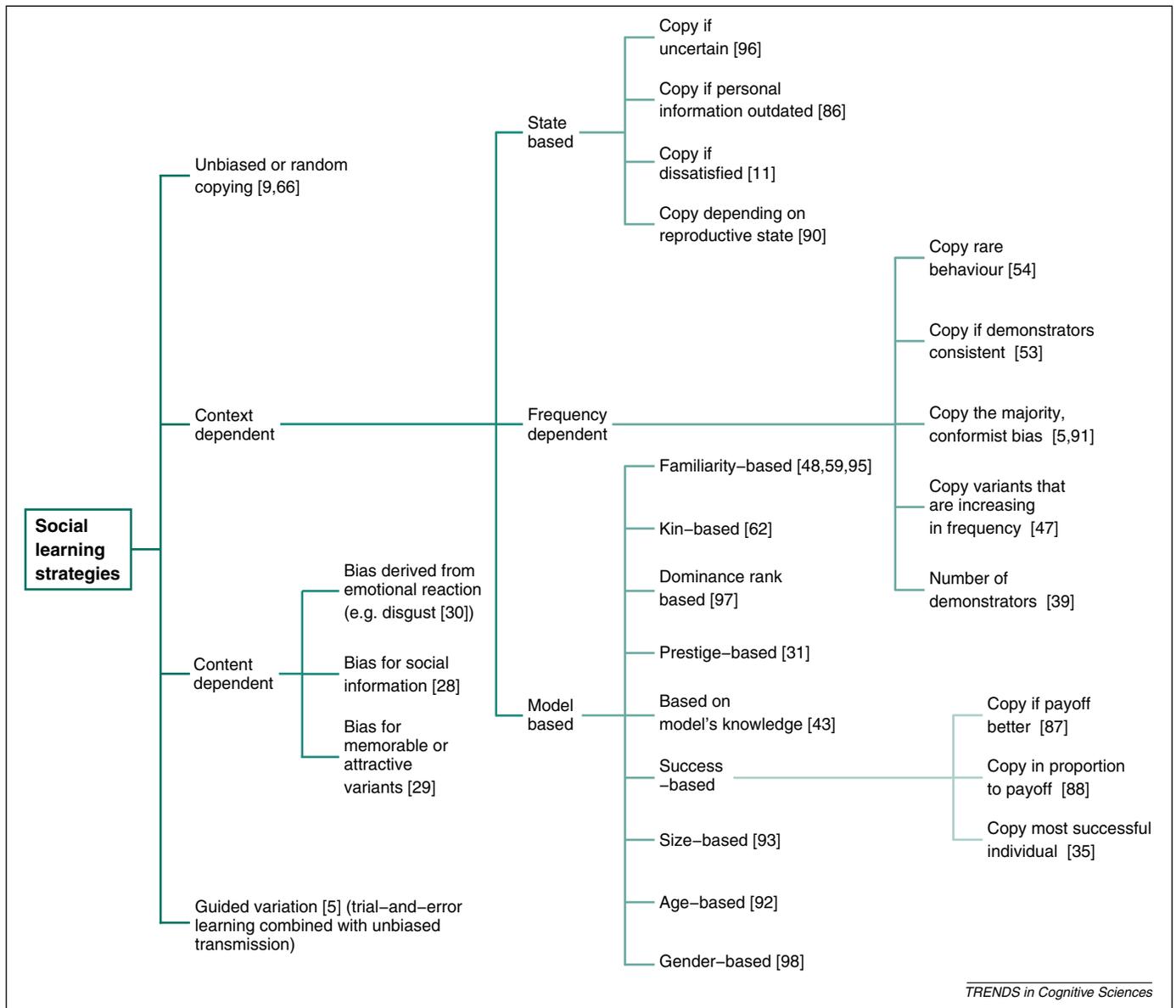
Table I. Probability that an individual acquires trait c given its frequency in the set of cultural role models

Number of role models with c	Probability that a focal individual acquires c
0	0
1	$\frac{1}{3} - \frac{D}{3}$
2	$\frac{2}{3} + \frac{D}{3}$
3	1

Figure I. Individual-level transmission biases produce different outcomes at the population level. The figure shows the time course of trait c when different biases are operating.

Key:
— Unbiased transmission (D=0)
— Frequency–dependent bias (D=0.5)
— Directly biased transmission (B=0.3)

TRENDS in Cognitive Sciences

Figure 1. Social learning strategies for which there is significant theoretical or empirical support. The tree structure is purely conceptual and not based on any empirical data on homology or similarity of cognition. The sources given are not necessarily the first descriptions or the strongest evidence, but are intended as literature entry points for readers.

to both when it is best to choose social sources to acquire information and from whom one should learn. These latter class are often referred to as learning biases [5]. These can be based on content (such as a preference for social information [28], attractive information [29], or content that evokes a strong emotion such as disgust [30]) as well as context, such as the frequency of a trait in a population (e.g. a conformist bias towards adopting the majority behaviour), the payoff associated with it (e.g. copy the most successful individual), or some property of the individuals from whom one learns (model-based biases such as copy familiar individuals).

Many studies have focussed on establishing the theoretical viability of a given strategy or a small number of strategies, and explored the conditions under which each is expected to prosper [5,11,12,15,16,18–21,31]. A different approach is to establish a framework within which the relative merits of a wide range of strategies can be evaluated

[11,32]. A recent example is the social learning strategies tournament [32], an open competition in which entrants submitted strategies specifying how agents should learn in order to prosper in a simulated environment (Box 4). This study relaxed some assumptions prevalent in the field, such as that asocial learning is more costly than social learning, to surprising effect. It revealed that copying pays under a far greater range of conditions than ever previously thought, even when extremely error-prone. In any given simulation involving the top-performing strategies, very little of the learning performed was asocial and learning for the winning strategy was almost exclusively social. The strength of this result depends in part on the tournament assumption that individuals build up a repertoire of multiple behaviour patterns, rather than focussing on a single acquired behaviour, as in most analytical theory. This meant that when a copied behaviour turned out to confer low fitness, agents could switch rapidly to an alternative behaviour in the
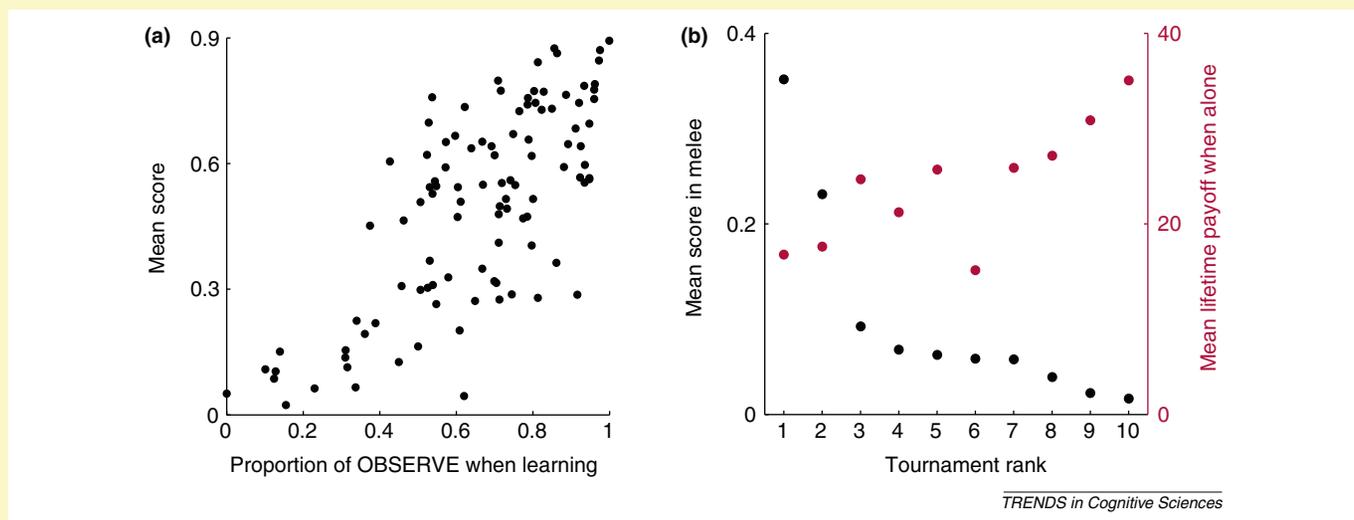
Box 4. The social learning strategies tournament

The social learning strategies tournament was a computer-based competition in which entrants submitted a strategy specifying the best way for agents living in a simulated environment to learn [32]. The simulation environment was characterized as a multi-armed bandit [11] with, in this case, 100 possible arms or behaviour patterns that an agent could learn and subsequently exploit. Each behaviour had a payoff, drawn from an exponential distribution, and the payoff could change over time (the rate of change was a model parameter).

This simulated environment contained a population of 100 agents, each controlled by one of the strategies entered into the tournament. In each model iteration, agents selected one of three moves, as specified by the strategy. The first, INNOVATE, resulted in an agent learning the identity and payoff of one new behaviour, selected at random. The second, EXPLOIT, represented an agent choosing to perform a behaviour it already knew and receiving the payoff associated with that behaviour (which might have changed from when the agent learned about it). The third, OBSERVE, represented an agent observing one or more of those agents who chose to play EXPLOIT, and learning the identity and payoff of the behaviour the

observed agent was performing. Agents could only receive payoffs by playing EXPLOIT, and the fitness of agents was determined by the total payoff received divided by the number of iterations through which they had lived. Evolution occurred through a death–birth process, with dying agents replaced by the offspring of survivors; the probability of reproduction was proportional to fitness. Offspring would carry the same strategy as their parents with probability 0.98, such that successful strategies tended to increase in frequency, and another strategy with probability 0.02, so that strategies could invade and re-invade the population.

The most important finding was the success of strategies that relied almost entirely on copying (i.e. OBSERVE) to learn behaviour (Figure Ia). Social learning in this context proved an extremely robustly successful strategy because the exploited behaviour patterns available to copy constituted a select subset that had already been chosen for their high payoff (see the main text). The results also highlighted the parasitic nature of social learning, because successful strategies did worse when fixed in the population than when other strategies were present and providing information (Figure Ib).

Figure I. Social learning strategies tournament results [32]. (**a**) Strategy score plotted against the proportion of the learning moves that were OBSERVE for that strategy. (**b**) Final score for the top ten strategies when competing simultaneously with other strategies (black) and individual fitness, measured as mean lifetime payoff, in populations containing only single strategies (red).

repertoire, thereby removing one of the drawbacks to copying identified in the analytical literature.

The tournament also highlighted the role of copied individuals as filters of information. Previous theory had placed the onus on learners to perform this adaptive filtering [15], demanding selectivity, and therefore specific cognitive capabilities, on the part of the copier. However, the tournament established that even nonselective copying is beneficial relative to asocial learning, because copied individuals typically perform the highest payoff behaviour in their repertoire generating a non-random sample of high-performance behaviour for others to copy. These insights go some way to explaining the discrepancy between Rogers' analysis and the empirical fact of human reliance on social information. They also help to explain why social learning is so widespread in nature, observed not just in primates and birds [3], but even in fruit flies and crickets [4]: even indiscriminate copying is generally more efficient than trial-and-error learning. However, because of its design, the tournament provided no information on the issue of from whom one should learn. A similar study incorporating individual identities would be potentially

informative, and we suspect that selectivity here would confer additional fitness benefits.

Conclusions as to which strategies are likely to prosper depend inevitably on the assumptions built into the models. For example, the conditional strategies described above depend on individuals knowing immediately the payoff of a behavioural option, but this information is not always available. If everyone else is planting potatoes, should you plant potatoes or another crop? Information on the relative payoffs will not be available for months, so a simple conditional strategy is not viable. An influential view is that under such circumstances, it pays to conform to the local traditions [4,16]. Indeed, theoretical models suggest that natural selection should favour such a conformist bias over most conditions that favour social learning [16], which brings us closer to an evolutionary understanding of the behavioural alignment prevalent in human herding behaviour [33]. However, this view has been challenged by subsequent analyses pointing out that conformity can hinder the adoption of good new ideas (and, by inference, cumulative cultural evolution), and therefore can be expected to perform relatively poorly in some circumstances,

particularly in changing environments [19,20]. More recent analyses suggest, however, that the strength of conformity is expected to vary with environmental stability and learning costs [18,21]. One way through this debate stems from the suggestion that conformity is only widely favoured when weak, because weak conformity acts to increase the frequency of beneficial variants when they are common, but its action is insufficient to prevent their spread when rare [17]. Such debates, and the formal theory in general, have stimulated an increase in empirical research on the strategic nature of human social learning (Figure 1) that sets out to determine whether copying behaviour fits with the theoretical predictions.

Empirical studies

Empirical investigations of social learning strategies in humans span a range of scales, from laboratory studies that pick apart the factors affecting minute-by-minute decisions at the individual level [34,35] through to observational work that seeks to explain the population-level frequencies of socially transmitted traits in historical and archaeological data [36–38].

Laboratory-based experiments have been successful in revealing the variety and subtlety of human social information use. Although there is a long tradition of these studies in social psychology [39], the new wave of research that we review here is different because it is rooted in the formal evolutionary theory described above [40]. Thus, whereas social psychology can provide immediate descriptions of the way in which people use social information, more recent research on social learning strategies seeks to link such observations with functional evolutionary explanations [40]. The use of micro-societies [41] and transmission chains [28], in which social learning is studied experimentally in small groups or chains of subjects that change composition, has been very productive. Such experiments have provided evidence of many of the biases explored in the theoretical literature. Examples include a bias for copying successful [35,42] or knowledgeable [43] models, a tendency to conform to route choices [44] and increased reliance on social information when payoff information is delayed [45] or at low rates of environmental change [46]. These experiments have also provided new insights not anticipated by theory; for example, it has been shown that people prefer variants that are increasing in frequency [47] and that in some circumstances people pay more attention to social information that originates outside their own sociocultural group [48].

Recently, some researchers in economics have started to introduce social learning into the experimental study of strategic games. Studies have shown that introduction of intergenerational social information can establish long-term social conventions that do not necessarily represent the predicted optimal strategy for any player [49,50], can drive up contributions in public-goods games [51], and can reveal unexpected biases in people's valuation of information sources, such as an over-weighting of private information in some conditions [52]. However, this research has yet to overlap with research on social learning strategies, which can potentially provide explanations for this apparently suboptimal behaviour in terms of the inherent biases people have about using social information.

Importantly, these studies can also throw up significant challenges to existing theory, such as individual variation in people's responses to social information, which has not yet been considered in the theoretical literature. Some subjects show a greater propensity to use social information than others, and those who do use social information can do so in different ways [34,47,53]. In a recent study using a simple binary choice task (choose the red or the blue technology), only a subset of subjects behaved as predicted by the conformist learning model, with the remaining 'maverick' subjects apparently ignoring social information altogether [34]. In another example, reading positive reviews of a piece of music caused some subjects to increase their valuation of that tune, whereas a significant minority actually decreased their evaluations [53]. Social psychology studies suggest that people will switch between conformity and anti-conformity depending on the social context, and are more or less likely to use social information depending on their mood [54]. Such flexibility is not inconsistent with an evolutionary explanation, but rather implies context-specific use of strategies [7]. The extent to which current theory needs to incorporate state-dependent and contextual cues requires exploration, and new formal methods are becoming available that facilitate such extensions [55].

Another area in which empirical and theoretical studies can inform each other is the ontogeny of learning strategies. Early in life, a child is surrounded by adults who have presumably engaged in decades of the kind of knowledge filtering that can make social learning adaptive. Young children have a tendency to imitate even irrelevant actions indiscriminately [56], which might reflect this informational imbalance. Evidence from attention studies suggests that very young infants have evolved mechanisms to focus attention on subtle cues given by their carers that indicate when important information is being made available [57]. As they grow and interact with a wider range of people, the challenge becomes less a problem of when and more of from whom to learn. This is when model-based, payoff-based, or frequency-dependent biases would become more pertinent.

There is ample evidence of model-based learning biases in young children [58–60] and in a surprising number of instances these echo similar patterns observed in other animals (Box 2). For example, preschool-age children (~3 years) tend to trust information presented to them by familiar teachers more strongly than that given by unfamiliar teachers [59]. In a follow-on study, older children (~5 years) further increased their trust in the information supplied by a familiar teacher who presented information that the children knew to be accurate, but reduced trust when the teacher provided inaccurate information, whereas the trust of younger children in familiar teachers was unaffected by the accuracy of the information provided [61], an example of the way we might expect adaptive social learning strategies to vary ontogenetically. More studies of how learning biases change during life, extending into adolescence and adult life, would be highly instructive in both humans and other animals.

Recent empirical work on social learning has also escaped the laboratory, which is vital for external validity. For instance, studies in traditional Fijian populations have found that food taboos that lead pregnant and lactating females to avoid consumption of toxic fish are initially transmitted through families, but as individuals get older they preferentially seek out local prestigious individuals to refine their knowledge [62]. Formal theory suggests that such learning strategies are highly adaptive [5]. Another study used the two-technology choice task in the subsistence pastoralist population of the Bolivian Altiplano, where a comparative lack of reliance on social information demonstrated that subtle effects of setting and cultural background probably play an important role in human social learning [63]. These results emphasize flexibility in the use of social information.

The combination of novel theory with empirical data has also been successful in understanding the spread of cultural traits across populations. Different social learning strategies lead to different transmission dynamics at the population level, generating detectable signatures in the frequency distributions and temporal dynamics of cultural traits. Comparison of real data with expected distributions can therefore indicate the processes behind the spread of ideas, trends and interests. This approach has been successful in highlighting several cultural domains where unbiased, or random, copying seems to dominate, such as the popularity of baby names, music and choice of dog breeds [37], and of the use of complementary and traditional medicines [64]. It has also illustrated the interactions between independent decisions and social transmission in the spread of interest in disease pandemics such as H5N1 and bird flu virus [65]. Here, random copying refers to unbiased copying in direct proportion to the rate a trait is observed, and does not imply that individual decision-making is random. For instance, in spite of all of the thought and care that individual parents put into choosing their child's name, parents as a group behave in a manner that is identical to the case in which they choose names at random [37]. The reason for this is nothing more than that common names are more likely to be observed and considered by parents than obscure names, and the likelihood that a name is chosen is approximately proportional to its frequency at the time. These studies also reveal how the drift-like dynamics that result from random copying can be perturbed by the influence of key events, such as a spike in popularity of the Dalmatian dog breed after the re-release of *101 Dalmatians*, a film that artificially inflated the number of Dalmatians observed [37]. This work is important because it provides potential tools for interpreting more ancient data when we have much less knowledge of the social context at the time [38,66,67].

Concluding remarks

The work we have reviewed here opens up a rich seam of opportunities for future development in several disciplines, from anthropology and cultural evolution through to economics and artificial life. Here we focus on just three. The first is related to the study of cooperation. One of the more intriguing results from the social learning strategies tournament was the parasitic effect of strategies that used only social learning. The way that a population learns can be viewed as a cooperation problem: innovators who engage in asocial learning are altruistic cooperators who introduce new information, whereas copiers are defectors who exploit that information. The tournament showed how, at the individual level, the temptation to defect (i.e. copy) is very powerful, but also that populations of defectors do worse than more mixed populations, which creates a classical cooperation dilemma. Although some have recognized the link [5,25,68], there is much to be done before the interactions between social learning strategies, cultural evolution and the evolution of cooperation are fully understood [69,70].

Second, we highlight the way in which computer scientists are now starting to use the concept of strategic social learning, and its interactions with individual learning and genetic evolution, to develop novel algorithms for evolutionary computing [71,72]. These studies show that social learning using a fixed strategy of copying from the most successful individuals significantly increases the success of agents exploring a complex fitness landscape (specifically the *NK* landscape widely adopted as a test bed for evolutionary computation), a result that striking parallels anthropological research on human social learning [35]. The prospect that research on social learning strategies can simultaneously provide inspiration for those working at the cutting edge of technology while benefiting from the novel insights such a dynamic field can produce is tremendously exciting.

Finally, we see open fields for research into the neurobiological basis of social learning. Hitherto, most experimental neuroscience concerned with learning and decision-making has focused largely on asocial learning, in spite of the important role of social influences on human learning. Research exploring the brain pathways and structures used in social learning and socially biased decision-making is needed. One pressing question is to what extent different social learning processes and strategies map onto different neural circuits. A pioneering study exploring how the opinion of others affects the valuation of objects has revealed that the human anterior insula cortex or lateral orbitofrontal cortex uniquely responds to the unanimous opinions of others [53]. This finding is suggestive of an evolved neural sensitivity to consistency in demonstrator behaviour, and is consistent with an economics experiment that suggests that people are more reinforced by following social information than otherwise expected by payoff alone [8]. Another key issue is whether our brains contain circuitry specific to social information processing, or whether these processes piggyback on established reinforcement learning circuitry. Recent evidence is suggestive of the latter [73], but our general lack of knowledge in this area is profound.

Clearly, the study of social learning strategies is a rapidly growing field with implications for multiple fields of research (Box 5). The empirical studies reviewed here reveal the subtlety and complexity of the learning strategies used by humans. An important contribution of this work, in parallel with studies on non-humans, is to challenge the notion of a single best strategy, or a strategy associated with a particular type of individual, or species.

Box 5. Questions for future research

- How are the performances of various learning strategies generalized across different learning environments?
- Can social learning be studied as a cooperation game? Innovators who engage in asocial learning could be viewed as altruistic cooperators who introduce new information, whereas copiers are defectors who exploit that information. Conversely, how might social learning strategies affect the establishment and maintenance of cooperation?
- Can social learning be used to develop novel algorithms for evolutionary computing and robotics?
- Do our brains contain circuitry specific to social information processing, or do these processes piggyback on established reinforcement learning circuitry?

Rather, recent work emphasizes instead the way in which the flexible context-dependent use of a range of subtle biases is a general feature of social learning, in both humans and other animals. In future, this should inspire theoretical researchers in turn to take on the challenge of incorporating meta-strategies into their models.

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