

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].

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