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The evolution of individual and cultural variation in social learning

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Highlights:

- 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

22 **Abstract:**

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

32 **Social learning across species...and individuals?**

33 There has recently been huge growth in studies of *social learning* and *culture* (see Glossary) across
34 diverse species [1,2], including fish [3], insects [4], birds [5], and mammals [6] such as cetaceans
35 [7], rodents [8], monkeys [9] and great apes [10], using multiple methods including field
36 observations [11,12], lab and field experiments [2,13] and theoretical models [14,15]. Social
37 learning (and social information use more broadly: Box 1) now constitutes a major area of study
38 within behavioural and evolutionary biology, shown to affect multiple domains including mate
39 choice, foraging, predator recognition, tool use and communication [1], and having concrete
40 evolutionary consequences such as the structuring of social groups [16] and even speciation [17].
41 Much effort has also gone into explaining human culture in a manner consistent with this
42 comparative evidence and with evolutionary principles, focusing on how relatively high-fidelity
43 human social learning [18,19] can uniquely support the cumulative cultural evolution [20–22] that
44 underlies our species' great ecological success [23].

45

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

52

53 In experiments, typically the demonstration of social learning, or a particular mechanism or strategy
54 of social learning, in enough individuals or on enough trials to reach statistical significance leads to
55 the claim that this phenomenon is present in this particular species. The authors of one recent study
56 claimed, for example, that their findings “constitute strong support for the view ... that cumulative
57 culture requires a package of key psychological processes— specifically, teaching through verbal

58 instruction, imitation, and prosocial tendencies—that are present in humans but are absent or
59 impoverished in chimpanzees and capuchins.” [26 p.1117]. Another stated that “we show
60 experimentally that wild vervet monkeys will abandon personal foraging preferences in favor of
61 group norms new to them” [27 p.483]. While not detracting from the validity and importance of
62 these findings on their own terms, there is implicit extrapolation here from the small number of
63 individuals tested in these experiments to all humans, all chimpanzees, all capuchins or all vervets.

64

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

71

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

78

79 But is this really the case? While adopting the phenotypic gambit may have been useful in the initial
80 study of social learning, here we argue that there is now substantial evidence, reviewed below, that
81 (i) individuals within a species often differ systematically in their tendency to learn from others, and
82 their use of different social learning strategies and mechanisms; and (ii) the causes of these
83 individual differences are varied, including at least partly genetically-inherited differences in

84 personality traits, cues of developmental stress and current physiological condition, past associative
85 learning histories, and (in humans, at least) cultural background. This individual variation has
86 important implications for how social learning is studied comparatively, and for our understanding
87 and interpretation of previous findings. Moreover, it can have significant evolutionary
88 consequences, potentially driving populations to behavioural equilibria different to what we would
89 expect if social learning were under tight genetic control, and casting doubt on the validity of a
90 phenotypic gambit approach that ignores the extent and causes of individual variation.

91

92 **Causes of individual variation in social learning**

93 In Supplementary Table S1 we summarise all experimental studies we could find that have
94 documented and attempted to explain individual variation in social information use (incorporating
95 social learning) within the same task and experimental condition. We exclude studies that found
96 individual variation but did not offer potential explanations for that variation (e.g. [29]), and studies
97 that found variation across different experimental tasks or conditions (e.g. different numbers or
98 identities of demonstrators, or task difficulty), but not systematically across different individuals
99 within the same task (e.g. [30]). For brevity, we also exclude age and sex differences, which are
100 more well-studied and discussed separately in Box 2. Studies in Table S1 are grouped according to
101 five broad categories.

102

103 *Stable 'personality' traits or individual learning ability*

104 Several studies have linked social information use to stable individual differences that appear
105 relatively fixed over the lifespan and to some degree genetically heritable. Some studies have linked
106 social information use to individual variation in exploratory behaviour when alone, sometimes
107 conceptualised as a 'boldness-shyness' personality continuum [31]. Findings are mixed, however,
108 with some studies showing that more exploratory individuals exhibit more social information use
109 [32,33], others that they exhibit less social information use [34–36], others finding no relationship

110 [37]. There is some evidence, albeit mixed, that boldness is heritable: one study found high
111 heritability ($h^2=0.76$) in zebrafish [38], another found substantial non-genetic inheritance in zebra
112 finches [39], another found both genetic and environmental influences in a tropical fish [40].
113 Notably, one study with *Drosophila* has shown that social information use is influenced by a
114 specific genetic polymorphism at the *foraging* locus, which also influences exploratory behaviour
115 when alone [36]. Others have found that performance in an asocial learning task subsequently
116 predicts social information use, although again in opposite directions: two studies found that better
117 individual learners were more likely to use social information [41,42], two studies that they were
118 less likely [43,44]. Three studies with humans have linked social learning to relatively stable
119 individual differences, specifically social dominance [45], collectivism [46] and IQ [47].

120

121 The contradictory results relating to individual exploration and learning might simply be due to low
122 power: many studies feature small sample sizes and marginally significant correlations. Species
123 differences (i.e. phylogeny) might also play a role, but the small number of species tested makes it
124 hard to identify any systematic relationship between the species studied and the direction of the
125 relationship. Theoretically, both relationships are plausible. A negative relationship (more
126 exploratory individuals and/or better individual learners show less social information use) might
127 indicate a frequency-dependent equilibrium between information producers (bold explorers and/or
128 good individual learners) and information scroungers (shy observers and/or poor individual
129 learners), as has been well-explored theoretically [48]. A positive relationship (more exploratory
130 individuals and/or better individual learners show more social information use) might reflect a
131 common cognitive ability or activity level underlying both individual exploration or learning and
132 social information use, as previously shown across, rather than within, species [49], and as
133 previously shown to underlie different cognitive abilities in the same species [50]. Finally, the
134 contradictory results might stem from conflating social learning with social information use (see
135 Box 1), particularly in non-primate studies of animal personality. The final three human studies

136 listed in Table S1 under this category all use verbal questionnaires, and it is unclear how they relate
137 to the behavioural findings. IQ likely predicts individual learning ability, and is substantially
138 heritable [51]; whether social dominance or collectivism are heritable is unknown.

139

140 *Developmental stress or deprivation*

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

150

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

161

162 *Reproductive state*

163 One study has shown that adult physiological condition can influence social learning, with pregnant
164 female ninespine sticklebacks exhibiting more social learning than non-pregnant females, and non-
165 reproductive males showing more social learning than reproductive males [57]. Like the
166 developmental cues just discussed, these might be adaptively fixed responses to specific cues.
167 Pregnant females, who are more vulnerable to predation, should avoid risk and so avoid potentially
168 dangerous individual learning, while reproductive males should show more risky individual
169 learning if it leads to greater access to females [57]. The degree to which this reflects the specific
170 cue of reproductive state, rather than operating via exploratory behaviour (see above) or some
171 general estimation of risk, remains to be determined.

172

173 *Past experience of demonstrator success or cues of demonstrator quality*

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

181

182 Heyes and colleagues [62,63] have taken this further, arguing that *all* forms of social learning,
183 including different social learning strategies and mechanisms, can be explained in terms of domain-
184 general associative learning processes. This can potentially explain otherwise puzzling findings
185 such as that solitary species, including tortoises and octopuses, can learn socially [62]. On the other
186 hand, it is difficult to explain certain inter-species differences in social learning without invoking
187 some kind of adaptive specialisation for social information use, particularly when those species are

188 exposed to the same environmental cues. For example, ninespine but not threespine sticklebacks use
189 social information in the same task and with the same opportunities for associative learning [64],
190 suggesting adaptive specialisation in the ninespine species (although it remains to be determined
191 whether the adaptive specialisation is for social learning specifically, or lower-level capacities such
192 as social attention). Irrespective of the wider argument, the studies listed in Table S1 suggest that at
193 least some intra-specific variation in social learning can arise through individual learning of the
194 reliability of social information. It is unclear how stable these effects are, however, and whether this
195 individual learning of social learning effectiveness continues throughout the lifetime resulting in
196 within-individual temporal variation in social learning use, or whether it is more likely to occur
197 early in life (see Box 2).

198

199 *Cultural background*

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

207

208 The notion that there is structured and stable cultural variation in social learning in humans fits with
209 broader proposals that humans have unusually high-fidelity and open-ended (i.e. domain-general)
210 social learning [18–20] that generates strong and long-lasting cultural traditions [23,69]. However,
211 stable cultural traditions are also present in other species [11,12], raising the possibility of the social
212 learning of social learning in non-human species also. Once social learning itself can be socially
213 learned, we might expect novel cultural evolutionary dynamics that drive behaviour to new

214 equilibria that would not exist if social learning were genetically fixed or individually learned (Box
215 3).

216

217 **Integration of findings**

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

221

222 First, some of the effects listed at the top of Table S1 likely reflect heritable and stable personality
223 differences that appear fixed at birth. These might be genetic polymorphisms, with little if any
224 postnatal phenotypic plasticity. Here, genes act as cues to (i.e. correlate with) the state of the social
225 environment [71]. Assuming that underlying allele frequencies reflect a history of frequency-
226 dependent selection (e.g. producer-scrounger dynamics) experienced by lineages, there would be no
227 need for any postnatal plasticity as the relevant environment is conspecifics from whom to learn,
228 whose presence is predicted by the frequencies of the underlying polymorphism. In other words,
229 when the value of social learning is predictable across generations, then individual variation will be
230 genetically determined.

231

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

237

238 Third, the individual learning of social learning represents greater plasticity, with the possibility that
239 different individuals who experience different reinforcement schedules end up with different social

240 learning frequencies or strategies. This might reflect a fine-tuning mechanism to deal with more
241 rapid and unpredictable within-generational change.

242

243 Finally, the social learning of social learning opens up a second (cultural) inheritance system
244 through which social learning can evolve inter-generationally, in addition to genetic inheritance
245 [73]. Here, for humans at least, the relevant environment is the society within which individuals
246 live, an environment which is itself socially constructed [74]. The best cue here would be the social
247 learning strategy of other individuals in that society, the one that existing institutions (e.g.
248 educational systems: see Box 3) are geared towards.

249

250 Our unidimensional scheme is, of course, an over-simplification, and any specific instance of social
251 learning may be influenced by more than one of these causes (e.g. a genetically or culturally
252 inherited tendency may subsequently be modified by developmental conditions or individual
253 learning). Nevertheless, we consider it a useful initial heuristic to synthesise the findings listed in
254 Table S1, which often remain unconnected in the literature. Further consideration of individual and
255 cultural variation in social learning in the context of environmental and genetic cue reliability
256 [71,72] might point to fruitful hypotheses. For example, we might predict that maladaptive side-
257 effects or runaway processes, such as informational cascades [48], are more common towards the
258 right hand side of Figure 1 where there is the least genetic control over social learning.

259

260 **Implications and future directions**

261 It is clear that there is individual variation in the use of social learning in many species, and that this
262 individual variation is not mere noise or error. Consequently, we suggest that broad claims such as
263 ‘species X shows conformity’ or ‘species Y exhibits imitation’ can give the misleading impression
264 that every member of that species exhibits these abilities. Such impressions are likely to be
265 incorrect, particularly when based on the results of a single study with just a few individuals, and

266 where those individuals have unknown or similar genetic variation, developmental experiences or
267 learning histories. While such studies can demonstrate that a certain ability is within the capacity of
268 at least one member of that species, they can say little about the prevalence or universality of that
269 ability.

270

271 An equivalent argument has been made regarding cognitive performance [75], where species-
272 typical cognitive abilities are claimed based on the performance of one or a few ‘genius’ individuals
273 such as Alex (the parrot) or Kanzi (the bonobo) without taking into account extensive inter-
274 individual variation. A similar argument has also been made regarding human psychology [76],
275 where psychological processes documented in people from Western, Industrialised, Educated, Rich,
276 Democratic (‘WEIRD’) countries have often been considered human universals, without taking into
277 account extensive cultural variation in those processes. Our review reinforces the points made in
278 those previous papers [75,76]: studies should avoid over-generalising from small samples to entire
279 species, use as large sample sizes as are feasible, report rather than ignore individual variation in
280 performance, and standardise tasks to be used across as many species (or, in humans, societies) as
281 possible.

282

283 We can also make some novel points specific to the study of social learning. If social learning can
284 itself be learned, it is particularly problematic to over-generalise from hand-reared or enculturated
285 members of non-human species who have learned to socially learn from their handlers. Indeed,
286 findings that enculturated but not mother-raised chimpanzees show certain forms of imitation
287 [77,78] lend support (albeit circumstantial) to our argument that individuals can learn from others
288 how to learn from others. Furthermore, if developmental cues and learning histories can influence
289 social learning, then comparisons between social learning in human children and adult non-human
290 primates become difficult to interpret given that putative species differences are confounded by
291 possible developmental differences. Finally, incorporating the possibility that social learning can

292 itself be learned into evolutionary models of social learning might resolve apparent contradictions
293 between modelling results and experimental findings, such as that humans copy others less than
294 they should do [30,41]. It might be that people are bringing their individually or socially learned
295 social learning strategies into the lab with them. Models that explicitly incorporate the individual or
296 social learning of social learning strategies might more accurately predict experimental behaviour.

297

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

311

312 Let us return to the phenotypic gambit question posed at the outset: does any of this individual
313 variation matter for our understanding of the evolution of social learning, beyond the more cautious
314 interpretation of empirical findings? We think that it does. Models assuming that social learning
315 strategies change slowly via the natural selection of genetic variation [14] might greatly
316 underestimate the speed with which populations can respond to environmental change, if those
317 learning strategies are actually phenotypically plastic. Rather than natural selection acting on social

318 learning strategies, it would act instead on the mechanisms of phenotypic plasticity outlined in
319 Figure 1. This greater disconnect between genes and learning strategies not only allows faster
320 adaptation to novel or changing environments, it also potentially makes it more likely that
321 maladaptive behaviour will spread [23,48]. Imagine an informational cascade in which not only is a
322 maladaptive behavioural trait copied, but also the tendency to copy that maladaptive trait: the
323 cascade would be magnified, possibly exponentially. On the other hand, if learning strategies are
324 more flexible, then such maladaptive cascades might be prevented more easily earlier on. Formal
325 models are needed of these situations. The few models that have explicitly addressed the social
326 learning of social learning [79–81] confirm that novel dynamics can emerge that would not be
327 expected if learning strategies were genetically specified (Box 3).

328

329 In conclusion, we hope to have highlighted both that there is evidence for meaningful individual
330 and cultural variation in social learning within species, but also that key questions remain
331 unanswered in the effort to explain this variation within a comparative, evolutionary framework
332 (Box 4). Our continuum of phenotypic plasticity is a first step towards integrating existing findings
333 according to the different sources of information that adaptively, and potentially maladaptively,
334 influence individuals' reliance on social information.

335

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344

345 **Supplementary Material**

346 Supplementary Material associated with this article can be found at doi:XXXXXXX'

347 **Figure captions**

348 **Figure 1.** A schematic continuum representing the degree of phenotypic plasticity in social
349 learning. At the left are the studies near the top of Table S1, where genetic polymorphisms generate
350 different phenotypes fixed from birth. Further towards the right are cases where phenotypes switch
351 in response to specific developmental cues (e.g. of stress) or specific adulthood physiological states
352 (e.g. reproductive state). Further right are cases of apparent individual learning of associations
353 between conspecifics and rewards, with little or no domain-specificity. At the extreme right are
354 cases – possibly restricted to humans – where social learning is acquired from others via social
355 learning.

Low
phenotypic
plasticity

High
phenotypic
plasticity



Heritable
individual
differences
(e.g. in
exploration)
fixed at birth



Facultative switching
in response to specific
developmental cues,
e.g. stress, or
physiological state,
e.g. pregnancy



Individual
learning of
the reliability
of social
learning



Social
learning of
social
learning

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1 **Glossary**

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

4 **Social learning:** long-term changes in rules for responding to stimuli that are derived from the
5 observation of, or interaction with, another individual or its products [1]. Can be contrasted with
6 individual (or asocial) learning, in which learning occurs with no social input. Social learning
7 represents a specific form of social information use (see Box 2).

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

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

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

1 **Box 1: Social learning and social information use**

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

1 **Box 2: Age and sex differences in social learning**

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

7 *Sex differences*

8 Some forms of social learning are specific to one sex simply because the trait being copied is only
9 exhibited by that sex. For example, in many songbird species, only male birds sing, and so only
10 juvenile males learn songs, typically from their fathers [86]. In other cases sex-specific social
11 organisation restricts social learning to one sex. For example, male humpback whales are quasi-
12 solitary and so fail to learn female-specific vocalisations that delineate the social groups in which
13 females live [87]. More interesting are cases in which both sexes of a species have opportunities to
14 learn a trait that is non-sex-specific. Studies of chimpanzee tool-use acquisition show that juvenile
15 females exhibit more effective social learning than juvenile males, most likely because females pay
16 greater attention to their mothers [88]. This can have important implications for cultural diversity,
17 with the number of cultural traits in chimpanzee societies correlating with the number of females,
18 not males [89]. Sex-specific social learning will also determine the spread of cultural traits between
19 groups in species with sex-specific dispersal patterns [90]. In humans, socially proscribed roles (e.g.
20 economic divisions of labour) will often limit social learning opportunities. In one small-scale
21 society, for example, only boys learn honey collecting skills, because only men perform this activity
22 [91]. However, lab experiments with adults and children from a range of cultural backgrounds
23 typically find no sex differences in social learning performance, frequency or strategy [29,41,65,66].

25 *Age differences*

26 The juveniles of many species show more social learning than adults, which is perhaps

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

1 **Box 3: The social learning of social learning in humans: Evidence, causes and consequences**

2 *Cultural variation in social vs individual learning*

3 There is much circumstantial evidence for cultural variation in social learning in humans, that is,
4 stable between-population differences in the frequency of social learning, or type of social learning
5 strategy used, that are unlikely to be genetic or individually learned [98]. Collectivistic countries
6 such as Japan or Korea have educational systems more focused around social learning (e.g. rote
7 learning, respect for teachers) while more individualistic countries such as the UK or USA have
8 educational systems more focused around individual learning (e.g. emphasising creativity and
9 personal discovery) [98,99]. There is faster diffusion of new products through more collectivistic
10 societies than through individualistic societies, suggesting stronger social learning of product choice
11 [100]. These broad differences are supported by experimental tasks [65]. Nevertheless, there is a
12 great deal of research needed to more broadly map variation in social learning beyond this
13 simplistic East-West dichotomy, as well as whether this variation is task or situation independent,
14 or only occurs in specific domains.

15

16 *The origin and persistence of cultural variation in social learning*

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

27

28 *The consequences of the social learning of social learning*

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

1 **Box 4: Outstanding questions**

- 2 • Are the stable and heritable individual differences listed at the top of Table S1 the result of
3 frequency-dependent selection (e.g. producer-scrounger dynamics) or a by-product of
4 natural variation in a single dimension (e.g. activity levels of some general ‘g’-like cognitive
5 ability)? Can this explain the contradictory findings?
- 6 • What other developmental or physiological cues provoke a switch in social learning
7 frequency or strategy, other than stress and reproductive state? What proximate mechanisms
8 link stress or reproductive state to learning behaviour?
- 9 • Are all organisms that can learn associatively able to learn to associate conspecifics with
10 rewards, as demonstrated in bees [59]?
- 11 • What are the fitness consequences of individual variation in social learning, given the
12 different levels of phenotypic plasticity specified in Table S1?
- 13 • What are the proximate and ultimate causes of cultural variation in social learning in
14 humans? Do any other species show stable between-group differences in social learning that
15 cannot be attributed to genetic variation or individual learning?

Table S1. Summary of experimental studies that have tested for within-species variation in social learning frequency or strategy within the same task and experimental condition.

Study	Species	Details
1. Stable ‘personality’ traits or individual learning ability		
Marchetti & Drent 2000 [1]	Great tits (<i>Parus major</i>)	Individuals who showed more exploratory behaviour when alone subsequently showed <i>more</i> social learning of food location
Bouchard et al. 2007 [2]	Pigeons (<i>Columba livia</i>)	Individuals who showed better individual learning in an asocial task subsequently showed <i>more</i> social learning
Nomakuchi et al. 2008 [3]	Three-spined stickleback (<i>Gasterosteus aculeatus</i>)	Individuals who showed more exploratory behaviour when alone subsequently showed <i>more</i> social learning of food location
Burkart et al. 2009 [4]	Common marmosets (<i>Callithrix jacchus</i>)	Individuals who showed better individual innovativeness (switching to a superior solution) showed <i>less</i> social learning in a foraging task
Harcourt et al. 2010 [5]	Threespine stickleback (<i>Gasterosteus aculeatus</i>)	No effect of individual exploratory behaviour on subsequent social learning of food location
Kurvers et al. 2010 [6]	Barnacle geese (<i>Branta leucopsis</i>)	Individuals who showed more exploratory behaviour when alone subsequently showed <i>less</i> social learning of food location
Katsnelson et al. 2010 [7]	House sparrow (<i>Passer domesticus</i>)	Individuals who showed better individual learning in an asocial foraging task subsequently showed <i>less</i> social learning in group foraging
Mesoudi 2011 [8]	Humans (<i>Homo sapiens</i>)	Individuals who showed better individual learning in an asocial practice session of a computer task subsequently showed <i>more</i> social learning
Rosa et al. 2012 [9]	Zebra finches (<i>Taeniopygia guttata</i>)	Individuals who showed more exploratory behaviour when alone subsequently showed <i>less</i> social learning of food location
Foucaud et al. 2013 [10]	Fruitflies (<i>Drosophila melanogaster</i>)	Individuals with the more-exploratory <i>rover</i> allele, associated with more exploratory behaviour, at the <i>foraging</i> locus showed <i>less</i> social learning than individuals with the <i>sitter</i> allele, associated with less exploratory behaviour
Cook et al. 2014 [11]	Humans (<i>Homo sapiens</i>)	Socially dominant individuals showed <i>more</i> social learning, and aggressively dominant individuals showed <i>less</i> social learning, in a computer task
Toelch et al. 2014 [12]	Humans (<i>Homo sapiens</i>)	Individuals with higher collectivism showed <i>more</i> social learning in two computer tasks (individualism and narcissism showed no association)
Muthukrishna et al. 2015 [13]	Humans (<i>Homo sapiens</i>)	High-IQ individuals showed <i>less</i> social learning in a perceptual task, although conformity showed a

Study	Species	Details
		U-shaped relationship (very high and very low IQ predicted high conformity). Prestige, dominance and cultural background had no effect.
2. Developmental stress or deprivation		
Levy et al. 2003 [14]	Rats (<i>Rattus norvegicus</i>)	Maternally deprived individuals failed to learn food preferences socially, despite unimpaired performance on a spatial (non-social) task
Melo et al. 2006 [15]	Rats (<i>Rattus norvegicus</i>)	Maternally deprived individuals failed to learn food preferences socially. Partially reversed by same-age, same-sex conspecific interaction
Lindeyer et al. 2012 [16]	Rats (<i>Rattus norvegicus</i>)	Pups of low licking-grooming mothers, indicative of high stress, show less social learning of food preferences
Farine et al. 2015 [17]	Zebra finches (<i>Taeniopygia guttata</i>)	Administration of avian stress hormone during development causes a shift from vertical (from parents) to oblique (from older non-parents) social learning in a foraging task
3. Reproductive state		
Webster & Laland 2011 [18]	Ninespine sticklebacks (<i>Pungitius pungitius</i>)	Pregnant females show more social learning of food location than non-pregnant females; reproductive males show less social learning than non-reproductive males
4. Past experience of demonstrator success or cues of demonstrator quality		
Katsnelson et al. 2008 [19]	House sparrow (<i>Passer domesticus</i>)	Groups imprinted on successful parental models showed more social learning than groups imprinted on unsuccessful models
Corriveau & Harris 2008 [20]	Humans (<i>Homo sapiens</i>)	4 and 5 year olds switched from copying familiar teachers to unfamiliar teachers when unfamiliar teachers were more accurate (but not when they were less accurate)
Dawson et al. 2013 [21]	Bumblebees (<i>Bombus terrestris</i>)	Bees previously rewarded for joining conspecifics subsequently copy flower colour preferences; bees not rewarded did not.
5. Cultural background		
Correa-Chávez & Rogoff 2009 [22]; López et al. 2010 [23]	Humans (<i>Homo sapiens</i>)	Children with less exposure to Western schooling pay more attention to, and learn more from, instruction directed towards their siblings, compared to children with more exposure to Western schooling
Mesoudi et al. 2015 [24]	Humans (<i>Homo sapiens</i>)	Individuals from mainland China showed more social learning in a computer task than individuals from the UK, Hong Kong and Chinese students in the UK
Berl & Hewlett	Humans (<i>Homo sapiens</i>)	Aka hunter-gatherers and Ngandu horticulturalists

Study	Species	Details
2015 [25]		showed less over-imitation in opening a puzzle box than Western children and adults (although see [26])

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