## Review

# Social Learning Strategies: Bridge-Building between Fields

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While social learning is widespread, indiscriminate copying of others is rarely beneficial. Theory suggests that individuals should be selective in what, when, and whom they copy, by following 'social learning strategies' (SLSs). The SLS concept has stimulated extensive experimental work, integrated theory, and empirical findings, and created impetus to the social learning and cultural evolution fields. However, the SLS concept needs updating to accommodate recent findings that individuals switch between strategies flexibly, that multiple strategies are deployed simultaneously, and that there is no one-to-one correspondence between psychological heuristics deployed and resulting population-level patterns. The field would also benefit from the simultaneous study of mechanism and function. SLSs provide a useful vehicle for bridge-building between cognitive psychology, neuroscience, and evolutionary biology.

## Social Learning Strategies Shape What, When and Whom to Copy

Learning that is facilitated by observation of, or interaction with, another individual or its products, is known as '**social learning**' (see Glossary) [1,2]. Social learning is common in animals [2], reaching its zenith in the uniquely powerful, cumulative, and diverse culture of humanity [3]. Such social learning is undoubtedly partially reliant on the same, or similar, mechanisms as **asocial learning** (namely associative learning), although, we argue, social learning is not solely reliant on associative learning mechanisms (Box 1). While social learning (or copying) appears intuitively useful, over the past 30 years, researchers from several fields have increasingly come to recognise that it is not inherently adaptive. Certainly, animals (including humans) may gain fitness benefits by learning from others insofar as they acquire adaptive information while avoiding some of the costs associated with the acquisition of **asocial information**, such as time and/or energy loss, opportunity costs, and exposure to predation while engaging in trial-and-error learning. However, the use of **social information** does not guarantee success [4–7]. Theoretical models predict that social learning will not be used in an indiscriminate manner [5,8]. Instead, heuristics, or **SLSs** (also termed 'transmission biases'), are expected to bias individuals to copy particular behaviours ('what' strategies), performed by specific others ('who' strategies), under suitable circumstances ('when' strategies) [5,8].

The SLS concept does not require that individuals be consciously aware of following a strategy and implies nothing about the underlying neural mechanisms [8]. Understanding the extent to which such strategies are products of evolution and/or learning requires detailed experimentation [9,10]. Nonetheless, selectivity in social learning may have important consequences, including facilitating the cultural inheritance of information and helping to promote **cumulative culture** by ensuring accurate copying of traits with high utility [whether instrumentally ('success bias') or conventionally ('prestige bias')] as well as the incorporation of novel beneficial modifications ('payoff bias') (Figure 1).

### Highlights

Accumulating evidence supports theoretical predictions that humans and nonhumans are selective in what, when, and whom they copy, suggesting the use of SLSs.

Recent studies indicate that SLS use is flexible and changes with ontogeny, experience, state, and context.

Multiple SLSs may be adopted simultaneously in the same population, and even by the same individual. The SLSs of individuals do not necessarily correspond to apparent population-level patterns.

SLSs likely involve associative learning processes and social learning mechanisms; experimental controls indicate that associative learning alone cannot explain all SLS findings.

Recent neuroscientific data suggest that the anterior cingulate cortex in the gyrus (ACCg) is specialised for processing the social information of relevance to SLSs.

The role of metacognition in SLSs requires investigation.

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### Box 1. Mechanisms of Asocial and Social Learning

Some authors have proposed that associative learning mechanisms can explain all social learning, and even suggested that the term 'social learning' is misleading because the underlying mechanisms are not distinctively social [10,80]. However, attributing social learning only to associative learning mechanisms relies on a narrower definition of social learning than standard [1,2], excluding language and teaching, which are reliant on specialist mechanisms. Here, we review key evidence regarding the debate.

Social learning in 'asocial' species has been interpreted as evidence that social learning relies on only asocial mechanisms [10,80]. However, social learning from heterospecifics is well established [84,117], and all animals, even solitary, are exposed to social information (observation and/or products), from mates, broodmates, or territorial neighbours [118]. Hence, it is dubious to infer that solitary species should not experience selection for social learning, or that their social learning relies on asocial mechanisms only. However, we may ask how evolutionary histories of group living shape the evolution of social learning [118]. Currently, it is not known whether social species exhibit evolved enhancements in social learning.

Social and asocial learning abilities co-vary across primates [119], but this does not negate the possibility of separate capacities that have coevolved. The correlation is imperfect, leaving variation potentially explainable by evolved adaptive specialisation in social learning, as seen in vocal learning in songbirds, cetaceans, and humans [120], public-information use in sticklebacks [84], and teaching in humans and other animals ([118] Box 4). Experimental studies are equivocal, with some reporting a positive (humans [121] and birds [38]), and others a negative (sparrows [122] and marmosets [123]) relationship between asocial and social learning performance.

Bumblebee research is enlightening here. It has been hypothesised that social learning is second-order conditioning whereby bees associate conspecific presence with reward and then associate conspecifics with a rewarding flower colour [124]. However, bumblebees learn differently when trained with social versus inanimate cues [125], and rely on social, over asocial, learning when tasks are complex [25] or the environment variable [126]. These experiments and 'ghost controls' in several other species [103] indicate animals respond differently to social and asocial information, again implying that enhancements in social learning performance can evolve.

Although there is undoubtedly overlap between social and asocial learning, whether (language and teaching aside) they rely entirely on the same mechanisms remains unknown. Indeed, for many social species learning occurs more frequently in social than in asocial contexts. These species may have experienced selection for proficient social learning, with enhanced asocial learning likely a by-product (e.g., humans [87]).

Here, we evaluate the status of SLS research for a cognitive science audience, briefly summarising theoretical predictions and empirical evidence, discussing challenges to the SLSs approach, and providing a perspective on future progress that emphasises the need for interdisciplinary work integrating mechanism and function. Our objective is to update and tighten the concept of SLSs and, in the process, build bridges between the disciplines that study social learning, including cognitive psychology (e.g., [14]), comparative psychology (e.g., [15,16]), developmental psychology (e.g., [17]), anthropology (e.g., [18]), archaeology (e.g., [19]), behavioural ecology (e.g., [20]), neuroscience (e.g., [21]) evolutionary biology (e.g., [22]), and behavioural economics (e.g., [23]).

## Findings of Social Learning Strategy Research

There is now evidence for various SLSs that shape when, what, and whom to copy (Figure 1). Thus far, most species studied appear to show evidence of multiple SLSs. However, more systematic research is required to identify any phylogenetic patterns in the adoption of specific SLSs. Here, we give a nonexhaustive review of these findings.

### Copy when Asocial Learning Would Be Costly

Theoretical analyses conclude that, as the costs associated with acquiring accurate but expensive personal information increase, reliance upon less accurate but cheap social information should increase [5,24]. Empirical support is provided by experimental studies of humans [9], bees [25], fish [26], and monkeys [27], where individuals were found to be more likely to use

social information when the task difficulty (and, thus, the energetic or time costs of acquiring the task solution asocially) increased. For example, humans required to decide whether two pictures represented the same shape seen from different angles, or different shapes were more likely to choose to view social information on harder than on easier trials, and after previously incurring high (versus low) costs of asocial information [9].

### Copy when Uncertain

Other theory predicts that individuals should use social information when they are uncertain, either because they have no relevant prior information because their prior personal information is unreliable or outdated [5], or because, in relative terms, the accumulated knowledge of conspecifics is more reliable [4]. Empirical studies have supported these ideas. High-fidelity copying is observed among children who lack relevant personal information (e.g., [13]). Children even copy causally irrelevant actions when they are confronted with a difficult task and are uncertain how to solve it [28]. Adult humans reporting low confidence in task-related decisions [9] or unreliable personal knowledge [29] are most likely to use social information. Subsequent analyses establish that copying when uncertain is an adaptive strategy in enhancing task success [9].

In addition to humans, uncertainty due to a lack of personal information has a powerful effect on increasing reliance on social learning across multiple taxa, including fish [30], chimpanzees [31], and ants [32]. Moreover, the opposite is also the case; children are more likely to **innovate** and devise a novel method when the demonstrated method is unreliable in providing rewards than when they observe reliable demonstration [17].

### Other State-Based Strategies

The decision to use social information is affected by other factors, including the age, social rank, and reproductive state [33] of the learner. There is experimental evidence that children choose to use social information more than do adults [17,34], perhaps because task-relevant knowledge is accumulated during childhood. Similarly, infant and juvenile capuchin monkeys pay more attention to the foraging behaviour of others than do adults [35] and, likewise, in chimpanzees, individuals are most sensitive to socially learning nut-cracking [36], and humans or birds to learn speech or song [37] when juvenile. Low- and mid-ranking chimpanzees are more likely to use social information than are high-ranking individuals [31], a pattern replicated in blue tits [38], and perhaps resulting from a tendency to attend to higher-status individuals. Early-life stress (e.g., unpredictable food) can also shape SLSs later in life [39,40]. Finally, empirical tests with bats [41] and bumblebees [42] indicate that individuals copy others when dissatisfied with the payoff of their current behaviour [43].

### Model-Based Biases or 'Who' Strategies

Another important insight of theoretical models is that social learning may be indirectly biased. That is, individuals may copy any aspect (e.g., the haircut or diet choices) of an individual who is, for example, of high status, whether or not that trait helped the model attain high status [5]. There is considerable empirical evidence for model-based biases in both humans and other animals. For example, children prefer to copy high-status individuals, where status is evidenced by their older age, popularity, and social dominance [44], and they distinguish between unfamiliar adults, copying the most 'prestigious' (or most attended to) among them [45]. Moreover, for the acquisition of skills, children prefer to copy adults over their same-age peers, even when the peer appears to have greater task-relevant knowledge than the adult [12]. Adults also display prestige bias. For example, Fijian villagers trust the advice of a successful yam grower with regard to a different domain, the use of medicinal plants [11].

**Innovation:** we adhere to existing definitions in recent literature [17,3,49]: 'a new, useful, learned behaviour that may be transmitted to others, arising from asocial learning alone or in combination with social learning, that is produced to successfully solve a novel problem or an existing problem in a novel manner'. Novelty is often considered to be at the population level.

**Metacognition:** processes used to plan, monitor, and evaluate one's knowledge and performance (e.g., thinking about thinking), or the knowledge and/or performance of others. In the context of SLSs, metacognition refers to 'knowing who knows' and 'knowing what is known'.

**Social information:** information acquired by an individual through some form of social influence (including social learning).

**Social learning:** 'learning that is facilitated by observation of, or interaction with, another individual (or its products)' ([1] p. 207).

**Social learning strategies (SLSs):** flexible rules that specify or bias when or how individuals should use social information, under various circumstances, to meet functional goals [7]. The term 'transmission biases' has, similarly, been used [5] to detail when, what, and from whom individuals acquire social information (see [66,81]).

**(A)**



**(B)**
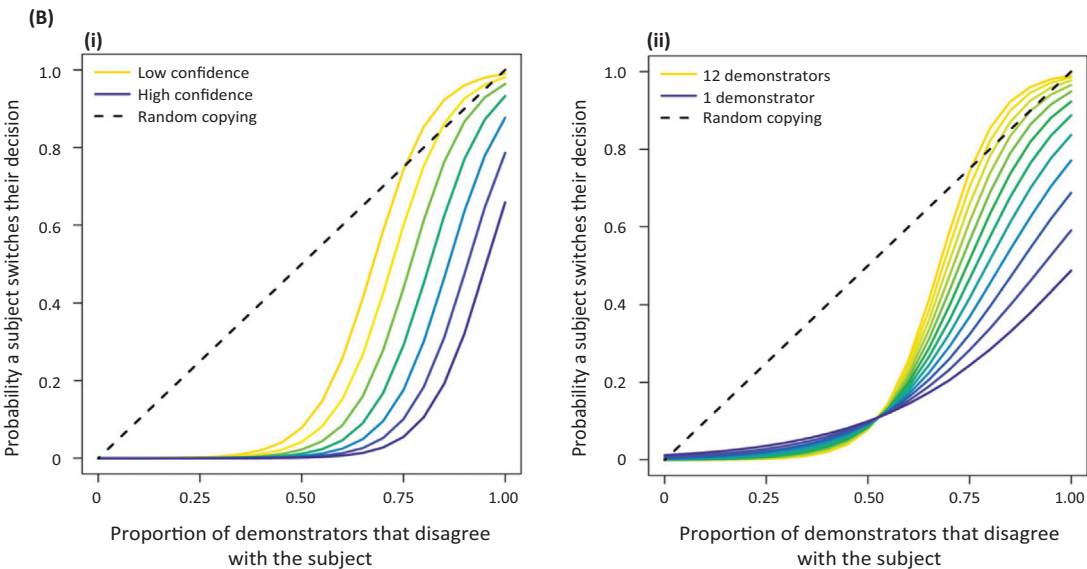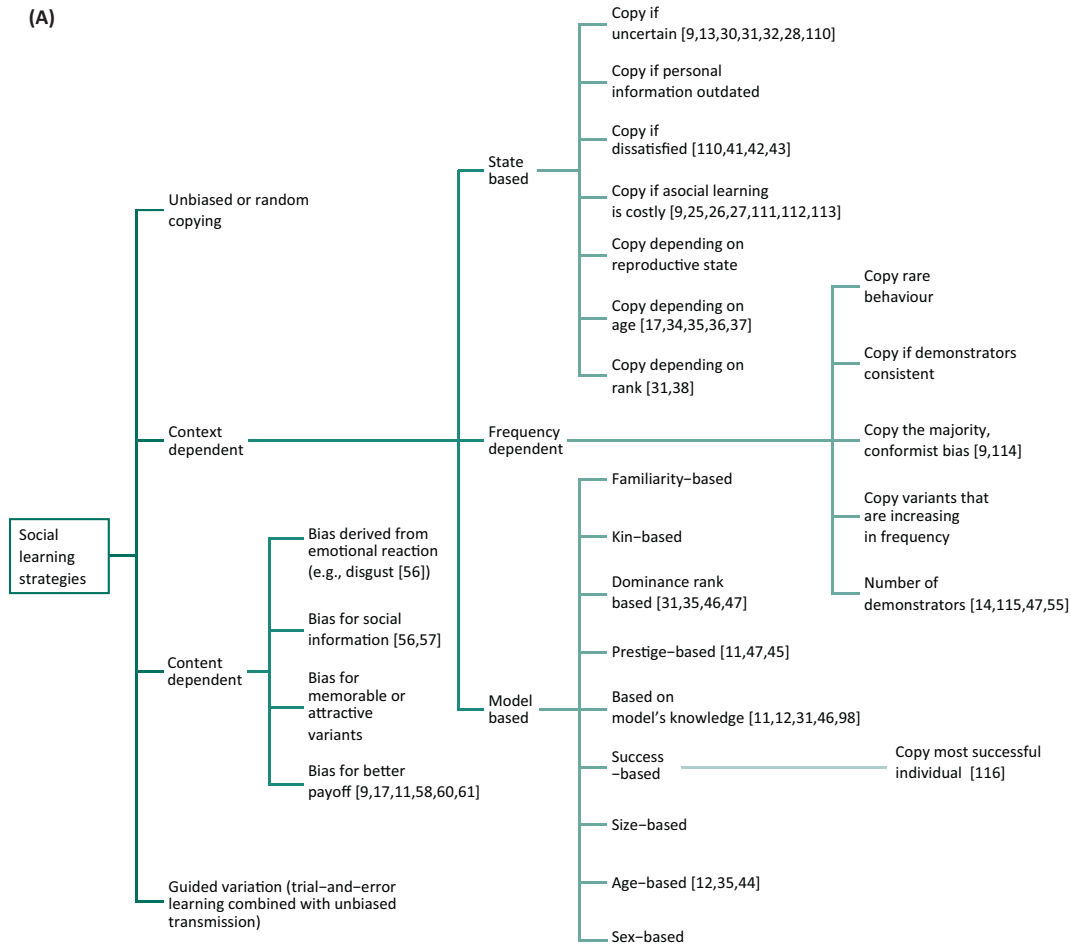


Trends in Cognitive Sciences

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In nonhumans, capuchins preferentially attend to, and learn from, older and higher-ranking over younger and/or lower-ranking individuals [35], while chimpanzees preferentially observe and copy dominants [31,46] as well as those with a history of proficiency in similar tasks (L.A. Wood, PhD thesis, Durham University, 2013) [46]. These strategies are heuristics thought to lead to the copying of successful individuals (e.g., in reaching older ages or higher dominance rank) that are assumed to display behavioural traits worth adopting.

### Frequency-Dependent Biases or 'Copy the Majority' Strategies

A positive frequency-dependent bias (aka 'conformist transmission' or 'copy-the-majority') occurs when the most common variant in a population is disproportionately more likely to be adopted, allowing individuals to benefit from the collective wisdom of others. Whether and under what circumstances individuals are expected to display this bias has excited controversy among theoreticians [5,47,55], and the empirical evidence is somewhat equivocal [9,47,48]. A key, although hotly debated, question is whether the behaviour of the majority of individuals should be copied, not simply the behaviour seen most [49–51]. In agreement with the emphasis on individuals rather than behaviour, children and chimpanzees will copy the behaviour demonstrated by three different individuals over the behaviour demonstrated, three times, by one individual [52]. To some extent, the debate is alleviated by recognition that conformity is often just one of several simultaneous influences on behaviour (see 'Multiple Strategies Are Deployed Simultaneously' and Figure 1) and is sensitive to context. Children show higher-fidelity imitation when demonstrations involve two simultaneous models, rather than one model [53]. Likewise, children will copy with higher fidelity when provided with linguistic cues, indicating that there is a convention to be followed compared with when instrumental language cues are provided [53,54]. Other studies of humans suggest that the likelihood of conforming is context [47] and individual dependent [55], and sensitive to whether the demonstrators have obtained their information from independent sources or from each other [14].

### Content-Dependent Biases or 'What' Strategies

Content-dependent (aka 'direct') strategies express biases regarding what is learned, with individuals adopting behaviours following direct assessment of the (relative or perceived) value of the trait. This assessment can be based on the nature of the information itself, or its effectiveness. In the former case, humans express a preference for social (e.g., relationships) over physical (e.g., the weather and/or environment) content when transmitting stories, urban legends, or gossip [56,57], and for content that evokes strong emotions (e.g., disgust) or is of survival relevance [56]. Such preferences are usually referred to as content biases. The payoff associated with a trait is also known to affect transmission ('payoff bias' e.g., [58]). There is empirical evidence of preferences for more effective solutions (i.e., copy a trait if its payoff is better than your own) across a range of species, including sticklebacks [59] and chimpanzees [58,60,61].

### Novel Insights from Theoretical and Empirical Findings

Several key insights have emerged over the recent years of intensive investigation of SLSs. These include findings of considerable flexibility in the use of SLSs at both the individual and population level, and of several SLSs being deployed simultaneously. Accordingly, it is now

Figure 1. Summarising identified social learning strategies (SLSs) and their use. (A) SLSs for which there is significant theoretical or empirical support. The tree structure is purely conceptual and does not imply similarity of cognition. Sources [9,11–14,17,25–28,30–32,34–38,41–47,55–58,60,61,98,110–116] are purely for illustration as recent literature entry points for readers (see [82] for additional illustrative sources). (B) The panels, which derive from an experimental study of human social learning [9], illustrate how behavioural outputs can result from the simultaneous deployment of multiple SLSs. (i) shows how subjects' decisions were affected by both their personal confidence and consensus among demonstrators, while (ii) shows the combined effects of the number of demonstrators and the consensus among them. Based on Figure 1 in [82] (A), and Figure 2A (Bi) and 2B (Bii) in [9].

understood that population-level patterns are not necessarily indicative of particular SLSs. Finally, because SLSs are imperfect heuristics, they can result in the acquisition and spread of maladaptive behaviour.

### Flexible Strategy Use

SLSs, and the behaviours that underpin them, are subject to natural selection. This has led some researchers to characterise SLSs as implying inflexible decision rules [62], but the fact that a strategy may have evolved does not imply anything about the flexibility of the behaviour it generates (neither is the flexible use of SLSs evidence that the SLSs have not evolved) [63]. Several recent studies have shown that individuals from the same population can adopt different strategies depending on subtle differences in context [64], developmental experience [40,65], or other interindividual variation [29,66] accounting for different patterns of behaviour. For instance, whom children copy (e.g., parents versus peers) varies with task domain [64], with new skills learned preferentially from adults, but toy, clothing, and dietary preferences dispro-portionately learned from other children. Likewise, children's learning strategies change as they age, with younger children influenced by unanimity, but older children sensitive to majorities [67]. Moreover, there is increasing evidence for cultural variation in reliance on social learning due to cultural differences in experience during ontogeny, for example regarding care-giving practices [68], pedagogical styles [69], or other emphases [70]. In humans, cumulative culture relies on psychological adaptations that are 'sufficiently flexible to support the acquisition of highly variable behavioural repertoires' ([71] p. 7877). Together, these findings need not imply active or executive control of decision-making, although that is a possibility. Hence, SLSs are best regarded as biases shaping behaviour, not hard-and-fast rules blindly applied across all individuals or contexts.

### Multiple Strategies Are Deployed Simultaneously

There is now clear evidence for multiple strategies being deployed by the same species (e.g., humans [72] or capuchins [35]), often simultaneously (chimpanzees [31], sticklebacks [26]; or humans [9]; Figure 1). For example, young children can combine different model-based biases (specifically 'copy adults over peers' and 'copy knowledgeable over ignorant individuals') contingent on whether the specific model characteristics intersect [12]. Learning biases can also interact flexibly to produce effective decision-making and higher payoffs in adults (e.g., individuals conform to the majority only when there is good consensus among demonstrators [9]; Figure 1). One study alone has provided evidence for the simultaneous deployment of nine strategies across a population of human adults [9], implying that SLSs likely operate in concert as biases rather than being combined into fine-grained decision rules [2] (although most studies lack the resolution to distinguish between different individuals pursuing alternative strategies and individuals pursuing multiple strategies simultaneously). These findings undermine any research agenda dedicated to working out the strategy implemented by a particular species. Rather, the challenge is to determine the complex of strategic copying influences that shape behaviour in any given instance.

### Psychological Heuristics and Population-Level Patterns

In the SLS literature, the term 'strategy' has often been used to describe both the psychological rule deployed by the learner and the pattern of behaviour that this rule produces across the population. However, this has proven problematic, since studies have established that there is not necessarily a one-to-one correspondence between the two. For example, theory predicts that the conformist rule 'copy the majority behaviour' results in the disproportionate adoption of popular traits at the expense of rare traits, producing at the population level an S-shaped relationship between trait frequency and probability of adoption [5]. However, conformist social

learning does not result in the expected (S-shaped) population-level outcome when other, simultaneously operating, biases have a masking effect [9]. Humans are only seen to be conforming to the majority when the effects of other biases have been statistically removed [9]. This insight helps to explain conflicting findings over the extent of conformity.

Likewise, strategies such as 'copy kin', 'copy friends', 'copy dominants', or where preferences differ between individuals (e.g., for dog breeds or baby names), can result in population-level patterns that resemble random or 'unbiased' copying (e.g., [73]) or, indeed, conformist transmission [50]. Given that multiple learning rules can generate the same population-level pattern, while a particular learning rule can generate multiple population-level outcomes, it is recommended that the term 'strategy' be restricted to cognitive rules and not population-level patterns of behaviour [2].

### Herding and the Spread of Misinformation

When the cost of collecting personal information and of individually vetting every trait for its potential contribution to fitness is prohibitive, individuals may rely on imperfect heuristics that enable them to adopt reasonably good behaviour through social learning now. As a consequence, some maladaptive behaviours will be acquired [74]. For example, reliance on social learning has resulted in the copying of obviously causally irrelevant behaviours in children (e.g., [17,75,76]) and potentially the recent spread of fake news, where content-dependent biases may have an important role [77]. Maladaptive information cascades [4], whereby individuals disregard their own personal information in favour of following the decisions of others (not the cues on which those decisions are based), may also occur. This may explain the explosive spread of behaviours such as economic market crashes, mob violence, panic rushes in crowds, and even suicides, as well as the existence of witchcraft and fake medical treatments [74,78,79].

## Challenges to the Social Learning Strategy Concept

The strong empirical support for strategic copying has not prevented the SLS concept from attracting criticism. Here, we consider some major criticisms, which require a clarification and updating of the SLS concept.

### Do SLSs Imply Domain-Specific Mechanisms?

Comparative psychologists have claimed that the SLS perspective encourages the conclusion that SLSs are reliant on 'specialised', 'evolved', or '**domain-specific**' mechanisms that deploy 'conscious', 'voluntary' decision-making [10,16,62,80]. It has been claimed that such assumptions could be leading the field astray because such authors suggest that **domain-general** associative processes could also account for the findings of SLS experiments. *Prima facie*, this criticism would appear an attribution error, perhaps a consequence of differences between fields in their use of terms such as 'evolved' (which, as we deploy it, applies to exaptations and products of cultural evolution, not solely biological adaptations). The SLS literature has been explicit from the outset in disavowing any commitment to mechanism, or to conscious decision-making. The paper that introduced the SLS concept states ([8] p. 5):

> 'In accordance with behavioral ecologists' use of the phenotypic gambit (Grafen, 1984), it does not matter whether animals adopt such strategies as a consequence of evolved psychological mechanisms, learning, culture, or some combination of processes' and 'the adoption of such strategies would not require that the animals be aware that they are following a strategy, nor that they understand why such strategies may work.'

The subsequent SLS literature is replete with statements along these lines (e.g., [2,9,58,66,81,82]), highlighting that SLS researchers are not committed to the hypotheses that the behaviour is unlearned, under tight genetic control, and neither that decision making is

conscious. Naturally, the neutrality of the SLS concept does not preclude experimental findings suggesting the possibility of social learning adaptations. Recent research with children, chimpanzees, and gorillas may provide evidence of evolved aspects of SLSs; individuals showed enhanced learning from animate (compared with inanimate) models, which was not merely due to changes in input mechanisms (e.g., reduced attention), but to greater depth of encoding and enhanced memory with socially mediated events [83]. This may be due to an 'agentive match' between model and observer [83], implying that some SLSs may be manifestations of evolved enhancements in memory for and, thus, replication of, the actions of specific models, mediated by relatability of goal-directed actions between observer and model (Box 1).

However, any claim that the evolutionary reasoning of SLS leads researchers to expect that closely related species should exhibit similar strategies [62] is contentious. While closely related species are generally expected to exhibit trait similarities, behavioural traits are renowned for being evolutionarily labile. Experimental studies have shown different SLS use in closely related species, different populations of the same species [84,85], and different individuals within a group [29,66], while other studies imply that ecology may be more influential in SLS distribution than is phylogenetic relatedness [81,84]. There is a need for further research on the relationship between phylogenetic relatedness and SLS use, but the prevailing evidence suggests that, due to the demonstrated flexibilities in use of SLSs, their study requires no commitment to the nativist stance that SLSs are unlearned.

### Are SLSs an Alternative to Associative Learning?

The misattribution of domain-specific explanations to SLS studies has led to **associative learning theory** (ALT) being juxtaposed as providing alternative domain-general explanations to SLSs [10,16,62,80]. There is no question that the findings of social learning experiments can often be explained by associative learning, but SLS and ALT are not alternatives. SLSs provide a functional account of behaviour; they are explicitly mechanism neutral, and no substitute for the thorough analysis of mechanism. This is implicit in the literature, because SLS studies commonly deploy asocial learning controls, and consider ALT explanations for the results (e.g., [30,41,84,140]; Box 2).

However, the possibility that ALT could underlie SLS findings does not constitute evidence that alternative mechanistic explanations are wrong, as some researchers have implied [62,80]. For instance, researchers have argued that between-species differences in social learning, such as differences between humans and chimpanzees in imitation, reflect differences in 'input mechanisms' (i.e., perceptual or motivational factors), on the assumption that both species exhibit the same ALT learning processes [80]. However, it would appear implausible, given the extensive evidence for neurological and genetic differences between these species (e.g., [86,87]), to suggest that motivational variation could fully explain the differences in social learning between chimpanzees and humans. Equally, the possibility that humans learn through the same mechanism(s) as nonhumans, but with enhanced computational power resulting in faster operation and differing behavioural effects, merits attention [87].

### Is 'Blackboxing' of Mechanism Bad?

SLS research has relied heavily on an assumption known as the '**behavioural gambit**', the idea that mechanisms of implementation do not greatly constrain the adaptive behavioural rules that evolve [20]. This assumption has stimulated extensive theoretical work, which in turn allows SLS theory (e.g., [6,43,88,89]) to guide a great deal of empirical research [31,59,82,87]. However, other researchers have expressed concern that this 'blackboxing' of mechanism is 'no longer a tenable scientific strategy' ([15] p. 2). Is this the case, or have the perils been overstated?

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**Box 2. Storytelling and Science: Contention over SLS Experimental Investigations**

Criticisms of SLS experiments by learning theorists [62] have sparked debate. Here, we present three illustrative studies, then draw out general points.

**Foraging Bats**

Foraging frog-eating bats learn novel prey cues socially more readily when cues are rewarded only 50% of the time compared with 100% of the time (a 'copy-if-dissatisfied' or 'copy-when-asocial-information-is-unreliable' SLS) [41]. Learning theorists suggested that social learning in the 50%-rewarded treatment was an artefact of bats being more likely to visit the demonstrated cue source than in the 100%-rewarded treatment because intermittently rewarded stimuli are less attractive [62]. However, the findings of an asocial control treatment rule out this explanation.

**A Species Difference in Public-Information Use**

Three- and ninespine sticklebacks experienced two groups of fish feeding at different rates (rich and poor prey patches). Later, when tested in the absence of demonstrators, only ninespines showed a preference for the rich patch, perhaps because ninespines face greater predation risk than do threespines (a 'copy-when-collecting-asocial-information-is-costly' SLS) [84]. Learning theorists suggested that this finding is an artefact of fish detecting that more prey were delivered at the rich patch [62]. This explanation is not credible because: (i) the design explicitly prevented observers from seeing food; (ii) fish cannot locate the rich patch using odour cues alone [84]; and (iii) later studies using watertight chambers to house demonstrators and feeders separately obtain identical results [127]. Moreover, the ALT account cannot explain the between-species differences in public-information use under identical conditions.

**Minnows and Predation Risk**

Minnows were more likely to use social information when predation risk was high (a 'copy-when-asocial-learning-is-costly' SLS) [112]. Learning theorists proposed that predation risk caused conditioned suppression of the feeder–food association, reducing foraging motivation, leading fish to approach areas where conspecifics had been [62]. This is extremely unlikely because fish perceiving risks are more likely to remain in cover than join shoals in the open [112].

**General Points**

ALT is a powerful explanatory tool that can be fruitfully deployed to understand findings from social learning experiments. However, these examples illustrate how the utility of ALT does not guarantee that a particular ALT explanation is correct. The general point here is that mechanistic perspectives that ignore functional insights are no less prone to error than are functional perspectives that ignore mechanism. To move the field forward, rather than retrospective ALT storytelling, researchers must integrate perspectives and experimentally compare the relative merits of alternative mechanistic explanations for particular exhibited strategies.

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The critique focuses on the findings of a computer-based tournament that pitted learning strategies against each other in an evolutionary simulation [90]. The tournament revealed how individuals performing the highest-payoff behaviour in their repertoire inadvertently filter information for others to copy. Thus, social learning will be favoured in any exploration and/or exploitation dilemma, if there is an opportunity cost to exploration (asocial learning) and individuals can select the best behaviour known to them for exploitation. This general adaptiveness of social learning is an important explanation for the ubiquity of social learning in the animal kingdom [90].

Nonetheless, the conclusion that social learning is adaptive across a range of conditions, a robust finding of experimental studies and formal theory [2,5,72,82,91] has been described as 'misleading'. Critics argue that some asocial learning in the tournament (where individuals asocially obtained information about the payoff of a behaviour they had already learned by performing it) was not properly accounted for in the analysis and interpretation of the tournament results, effectively obscuring (or 'blackboxing') an important source of asocial information, and leading to an unwarranted emphasis on social learning [15]. However, this argument is

problematic, in two respects. First, it does not distinguish between two classes of learning represented in the tournament (learning how to perform a behaviour and learning its payoff) when the claims regarding the superiority of social learning were related explicitly, and specifically, to the former. Unravelling how individuals decide which of an almost infinite set of behaviours to learn is a serious scientific challenge, in comparison to which updating payoffs received for established behaviour appears straightforward. Second, and more importantly, disagreement over how to interpret learning about payoffs reflects little on the perils or merits of 'blackboxing'. The tournament organisers decided that details of exactly how learning about payoffs happened were peripheral to the analysis, and so these were abstracted out. Theoretical models must always strike a balance between accurately representing the process being studied and incorporating those assumptions that are judged critical, while deciding which details to leave out. In this respect, the critique of 'blackboxing' applies to any mathematical model. It is, of course, legitimate to evaluate any model on the extent to which it has accurately captured the key components of the process being studied. Nevertheless, it is a big step indeed to build on such critiques a proposal that the entire approach of not modelling every mechanism in detail is scientifically 'untenable'.

While systematically and uncritically ignoring mechanism would be problematic, evolutionary researchers are not unaware of these pitfalls; indeed, there is active debate within the field about the issue (e.g., [20]). There is no doubt that research on the neural mechanisms of social learning is important, but such research itself attests to the underlying biological reality of SLS, as well as neural adaptations for social learning competences (particularly in humans). Some of the latest neuroscience research is revealing just how profoundly social interactions are embedded in human and nonhuman brains. For example, there is growing, and methodologically diverse, evidence indicating that the anterior cingulate cortex lying in the gyrus (ACCg) is specialised for the processing of social information in humans and nonhumans, with ramifications specifically for SLSs ([92]; Box 3). Likewise, 'evolutionary neuroscience' experiments indicate that differences between primate species (including humans) in neural connectivity and responsivity of the mirror system link to species differences in the capacity for imitation and social learning of tool use [93]. In macaques and chimpanzees, most of this circuitry consists of frontal–temporal connections, while humans have more substantial temporal–parietal and frontal–parietal connections. Moreover, humans' comparatively expanded and plastic association cortex [94] may imply a greater role for developmental scaffolding [95] upon brain architecture underlying social learning capacities in humans versus nonhumans (but see [96]). Finally, connectome studies are revealing dedicated networks of neural connections underlying behavioural innovation [97] that link to regions of the primate brain (such as the lateral prefrontal cortex) that have expanded disproportionately during human evolution [130]. Such neuroscientific studies highlight how functional and mechanistic perspectives are complementary. Moreover, they leave the hypothesis that social learning abilities underlying SLSs derive solely from selection on input mechanisms (e.g., attention or motivation) [80] increasingly untenable.

### Metacognitive SLSs

It has been suggested [16] that the primary difference between cultural evolution in humans and other animals is that humans alone have domain-specific **metacognitive** SLSs, whereby individuals consciously assess who is knowledgeable, which in turn influences whom is copied (Box 4). In reality, the discrepancies between humans and other animals in this domain are multifaceted, and almost certainly reflect the aforementioned substantial evolved differences in the neural architecture of human brains [87], rather than a single cognitive competence. Nonetheless, an important role for metacognition in human culture is plausible. One possibility

## Box 3. The Neurobiology of Strategic Copying

Social neuroscientists now recognise 'deep homology' in the mechanisms and structures of the 'social brain' across diverse taxa [106], while primatologists emphasise how the brain of primates, particularly with respect to encephalisation and the neural basis of imitation, is organised for 'sociocultural' processing [107]. That social interactions are embedded in brains is also highlighted by the emerging field of 'network neuroscience', which argues that neural networks within the brain exhibit reciprocal interaction with social networks in the environment: neural activities shape patterns of learning and behaviour in humans' social networks, which in turn feed back to influence individuals' brain structure and function [108]. Human brains spontaneously encode social network positions of familiar others, highlighting how navigating complex social interactions could influence brain development and evolution [128] and hinting at rapid unconscious (see Box 4 in the main text) processes underlying model-based SLSs in humans and nonhumans. Collectively, these findings imply that the use of particular SLSs within a population may lead to characteristic patterns of neural connectivity within individual brains, potentially with signatures of implemented strategies manifest across diverse animal groups.

Increasingly, neuroscientific data are pointing to dedicated mechanisms for social learning. For instance, Hill *et al.* [129] discovered that the portion of the ACCg of humans showed neuronal activity corresponding to reinforcement (or trial-and-error) learning, but only when monitoring the behaviour of others. This allocentric pattern is distinct from other regions, implying it signals information crucial to social learning [21]. Neurophysiology, neuroimaging, lesion studies, and those of individuals with autistic spectrum disorder, all indicate a specialisation in the ACCg for processing social information in humans and nonhumans [92]. Other medial prefrontal cortex (mPFC) subregions mostly signal in an egocentric frame or in both egocentric and allocentric frames. Thus, these regions may contribute to integrating information regarding one's own actions and those of others to update behaviour [21], potentially underlying 'copy if better' SLSs. Likewise, considering frequency-dependent SLSs, there is evidence that the magnitude of activity in the anterior insula, rostral cingulate zone, and ventral striatum in response to consensus/nonconsensus between demonstrators or between self and demonstrators predicts changes in an individual's behaviour (reviewed in [139]). It remains to be established to what extent different humans, societies, and species implement the same behavioural strategies in different ways in their brains, but this issue affords rich opportunities for comparative work.

## Box 4. Metacognition and Social Learning Strategies

Metacognition is a sophisticated cognitive capacity developing late in human ontogeny [131], considered uniquely human by some [16]. It uses forms of learning (e.g., ALT) and/or other aspects of cognition (e.g., memory or mental simulation) to generate responses not directly related to them (i.e., thinking about thinking). Thus, metacognition is sometimes labelled a 'system 2' process, being top-down (executively controlled), available to conscious awareness, in contrast to and serving to augment 'system 1' activities, which are bottom-up (stimulus driven), involuntary, and based on information from genetic inheritance or associative learning (dual-process theory [132]). For example, humans may express their confidence (a metacognitive output) regarding their own abilities, verbally or physically (e.g., shrugging shoulders), or have knowledge about what others know.

The extent to which metacognitive capacities are seen in nonhumans is relevant to our understanding of their levels of self-awareness and evolution of the human mind. Although nonhuman abilities may be less varied and sophisticated (e.g., [133]) than those of humans, there is evidence in pigeons, rats, monkeys, and apes for monitoring of knowledge, uncertainty, and memory, as well as confidence levels (reviewed in [134]). For example, chimpanzees make spontaneous confidence judgements regarding the likelihood that they performed accurately enough in a task to gain a reward, and adjust their behaviour accordingly [134]. Likewise, strategic information seeking in nonhumans, where ALT explanations are discounted [135], reflects a response to perceived uncertainty. For example, orangutans and chimpanzees demonstrate that they know when they do not know which of three tools is appropriate to reach a reward (due to their length being occluded) by changing position to determine this [136].

Whether explicit metacognitive capacities are manifest in SLSs, such that the accuracy and reliability of cognitive processes in the self and others is consciously assessed [16], is open to question. Most contexts where 'copy when uncertain' SLSs have been reported need not require explicit (versus implicit) metacognition, but other strategies representing 'who knows' (e.g., chimpanzees (L.A. Wood, PhD thesis, Durham University, 2013) and humans [98,109,137]) might. While no more an alternative to SLS than ALT, metacognition potentially affords unique learning strategies (especially if explicit). These include enabling accurate inference of others' intentions and, hence, what to copy, and teaching that is contingent upon, or enhanced by, knowledge of the pupil's level of understanding. Thus, metacognition may have had an important role in human cognitive and cultural evolution, and may help to explain how humans teach across such a broad range of tasks, in contrast to the rare and specialist teaching reported in other animals [87,138]. However, whether explicitly (conscious) metacognitive SLSs are unique to humans and must produce reportable (verbally or otherwise) representations of 'who knows' to promote culture [16], is currently difficult to assess.

is that human-unique metacognitive SLSs produce reportable representations of 'who knows', thereby supporting the cultural inheritance of 'wise' SLSs dictating high-fidelity copying from recognised experts (and avoiding copying amateurs), which over generations promotes cumulative cultural evolution [16]. Importantly, for arguments that emphasise the importance of culture for the ecological dominance of humanity [99–101], these metacognitive strategies enable individuals to copy the best trait in a given domain, despite the reason for its success being cognitively opaque. By allowing inferences to be made about the goals and intentions of others, a metacognitive capability potentially affords more accurate reconstruction of the nature of the task to be copied, while the same capabilities potentially help tutors tailor their teaching and scaffolding to pupils' knowledge levels. Although SLSs have thus far been constrained to the perspective of the learner, it might be fruitful to explore how SLSs may be extended to include strategic information provisioning by experts.

While the 'metacognition underlies human culture' argument was presented as an alternative to a SLS explanation [16], this juxtaposition is misleading, both because to our knowledge, no strong claims about SLSs underlying human–animal differences appear in the literature, and because metacognition itself may be a mechanism underpinning some SLSs. The SLS concept covers a diversity of mechanisms for achieving efficient social learning, from genetically heritable variation between individuals through to the social learning of social learning [66] and the cultural diversity the latter entails [70,100]. Given that the phylogenetic distribution of metacognition is an active area of research [102], it would appear premature simply to assume that 'all animal behaviour . . . conforming to SLSs, is based on domain-general processes of associative learning' ([16] p. 209, emphasis added; Box 1). Nonetheless, increased attention to the role of metacognition in social learning and teaching, in humans and other animals, is required (Box 4). The hypothesis that metacognitive SLSs are uniquely human also merits further attention.

## Concluding Remarks

The SLS perspective has proven productive not least because the approach provides a vehicle for integrating cognitive, behavioural, and evolutionary perspectives, as well as empirical work and theory. A complete understanding of behaviour requires that (at least) **four questions** are addressed [104]. Analyses of social learning and cultural evolution that focus on function to the exclusion of mechanism are necessarily incomplete. However, SLS researchers have conducted numerous investigations of social learning mechanisms, including drawing on associative learning interpretations (e.g., [103,105,140]). To move forward, what is now required are not retrospective narrative accounts but experimental tests, based upon *a priori* specification of differing predictions, designed to distinguish purported alternative explanations of social learning behaviour (see Outstanding Questions). There are exciting opportunities for integrating functional, evolutionary, developmental, and mechanistic analyses in this domain, for example, by exploring the mechanistic and neuroscientific bases of strategy use (Box 3), studying how learning strategies change over developmental time as cognitive capabilities change, investigating the phylogenetic distribution and adaptive value of the use of a particular SLS, and exploring the role of metacognition in human culture (Box 4). The advantages of interdisciplinary work in these domains extend beyond the benefits that return to social learning researchers. For instance, it may be possible for developmental psychologists, comparative psychologists, and cognitive neuroscientists to make sense of population or individual differences in cognitive development or neural connectivity in terms of alternative SLS deployment. Likewise, species differences in brain architecture, and its development throughout ontogeny, will likely be strongly tied to the details of the functional questions those brains have evolved to answer. In comparison to the cruder categories of 'social learning' or 'imitation', specification of SLSs characterises, for instance, whether the learner will be

attending to payoff, consensus, or status information, each of which are seemingly associated with distinctive patterns of neural connectivity (Box 3). Given their impressive track record of integrating empirical and theoretical insights, as well as findings from behavioural and evolutionary biology, cognitive neuroscience, and developmental psychology, SLSs potentially provide a useful vehicle for bridge-building between fields.

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## Outstanding Questions

What mechanisms underpin SLSs? Investigating the behavioural and neurobiological underpinnings of SLSs is central to progress in the field. Can we design studies with differing *a priori* predictions regarding learning mechanisms involved in SLSs? Feasibly, the types of test (including ALT controls; see Box 2 in the main text) deployed with bumble-bees (see Box 1 in the main text) could be extended to other systems.

Do particular SLSs involve characteristic neural circuitries? Do individuals, societies, or species implement behavioural strategies in similar ways in their brains? Is there a characteristic connectome for each SLS? Can neurobiological studies (see Box 3 in the main text) shed light on the role of ALT in SLSs implemented by different species? How is SLS use influenced by individual differences?

How do SLSs develop over the lifetime? The ontogeny of SLSs is understudied yet contributes to flexibility in SLS use. How does the deployment of SLSs shift over ontogeny? To what extent is this contingent on general aspects of brain and cognitive development? How do individuals alter use of SLSs with personal experience and changing context (e.g., stage of tradition formation)?

What is the evolutionary history of SLSs? Can phylogenetic techniques (e.g., comparative studies of SLSs in multiple pairs of closely related species) contribute to the debate over the extent to which SLSs are evolved adaptations and/or learned heuristics? Do differing evolutionary histories of group living influence the use or sophistication of SLSs?

What is the adaptive value of SLSs? SLSs likely vary in their fitness consequences, but this is understudied and relies on identifying SLSs in natural contexts. How do SLSs affect foraging success and success in other domains (e.g., nest building and predator evasion)?

What role does metacognition have in human culture? What is the phylogenetic distribution of metacognitive SLSs (see Box 4 in the main text)? How do they promote culture? Is knowledge of 'who knows (what)' critical for model-based SLSs and teaching?

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