Chapter prepared for
Evolution of Learning and Memory Mechanisms (Mark Krause, Karen L Hollis, Mauricio R Papini, Eds) Cambridge University Press

Social Learning Strategies

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Social learning, defined as “learning that is facilitated by observation of, or interaction with, another individual (or its products)” (Heyes, 1994, p. 207), is often characterized as relatively cheap and risk free when compared to individual learning (Hoppitt & Laland, 2013). Accordingly, social learning is an adaptive way to gain information about the environment, explaining why it is taxonomically widespread, having been found in mammals, birds and insects, and across a variety of behavioral domains including skills, calls, predation, mate choice and resource use(Hoppitt & Laland, 2013). Different types of social learning have been described in terms of what information an individual attends to and processes when learning from others. (e.g., Galef, 1988; Heyes, 1994; Hoppitt & Laland, 2013; Whiten & Ham, 1992). There is consensus on their basic categorization, which vary from an inadvertent process, such as when an individual’s attention is drawn to a new resource by another individual “going about its business” after which it learns for itself (asocially), to active teaching of skills by experienced individuals to naïve ones.

Social learning is often contrasted with asocial (or individual) learning and arguments abound as to whether there is anything different or special about social, compared with asocial learning, and whether social learning can be adequately explained in conditioning terms (see Kendal et al., 2018). Social learning abilities have been found in solitary species such as the common octopus and red-footed tortoise (Fiorito & Scotto, 1992; Wilkinson et al., 2010), which might not be expected if social learning evolved independently of asocial learning and in response to the selection pressures of social living. However, it is unrealistic to assume that solitary species never interact with conspecifics or heterospecifics, thus social learning remains useful to them (Kendal et al., 2018). Moreover, one popular argument (Heyes, 2012) is that, at the cognitive level, all that is "social about social learning" is the biasing or tuning of input mechanisms (perception, attention, and motivation) towards other agents, as the actual long-term encoding of information is mediated by general learning mechanisms. In section 2.3, I provide an alternative, and more in-depth, discussion of the biological basis of social learning.

Where social information transmission is sufficient to propagate the diffusion of novel behavior patterns through populations, it may result in distinct behavioral traditions between different populations of the same species. Such traditions, whether in humans or nonhuman species, can be described as "culture" (Laland & Janik, 2006). In this context, the use of the term "culture" indicates that the behavior concerned has been socially learned. Whether the species has a repertoire of behavioral traditions (Whiten & van Schaik, 2007) and cultural norms, or indeed exceptional linguistic or cognitive capabilities (Tylor, 1871) are further features on which some may insist in their definitions of culture. Moreover, social learning is regarded as pivotal to a number of social intelligence hypotheses, which maintain that the evolution of high intelligence or large brains was driven by a capacity for social learning and culture. Explaining the extent of continuity of culture between humans and nonhumans is a key aim of many researchers. Species differences in the types of social learning processes and presence of biases in social learning often feature in these explanations. I will now consider key social learning processes before discussing cultural transmission biases (i.e., social learning strategies) in more depth.

1. Social Learning Processes

Although social learning, as an umbrella term, may include active teaching (see Hoppitt et al., 2008) or explicit communication, researchers of non-humans mean no more by the term than the acquisition of information by "observers" from other individuals, called "demonstrators", who inadvertently emit information when going about their business. The simplest social learning processes do not affect the form of a learned behavior, influencing only *when* animals perform it. *Social facilitation* occurs when a conspecific's presence increases the likelihood that an individual performs an action (e.g., bird song: Jesse & Riebel, 2012), whether or not the conspecific is performing that action (Hoppitt & Laland, 2013). Similarly, we see *response facilitation* when a conspecific's behavior (e.g., placing a blade of grass in the ear in chimpanzees: van Leeuwen et al., 2014) triggers performance of the behavior in others that already had the behavior in their repertoire (Byrne, 1994).

Animals may also learn the form of a behavior asocially after their attention is drawn to a particular location (*local enhancement,* Spence, 1937) or stimulus *(stimulus enhancement,* Thorpe, 1956*)* by another individual's behavior. Wild British blue tits and great tits (*Paridae*) learned to peck open milk bottles to drink the cream (Hinde and Fisher, 1951) because the by-products (open tops) of feeding birds' behavior attracted their attention to milk bottles (Sherry & Galef, 1990). Likewise, due to a shoaling tendency in fish, knowledgeable guppies may lead naïve individuals to novel resource locations (Laland & Williams, 1997). “Observational conditioning” occurs when the observer learns under what circumstances a specific behavioral response should occur. For example, infant rhesus macaques learn to fear and avoid snakes through observations of adults behaving fearfully when exposed to snakes (Mineka & Cook, 1988).

Observational learning occurs when an observer learns a relationship between a behavior and its outcome. *Imitation* is within this class of social learning processes and occurs when “B learns from A some part of the form of a behavior” (Whiten & Ham, 1992, p. 247). Actions are not learned by trial-and-error (asocial) learning but by recreating them after observing a demonstrator perform the behavior. The “two-action method” (Dawson & Foss, 1965) is widely used to infer imitation. For example, a puzzle box that can be solved in two ways (e.g., “lift” or “poke”, Whiten et al. 2005) to gain a food reward, is given to two groups of animals (e.g., chimpanzees), each seeded with a demonstrator trained to use only one method. Imitation may be claimed when naïve individuals within the group are more likely to adopt the method they had witnessed than the alternative. Imitation is, however, the most contentious of all of the social learning processes with researchers calling for various additional delineations to the definition (see Hoppitt & Laland, 2008, 2013, for details). Likewise, there are various forms of *emulation* (Byrne, 2002) whereby individuals copy the results of a demonstrator’s behavior rather than the actions themselves (see Hoppitt & Laland, 2008). Famously, chimpanzees (unlike children) parse out causally irrelevant actions produced by a demonstrator to retrieve a reward when given an opportunity to attempt a puzzle box themselves (Horner & Whiten, 2005).

Key in the many delineations for both imitation and emulation is the question of the observer’s intentionality. Although the role of intentional action is disputed, social learning is inextricably linked to other factors believed pivotal in the evolution of humanity's socio-cognitive niche (Whiten & Erdal, 2012). In the cultural niche theory of human evolution (Boyd et al., 2011), imitation and teaching are vital in promoting the high-fidelity transmission deemed necessary for cumulative culture. Note that *teaching* is the only non-inadvertent social learning process, whereby the demonstrator intentionally conveys information to the observer to hasten its learning (Hoppitt et al., 2008). The cumulative cultural ability to generate complex traits by building upon existing behavior patterns, generation after generation, is widely thought to enable the extraordinary achievements of humans (Boyd & Richerson, 1985; Galef, 1992; Tomasello, 1994). Accordingly, a major unanswered question in the social learning field is why nonhumans do not have, or have impoverished forms of, cumulative culture (Dean et al., 2014). One, of many, explanations (see Dean et al., 2012) is differential prevalence of social learning strategies across species, a topic I turn to next.

2. Social Learning Strategies

Although social learning is intuitively useful, researchers from several fields have, over the last 30 years, increasingly recognized that it is not inherently adaptive. Individuals certainly can gain fitness benefits by learning from others as they may acquire adaptive information yet avoid costs associated with the acquisition of asocial information, such as time or energy loss, opportunity costs, and predation. However, theoretical (Boyd & Richerson, 1985; Rendell et al., 2011) and empirical (Avarguès-Weber et al., 2018; Rieucau & Giraldeau, 2011) research indicates that social information use does not guarantee success. Theoretical models predict that social learning will not be employed in an indiscriminate manner (Boyd & Richerson, 1985; Laland, 2004). Instead, heuristics, or *social learning strategies* (also termed "transmission biases") should bias individuals to copy particular behaviors ("what" strategies), performed by specific others ("who" strategies), under suitable circumstances ("when" strategies). However, individuals need not be consciously aware of following a strategy, and the underlying neural mechanisms are, as yet, unknown (Kendal et al., 2018). Moreover, an understanding of the extent to which social learning strategies are products of evolution and/or learning requires detailed experimentation (Heyes, 2015; Morgan et al., 2011) and increased interdisciplinary work capable of integrating mechanism and function (see Kendal et al., 2018).

Theoretical analyses have explored the circumstances under which natural selection will favor reliance on social learning, as opposed to asocial learning or evolved nonlearned behavior (see Laland et al., 1996, for an overview). A consensus has been reached that the issue hangs, in part, on patterns of variability in the environment. In an environment that is changing comparatively slowly or that exhibits relatively little spatial heterogeneity in resources, populations are able to evolve appropriate behavior patterns through natural selection, and learning is of little adaptive value. By contrast, in rapidly changing or highly variable environments asocial learning pays. Here, natural selection cannot track environmental fluctuations quickly enough, while social learning is unreliable because it may lead individuals to acquire outdated or locally inappropriate behaviors. Intermediate rates of change and patterns of spatial heterogeneity favor social learning, and within this window vertical transmission of information (social learning by offspring from parents) is thought to be an adaptation to slower rates of change than horizontal transmission (social learning among unrelated individuals of the same cohort).

2.1. Evidence for Social Learning Strategies

There is now evidence for various social learning strategies that shape when, what, and whom to copy (Table 1). What follows is a brief, nonexhaustive, review.

2.1.1. "When" Strategies (state-based biases)

Individuals should use social information when uncertain, either because they possess no relevant prior information, or because their personal information is outdated or unreliable (Boyd & Richerson, 1985), or because the accumulated knowledge of conspecifics is more reliable (Rieucau & Giraldeau, 2011). Across multiple taxa, a lack of personal information increases reliance on social learning (e.g., fish: Kendal et al., 2004; chimpanzees: Kendal et al., 2015; ants: Stroeymert et al., 2017; humans: Wood et al., 2013). Stickleback fish are more likely to use social information pertaining to foraging when their personal information is outdated or unreliable (van Bergen et al., 2004). Likewise, adult humans use social information when lacking reliable personal knowledge (Toelch et al., 2014) or confidence, and this is an adaptive strategy in enhancing task success (Morgan et al., 2011). The reverse can also be the case of course; individuals may innovate more when social demonstrations are unreliable (e.g., children: Carr et al., 2015).

Reliance on cheap, but less accurate, social information should increase as the costs associated with asocially acquiring accurate information increase (Boyd & Richerson, 1985; Feldman et al., 1996). Indeed, evidence from multiple taxa indicates that individuals use social information more as task difficulty (and associated energetic or opportunity costs of solving the task asocially) increases (e.g., humans: Morgan et al., 2011; bees: Baracchi et al., 2017; fish: Laland et al., 2011; monkeys: Kendal et al., 2009a). Likewise, individuals are more likely to collect social information whenever learning for themselves exposes them to predation risk (e.g., minnows: Webster & Laland, 2008; guppies: Kendal et al., 2004; but see Galef & Yarkovsky, 2009).

Other state-based biases of the learner, such as age, social rank, and reproductive state (Webster & Laland, 2011), also influence the use of social information. For example, juvenile primates pay more attention to others' foraging behavior than do adults (Coelho et al., 2015; Matsuzawa, 1994), and in humans and birds, juveniles socially learn vocalizations (Bolhuis et al., 2010). Likewise, children use social information more than adults (Carr et al., 2015; Flynn et al., 2016), perhaps because it is mostly during childhood that task-relevant knowledge is accumulated. Moreover, lower-ranking blue tits (Aplin et al., 2013) and chimpanzees (Kendal et al., 2015) are more likely to use social information than high-ranking individuals. Early-life stress can also shape social learning strategies in later life (Boogert et al., 2013; Farine et al., 2015). Finally, bumblebees (Jones et al., 2015), bats (Jones et al., 2013), and chimpanzees (Vale et al., 2017) use social information when the payoff of their own current behavior is poor (Schlag, 1998), known as a "copy if dissatisfied" strategy (Laland 2004).

2.1.2 Frequency-dependent Strategies (context-dependent biases)

A "copy the majority" strategy, where the most common behavioral variant in a population is disproportionately adopted, harnesses the collective wisdom of others. There is much theoretical work regarding the circumstances under which individuals are expected to display this conformist bias (Boyd & Richerson, 1985; Efferson et al., 2008; Eriksson et al., 2007), but the evidence is mixed (Efferson et al., 2008; Henrich & Boyd, 1998; Morgan et al., 2011). Conformity has been observed in fruit flies choosing mates (Danchin et al., 2018) and implicated in foraging choices of wild great tits (Aplin et al., 2015; 2017), immigrant chimpanzees (Luncz et al., 2012), and vervet monkeys (van de Waal et al., 2013; but see van Leeuwen et al., 2015, 2016).

A key question of evolutionary relevance is whether the behavior copied is the one actually exhibited by the majority of individuals, or just the behavior observed most frequently by the individual (Aplin et al., 2015; van Leeuwen et al., 2015; 2016). In support of an emphasis on individuals as representing collective wisdom, children and chimpanzees copy the behavior demonstrated by three different individuals over the behavior demonstrated, three times, by one individual (Haun et al., 2012). Yet the likelihood of conforming is culture- (Clegg & Legare, 2016), context- (Toyokawa et al., 2019), and individual-dependent (Efferson et al., 2008). Moreover, conforming is sensitive to whether the demonstrators have obtained their information from independent sources or from each other (Whalen et al., 2017), as well as to the apparent efficacy of the behavior demonstrated by the majority (Evans et al., 2018).

2.1.3. “Who” Strategies (context-dependent biases)

Social learning may be *indirectly* biased, whereby individuals copy any trait displayed by an individual who is, for example, high status, whether or not that trait helped the individual attain high status (Boyd & Richerson, 1985). We see such *model-based biases* in many taxa. Capuchin monkeys preferentially learn from older/higher-ranking over younger/lower-ranking individuals (Coelho et al., 2015), and chimpanzees preferentially observe and copy dominants (Horner & Whiten, 2005; Kendal et al., 2015; but see Watson et al., 2017) as well as apparent task experts (Horner & Whiten, 2005; Wood, 2013). In the wild, vervet monkeys learn from dominant philopatric females, who likely possess more ecologically relevant information, rather than dominant immigrant males (van de Waal et al., 2010; Canteloup et al., 2020); long-tailed macaques preferentially attend to closer, older, and better tool users (Tan et al., 2018); meerkats learn foraging preferences from older individuals (Thornton & Malapert, 2009); and, orca preferentially learn from older females (Brent et al., 2015).

In humans, children tend to copy high-status (older, popular, socially dominant) individuals (Flynn & Whiten, 2012), and copy the most "prestigious" (or most attended to) individual of two unfamiliar adults (Chudek et al., 2012). Moreover, they copy adults over their same-age peers, even when the peer professes greater task-relevant knowledge than the adult (Wood et al., 2012). Adults also display prestige-bias: Fijian villagers trust the advice of a successful yam grower with regard to use of medicinal plants, as success at the latter is difficult to determine (Henrich & Broesch, 2011). The use of celebrities in marketing campaigns clearly taps into our prestige bias. Although model-based biases may be prone to error, such heuristics generally lead to the copying of successful individuals (those reaching older ages, higher dominance rank, or, in humans, higher social status), who presumably display behavioral traits worth adopting.

2.1.4. "What" Strategies (content-dependent biases)

These strategies are considered “direct” as *what* is learned is influenced by the observer’s direct assessment of a displayed trait’s value. This assessment can be based on the nature of the information itself, or its relative/perceived effectiveness. In the former case, humans express a preference for social content (e.g., gossip), emotional content (e.g., disgust), threat or survival content, and minimally counterintuitive content (e.g., ghosts) when transmitting stories, urban legends, or “fake news” (Mesoudi et al., 2006, Stubbersfield et al., 2015; Vosoughi et al., 2018; Acerbi, 2019). Such preferences are sometimes referred to as “cognitive attractors” particularly in the field of cultural attraction (Sperber & Hirschfield, 2004). There is comparatively little evidence of these types of attractor biases in nonhumans, although we know that socially learned antipredator behavior is more likely when fear-relevant rather than fear-irrelevant stimuli are paired with the observation of conspecific fear responses (Griffin, 2004).

Another type of “what” social learning strategy or content bias constitutes an assessment of payoffs associated with a behavioural trait (Schlag, 1998), for example the richness of a food resource correlated with a foraging strategy, and has been observed to influence transmission in both humans and nonhumans. Payoff biases are arguably the most accurate, yet most cognitively difficult, social learning strategies an individual can implement. Accordingly, studies have reported that payoff bias is adaptive and used in preference to other social learning strategies in humans (McElreath et al., 2008; Mesoudi, 2011) and chimpanzees (van Leeuwen et al., 2013). An ability to copy the highest payoff foraging behavior has also been reported recently in wild capuchin monkeys (Barrett et al., 2017) and male vervet monkeys (Bono et al., 2018), in the latter case overriding the previously mentioned bias to copy the dominant (philopatric) female. There is also empirical evidence of a “copy if better” type strategy where the behavioral payoffs of others are compared to your own; this strategy could be important for cumulative cultural evolution. A version of this strategy has been reported in captive sticklebacks (Kendal et al., 2009b) and young children (Vale et al., 2017). It has also been investigated in chimpanzees (Vale et al., 2017; van Leeuwen & Call, 2017), where it seems individuals do not compare their behavior to that of others, but rely on an assessment of their own behavioral payoff only (a “when” strategy of “copy if dissatisfied”).

2.2. Insights Regarding the Evolution and Use of Social Learning Strategies

Several key insights have resulted from the increasing body of research of SLSs (Kendal et al., 2018). Two of these insights are of particular importance. First is the finding of individual- and population-level flexibility in use of SLSs. Several recent studies have shown that individuals from the same population can adopt different strategies depending on subtle differences in context (Wood et al., 2013), developmental experience (Farine et al., 2015, Leris & Reader, 2016) or other individual-level variation (reviewed by Mesoudi et al., 2016). Although flexible use of SLSs is not evidence that a SLS has not evolved (Call, 2017), they are best regarded as biases shaping behaviour, not rigid rules blindly applied by all individuals or in all contexts (Kendal et al., 2018).

Second, multiple social learning strategies may be deployed simultaneously in any one learning event (e.g., chimpanzees: Kendal et al., 2015; vervet monkeys: Bono et al., 2018; sticklebacks: Laland et al., 2011; humans: Morgan et al., 2011). As is the case for social learning processes, SLSs are likely to operate in concert to bias learning, rather than merging into fine-grained decision rules (Hoppitt & Laland, 2013). More systematic research is required to identify any phylogenetic patterns in the use of SLSs that may explain, for example, the taxonomic distribution of cumulative culture (Vale et al., 2017). In this endeavor, we should note that multiple SLSs can generate the same population-level pattern of behavior, and a particular SLS can generate different population-level outcomes (Morgan et al., 2011, van Leeuwen et al., 2015). Thus, population-level patterns do not provide a robust signature of particular cognitive heuristics or social learning strategies. Moreover, consideration of the temporal phase of a tradition's establishment is key, as the utility of different social learning strategies will change over time. Soon after the first innovation, individuals will use more accurate but costly SLSs (e.g., Payoff bias) as skilled practitioners of the establishing tradition will be few. Once the innovation has become an established tradition, individuals may use less accurate but easily implemented SLSs (e.g., Model-based biases) as the behavior is more prevalent, for example being displayed by all adults (Coelho et al., 2015).

2.3. Insights Regarding the Mechanisms Underlying SLSs

The research reviewed here assumes that the underlying mechanisms do not greatly constrain the adaptive social learning strategies that evolve (Fawcett et al., 2013). This assumption has enabled theoretical work (e.g., Enquist et al., 2007; Kendal et al., 2009c; Rendell et al., 2010; Schlag, 1998) to stimulate and guide empirical research (e.g., Mesoudi, 2011; Rendell et al., 201; Vale et al., 2017). This "blackboxing" (Heyes, 2016) has, however, led to much debate regarding whether social learning strategies are domain-specific or domain-general mechanisms, and whether they are an alternative to associative learning mechanisms (Heyes & Pearce, 2015; see Kendal et al., 2018, for a review).

The SLS field has been explicit since its inception in its lack of commitment to mechanism and to conscious decision-making (Laland, 2004). Accordingly, use of the term strategy (as indicated in section 3.2) does not imply domain specificity, or that strategies are unlearned or under tight genetic-control. Researchers of social learning strategies view them as products of cultural and/or biological evolution. Nevertheless, recent research may provide evidence of evolved aspects of SLSs. For example, children, chimpanzees, and gorillas showed enhanced learning from animate (versus inanimate) models, which is not merely due to changes in input mechanisms such as reduced attention (Heyes, 2012), but to deeper encoding and enhanced memory of socially mediated events (Howard et al., 2017). The authors have suggested relatability of goal-directed actions between observer and model as an explanation, and such may mediate evolved enhancements in memory for, and thus replication of, the actions of specific models, represented in specific social learning strategies.

Although domain-general associative learning processes can often explain the findings of many social learning experiments (Heyes, 2012; Heyes & Pearce, 2015), it is worth noting that social learning strategies and associative learning theories are not alternatives (Kendal et al., 2018). This is because SLSs are explicitly a functional account of behaviour and agnostic regarding mechanism, although researchers of SLSs do routinely employ asocial learning controls and consider associative learning explanations (Coolen et al., 2003; Jones et al., 2013; Kendal et al., 2004). However, we ought to consider that the extensive evidence for neurological and genetic differences between chimpanzees and humans (e.g., Boyd et al., 2015; Laland, 2017) make it unlikely that attentional or motivational variation, aligned with general associative learning processes, could fully explain the differences in social learning between chimpanzees and humans (Kendal et al., 2018). Further research is also required to determine whether such species differences in social learning represent the effect of differing computational power aligned with general underlying learning mechanisms.

In fact, neuroscience research is revealing that social interactions are heavily embedded in human and nonhuman brains. For instance, a brain region known as the ACCg, a sub-region of the anterior cingulate cortex lying in the gyrus, appears to be specialised for the processing of social information in humans and nonhumans, as evidenced by neurophysiology, neuroimaging, lesion studies, and studies of individuals with autistic spectrum disorder (Apps et al., 2016; Hill et al., 2016). In combination with other brain regions that signal in a more egocentric frame, this allocentrically signalling brain region (ACCg) may enable integration of information regarding the actions of oneself and those of others (Apps & Sallet, 2017), which could potentially enable the payoff bias of "copy if better". Moreover, there is indicative evidence that frequency dependent biases may be facilitated by specific brain regions (anterior insula, rostral cingulate zone, and ventral striatum) whose activity increases in response to consensus or lack of consensus between demonstrators which predicts changes in behavior (Morgan & Laland, 2012)Such studies and others in the area of evolutionary neuroscience (reviewed in Kendal et al., 2018) highlight the possibility for some social learning processes and social learning strategies to derive from domain specific capacities.

Social learning strategies provide an exciting avenue for investigation of the complementarity between functional and mechanistic perspectives. Such studies will be fruitful in perhaps identifying distinctive patterns of neural connectivity associated with different social learning strategies. Moreover, such studies may assist developmental and comparative psychologists as well as cognitive neuroscientists in understanding population- or individual-level differences in cognitive development or neural connectivity in terms of alternative SLS deployment. Likewise, the detailed functional questions brains have evolved to deal with, as exemplified by social learning strategies, may explain differences in brain architecture between species. Although consideration that any apparent domain specific capacities necessarily involve brain regions that participate in a variety of other functions will be required.

3. Conclusion

Social learning strategies influence when individuals learn from others, as opposed to innovating, as well as what they socially learn and whom they learn from. Such strategies, though not necessarily consciously applied, enable individuals to acquire useful skills, or information, with minimal opportunity or predation costs. The many different social learning strategies can be classified into those that are dependent upon the context in which individuals find themselves – including their own state, the frequency of traits they observe around them, and the characteristics of models, or demonstrators, displaying those traits – and, the content of the trait in question. The strategies differ in the ease with which they may be applied and their likely accuracy in enabling the observer to acquire the ”best” information. Recent research has highlighted that (i) SLS use is widespread in the animal kingdom; (ii) SLSs are often used in combination; and, (iii) a SLS does not have a particular population-level signal. These considerations will influence research regarding the role of SLSs in the evolution of social intelligence or cumulative culture, for example. Finally, although the precise mechanisms underlying social learning strategies remain unknown, recent findings highlight that SLSs may involve both domain-general and domain-specific capacities. Accordingly, the SLSs field is ripe for a combined functional and mechanistic investigation of social learning. Such may be particularly interesting regarding the utility of metacognitive SLSs in cumulative cultural evolution (Dunstone & Caldwell 2018; Heyes 2016).

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Table 1. The classification scheme of cognitive heuristics or ”rules of thumb” known variously as social learning strategies or transmission biases in the social learning field. The examples given all have empirical support as either discussed in this chapter or cited in Rendell et al. (2011) and Kendal et al. (2018). The shaded portions of the table indicate the social learning strategies that I focus upon in this chapter.

Transmission Bias	**Unbiased (Random)**	**Context Dependent (Indirect)**			**Content Dependent (Direct)**	**Guided Variation**
Strategy Type		***“When”*** **State-based**	***“Who”*** **Frequency-dependent**	***“Who”*** **Model-based**	***“What”*** **(most accurate)**	
Examples	“copy friends”	“copy if uncertain”	“copy the majority”	“copy males”	“copy if better” (payoff bias)	Trial and error learning combined with unbiased transmission
	“copy kin”	“copy if hungry”	“copy rare behaviour”	“copy dominants”	Bias for social information	
		“copy if low-ranking”	“copy variants increasing in frequency”	“copy adults”	Bias for emotional information	
		“copy if pregnant”		“copy prestigious”		

Citation on deposit: Kendal, R. L. (2022). Social Learning Strategies. In M. A. Krause, K. L. Hollis, & M. R. Papini (Eds.), Evolution of Learning and Memory Mechanisms (247-264). Cambridge University Press. https://doi.org/10.1017/9781108768450.017