

## Review

## The Evolution of Individual and Cultural Variation in Social Learning

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It is often assumed in experiments and models that social learning abilities – how often individuals copy others, plus who and how they copy – are species-typical. Yet there is accruing evidence for systematic individual variation in social learning within species. Here we review evidence for this individual variation, placing it within a continuum of increasing phenotypic plasticity, from genetically polymorphic personality traits, to developmental plasticity via cues such as maternal stress, to the individual learning of social learning, and finally the social learning of social learning. The latter, possibly restricted to humans, can generate stable between-group cultural variation in social learning. More research is needed to understand the extent, causes, and consequences of this individual and cultural variation.

### Social Learning across Species... and Individuals?

There has recently been huge growth in studies of **social learning** and **culture** (see [Glossary](#)) across diverse species [1,2], including fish [3], insects [4], birds [5], and mammals [6], such as cetaceans [7], rodents [8], monkeys [9], and great apes [10], using multiple methods including field observations [11,12], lab and field experiments [2,13], and theoretical models [14,15]. Social learning (and **social information use** more broadly, [Box 1](#)) now constitutes a major area of study within behavioural and evolutionary biology, shown to affect multiple domains including mate choice, foraging, predator recognition, tool use, and communication [1], and having concrete evolutionary consequences such as the structuring of social groups [16] and even speciation [17]. Much effort has also gone into explaining human culture in a manner consistent with this comparative evidence and with evolutionary principles, focusing on how relatively high-fidelity human social learning [18,19] can uniquely support the cumulative cultural evolution [20–22] that underlies our species' great ecological success [23].

While much effort has gone into empirically demonstrating the presence of social learning in different species, and the presence of different **social learning mechanisms** (e.g., stimulus enhancement, local enhancement, imitation [19,24]), and **social learning strategies** (e.g., copying successful individuals or copying the majority [13,25]), much less attention has been devoted to documenting and explaining individual variation in these phenomena within species, or among groups of individuals (e.g., populations) within species.

In experiments, typically the demonstration of social learning, or a particular mechanism or strategy of social learning, in enough individuals or on enough trials to reach statistical significance leads to the claim that this phenomenon is present in this particular species. The authors of one recent study claimed, for example, that their findings 'constitute strong support for the

#### Trends

Social learning is often assumed to be a universal, species-typical capacity.

We review evidence showing non-trivial individual variation in social learning.

This individual variation has multiple causes, reflecting phenotypic plasticity.

Individual variation in social learning has important evolutionary consequences.

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### Box 1. Social Learning and Social Information Use

In recent years, interest in the use of information derived from the behaviour of other animals has burgeoned among evolutionary and behavioural ecologists [82–84]. This is referred to as ‘social information use’ and encompasses a broader range of phenomena than is typically considered in the social learning literature. For instance, researchers will often consider any signalling interaction as social information use; indeed, social information use is functionally subdivided into ‘inadvertent’ and ‘evolved’, according to whether the source (e.g., behaviour or morphological trait) has been directly selected upon for its capacity to transfer information among individuals or not [82,83]. Thus, even behaviour that is ‘innately’ stimulated such as the tendency of female guppies to approach orange objects due to a sensory bias towards the flesh of fallen fruit [85] will be classed as social information use if it results in spending the most time with the most-orange male guppies. Such phenomena do not necessarily involve any learning (i.e., change in response to a stimulus as a result of experience). Therefore, social learning as we define it here (see ‘Glossary’) is clearly a form of social information use, but the terms are not interchangeable. Care must be taken when generalising about the evolution and maintenance of social learning from studies of social information use in the evolutionary ecology literature (typically done on non-primate taxa).

view . . . that cumulative culture requires a package of key psychological processes – specifically, teaching through verbal instruction, imitation, and prosocial tendencies – that are present in humans but are absent or impoverished in chimpanzees and capuchins.’ ([26], p. 1117). Another stated that ‘we show experimentally that wild vervet monkeys will abandon personal foraging preferences in favor of group norms new to them’ ([27], p. 483). While not detracting from the validity and importance of these findings on their own terms, there is implicit extrapolation here from the small number of individuals tested in these experiments to all humans, all chimpanzees, all capuchins, or all vervets.

Similarly, many theoretical models have examined the evolution of social learning [14] and of specific social learning strategies [15,28]. Yet these models typically assume that the capacity for social learning, or for different social learning strategies, is under direct genetic control and evolves by natural selection. For example, a recent review of 11 influential models of the evolution of social learning highlights the common assumption of all that ‘[e]ach learning strategy is assumed to be genetically determined and . . . not modifiable by learning.’ ([14], p. 3).

To some extent this is a modelling convenience, and in principle the findings of such models could hold if the inheritance of learning strategies is cultural rather than genetic. Empirical research, too, can in principle proceed according to the phenotypic gambit: ‘it does not matter whether animals adopt such [social learning] strategies as a consequence of evolved psychological mechanisms, learning, culture, or some combination of processes. Strategies can still fruitfully be studied as if the simplest genetic system controlled them.’ ([25], p. 5).

But is this really the case? While adopting the phenotypic gambit may have been useful in the initial study of social learning, here we argue that there is now substantial evidence, reviewed below, that (i) individuals within a species often differ systematically in their tendency to learn from others, and their use of different social learning strategies and mechanisms; and (ii) the causes of these individual differences are varied, including at least partly genetically inherited differences in personality traits, cues of developmental stress and current physiological condition, past associative learning histories, and (in humans, at least) cultural background. This individual variation has important implications for how social learning is studied comparatively, and for our understanding and interpretation of previous findings. Moreover, it can have significant evolutionary consequences, potentially driving populations to behavioural equilibria different to what we would expect if social learning were under tight genetic control, and casting doubt on the validity of a phenotypic gambit approach that ignores the extent and causes of individual variation.

### Causes of Individual Variation in Social Learning

In Table S1 in the supplemental information online, we summarise all experimental studies we could find that have documented and attempted to explain individual variation in social

### Glossary

**Culture:** at a minimum, simply denotes the presence of social learning within a population [1]; narrower definitions require the presence of stable between-population differences in behaviour as a result of social learning (‘cultural traditions’ [9,12]) or the accumulation of information via social learning over successive generations (‘cumulative culture’ [22]).

**Social information use:** changes in behaviour as a result of responding to stimuli derived from the behaviour of other individuals.

**Social learning:** long-term changes in rules for responding to stimuli that are derived from the observation of, or interaction with, another individual or its products [1]. Can be contrasted with individual (or asocial) learning, in which learning occurs with no social input. Social learning represents a specific form of social information use (Box 1).

**Social learning mechanisms:** lower-level descriptions of how or what one individual learns from another [19]. These include imitation (copying another’s motor actions), emulation (copying the end state or outcome of another’s actions), local enhancement (learning to attend to a particular location as a result of social cues), or stimulus enhancement (learning to attend to a particular object as a result of social cues).

**Social learning strategies:** relatively high-level heuristics that describe from whom individuals learn (e.g., copy successful individuals or copy the majority) and when they learn from others (e.g., copy when uncertain or copy when unsuccessful) [25].

### Box 2. Age and Sex Differences in Social Learning

In Table S1 we focus on individual variation within age or sex classes, as these have received the least attention in the field. However, there is also evidence for systematic age and sex differences in social learning, although similar to the other sources of individual variation discussed in the main text, several outstanding questions remain regarding their universality and causes.

#### Sex Differences

Some forms of social learning are specific to one sex simply because the trait being copied is only exhibited by that sex. For example, in many songbird species, only male birds sing, and thus only juvenile males learn songs, typically from their fathers [86]. In other cases, sex-specific social organisation restricts social learning to one sex. For example, male humpback whales are quasi-solitary and thus fail to learn female-specific vocalisations that delineate the social groups in which females live [87]. More interesting are cases in which both sexes of a species have opportunities to learn a trait that is non-sex-specific. Studies of chimpanzee tool-use acquisition show that juvenile females exhibit more effective social learning than juvenile males, most likely because females pay greater attention to their mothers [88]. This can have important implications for cultural diversity, with the number of cultural traits in chimpanzee societies correlating with the number of females, not males [89]. Sex-specific social learning will also determine the spread of cultural traits between groups in species with sex-specific dispersal patterns [90]. In humans, socially proscribed roles (e.g., economic divisions of labour) will often limit social learning opportunities. In one small-scale society, for example, only boys learn honey collecting skills, because only men perform this activity [91]. However, lab experiments with adults and children from a range of cultural backgrounds typically find no sex differences in social learning performance, frequency, or strategy [29,41,65,66].

#### Age Differences

The juveniles of many species show more social learning than adults, which is perhaps understandable given their relative lack of knowledge. Juvenile meerkats, for example, show greater social learning of foraging skills than adults [92]. Many vocalising bird and cetacean species acquire their vocalisations during a juvenile sensitive period [7,86]. In humans, field studies have shown transitions in learning from strong vertical (parental) social learning in childhood, to greater oblique (non-parental) and horizontal (peer-based) social learning in adolescence, to greater individual learning in adulthood [91,93]. Some have argued that human children possess specialised adaptations for acquiring knowledge from adults with little understanding of the benefits or uses of that knowledge [94,95], which would preclude any type of individual learning. The general pattern of more social learning in youth accords with theoretical models showing that social learning is most effective when combined with subsequent individual learning later in life [96,97]. While there have been many studies showing differences in social learning between age cohorts, more work is needed to track social learning within the same individual longitudinally, and particularly to test whether the individual variation reviewed in the main text is stable over a lifetime.

information use (incorporating social learning) within the same task and experimental condition. We exclude studies that found individual variation but did not offer potential explanations for that variation (e.g., [29]), and studies that found variation across different experimental tasks or conditions (e.g., different numbers or identities of demonstrators, or task difficulty), but not systematically across different individuals within the same task (e.g., [30]). For brevity, we also exclude age and sex differences, which are more well-studied and discussed separately in Box 2. Studies in Table S1 are grouped according to five broad categories.

#### Stable 'Personality' Traits or Individual Learning Ability

Several studies have linked social information use to stable individual differences that appear relatively fixed over the lifespan and to some degree genetically heritable. Some studies have linked social information use to individual variation in exploratory behaviour when alone, sometimes conceptualised as a 'boldness–shyness' personality continuum [31]. Findings are mixed, however, with some studies showing that more exploratory individuals exhibit more social information use [32,33], others that they exhibit less social information use [34–36], and others finding no relationship [37]. There is some evidence, although mixed, that boldness is heritable: one study found high heritability ( $h^2 = 0.76$ ) in zebrafish [38], another found substantial non-genetic inheritance in zebra finches [39], another found both genetic and environmental influences in a tropical fish [40]. Notably, one study with *Drosophila* has shown that social information use is influenced by a specific genetic polymorphism at the foraging locus, which also influences exploratory behaviour when alone [36]. Others have found that performance in an asocial learning task subsequently predicts social information use, although again in opposite directions:

two studies found that better individual learners were more likely to use social information [41,42], and two studies that they were less likely [43,44]. Three studies with humans have linked social learning to relatively stable individual differences, specifically social dominance [45], collectivism [46], and IQ [47].

The contradictory results relating to individual exploration and learning might simply be due to low power: many studies feature small sample sizes and marginally significant correlations. Species differences (i.e., phylogeny) might also play a role, but the small number of species tested makes it difficult to identify any systematic relationship between the species studied and the direction of the relationship. Theoretically, both relationships are plausible. A negative relationship (more exploratory individuals and/or better individual learners show less social information use) might indicate a frequency-dependent equilibrium between information producers (bold explorers and/or good individual learners) and information scroungers (shy observers and/or poor individual learners), as has been well-explored theoretically [48]. A positive relationship (more exploratory individuals and/or better individual learners show more social information use) might reflect a common cognitive ability or activity level underlying both individual exploration or learning and social information use, as previously shown across, rather than within, species [49], and as previously shown to underlie different cognitive abilities in the same species [50]. Finally, the contradictory results might stem from conflating social learning with social information use (Box 1), particularly in non-primate studies of animal personality. The final three human studies listed in Table S1 [45–47] under this category all use verbal questionnaires, and it is unclear how they relate to the behavioural findings. IQ likely predicts individual learning ability, and is substantially heritable [51]; whether social dominance or collectivism are heritable is unknown.

#### Developmental Stress or Deprivation

Other studies show that specific developmental cues influence social learning, introducing some degree of postnatal phenotypic plasticity. Three studies, all with rats, show that maternal deprivation or markers of high maternal stress (infrequent licking and grooming) reduce the subsequent social learning of food preferences from unfamiliar demonstrators [52–54]. This facultative switching in response to specific developmental cues might represent an adaptively limited degree of phenotypic plasticity: maternal deprivation or stress might indicate a recent environmental shift to which mothers are poorly suited, making it adaptive to rely less on others' potentially outdated knowledge (although see [55] for caution regarding anticipatory parental effects).

This response can be even more specific than simply switching from social to asocial learning. Farine *et al.* [56] found that zebra finches switch from vertical (parental) to oblique (non-parental) social learning in response to developmental stress. This might be adaptive when one's parents specifically possess outdated or inappropriate knowledge, while other conspecifics remain useful sources of information to be exploited. Further work is needed to test these adaptive hypotheses and rule out alternatives (although this is challenging [55]). We might predict, for example, that shifts in learning should depend on the severity of stress cues: very strong cues indicate dramatic recent environmental change and should provoke a wholesale shift from social to asocial learning, whereas more subtle cues indicate less severe environmental change and should provoke more subtle shifts such as from vertical to oblique social learning.

#### Reproductive State

One study has shown that adult physiological condition can influence social learning, with pregnant female ninespine sticklebacks exhibiting more social learning than non-pregnant females, and non-reproductive males showing more social learning than reproductive males [57]. Like the developmental cues just discussed, these might be adaptively fixed responses to specific cues. Pregnant females, who are more vulnerable to predation, should avoid risk and

thus avoid potentially dangerous individual learning, while reproductive males should show more risky individual learning if it leads to greater access to females [57]. The degree to which this reflects the specific cue of reproductive state, rather than operating via exploratory behaviour (as discussed earlier) or some general estimation of risk, remains to be determined.

#### Past Experience of Demonstrator Success or Cues of Demonstrator Quality

Three studies hint that social learning can be even more flexible than responding to specific cues, and that individuals can learn over time whether social learning leads to rewards [58–60]. In the clearest demonstration, bees previously rewarded for joining conspecifics subsequently showed more social learning of food location [59]. These authors argued that social learning here can be explained entirely through domain-general associative learning, rather than any specialised, domain-specific adaptation for social learning. In other words, social learning is just associative learning but with conspecifics as conditioned stimuli [61].

Heyes and colleagues [62,63] have taken this further, arguing that all forms of social learning, including different social learning strategies and mechanisms, can be explained in terms of domain-general associative learning processes. This can potentially explain otherwise puzzling findings such as that solitary species, including tortoises and octopuses, can learn socially [62]. On the other hand, it is difficult to explain certain interspecies differences in social learning without invoking some type of adaptive specialisation for social information use, particularly when those species are exposed to the same environmental cues. For example, ninespine but not threespine sticklebacks use social information in the same task and with the same opportunities for associative learning [64], suggesting adaptive specialisation in the ninespine species (although it remains to be determined whether the adaptive specialisation is for social learning specifically, or lower-level capacities such as social attention). Irrespective of the wider argument, the studies listed in Table S1 suggest that at least some intraspecific variation in social learning can arise through individual learning of the reliability of social information. It is unclear how stable these effects are, however, and whether this individual learning of social learning effectiveness continues throughout the lifetime resulting in within-individual temporal variation in social learning use, or whether it is more likely to occur early in life (Box 2).

#### Cultural Background

Finally, humans appear to show cultural variation in social learning, that is, stable between-group differences (cultural traditions) in social learning use or strategy that arise when individuals learn from others how and when to learn from others: the ‘social learning of social learning’. This can be distinguished from the individual learning of social learning discussed in the previous subsection because there is no requirement that conspecifics must be associated with tangible rewards. There is much circumstantial evidence for cultural variation in social learning in humans (Box 3), but only a few studies have tested this experimentally using robust methods [65–68].

The notion that there is structured and stable cultural variation in social learning in humans fits with broader proposals that humans have unusually high-fidelity and open-ended (i.e., domain-general) social learning [18–20] that generates strong and long-lasting cultural traditions [23,69]. However, stable cultural traditions are also present in other species [11,12], raising the possibility of the social learning of social learning in non-human species also. Once social learning itself can be socially learned, we might expect novel cultural evolutionary dynamics that drive behaviour to new equilibria that would not exist if social learning were genetically fixed or individually learned (Box 3).

#### Integration of Findings

One potentially useful way to integrate these findings, summarised in Figure 1, is according to the presumed degree of phenotypic plasticity involved [70], and by extension the reliability of cues to current and future environmental conditions [71,72].

## Box 3. The Social Learning of Social Learning in Humans: Evidence, Causes, and Consequences

**Cultural Variation in Social versus Individual Learning**

There is much circumstantial evidence for cultural variation in social learning in humans, that is, stable between-population differences in the frequency of social learning, or type of social learning strategy used, that are unlikely to be genetic or individually learned [98]. Collectivistic countries such as Japan or Korea have educational systems more focused around social learning (e.g., rote learning, respect for teachers), while more individualistic countries such as the UK or USA have educational systems more focused around individual learning (e.g., emphasising creativity and personal discovery) [98,99]. There is faster diffusion of new products through more collectivistic societies than through individualistic societies, suggesting stronger social learning of product choice [100]. These broad differences are supported by experimental tasks [65]. Nevertheless, there is a great deal of research needed to more broadly map variation in social learning beyond this simplistic East–West dichotomy, as well as whether this variation is task- or situation-independent, or only occurs in specific domains.

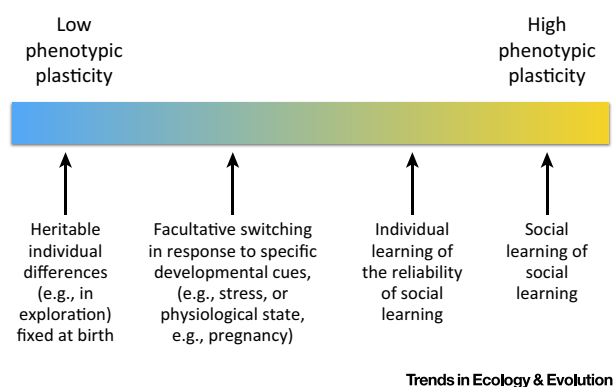
**The Origin and Persistence of Cultural Variation in Social Learning**

Documenting cultural variation is one step, but explaining it is entirely another. At a proximate level, it is not known how putative cultural variation in social learning is maintained over time. The unusual genetic homogeneity of our species, along with evidence that recent migrants adopt local patterns of social learning [65], counts against a genetic basis for this variation, but the precise cultural transmission pathways are unknown. It might be via educational systems (as discussed earlier), parental transmission, or peer influence. At a more ultimate level, Chang *et al.* [98] have argued that East–West differences in social learning arose as cultural responses to different historical rates of environmental change in Ancient China and Western Europe, respectively, given theoretical findings that social learning is most effective at relatively slow rates of environmental change, such that others' information is not outdated.

**The Consequences of the Social Learning of Social Learning**

Does it matter if social learning is socially learned? Ghirlanda and colleagues [79–81] addressed this question in a series of models. In the first [79], individuals possess the trait 'openness', defined as the probability of learning from a demonstrator, and which can itself be socially learned. This simple model resulted in the decrease of openness to its minimum initial value in the population. This is because more-open individuals learn to be less open from less-open demonstrators, but the reverse does not occur: less-open individuals do not learn to be more open from more-open individuals because less-open individuals do not learn from others. A subsequent model [80] showed that openness can be maintained but only when openness, and effectiveness as a demonstrator, are determined by multiple traits, such that individuals must first remain open to learn all of the traits needed to be effective demonstrators, before becoming conservative. Irrespective of these particular conclusions, these models demonstrate that when the tendency to learn from others can itself be learned from others, then cultural dynamics emerge that we would not expect if social learning were genetically fixed and stable over a lifetime.

First, some of the effects listed at the top of Table S1 likely reflect heritable and stable personality differences that appear fixed at birth. These might be genetic polymorphisms, with little if any postnatal phenotypic plasticity. Here, genes act as cues to (i.e., correlate with) the state of the social environment [71]. Assuming that underlying allele frequencies reflect a history of frequency-dependent selection (e.g., producer–scrounger dynamics) experienced by lineages,



**Figure 1. A Schematic Continuum Representing the Degree of Phenotypic Plasticity in Social Learning.** At the left are the studies near the top of Table S1, where genetic polymorphisms generate different phenotypes fixed from birth. Further towards the right are cases where phenotypes switch in response to specific developmental cues (e.g., of stress) or specific adulthood physiological states (e.g., reproductive state). Further right are cases of apparent individual learning of associations between conspecifics and rewards, with little or no domain specificity. At the extreme right are cases – possibly restricted to humans – where social learning is acquired from others via social learning.

there would be no need for any postnatal plasticity as the relevant environment is conspecifics from whom to learn, whose presence is predicted by the frequencies of the underlying polymorphism. In other words, when the value of social learning is predictable across generations, then individual variation will be genetically determined.

Second, the developmental and physiological effects represent a limited degree of postnatal phenotypic plasticity in response to specific cues (e.g., maternal stress, pregnancy) that reliably indicate changeable environmental conditions. For example, maternal stress might be a good indicator of recent between-generational environmental change, and thus provokes a shift from social to individual learning.

Third, the individual learning of social learning represents greater plasticity, with the possibility that different individuals who experience different reinforcement schedules end up with different social learning frequencies or strategies. This might reflect a fine-tuning mechanism to deal with more rapid and unpredictable within-generational change.

Finally, the social learning of social learning opens up a second (cultural) inheritance system through which social learning can evolve intergenerationally, in addition to genetic inheritance [73]. Here, for humans at least, the relevant environment is the society within which individuals live, an environment which is itself socially constructed [74]. The best cue here would be the social learning strategy of other individuals in that society, the one that existing institutions (e.g., educational systems, Box 3) are geared towards.

Our unidimensional scheme is, of course, an oversimplification, and any specific instance of social learning may be influenced by more than one of these causes (e.g., a genetically or culturally inherited tendency may subsequently be modified by developmental conditions or individual learning). Nevertheless, we consider it a useful initial heuristic to synthesise the findings listed in Table S1, which often remain unconnected in the literature. Further consideration of individual and cultural variation in social learning in the context of environmental and genetic cue reliability [71,72] might point to fruitful hypotheses. For example, we might predict that maladaptive side effects or runaway processes, such as informational cascades [48], are more common towards the right-hand side of Figure 1 where there is the least genetic control over social learning.

### Implications and Future Directions

It is clear that there is individual variation in the use of social learning in many species, and that this individual variation is not mere noise or error. Consequently, we suggest that broad claims such as 'species X shows conformity' or 'species Y exhibits imitation' can give the misleading impression that every member of that species exhibits these abilities. Such impressions are likely to be incorrect, particularly when based on the results of a single study with just a few individuals, and where those individuals have unknown or similar genetic variation, developmental experiences, or learning histories. While such studies can demonstrate that a certain ability is within the capacity of at least one member of that species, they can say little about the prevalence or universality of that ability.

An equivalent argument has been made regarding cognitive performance [75], where species-typical cognitive abilities are claimed based on the performance of one or a few 'genius' individuals such as Alex (the parrot) or Kanzi (the bonobo) without taking into account extensive interindividual variation. A similar argument has also been made regarding human psychology [76], where psychological processes documented in people from Western, Industrialised, Educated, Rich, Democratic ('WEIRD') countries have often been considered human universals, without taking into account extensive cultural variation in those processes. Our review reinforces

the points made in those previous papers [75,76]: studies should avoid overgeneralising from small samples to entire species, use as large sample sizes as are feasible, report rather than ignore individual variation in performance, and standardise tasks to be used across as many species (or, in humans, societies) as possible.

We can also make some novel points specific to the study of social learning. If social learning can itself be learned, it is particularly problematic to overgeneralise from hand-reared or enculturated members of non-human species who have learned to socially learn from their handlers. Indeed, findings that enculturated but not mother-raised chimpanzees show certain forms of imitation [77,78] lend support (although circumstantial) to our argument that individuals can learn from others how to learn from others. Furthermore, if developmental cues and learning histories can influence social learning, then comparisons between social learning in human children and adult non-human primates become difficult to interpret given that putative species differences are confounded by possible developmental differences. Finally, incorporating the possibility that social learning can itself be learned into evolutionary models of social learning might resolve apparent contradictions between modelling results and experimental findings, such as that humans copy others less than they should do [30,41]. It might be that people are bringing their individually or socially learned social learning strategies into the lab with them. Models that explicitly incorporate the individual or social learning of social learning strategies might more accurately predict experimental behaviour.

As is evident from Table S1, individual variation in social learning has been explored experimentally in only a select few species, making it difficult to know whether contradictory results are due to species differences or some other difference. More attention is needed to the socioecological context within which decisions are made, in terms of the type of task and behaviour studied, and within what type of social organisation. More long-term studies are needed of the stability of social learning strategies over a lifetime. This is difficult in some long-lived species (e.g., great apes, cetaceans), but not as challenging in others. Research with humans should avoid using questionnaires to measure traits such as dominance or collectivism, and instead use behavioural measures to maintain better continuity with non-human research and avoid problems that verbal responses to questionnaires might not necessarily reflect actual behaviour. Only one study has looked directly at the genetic basis of social learning [36], and only one study has properly demonstrated the associative learning of social learning [59]; both deserve replication in other species, including humans.

Let us return to the phenotypic gambit question posed at the outset: does any of this individual variation matter for our understanding of the evolution of social learning, beyond the more cautious interpretation of empirical findings? We think that it does. Models assuming that social learning strategies change slowly via the natural selection of genetic variation [14] might greatly underestimate the speed with which populations can respond to environmental change, if those learning strategies are actually phenotypically plastic. Rather than natural selection acting on social learning strategies, it would act instead on the mechanisms of phenotypic plasticity outlined in Figure 1. This greater disconnect between genes and learning strategies not only allows faster adaptation to novel or changing environments but it also potentially makes it more likely that maladaptive behaviour will spread [23,48]. Imagine an informational cascade in which not only is a maladaptive behavioural trait copied but also the tendency to copy that maladaptive trait: the cascade would be magnified, possibly exponentially. On the other hand, if learning strategies are more flexible, then such maladaptive cascades might be prevented more easily earlier on. Formal models are needed of these situations. The few models that have explicitly addressed the social learning of social learning [79–81] confirm that novel dynamics can emerge that would not be expected if learning strategies were genetically specified (Box 3).



## Concluding Remarks

In conclusion, we hope to have highlighted both that there is evidence for meaningful individual and cultural variation in social learning within species and also that key questions remain unanswered in the effort to explain this variation within a comparative, evolutionary framework (see Outstanding Questions). Our continuum of phenotypic plasticity is a first step towards integrating existing findings according to the different sources of information that adaptively, and potentially maladaptively, influence individuals' reliance on social information.

## Acknowledgments

We thank three anonymous reviewers for valuable comments. This research was funded by a bilateral Economic and Social Research Council (UK) and Research Grants Council (Hong Kong) grant no. ES/J016772/1 awarded jointly to A.M. and L.C., an Economic and Social Research Council (UK) research grant no. ES/J01916X/1 awarded to A.M., a Leverhulme Trust International Network Grant awarded to S.R.X.D., Peter Hammerstein, Olof Leimar, and John McNamara, a BBSRC David Phillips Fellowship to A.T. (BB/H021817/1), and an Economic and Social Research Council (UK) grant awarded to A.T., Christine Caldwell and Francesca Happé (ES/M006042/1).

## Supplemental Information

Supplemental information associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.tree.2015.12.012>.

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## Outstanding Questions

Are the stable and heritable individual differences listed at the top of Table S1 a result of frequency-dependent selection (e.g., producer–scrounger dynamics) or a by-product of natural variation in a single dimension (e.g., activity levels of some general ‘g’-like cognitive ability)? Can this explain the contradictory findings?

What other developmental or physiological cues provoke a switch in social learning frequency or strategy, other than stress and reproductive state? What proximate mechanisms link stress or reproductive state to learning behaviour?

Are all organisms that can learn associatively able to learn to associate conspecifics with rewards, as demonstrated in bees [59]?

What are the fitness consequences of individual variation in social learning, given the different levels of phenotypic plasticity specified in Figure 1?

What are the proximate and ultimate causes of cultural variation in social learning in humans? Do any other species show stable between-group differences in social learning that cannot be attributed to genetic variation or individual learning?

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