



REVIEW

Animal social learning: associations and adaptations [version 1; referees: 2 approved]

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Abstract

Social learning, learning from others, is a powerful process known to impact the success and survival of humans and non-human animals alike. Yet we understand little about the neurocognitive and other processes that underpin social learning. Social learning has often been assumed to involve specialized, derived cognitive processes that evolve and develop independently from other processes. However, this assumption is increasingly questioned, and evidence from a variety of organisms demonstrates that current, recent, and early life experience all predict the reliance on social information and thus can potentially explain variation in social learning as a result of experiential effects rather than evolved differences. General associative learning processes, rather than adaptive specializations, may underpin much social learning, as well as social learning strategies. Uncovering these distinctions is important to a variety of fields, for example by widening current views of the possible breadth and adaptive flexibility of social learning. Nonetheless, just like adaptationist evolutionary explanations, associationist explanations for social learning cannot be assumed, and empirical work is required to uncover the mechanisms involved and their impact on the efficacy of social learning. This work is being done, but more is needed. Current evidence suggests that much social learning may be based on 'ordinary' processes but with extraordinary consequences.

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Introduction

Animals learn from others. This phenomenon, termed ‘social learning’, is well established across numerous taxa and contexts, from fish learning mating sites by following others, to meerkats (*Suricata suricatta*) teaching pups to handle scorpions¹⁻⁵. Social information (information available due to the activities of other individuals) and social learning (learning from social information) can provide animals with a shortcut to adaptive behavior, minimizing the costs and risks of individual exploration⁶⁻⁸. For example, metabolic chamber studies demonstrate that socially acquired techniques result in considerable time and energy savings for black rats (*Rattus rattus*) extracting seeds from pine cones and red squirrels (*Tamiasciurus hudsonicus*) opening nuts^{9,10}. Black rat pups learn the efficient cone stripping technique by stealing partially opened cones from their mothers, and the invention and spread of this technique has allowed black rats to invade newly planted pine forests in Israel, opening up a previously unexploited niche¹⁰. As well as positive effects on animal success, several research groups have noted that the loss of socially learned behavior patterns may impact animal management and conservation (e.g. 11–15).

Such examples illustrate the manifold ecological and evolutionary consequences that social learning can have, and a considerable body of theoretical work indicates that social learning will be advantageous in changing environments where genetic change is too slow and individual learning too costly to track change⁵. However, social learning also raises the possibility of novel costs, such as increased competition over shared resources, or the acquisition of poor-quality or irrelevant information^{16,17}. Animals have thus been proposed to employ so-called social learning ‘strategies’ or ‘biases’ that determine when to learn from others and who to learn from, increasing the payoffs of social learning^{6,17,18}. Such considerations of costs and benefits, together with the fact that social learning is a major contribution to the success of our own species, as well as observations of species differences in social learning, have led researchers to consider how, why, and when social learning and different social learning strategies have evolved. In this brief review, I discuss some current controversies within the field of social learning. Although research on human social learning is relevant to these controversies, much attention has been given to aspects of social learning thought to be uniquely human (e.g. 19–23), and here I thus focus on non-human animals (henceforth ‘animals’). I also focus on the more general case of animals learning from cues inadvertently produced by the activities of other individuals, rather than learning from communication signals that are by definition evolved specializations²⁴.

What evolves?

Social learning is defined in terms of its outcome rather than its underlying process. It can thus result from varied processes and mechanisms, and several classification schemes exist, often differentiating on the basis of the psychological processes thought to be involved, but also on the basis of what is learned^{5,7,25–28}. Since multiple mechanisms may solve the same adaptive problem and multiple adaptive problems may be solved by a single mechanism²⁹, there need not be a one-to-one correspondence between social learning outcomes and mechanisms.

Considering how, why, and when social learning evolved has thus prompted researchers to ask, ‘what evolves?’^{30,31}. That is, what evolved processes underpin different instances of social learning, and have these evolved to facilitate social learning? More formally, have abilities to gather, assess, and utilize social information been specifically shaped by natural selection, resulting in derived adaptive specializations for social learning³²? Alternatively, is much social information use and social learning the product of general processes that have evolved or developed for other reasons? Or does most social learning instead result from a combination of these two possibilities? Social learning has often been assumed to involve at least some derived cognitive processes that evolve and develop independently, but this assumption is increasingly questioned.

A key counterargument to the adaptive specialization account has been the proposal that social learning propensities, strategies, biases, and processes are all products of general learning processes, with any adaptive specialization involving input systems rather than the learning mechanisms themselves^{7,28,31–42}. Heyes has been key in developing and examining these ideas^{7,28,36,41,42}. For example, the recent papers ‘What’s social about social learning?’ and ‘Not-so-social learning strategies’^{28,42} present considerable theory and evidence that social learning and social learning strategies depend on the same general learning mechanisms as individual (or ‘asocial’) learning. That is, while these learning mechanisms are themselves products of evolution, they have not evolved and are not specialized *for* social learning, nor have they subsequently been shaped by evolution to facilitate social learning. Instead, individual experience is argued to shape and specialize social learning.

Current, recent, and early life experience have all been shown to predict the reliance on social information⁴³, and thus experiential effects rather than evolved differences could indeed explain variation in social learning propensities between individuals, populations, and species, consistent with the general process account. For example, early maternal care predicts whether adult rats socially acquire food preferences^{44–46}. However, flexibility alone is insufficient to rule out evolved social learning mechanisms, since flexibility could be genetically encoded. For example, individuals could follow evolved unlearned rules-of-thumb of when, where, and how to employ social information¹⁷. Recent studies, in a variety of species but limited in number, have directly manipulated the value of social information. Such manipulations provide compelling evidence that social information use may indeed emerge as the result of within-lifetime learning rather than adaptive specializations^{31,47}. For example, through simple associative learning, bees can be trained to approach but also to avoid flower colors that were previously marked by a social cue, just as they might learn the value of an asocial cue⁴⁸.

Data comparing individuals and species provide some further, albeit correlational, support for the idea that social learning is not independent from other processes^{49,50}. For example, experimental tests of social learning and individual learning show that performance on these tests correlates across five species of birds, consistent with these traits evolving together³². Similarly, in primates, the number of reported observations of social learning per species

co-varies with both observational measures of behavioral flexibility and experimental measures of cognitive performance^{40,51,52}, although social learning may also carry specific costs in terms of parasite exposure⁵². There is also comparative evidence consistent with evolved adaptive specializations in social learning. For example, Templeton *et al.*⁵³ found enhanced social learning in the more social of two corvid species over and above differences in individual learning, and human children were found to outperform two ape species on a variety of social measures, including social learning, while performance on physical tasks was more similar⁵⁴. Neither of the two study designs, however, fully eliminated developmental explanations or identified whether the specialization exists in learning mechanisms or input systems²⁸. A further issue relevant to all studies assessing reliance on social learning is the method of measurement. Typically, social learning is assessed as success or failure, or the speed of learning, but there are numerous additional ways to measure social learning performance, such as accuracy, longevity, generalization, number of demonstrations required to learn, the weight given to social information, the variety of acts acquired, and resistance to extinction. If these measures vary independently from one another or even negatively correlate (e.g. a speed-accuracy trade-off), ‘reliance on social learning’ may itself be a multidimensional trait.

Advantageous specializations in social learning could therefore be the result of genetic evolution, development, individual learning, or even social learning^{18,41,47,55}. Once a bias to favor or disfavor social information has arisen, it may be strengthened by positive feedback during development, with individuals becoming more adept in particular types of social learning with experience^{50,56}. While social and individual learning are often presented as alternatives, a view that has been criticized⁵⁷, a more fundamental distinction may lie in the degree that information is gathered for decision making, with certain individuals more likely to utilize both individual and social information⁵⁸.

Do mechanisms matter?

As several scholars have noted (e.g. 28,59), the neurocognitive mechanisms of social learning are woefully understudied, with some notable exceptions such as work on human fear learning and social influence (e.g. 60,61), rodent food preference learning (e.g. 62), and birdsong acquisition (e.g. 63). This is clearly a problem for research orientated towards understanding mechanisms, such as work on human psychopathologies linked to social learning, but this gap also matters more broadly, for example to researchers focused on the adaptive function and evolution of social learning.

There are several reasons that research on the outcomes of social learning should also attend to the mechanisms of social learning (see also 42,55). First, different mechanisms may have different transmission dynamics or fitness consequences (again a field of active debate⁵⁷). Second, if specializations in social learning do exist, they may allow valuable inferences to be made on the function of those processes, helping to establish the relevant costs and benefits⁶⁴. For example, uncovering evolved mechanisms that channel social learning to particular contexts or models would allow inferences to be drawn on when social cues provide useful information

and when the attendant costs of competition are low. Third, knowing the mechanisms that underpin social learning allows us to determine what (if anything) has to evolve for social learning to occur and thus its likely distribution and impact. If much social learning is the result of general associative learning processes, as seems likely, this is exciting, since it widens the realm of both social learning and adaptive biases in social learning to any animal able to form learned associations.

When opportunities for learning about the value of social information are limited, learning or errors are costly, or the optimal response to a social cue is highly predictable, we would expect the evolution of genetically encoded predispositions that impact social learning, such as a bias to attend to particularly informative social cues (e.g. fear responses or feeding behavior). Biases and constraints impacting individual learning have been widely documented, and are proposed to dramatically increase the benefits of individual learning by facilitating the use of relevant cues and actions while allowing the many irrelevant ones likely to be present to go ignored⁶⁵⁻⁶⁷. Indeed, experimental evolution in *Drosophila* demonstrates that this ‘prepared learning’ about reliable cues can evolve readily⁶⁷. Similarly, work on animal communication has documented numerous adaptations in both signalers and receivers⁶⁸, demonstrating that adaptive specializations readily evolve in this domain too. The absence of evolved predispositions that impact learning from inadvertent social cues would thus be a great surprise, given the potential fitness payoffs of using this social information. If such predispositions are not found, it suggests that either flexibility is vital to adaptive function (e.g. social cues have variable meanings that must be learned) or the evolution of predispositions is constrained⁵⁸. The broad affordances of associative learning and its broad taxonomic distribution may mean that adaptive systems come with little additional cost, reducing the likelihood of alternate evolved solutions. For example, shoaling fish may learn about locations within their environment due to a tendency to group with and follow others combined with general learning abilities^{1,69}, and thus in such cases the propensity to learn socially is intertwined with grouping propensities^{31,70}. That is, grouping animals may get social learning benefits ‘for free’ as an exaptive by-product of forming groups⁷¹. My view is that much variation in social learning can be explained as a result of experiential effects and general learning processes, or as a by-product of evolved changes in other traits, but that this will not be the whole story, and adaptive specializations that build upon pre-existing learning mechanisms are likely. These adaptive specializations may well be in input systems, but this does not make them unimportant.

Concluding remarks

Both evolution and associative learning are powerful processes, and thus can potentially be used to explain many phenomena. Just as plausible but untested evolutionary explanations of traits have been criticized as adaptationist “just-so” stories⁷², we must be cautious to avoid *associationist* “just-so” stories without empirical data and to ensure that underlying processes are carefully examined.

Associationist explanations are attractively parsimonious, since no new processes need evolve. However, without explicitly investigating processes, there is a danger of neglecting important

specializations in input systems, for example, that may make particular associations more likely to be learned²⁸. Such specializations may be subtle but still have significant effects due to positive feedback processes, and how evolution and development interact to produce these specializations will have ramifications for the expected impact, flexibility, and taxonomic distribution of social learning. Identifying where, how, and whether specializations occur is challenging but worthwhile (e.g. 73,74). Turning to general learning mechanisms, nonassociative learning processes such as habituation are proposed to underlie some instances of social learning, and thus should not be ruled out⁷. Within associative learning, an open possibility is that certain domain-general parameters (such as the initial learning or extinction rate⁷⁵) are or have been shaped by the ubiquity, properties, or importance of social information in certain taxa. In sum, social learning depends on both social cues and on learning, and so we should not neglect the potential impact of processes outside of general associative learning mechanisms in shaping social learning propensities.

To conclude, this is a rich time for studies of social learning and social information use, with increasing work using novel experimental and mathematical methods to demonstrate the breadth of influence of social learning, often in large-scale studies of wild

populations (e.g. 76–80). Interdisciplinary integration has been key in this progress, and further integration between studies of mechanism and function provides exciting opportunities for new discoveries. Diverse fields thus have much to offer to our understanding of the causes and consequences of social learning.

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References



- Warner RR: **Male versus female influences on mating-site determination in a coral reef fish.** *Anim Behav.* 1990; **39**(3): 540–8.
[Publisher Full Text](#)
- Heyes CM, Galef BG Jr.: **Social Learning in Animals: The Roots of Culture.** London: Academic Press. 1996.
[Reference Source](#)
- Thornton A, McAuliffe K: **Teaching in wild meerkats.** *Science.* 2006; **313**(5784): 227–9.
[PubMed Abstract](#) | [Publisher Full Text](#) | [F1000 Recommendation](#)
- Reader SM, Biro D: **Experimental identification of social learning in wild animals.** *Learn Behav.* 2010; **38**(3): 265–83.
[PubMed Abstract](#) | [Publisher Full Text](#)
- Hoppitt W, Laland KN: **Social Learning: An Introduction to Mechanisms, Methods, and Models.** Princeton: Princeton University Press; 2013.
[Publisher Full Text](#)
- Boyd R, Richerson PJ: **Culture and the Evolutionary Process.** Chicago: University of Chicago Press. 1985.
[Reference Source](#)
- Heyes CM: **Social learning in animals: categories and mechanisms.** *Biol Rev Camb Philos Soc.* 1994; **69**(2): 207–31.
[PubMed Abstract](#) | [Publisher Full Text](#)
- Galef BG Jr., Laland KN: **Social learning in animals: Empirical studies and theoretical models.** *BioScience.* 2005; **55**(6): 489–499.
[Publisher Full Text](#)
- Weigl PD, Hanson EV: **Observational learning and the feeding behavior of the red squirrel *Tamiasciurus hudsonicus*: The ontogeny of optimization.** *Ecology.* 1980; **61**(2): 213–8.
[Publisher Full Text](#)
- Terkel J: **Cultural transmission of feeding behaviour in the black rat (*Rattus rattus*).** In *Social Learning in Animals: The Roots of Culture* (ed. CM Heyes & BG Galef, Jr.), London: Academic Press. 1996; 17–48.
[Publisher Full Text](#)
- Suboski MD, Templeton JJ: **Life skills training for hatchery fish: Social learning and survival.** *Fish Res.* 1989; **7**(4): 343–52.
[Publisher Full Text](#)
- Brown C, Laland K: **Social learning and life skills training for hatchery reared fish.** *J Fish Biol.* 2001; **59**(3): 471–93.
[Publisher Full Text](#)
- van Schaik CP: **Fragility of traditions: the disturbance hypothesis for the loss of local traditions in orangutans.** *Int J Primatol.* 2002; **23**(3): 527–38.
[Publisher Full Text](#)
- Griffin AS: **Social learning about predators: a review and prospectus.** *Learn Behav.* 2004; **32**(1): 131–40.
[PubMed Abstract](#) | [Publisher Full Text](#)
- Carroll EL, Baker CS, Watson M, et al.: **Cultural traditions across a migratory network shape the genetic structure of southern right whales around Australia and New Zealand.** *Sci Rep.* 2015; **5**: 16182.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
- Seppänen J, Forsman JT, Mönkkönen M, et al.: **Social information use is a process across time, space, and ecology, reaching heterospecifics.** *Ecology.* 2007; **88**(7): 1622–33.
[PubMed Abstract](#) | [Publisher Full Text](#)
- Rendell L, Fogarty L, Hoppitt WJ, et al.: **Cognitive culture: theoretical and empirical insights into social learning strategies.** *Trends Cogn Sci.* 2011; **15**(2): 68–76.
[PubMed Abstract](#) | [Publisher Full Text](#)
- Laland KN: **Social learning strategies.** *Learn Behav.* 2004; **32**(1): 4–14.
[PubMed Abstract](#) | [Publisher Full Text](#)
- Tomasello M, Carpenter M, Call J, et al.: **Understanding and sharing intentions: the origins of cultural cognition.** *Behav Brain Sci.* 2005; **28**(5): 675–91; discussion 691–735.
[PubMed Abstract](#) | [Publisher Full Text](#) | [F1000 Recommendation](#)
- Beppu A, Griffiths TL: **Iterated learning and the cultural ratchet.** *Proceedings of the 31st Annual Conference of the Cognitive Science Society.* 2009; 2089–2094.
[Reference Source](#)
- Caldwell CA, Millen AE: **Social learning mechanisms and cumulative cultural evolution. Is imitation necessary?** *Psychol Sci.* 2009; **20**(12): 1478–83.
[PubMed Abstract](#) | [Publisher Full Text](#)
- Bryson JJ: **Cultural ratcheting results primarily from semantic compression.** In *The Evolution of Language: Proceedings of the 8th International Conference.*

- (ed. ADM Smith, M Schouwstra, B de Boer & K Smith) Hackensack, NJ: World Scientific. 2010; 50–57.
[Reference Source](#)
23. Heyes C: **Who Knows? Metacognitive Social Learning Strategies.** *Trends Cogn Sci.* 2016; **20**(3): 204–13.
[PubMed Abstract](#) | [Publisher Full Text](#)
 24. Danchin E, Giraldeau LA, Valone TJ, *et al.*: **Public information: from noisy neighbors to cultural evolution.** *Science.* 2004; **305**(5683): 487–91.
[PubMed Abstract](#) | [Publisher Full Text](#)
 25. Galef BG: **Imitation in animals: history, definition, and interpretation of data from the psychological laboratory.** In *Social Learning: Psychological and Biological Perspectives.* (ed. T Zentall & BG Galef), Hillsdale NY: Erlbaum. 1988; 3–25.
[Reference Source](#)
 26. Whiten A, Ham R: **On the nature and evolution of imitation in the animal kingdom: Reappraisal of a century of research.** *Adv Study Behav.* 1992; **21**: 239–283.
[Publisher Full Text](#)
 27. Giraldeau LA: **The ecology of information use.** In *Behavioural Ecology.* 4th Edition (ed. JR Krebs & NB Davies), Blackwell, Oxford, 1997; 42–68.
[Reference Source](#)
 28. **F** Heyes C: **What's social about social learning?** *J Comp Psychol.* 2012; **126**(2): 193–202.
[PubMed Abstract](#) | [Publisher Full Text](#) | [F1000 Recommendation](#)
 29. de Kort SR, Clayton NS: **An evolutionary perspective on caching by corvids.** *Proc Biol Sci.* 2006; **273**(1585): 417–23.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
 30. Morand-Ferron J, Doligez B, Dall SRX, Reader SM: **Social information use.** In *Encyclopedia of Animal Behavior.* (ed. MD Breed & J Moore), Oxford: Academic Press, 2010; **3**: 242–250.
[Publisher Full Text](#)
 31. Leadbeater E: **What evolves in the evolution of social learning?** *J Zool.* 2015; **295**(1): 4–11.
[Publisher Full Text](#)
 32. Lefebvre L, Giraldeau LA: **Is social learning an adaptive specialization?** In *Social Learning in Animals: the Roots of Culture.* (ed. CM Heyes & BG Galef Jr.); London: Academic Press, 1996; 107–128.
[Publisher Full Text](#)
 33. Miller NE, Dollard J: **Social learning and imitation.** New Haven: Yale University Press, 1941.
[Reference Source](#)
 34. Church RM: **Transmission of learned behavior between rats.** *J Abnorm Psychol.* 1957; **54**(2): 163–5.
[PubMed Abstract](#) | [Publisher Full Text](#)
 35. Caldwell CA, Whiten A: **Evolutionary perspectives on imitation: is a comparative psychology of social learning possible?** *Anim Cogn.* 2002; **5**(4): 193–208.
[PubMed Abstract](#) | [Publisher Full Text](#)
 36. Heyes C: **Four routes of cognitive evolution.** *Psychol Rev.* 2003; **110**(4): 713–27.
[PubMed Abstract](#) | [Publisher Full Text](#)
 37. Keyser C, Perrett DI: **Demystifying social cognition: a Hebbian perspective.** *Trends Cogn Sci.* 2004; **8**(11): 501–7.
[PubMed Abstract](#) | [Publisher Full Text](#)
 38. Laland KN, Bateson P: **The mechanisms of imitation.** *Cybernet Syst.* 2001; **32**(1–2): 195–224.
[Publisher Full Text](#)
 39. Leadbeater E, Chittka L: **Social learning in insects—from miniature brains to consensus building.** *Curr Biol.* 2007; **17**(16): R703–13.
[PubMed Abstract](#) | [Publisher Full Text](#)
 40. Reader SM, Hager Y, Laland KN: **The evolution of primate general and cultural intelligence.** *Philos Trans R Soc Lond B Biol Sci.* 2011; **366**(1567): 1017–27.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
 41. Heyes C: **Grist and mills: on the cultural origins of cultural learning.** *Philos Trans R Soc Lond B Biol Sci.* 2012; **367**(1599): 2181–91.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
 42. Heyes C, Pearce JM: **Not-so-social learning strategies.** *Proc Biol Sci.* 2015; **282**(1802): pii: 20141709.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
 43. Kendal RL, Coolen I, Laland KN: **Adaptive trade-offs in the use of social and personal information.** In *Cognitive Ecology II.* (ed. R Dukas & JM Ratcliffe), Chicago: University of Chicago Press, 2009; 249–271.
[Publisher Full Text](#)
 44. Lévy F, Melo AI, Galef BG Jr., *et al.*: **Complete maternal deprivation affects social, but not spatial, learning in adult rats.** *Dev Psychobiol.* 2003; **43**(3): 177–91.
[PubMed Abstract](#) | [Publisher Full Text](#)
 45. Melo AI, Lovic V, Gonzalez A, *et al.*: **Maternal and littermate deprivation disrupts maternal behavior and social-learning of food preference in adulthood: tactile stimulation, nest odor, and social rearing prevent these effects.** *Dev Psychobiol.* 2006; **48**(3): 209–19.
[PubMed Abstract](#) | [Publisher Full Text](#)
 46. Lindeyer CM, Meaney MJ, Reader SM: **Early maternal care predicts reliance on social learning about food in adult rats.** *Dev Psychobiol.* 2013; **55**(2): 168–75.
[PubMed Abstract](#) | [Publisher Full Text](#)
 47. Reader SM: **Experiential effects on mirror systems and social learning: implications for social intelligence.** *Behav Brain Sci.* 2014; **37**(2): 217–8.
[PubMed Abstract](#) | [Publisher Full Text](#)
 48. **F** Dawson EH, Avarguès-Weber A, Chittka L, *et al.*: **Learning by observation emerges from simple associations in an insect model.** *Curr Biol.* 2013; **23**(8): 727–30.
[PubMed Abstract](#) | [Publisher Full Text](#) | [F1000 Recommendation](#)
 49. Reader SM: **Innovation and social learning: Individual variation and brain evolution.** *Anim Biol.* 2003; **53**(2): 147–58.
[Publisher Full Text](#)
 50. Reader SM: **Causes of individual differences in animal exploration and search.** *Top Cogn Sci.* 2015; **7**(3): 451–68.
[PubMed Abstract](#) | [Publisher Full Text](#)
 51. Reader SM, Laland KN: **Social intelligence, innovation, and enhanced brain size in primates.** *Proc Natl Acad Sci U S A.* 2002; **99**(7): 4436–41.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
 52. McCabe CM, Reader SM, Nunn CL: **Infectious disease, behavioural flexibility and the evolution of culture in primates.** *Proc Biol Sci.* 2015; **282**(1799): 20140862.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
 53. Templeton JJ, Kamil AC, Balda RP: **Sociality and social learning in two species of corvids: the pinyon jay (*Gymnorhinus cyanocephalus*) and the Clark's nutcracker (*Nucifraga columbiana*).** *J Comp Psychol.* 1999; **113**(4): 450–5.
[PubMed Abstract](#) | [Publisher Full Text](#)
 54. Herrmann E, Call J, Hernández-Lloreda MV, *et al.*: **Humans have evolved specialized skills of social cognition: the cultural intelligence hypothesis.** *Science.* 2007; **317**(5843): 1360–6.
[PubMed Abstract](#) | [Publisher Full Text](#)
 55. Mesoudi A, Chang L, Dall SR, Thornton A: **The evolution of individual and cultural variation in social learning.** *Trends Ecol Evol.* 2016; **31**(3): 215–25.
[PubMed Abstract](#) | [Publisher Full Text](#)
 56. Toelch U, Bruce MJ, Newson L, *et al.*: **Individual consistency and flexibility in human social information use.** *Proc Biol Sci.* 2013; **281**(1776): 20132864.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
 57. Sterelny K: **Adaptable individuals and innovative lineages.** *Philos Trans R Soc Lond B Biol Sci.* 2016; **371**(1690): pii: 20150196.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
 58. Reader SM, Leris I: **What shapes social decision making?** *Behav Brain Sci.* 2014; **37**(1): 96–7.
[PubMed Abstract](#) | [Publisher Full Text](#)
 59. Galef BG: **Imitation and local enhancement: detrimental effects of consensus definitions on analyses of social learning in animals.** *Behav Processes.* 2013; **100**: 123–30.
[PubMed Abstract](#) | [Publisher Full Text](#)
 60. Olsson A, Phelps EA: **Social learning of fear.** *Nat Neurosci.* 2007; **10**(9): 1095–102.
[PubMed Abstract](#) | [Publisher Full Text](#)
 61. Stallen M, Sanfey AG: **The neuroscience of social conformity: implications for fundamental and applied research.** *Front Neurosci.* 2015; **9**: 337.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
 62. Munger SD, Leinders-Zufall T, McDougall LM, *et al.*: **An olfactory subsystem that detects carbon disulfide and mediates food-related social learning.** *Curr Biol.* 2010; **20**(16): 1438–44.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
 63. Jarvis ED, Güntürkün O, Bruce L, *et al.*: **Avian brains and a new understanding of vertebrate brain evolution.** *Nat Rev Neurosci.* 2005; **6**(2): 151–9.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
 64. Chouinard-Thuly L, Reader SM: **Does all teaching rest on evolved traits?** *Behav Brain Sci.* 2015; **38**: e36.
[PubMed Abstract](#) | [Publisher Full Text](#)
 65. Roper TJ: **Learning as a biological phenomenon.** In *Animal Behaviour: Genes, Development and Learning.* (ed. TR Halliday & PJB Slater), Oxford: Blackwell; 1983; **3**: 178–212.
 66. Bryson JJ: **Representations underlying social learning and cultural evolution.** *Interaction Studies.* 2009; **10**(1): 77–100.
[Publisher Full Text](#)
 67. **F** Dunlap AS, Stephens DW: **Experimental evolution of prepared learning.** *Proc Natl Acad Sci U S A.* 2014; **111**(32): 11750–5.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#) | [F1000 Recommendation](#)
 68. Searcy WA, Nowicki S: **The Evolution of Animal Communication: Reliability and Deception in Signaling Systems.** Princeton: Princeton University Press, 2005.
[Reference Source](#)
 69. Reader SM, Kendal JR, Laland KN: **Social learning of foraging sites and escape routes in wild Trinidadian guppies.** *Anim Behav.* 2003; **66**(4): 729–39.
[Publisher Full Text](#)
 70. Chapman BB, Ward AJ, Krause J: **Schooling and learning: Early social environment predicts social learning ability in the guppy, *Poecilia reticulata*.** *Anim Behav.* 2008; **76**(3): 923–9.
[Publisher Full Text](#)
 71. van der Post DJ, Hogeweg P: **Diet traditions and cumulative cultural processes as side-effects of grouping.** *Anim Behav.* 2008; **75**(1): 133–44.
[Publisher Full Text](#)

72. Pigliucci M, Kaplan J: **The fall and rise of Dr Pangloss: adaptationism and the Spandrels paper 20 years later.** *Trends Ecol Evol.* 2000; **15**(2): 66–70.
[PubMed Abstract](#) | [Publisher Full Text](#)
73. Thornton A, Raihani NJ: **The evolution of teaching.** *Anim Behav.* 2008; **75**(6): 1823–36.
[Publisher Full Text](#)
74. Chivers DP, Wisenden BD, Hindman CJ, *et al.*: **Epidermal ‘alarm substance’ cells of fishes maintained by non-alarm functions: possible defence against pathogens, parasites and UVB radiation.** *Proc Biol Sci.* 2007; **274**(1625): 2611–9.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
75. Behrens TE, Woolrich MW, Walton ME, *et al.*: **Learning the value of information in an uncertain world.** *Nat Neurosci.* 2007; **10**(9): 1214–21.
[PubMed Abstract](#) | [Publisher Full Text](#)
76. Doligez B, Danchin E, Clobert J: **Public information and breeding habitat selection in a wild bird population.** *Science.* 2002; **297**(5584): 1168–70.
[PubMed Abstract](#) | [Publisher Full Text](#)
77. Davies NB, Welbergen JA: **Social transmission of a host defense against cuckoo parasitism.** *Science.* 2009; **324**(5932): 1318–20.
[PubMed Abstract](#) | [Publisher Full Text](#)
78. **E** Aplin LM, Farine DR, Morand-Ferron J, *et al.*: **Experimentally induced innovations lead to persistent culture via conformity in wild birds.** *Nature.* 2015; **518**(7540): 538–41.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#) | [F1000 Recommendation](#)
79. Allen J, Weinrich M, Hoppitt W, *et al.*: **Network-based diffusion analysis reveals cultural transmission of lobsail feeding in humpback whales.** *Science.* 2013; **340**(6131): 485–8.
[PubMed Abstract](#) | [Publisher Full Text](#)
80. van de Waal E, Borgeaud C, Whiten A: **Potent social learning and conformity shape a wild primate’s foraging decisions.** *Science.* 2013; **340**(6131): 483–5.
[PubMed Abstract](#) | [Publisher Full Text](#)

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The referees who approved this article are:

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- 1 **Joanna Bryson**, Artificial Models of Natural Intelligence, University of Bath, Bath, UK
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- 2 **Luke Rendell**, Centre for Social Learning and Cognitive Evolution, School of Biology, University of St Andrews, Fife, UK
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