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Opinion

Who Knows? Metacognitive Social Learning Strategies

Q1 Cecilia Heyes^{1,2,*}

To make good use of learning from others (social learning), we need to learn from the right others; from agents who know better than we do. Research on social learning strategies (SLSs) has identified rules that focus social learning on the right agents, and has shown that the behaviour of many animals conforms to these rules. However, it has not asked what the rules are made of, that is, about the cognitive processes implementing SLSs. Here, I suggest that most SLSs depend on domain-general, sensorimotor processes. However, some SLSs have the characteristics tacitly ascribed to all of them. These metacognitive SLSs represent ‘who knows’ in a conscious, reportable way, and have the power to promote cultural evolution.

It Pays to Know Who Knows

Learning from others (social learning) can be a wonderful thing, but only if you learn from the right others. Whether you are trying to blend in with a new social group or tackling a new piece of technology, there is no point in copying another ingénue. Indeed, if the learning itself is laborious, or mistakes are expensive (one false move produces ostracism or a factory reset), taking a lead from the wrong people can be even more costly than going it alone. Sticking with old habits, or trying new things until you hit on something that works (asocial learning) can be better than copying the clueless (Box 1) [1,2]. To make social learning work for us, we need to keep track of who knows.

Over the past 10 years, researchers from a range of disciplines have been looking closely at transmission biases [3,4] or SLSs [5–7]. These are rules, such as ‘copy if uncertain’, ‘copy the majority’, and ‘copy the most successful’, that rational agents should use to maximise the efficiency of their social learning. Using mathematical modelling, behavioural ecologists and economists have devised a large number of SLSs, and found that these rules often predict when and who we copy in laboratory experiments [5,6,8]. In addition, the rules do not only apply to humans. The behaviour of an impressive array of animals, including rats [9], sticklebacks [10], fruit flies [11], and frog-eating bats [12], also conforms to SLSs.

Fortified by these achievements, ecologists and economists have proposed that SLSs provide a key to understanding two fundamental features of life on Earth: the evolution of social learning and human culture [5,13,14]. The first of these proposals is straightforward: social learning is ubiquitous in the animal kingdom [15]; even ants [16] and caddisfly larvae [17] can learn from others. The ubiquity of social learning would be a puzzle if creatures opted for social rather than asocial learning at random, and were just as likely to copy ignorant as knowledgeable conspecifics. In that case, social learning would amount to nothing more than indiscriminate recycling of behaviour. On average, it would not improve the efficiency of a creature or increase its reproductive fitness [18]. Therefore, research on SLSs helps to explain the evolution of social learning by showing that it could be, and often is, launched and targeted in ways that make it adaptive. Research on SLSs shows that it is not the tool itself (social learning) that is valuable, but the way it is used.

Trends

When agents learn selectively from others, they are using SLSs.

Mathematical modelling indicates that these strategies enhance the efficiency of social learning in humans and other animals.

SLSs are described as if they were rules, such as ‘copy when uncertain’ and ‘copy the most successful’, that are voluntarily deployed.

SLSs are thought to have contributed to the emergence of human culture.

Here I propose a dual-system psychological framework for research on the mechanisms and functions of SLSs.

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Box 1. Social and Asocial Learning Depend on the Same Psychological Processes

This article concerns the psychological processes controlling the deployment of social and asocial learning. Previous research, examining the intrinsic properties of these two types of learning, has shown that they exploit different sources of information: cues provided by other agents (social learning), and cues from the inanimate environment (asocial learning). However, four lines of evidence converge on the conclusion that information from these sources is processed by the brain using the same computations [15]: (i) social and asocial learning ability co-vary. Among birds [68] and among primates [69], species that perform well in tests of social learning also tend to perform well in tests of asocial learning, and this positive correlation is present even when statistical analyses control for body mass, brain volume, and phylogeny. (ii) Social learning in solitary animals. In laboratory tests, animals such as octopuses [70] and red-footed tortoises [71] (Figure 1), which lead solitary lives in the wild, prove themselves to be adept at learning from social cues. (iii) Common varieties. Social and asocial learning each come in the same three varieties (learning about single stimuli, about relations among stimuli, and about relations between stimuli and responses, or actions and outcomes) [15], and each type of social and asocial learning has been found in a wide range of species [16,72]. For example, social learning about actions and outcomes, which was once thought to be uniquely human, has now been found in birds [73,74]. (iv) Associative learning of social value. Studies of human decision-making, combining mathematical modelling with functional brain imaging, have found that the same computations, based on the calculation of prediction error, are involved in processing information from social partners (social learning) and personal experiences of reward (asocial learning) [26,75]. Processing of social and asocial cues is sometimes carried out in different brain areas [76]. However, evidence is emerging that, rather than being rigidly specialised for social and asocial learning, each brain area may be capable of processing social and asocial cues, and switches back and forth according to which type of cue is currently more relevant for action [77,78]. Together, these four lines of evidence suggest that, intrinsically, both social and asocial learning depend on domain-general, or 'generic' [75], processes of learning.



Trends in Cognitive Sciences

Figure 1. Social Learning in Solitary Animals. The red-footed tortoise *Chelonoidis carbonaria* engages in very little social interaction under free-living conditions, but is capable of social learning in laboratory tests [71]. Reproduced with permission from Peter Baumber and Anna Wilkinson.

Glossary

Associative learning: mechanisms that encode information about relations between events in excitatory and inhibitory links between sensory and motor representations. Traditionally, these mechanisms have been studied using conditioning procedures. The computations that control link formation depend on prediction error [64,65].

Domain-general: in this article, a process is domain-general if it applies the same computations to information from social and asocial sources. Therefore, a process mediating a SLS is domain-general if it selects between social and asocial inputs, among social inputs, and among asocial inputs, in the same way.

Implicit (System 1) versus explicit (System 2) cognition: implicit cognition, or System 1, is minimally dependent on working memory, and typically processes information rapidly and in parallel. We are seldom conscious of its operations, and many of them involve sensorimotor processes. By contrast, explicit cognition, or System 2, is highly dependent on working memory, and typically slow, serial, rule based, and conscious [66,67].

Implicit (System 1) versus explicit (System 2) metacognition: metacognition is a special kind of cognition that represents properties of cognitive processes (e.g., their speed or reliability), rather than properties of the world (e.g., the location or value of an object). Implicit metacognition represents cognitive processes in System 1 (e.g., rapidly, in parallel, with minimal dependence on working memory), whereas explicit metacognition represents cognitive processes in System 2 (e.g., slowly, serially, and in a conscious, reportable form).

Metacognition: the use of metacognitive representations. These represent properties of cognitive processes; for example, the reliability of a perceptual representation [32].

'When' and 'who' SLSs: 'when' SLSs are rules specifying the conditions in which an agent should engage in social learning rather than persist in using an established behaviour or engage in asocial learning. For example, copy when

45 The second proposal, that SLSs help to explain human culture, is harder to understand. Indeed,
46 it seems to conflict with the first proposal. If a range of animals use SLSs, and SLSs promote
47 culture, why is human culture so much richer than that of other animals? There is some evidence
48 that nonhuman primates and cetaceans show geographical variation in behaviour that is not due

49 to genetic or ecological differences [19,20], but why do rats, sticklebacks, fruit flies and frog-
 50 eating bats not show this kind of cultural diversity? Why do these species and many others,
 51 equipped with SLSs, not show cumulative cultural change (i.e., the accretion of wisdom over
 52 generations) through social learning, to produce sophisticated technology, elaborate social
 53 practices, and vast libraries of knowledge about the world? There can be no doubt that many
 54 human qualities, especially language, contribute to making us 'odd' animals [3]. The question
 55 here is whether the use of SLSs is one of those qualities and, if so, how it contributes to making
 56 humans such peculiar, cultural animals.

uncertain. 'Who' SLSs are rules specifying the type of agent to be copied. For example, copy older individuals [5].

57 Here, I suggest that some SLSs have the power that has been ascribed to all SLSs: the power to
 58 promote culture. The culture-promoting SLSs are based on a special kind of **metacognition**
 59 (see Glossary); psychological processes that produce explicit, reportable representations of
 60 'who knows'. These explicitly metacognitive SLSs are used only by humans. All other SLSs, in
 61 human and nonhuman animals, are supported by simpler, general-purpose psychological
 62 mechanisms. I argue that this deep divide, between metacognitive and other SLSs, has not
 63 been recognised before because research on SLSs has been dominated by ecology and
 64 economics, disciplines concerned with what agents do, not what they think [21]. When recent
 65 developments in cognitive science are brought to bear on SLSs, it becomes apparent that
 66 humans are the only animals that target their social learning by asking 'who knows?'

67 Animals Are Like Planets

68 Planetary motion conforms to certain rules, for example, 'the orbit of a planet is an ellipse with the
 69 Sun at one of two foci'. However, planets do not understand these rules or implement them
 70 deliberately. Planetary motion is law-like because it is driven by consistent internal and external
 71 forces, but the rules of planetary motion are in the minds of scientists, not in the minds of planets.
 72 Similarly, I suggest that the behaviour of nonhuman animals can be described and predicted by
 73 SLSs, but the strategies are in the minds of scientific observers, not of the animals themselves.

74 The language used in research on SLSs implies that they are rules in the minds of agents rather
 75 than scientific observers. To say that an agent 'uses' a strategy implies a voluntary act of
 76 deployment. To characterise the strategy itself in words, such as 'copy when uncertain', implies
 77 that what is deployed is a rule encoded in a reportable form, and 'copy' implies that the rule
 78 relates specifically to decisions about social learning. Even if few researchers would endorse
 79 these claims explicitly, the language of SLSs is potentially misleading. A recent analysis of
 80 the evidence indicates that the psychological forces driving animals to engage in social rather
 81 than asocial learning, and to copy one model rather than another, are not voluntarily deployed,
 82 domain-specific rules (Box 2) [22]. Instead, these forces comprise processes of **associative**
 83 **learning** that operate automatically, rather than in a controlled way, and are **domain-general**;
 84 that is, they select not only between social and asocial sources of information, and among social
 85 cues, but also among asocial or inanimate sources of information. They are products of
 86 biological evolution (natural selection operating on genetic variants) but they did not, as the
 87 language used in economic and ecological analyses implies, evolve specifically for the guidance
 88 of social learning. Their evolutionary purpose is to direct all learning towards objects and events
 89 that are most likely to carry useful information.

90 People Are (Sometimes) Like Cooks

91 Associative processes are powerful determinants of human as well as animal behaviour [23–26].
 92 Therefore, it is likely that these domain-general processes underpin much of the human
 93 behaviour that conforms to SLSs [6,27–31]. However, I suggest that humans sometimes
 94 use explicitly metacognitive SLSs (Box 3). These strategies, and only these, have the character-
 95 istics that previous research has tacitly ascribed to all SLSs, found in animals and humans. They
 96 are consciously represented, reportable, domain-specific rules. These rules are metacognitive in

Box 2. Frog-Eating Bats Copy When Dissatisfied

Heyes and Pearce [22] reviewed the most striking examples of SLSs in animals and found that they could be explained by domain-general processes of attention and associative learning. For example, in one of the experiments they examined, frog-eating bats initially learned to approach one of two auditory stimuli, A or B, for food [12] (Table I). For A-trained bats (the design was counterbalanced), food was always available from the loudspeaker playing A. In the second phase, these 'observer' bats were again able to retrieve food from the loudspeaker playing A, but now food could also be retrieved from the other loudspeaker, playing B. During this phase, food was available on the loudspeaker playing A on 100% of the trials for group 100-social, and on 50% of the trials for group 50-social and for group 50-solitary. The trials for group 100-social and group 50-social involved a second bat, a 'model', which was released at the same time as the observer, and which had been trained to find food on the loudspeaker playing B, but not A. Subsequent testing revealed a strong preference for A over B in groups 50-solitary and 100-social, but a preference for B over A in group 50-social.

The behaviour of the bats in this study conformed to the rule 'copy when dissatisfied'. Observation of a model that went to B encouraged the observers to reverse their original preference for A over B (social learning), when the rate of reward at A had recently declined ('dissatisfied' group 50-social), but not when it had been sustained ('satisfied' group 100-social). However, associative learning is sufficient to explain the behaviour of the bats. For example, on the associative account, when the bats had a choice between A and B on test, group 50-social approached A less than group 100-social and, therefore, by default, approached B more, because, during the second phase of training, approaches to A had been intermittently rewarded for group 50-social and consistently rewarded for group 100-social. Compared with consistent reward, intermittent reward yields a weaker association between the cue and the positive event that follows and, therefore, intermittent reward does not make a cue as attractive as consistent reward [79]. In support of this domain-general explanation, Jones and colleagues [12] found that, in a final test where B was presented without A, groups 50-social and 100-social were equally likely to approach B.

Table I. Key Elements of the Design Used by Jones *et al.* [12], Illustrated by the Groups of Bats Initially Trained to Approach Cue A

Phase of Training	Group	% Reward at A	% Reward at B
1	All	100	0
2	100-social	100	100 + model feeding at B
	50-social	50	100 + model feeding at B
	50-solitary	50	100 no model

97 that they represent properties of the cognitive processes of the rule-user and of other agents.
 98 They are distinct from other explicit metacognitive rules, such as those used to allocate study
 99 time during examination preparation, or to decide how much to bet on a perceptual judgement,
 100 because they specify conditions in which it is advisable to engage in social rather than asocial
 101 learning, and, in the former case, from whom one should learn.

102 Some of the labels currently in use make it obvious that SLSs can have metacognitive content,
 103 that is, that they can relate to 'who knows'. For example, 'copy when uncertain' clearly implies
 104 that agents should be biased in favour of social learning to the extent that they lack confidence in
 105 their own knowledge; to the extent that their own knowledge, or the process yielding that
 106 knowledge, is metacognitively represented as lacking precision or reliability. Other labels need
 107 unpacking to reveal their potential metacognitive content. For example, 'copy the majority'
 108 becomes 'copy the majority when the majority is likely to know best'.

109 When humans use explicitly metacognitive SLSs, they are like cooks rather than like planets.
 110 Cooks know the rules to which their behaviour conforms, and the conformity of their behaviour is
 111 due, in part, to their knowledge of the rules. They can tell you that 'a good cook never fries until
 112 they see blue smoke arise', and this explicit knowledge is part of what makes a cook wait until the
 113 oil is hot before putting food in the pan.

114 No research to date has been dedicated to finding out what kinds of psychological process
 115 mediate SLSs. However, the results of several studies provide evidence that, in adult humans,
 116 SLSs are sometimes implemented by explicit metacognitive rules (Box 4).

Box 3. Explicit Metacognition

Metacognition is broadly defined as cognition-about-cognition or thinking-about-thinking. **System 2** or **explicit metacognition** is a special kind of thinking-about-thinking [32] (Figure 1). In common with **System 1** or **implicit metacognition**, it represents properties of cognitive processes (e.g., their speed or reliability) rather than properties of the world (e.g., the location or value of an object). However, unlike implicit metacognition, explicit metacognition represents properties of cognitive processes in a conscious, reportable form. With explicit metacognition, an agent can think and say 'I'm sure' or 'I'm doubtful'.

More broadly, within dual systems models of the mind [66,67], and related theories [80,81], explicitly metacognitive representations are part of a cognitive system that tends to handle problems slowly and serially. Its functioning depends on working memory, and correlates with differences between people in general intelligence. By contrast, implicit metacognition, and many of the cognitive processes represented by explicit metacognition, including the processes of associative learning, are part of a cognitive system that tends to handle problems rapidly and in parallel, and that is minimally dependent on working memory. Explicit metacognition can be regarded as a component of System 2 without embracing controversial aspects of dual systems models [82,83]; for example, without assuming that the features of System 2 cognition are perfectly correlated, or that System 1 operation cannot be characterised using (planetary) rules [32,66].

Explicit metacognition is typically studied by cognitive scientists using judgements of learning and confidence judgements. When working towards an examination, students use explicitly metacognitive judgements of their own prior learning to exclude from future study materials they have already assimilated, and to prioritise material they have nearly, but not quite, mastered [84,85]. When making perceptual decisions, for example, about the presence or orientation of an object in a stimulus array, people use explicitly metacognitive confidence judgements to decide how much they should bet on the accuracy of their decisions, and to communicate the reliability of their decisions to cooperation partners [33,35,86]. The power of explicit metacognition to influence the operation of implicit processes is illustrated by studies showing that explicit metacognitive beliefs about self-control modulate eating behaviour, procrastination during an examination period, and performance on simple laboratory tasks requiring the inhibition of habitual responses [87–89].

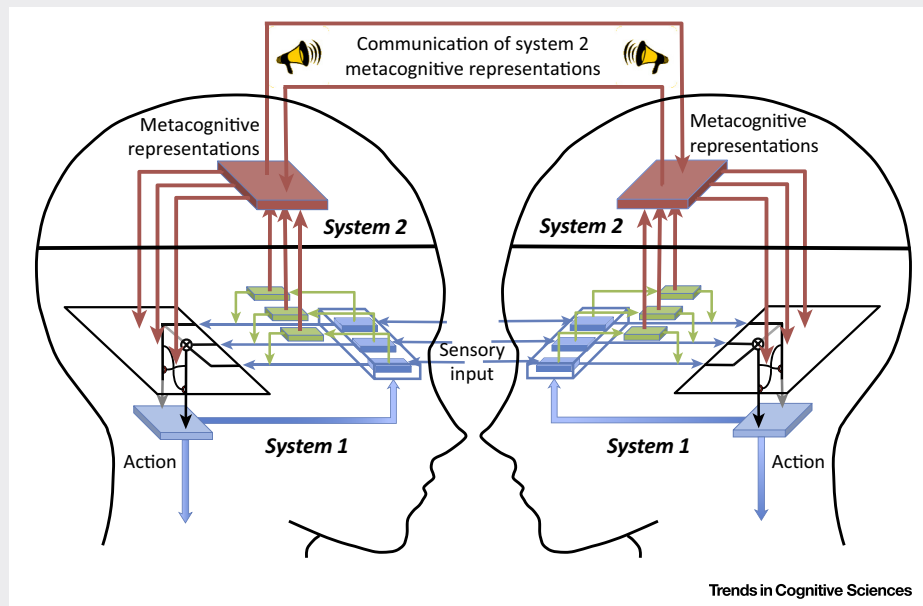


Figure 1. System 2 Metacognition. Shea *et al.* [32] argued that explicit or 'System 2' metacognition is for cognitive control across two agents. System 2 metacognitive representations are derived from information in System 1, but they are in a form available for report. For example, the reliability of a sensory signal can be reported in terms of confidence. When agents are cooperating, these reports can be used to optimise control by, for example, giving more weight to the more confident observer [90]. Reproduced with permission from [32].

Recipes Are Socially Learned

Research on metacognition in general indicates that explicitly metacognitive rules are learned [32,33]; this learning typically depends on social interaction [34–36] and consequently there is marked cultural variation in explicit metacognition [37–40]. For example, children learn by

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Box 4. Explicitly Metacognitive SLSs

There is evidence that both ‘when’ and ‘who’ SLSs can be explicitly metacognitive. In a study relating to ‘when’ strategies, people were asked to make a preliminary decision in foraging and perceptual tasks, and an explicit judgement of their confidence in that decision, before being given the opportunity to use social information to make a final decision [91]. The participants’ confidence judgements were accurate (they had lower confidence in wrong rather than right preliminary decisions) and, crucially, they were increasingly likely to use social information as their confidence declined, suggesting that they deliberately applied the rule ‘copy when uncertain’. In a study relating to ‘who’ strategies, people given the opportunity to copy members of their own or an opposing team were able to report the strategies they had adopted in a post-test questionnaire [92]. Similarly, in another study, participants preferentially copied popular choices when other people’s payoffs were visible, but preferentially copied unpopular choices when their payoffs were invisible [6]. A potential explanation for this unpopularity bias is that people were deliberately avoiding an ‘information herd’ [21,93]; their social learning was guided by explicit knowledge, acquired from others, that majorities know best only when they have access to information about payoffs.

Further evidence that SLSs can be explicitly metacognitive comes from an exciting new field of cognitive neuroscience with great potential to illuminate SLSs. This field uses computational modelling of behavioural and neuroimaging data to identify the psychological and neural processes mediating social and asocial learning [76,94–96]. As yet, these techniques have not been used deliberately to investigate SLSs, but they have already provided evidence that social and asocial learning depend on the same psychological processes (Box 1, main text), and that, in adult humans, ‘who’ SLSs can be explicitly metacognitive. For example, in a foraging task, people made use of social information (advice about which of two options to choose) to the extent that they believed the advisor to be motivated to help rather than to mislead them [95]. These beliefs were explicitly stated, and the basic effect (co-variation between the advisors’ incentives and the participants’ use of social information) disappeared when participants were told that the advisors did not know which option they were recommending. Therefore, these results suggest that the participants used an explicitly metacognitive strategy, such as ‘copy when the model intends to help’.

121 instruction to use ‘semantic clustering’ to retrieve the names of animals from memory [34] (e.g. think of birds first, then mammals...), and adults learn through social interaction explicitly to
 122 metarepresent their confidence in ways that make two heads better than one [35,36].
 123

124 Given these findings from research on metacognition in general, one would expect explicitly
 125 metacognitive SLSs also to be products of learning through social interaction, and to vary across
 126 cultures. Evidence consistent with the first of these predictions indicates that preschool children
 127 are more like planets than like cooks. When children under 4- or 5-years of age observe the
 128 nonverbal actions of others, their behaviour conforms to rules such as ‘copy when uncertain’
 129 [41], ‘copy the in-group’ [42], and ‘copy prestigious individuals’ [43,44], but I have argued in two
 130 reviews of the empirical evidence that their choices can be explained by domain-general
 131 psychological processes [45,46]. This suggests that domain-specific SLSs do not come
 132 online until relatively late in development, when there has been plenty of opportunity for them
 133 to be learned through social interaction. Evidence consistent with the second prediction shows
 134 that there is marked cross-cultural variation among the SLSs used by adults [47–51]. For
 135 example, in contrast with Westerners, Fijians are less likely to seek advice from people with more
 136 formal education [50] and, in contrast with Britons, people from mainland China engage in more
 137 social learning, and their social learning is less dependent on uncertainty [47].

138 Concluding Remarks

139 This article asks, for the first time, what SLSs are made of, about the cognitive mechanisms that
 140 direct social learning to the right ‘others’. It proposes that most SLSs are implemented by
 141 domain-general sensorimotor processes (planetary SLSs), while a small proportion, found only
 142 in humans, are explicitly metacognitive (cook-like SLSs). This dual systems account provides a
 143 framework for future research on SLSs (see Outstanding Questions), and casts further light on
 144 the roles of SLSs in the evolution of social learning and of human culture.

145 Economists and ecologists write about SLSs as if they were all domain-specific rules produced
 146 by genetic evolution; rules about the use of social information (not information in general),
 147 produced by the slow process of natural selection operating on genetic variants. If this were true,

Outstanding Questions

Under what range of conditions are explicitly metacognitive SLSs more accurate and precise than other SLSs? For example, they may be especially advantageous when payoffs are invisible and the copying process is itself costly.

Do metacognitive SLSs sometimes conflict with other SLSs and, if so, what are the neurocognitive mechanisms that resolve these conflicts?

What is the nature and extent of cultural variation in metacognitive SLSs?

Are nonhuman primates capable of using metacognitive SLSs? If so, can they communicate these strategies to others?

When do children begin to use metacognitive SLSs? Is this related to the development of executive function?

How do sensorimotor and explicitly metacognitive processes contribute to the resolution of other ‘explore versus exploit’ dilemmas?

148 it is likely that SLSs would be highly inflexible over time. By contrast, I have suggested that all
149 animal behaviour, and much human behaviour, conforming to SLSs is based on domain-
150 general processes of associative learning. These learning processes are products of genetic
151 evolution, but, because they are minimally canalised or genetically constrained, they allow SLSs
152 to change rapidly over time. For example, if the younger members of a population discovered
153 some clever foraging techniques [52], associative learning could quickly convert ‘copy older
154 individuals’ to ‘copy younger individuals’ in that population [22]. Therefore, the idea that animals
155 are like planets (their SLSs are based on associative learning) casts further light on the ubiquity of
156 social learning in the animal kingdom. Social learning is a valuable tool because it can be used,
157 not only selectively, but also with a selectivity that can be adjusted rapidly over time to track
158 changes in the social and asocial environment.

159 My proposal that most SLSs are based on associative learning implies that they are smarter
160 (more supple and adaptive) than was previously thought. However, if planetary SLSs are so
161 smart, what are the advantages of cook-like, explicitly metacognitive SLSs; of rules that are
162 domain specific and socially learned? I suggest that cook-like SLSs have the edge because they
163 can isolate ‘who knows’ with greater accuracy and precision than planetary SLSs. They can be
164 more veridical and specific in identifying sources of superior knowledge because metacognitive
165 SLS can be based on collective wisdom accumulated over generations [53]. Planetary SLSs
166 change as a function of the user’s own, recent experience; for example, if a monkey finds that
167 information from females has yielded higher payoffs recently, it will turn its attention from males to
168 females [22,54]. By contrast, because they are socially learned, metacognitive SLSs can distil
169 the experience of many agents over an extended period of time. For example, ‘copy the majority
170 only when payoffs are visible’ (Box 4) [6] is based on the experience of many people in a range of
171 environments, and anyone who has learned from others about the dangers of herding is likely to
172 stick with this rule even when they encounter exceptions. Furthermore, metacognitive SLSs can
173 comprise hierarchies of rules [55], in which some of the conditions are socially defined activities
174 and roles. For example, when uncertain about a health problem, copy the medicinal plant expert
175 with highest prestige; when uncertain about a boat-building problem, copy the boat builder with
176 the largest fleet. Or, in contemporary Western society, when you do not know much about
177 maths or science, place more trust in science accompanied by mathematical equations [49].

178 Evidence that nonhuman animals use explicit metacognition in solitary tasks [56,57], although
179 controversial [32,58], raises the possibility that some can also represent ‘who knows’ in social
180 tasks. However, the advantages of cook-like SLSs depend on them being constructed from the
181 experience of many agents. Consequently, for nonhuman animals to reap the benefits of
182 metacognitive SLSs, they would need not only to be capable of representing ‘who knows’,
183 but of communicating these beliefs to others. It is not inconceivable that this could be done
184 without language, but it is unlikely that it could be done on any significant scale, and in a way that
185 allows wisdom about ‘who knows’ to accumulate over time.

186 SLSs that identify ‘who knows’ with high accuracy and precision could not only benefit the
187 individual, but also promote cultural evolution by making it safer for learners to: (i) copy one or a
188 small number of models; (ii) copy them blindly, without introducing innovations based on asocial
189 learning; and (iii) invest in the development and use of high-fidelity copying mechanisms, such as
190 teaching and imitation [46,59]. It is now widely acknowledged that these high-fidelity mechanisms
191 are not sufficient for cultural evolution, but it remains likely that they contribute [60,61]. All three of
192 these effects (i–iii) would enhance ‘parent–offspring relations’ [62] (the heritability of differentially fit
193 cultural variants) which is one of the three, major conditions for Darwinian evolution [63].

194 Previous discussions of the relation between SLSs and human culture have also emphasised the
195 importance of high-fidelity copying mechanisms, such as language, teaching, imitation, and

196 mental time travel [13,14]. These discussions imply that there is some connection between SLSs
 197 and high-fidelity copying, but they do not specify the nature of this connection, or explain why
 198 SLSs are special; how their role in the emergence and operation of high-fidelity copying differs
 199 from the roles of other psychological capacities, such as perceiving, remembering, and learning.
 200 By contrast, the dual systems account explains the relation between SLSs and human culture,
 201 including the emergence of high-fidelity copying. It suggests that SLSs of one, comparatively
 202 rare type (the cook-like SLSs, based on explicit metacognition) improve the accuracy and
 203 precision with which agents can track 'who knows', and thereby create conditions in which high-
 204 fidelity mechanisms can evolve, develop, and operate.

205 I began with a question: If a wide range of animals use SLSs, and SLSs promote culture, why is
 206 human culture so much richer than that of other animals? I have argued that the answer is that
 207 the SLSs found in other animals, including rats, sticklebacks, fruit flies and frog-eating bats, do
 208 not promote cumulative cultural change because they are based on general-purpose cognitive
 209 processes. These processes make planetary SLSs impressively supple, but do not enable them
 210 to achieve the accuracy and precision of metacognitive SLSs. Metacognitive SLSs, found only in
 211 humans, focus social learning on knowledgeable agents so precisely that they encourage blind,
 212 high-fidelity copying (a key requirement for cumulative cultural change). Metacognitive SLSs (the
 213 ones that really concern 'who knows') are an integral part of what makes us such peculiar,
 214 cultural animals.

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