



Heriot-Watt University
Research Gateway

Beyond social learning

Citation for published version:

Singh, M, Acerbi, A, Caldwell, C, Danchin, E, Guillaume, I, Molleman, L, Scott-Phillips, T, Tamariz, M, van den Berg, P, van Leeuwen, EJC & Derex, M 2021, 'Beyond social learning', *Philosophical Transactions of the Royal Society B: Biological Sciences*.

Link:

[Link to publication record in Heriot-Watt Research Portal](#)

Document Version:

Peer reviewed version

Published In:

Philosophical Transactions of the Royal Society B: Biological Sciences

General rights

Copyright for the publications made accessible via Heriot-Watt Research Portal is retained by the author(s) and / or other copyright owners and it is a condition of accessing these publications that users recognise and abide by the legal requirements associated with these rights.

Take down policy

Heriot-Watt University has made every reasonable effort to ensure that the content in Heriot-Watt Research Portal complies with UK legislation. If you believe that the public display of this file breaches copyright please contact open.access@hw.ac.uk providing details, and we will remove access to the work immediately and investigate your claim.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B

BIOLOGICAL SCIENCES

Beyond social learning

Journal:	<i>Philosophical Transactions B</i>
Manuscript ID	RSTB-2020-0050.R1
Article Type:	Review
Date Submitted by the Author:	24-Nov-2020
Complete List of Authors:	Singh, Manvir; Harvard University, Department of Human Evolutionary Biology; Institute for Advanced Study in Toulouse Acerbi, Alberto; Brunel University London, Center for Culture and Evolution Caldwell, Christine; University of Stirling, Department of Psychology Danchin, Etienne; Université de Toulouse, Laboratoire Évolution & Diversité Biologique Isabel, Guillaume; Université Toulouse III Paul Sabatier, Centre de Recherches sur la Cognition Animale (CRCA) Molleman, Lucas; University of Amsterdam, Amsterdam Brain and Cognition Scott-Phillips, Thom; Central European University, Tamariz, Monica; Heriot Watt University, Department of Psychology van den Berg, Piet; KU Leuven, Lab of Socioecology and Social Evolution van Leeuwen, Edwin; University of Antwerp Department of Biology, ; Royal Zoological Society of Antwerp, Centre for Research and Conservation Derex, Maxime; Institute for Advanced Study in Toulouse
Issue Code (this should have already been entered and appear below the blue box, but please contact the Editorial Office if it is not present):	FOUNDATIONS
Subject:	Cognition < BIOLOGY, Behaviour < BIOLOGY, Evolution < BIOLOGY
Keywords:	cultural evolution, social learning, culture, cumulative culture, adaptation, mechanism

SCHOLARONE™
Manuscripts

Beyond social learning

Manvir Singh^{*1,2}, Alberto Acerbi³, Christine Caldwell⁴, Étienne Danchin⁵, Guillaume Isabel⁶,
Lucas Molleman⁷, Thom Scott-Phillips⁸, Monica Tamariz⁹, Pieter Van den Berg¹⁰, Edwin J. C.
van Leeuwen^{11, 12}, & Maxime Derex^{*2}

¹ Department of Human Evolutionary Biology, Harvard University, Cambridge, MA 02138, USA

² Institute for Advanced Study in Toulouse, Toulouse 31015, France

³ Center for Culture and Evolution, Brunel University London, Middlesex UB8 3PH, UK

⁴ Department of Psychology, University of Stirling, FK9 FLA Stirling, UK

⁵ Laboratoire Évolution and Diversité Biologique, Université Fédérale de Toulouse, F-31062
Toulouse cedex 9, France

⁶ Centre de Recherches sur la Cognition Animale, Centre de Biologie Intégrative, Université
Fédérale de Toulouse, F-31062 Toulouse cedex 9, France

⁷ Amsterdam Brain and Cognition, University of Amsterdam, 1018 WT Amsterdam, The
Netherlands

⁸ Department of Cognitive Science, Central European University, Budapest 1051, Hungary

⁹ Department of Psychology, Heriot-Watt University, Edinburgh EH14 4AS, UK

¹⁰ Department of Biology, KU Leuven, B-3000 Leuven, Belgium

¹¹ Department of Biology, University of Antwerp, 2610 Wilrijk, Belgium

¹² Centre for Research and Conservation, Royal Zoological Society of Antwerp, B 2018
Antwerp, Belgium

*Corresponding authors: manvir.singh@iast.fr; maxime.derex@iast.fr

24 **Abstract**

25 Cultural evolution requires the social transmission of information. For this reason, scholars have
26 emphasized social learning when explaining how and why culture evolves. Yet cultural evolution
27 results from many mechanisms operating in concert. Here, we argue that the emphasis on social
28 learning has distracted scholars from **appreciating both the full range of mechanisms contributing**
29 **to cultural evolution and how interactions among those mechanisms and other factors affect the**
30 **output of cultural evolution.** We examine understudied mechanisms and other factors and call for
31 a more inclusive program of investigation that probes multiple levels of organization, spanning
32 the neural, cognitive-behavioural, and populational levels. To guide our discussion, we focus on
33 **factors** involved in three core topics of cultural evolution: the emergence of culture, the
34 emergence of cumulative cultural evolution, and the design of cultural traits. Studying
35 mechanisms across levels can add explanatory power while revealing gaps and misconceptions
36 in our knowledge.

37
38 **Keywords:** adaptation, culture, cumulative culture, cultural evolution, mechanism, social
39 learning

1. Introduction

Scholars studying how and why culture evolves have long focused on social learning. This makes sense. For many researchers, culture *is* socially-learned information [1–3], making social learning central in the emergence of culture and a natural starting point when studying cultural evolution. In line with this focus, scientists aiming to explain the uniqueness of human culture began by asking how social learning differs between humans and our closest relatives [4], inspiring comparative research directed at pinpointing the learning capacities that set humans apart [5,6]. Similarly, scientists interested in the origins of cultural adaptations (e.g., igloos, food-processing) began by asking how social learning, when iterated, gives rise to adaptive, cultural evolutionary processes [7,8]. This focus has been productive, yielding valuable insights about cultural transmission, cultural adaptation, and capacities that distinguish humans from other primates [6,9,10].

Despite the value of studying social learning—defined here as learning that occurs through the acquisition of information from a social source—the current focus has two major limitations. First, it distracts from other important factors. Growing evidence suggests that many mechanisms aside from social learning contribute to cultural evolution. The emergence of culture hinges not only on social transmission but on cognitive capacities enabling innovation, too. Cumulative cultural evolution depends on high-fidelity transmission, yes, but just as critically on cognitive flexibility and the frequency of interaction between cultural learners. And cultural traditions exhibit features that are crucially shaped by factors such as status asymmetries, biases involved in traits' evaluation, and the distribution of beliefs within groups. We do not deny that social learning is important, nor do we assert that scholars do not appreciate that other mechanisms contribute. Rather, we contend that the focus on social learning may distract from

1
2
3 63 complementary mechanisms that help explain central research foci, such as why some species
4
5 64 have culture or how cumulative cultural evolution emerges.
6
7

8 65 A second limitation of the focus on social learning is that researchers commonly treat it
9
10 66 simply as an expressed behaviour, blackboxing underlying mechanisms [9,11]. Blackboxing is,
11
12 67 of course, a necessary first step when explaining any behaviour. A researcher trying to explain
13
14 68 the spread of prosocial religion might point to its effects on cooperation, abstracting the
15
16 69 molecular interactions and neural processes involved in cooperative decision-making. To do
17
18 70 otherwise—to consider each molecule or firing neuron—would be unmanageable. But
19
20 71 blackboxing also carries risks. In the case of social learning, one problematic consequence is the
21
22 72 resulting assumption that different behaviours, such as social and non-social learning, have
23
24 73 distinct neurocognitive foundations and thus constitute independently evolving “traits” [12]. A
25
26 74 related risk is that ignoring the underpinnings of social learning overlooks the possibility that
27
28 75 many learning behaviours may be the products of less specialized cognitive building blocks (see
29
30 76 [13] for a similar argument as applied to other apparently derived human abilities). A complete
31
32 77 understanding of cultural evolution requires considering mechanisms and other factors (“factors”
33
34 78 from here onwards) across levels of organization and appreciating how interactions among
35
36 79 factors affect the output of cultural evolution.
37
38
39
40
41

42 80 Here we review promising and understudied factors contributing to cultural evolution.
43
44 81 We organize these into three levels of organization: neural, cognitive/behavioural, and
45
46 82 populational (Box 1). Our goal is to identify factors that add explanatory power while revealing
47
48 83 erroneous assumptions and gaps in our knowledge of how and why culture evolves. We also
49
50 84 review the mechanistic underpinnings of social learning to demonstrate how peering into the
51
52 85 black box can transform our understanding of culture.
53
54
55
56
57
58
59
60

1
2
3 86 Our aim is not to comprehensively enumerate the factors that affect cultural evolution.
4
5
6 87 Instead, it is to point readers towards overlooked factors while illustrating the value of a
7
8 88 multilevel approach. In that vein, we focus three questions that have arguably attracted the most
9
10 89 attention in cultural evolutionary research:

11
12 90 1. What explains the emergence of culture?

13
14
15 91 2. What explains cumulative cultural evolution?

16
17 92 3. What explains the design of cultural traits?
18
19 93

20
21
22 94 **Box 1. *Three levels of organization***

23
24 95 We structure our discussion of mechanisms and other factors into three levels of
25
26 96 organization:

27
28 97 1. The neural level concerns neurons and their interaction. Neural factors include
29
30 98 neurophysiology, the structure of neural networks, and the density of neurons.

31
32
33 99 2. The cognitive-behavioural level concerns both mental computations and their
34
35 100 behavioural outputs. Mental computations include algorithms involved in
36
37 101 perception, kin detection, and representations of possibility. Behavioural outputs
38
39 102 consist of actions resulting from the interaction between individuals' internal
40
41 103 processes and their environment. Although cognition and behaviour are often
42
43 104 regarded as distinct levels of organization, we treat them together here because of
44
45 105 the difficulty of sometimes isolating mental computations from their behavioural
46
47 106 outputs.
48
49
50
51
52
53
54
55
56
57
58
59
60

1
2
3 107 3. The populational level concerns features of populations such as size, structure,
4
5 108 and density, as well as by traits that only exist at the group-level, such as markers
6
7
8 109 of group identity.
9

10 110 Readers should note three complexities. First, these levels are hierarchically
11
12 111 structured. Cognition, for instance, consists of mental computations that emerge from
13
14
15 112 interactions among neurons. Second, there are other levels of organization buried within
16
17 113 these three levels. Interactions among neurons, for instance, may give rise to neural
18
19 114 networks, whose interaction might in turn manifest as cognition. Finally, a phenomenon at
20
21 115 any level can be influenced by entities at both lower and higher levels. Cognitive algorithms
22
23
24 116 are patterned abstractions of neural activity, but they can take as inputs information about
25
26 117 population-level variables, such as levels of competition.
27
28
29 118

30 31 119 **2. Factors contributing to the emergence of culture**

32
33 120 Why do some species have culture, while others do not? Given that culture relies on the social
34
35
36 121 transmission of behaviour, attention has focused on social learning capacities, mostly in
37
38 122 vertebrates, but in insects as well [6,14]. Yet although culture necessitates social learning, social
39
40 123 learning does not necessarily result in culture. For a behaviour to qualify as a cultural tradition, it
41
42
43 124 must be shared by two or more individuals and persist over time [15]. Recognizing this, we here
44
45 125 examine social learning at different levels of explanation and consider other factors potentially
46
47 126 involved in the emergence of culture. We review evidence that species such as bumblebees
48
49 127 engage in cultural transmission using general-purpose learning mechanisms. Given that these
50
51 128 general learning mechanisms are shared widely among animals—and are likely much more
52
53
54
55
56
57
58
59
60

1
2
3 129 widespread than culture—we consider how capacities aside from social learning, such as
4
5 130 memory, innovation, and social interaction, may underlie the emergence of culture.
6
7

8 131

9 10 132 **2.1. Neural**

11
12 133 Research on neural mechanisms helps specify which faculties are involved when an individual
13
14 134 learns from another, resolving whether particular neural specializations are necessary for cultural
15
16 135 transmission. Studies of the neurogenetics of social learning among model species where genetic
17
18 136 and molecular tools are available show that the neural machinery for social learning overlaps
19
20 137 considerably with that of non-social learning and that such machinery exhibits commonalities
21
22 138 across taxa. In primates and rodents, social information triggers activity in the same reward
23
24 139 pathways involved in non-social learning, such as the ventral striatum and medial prefrontal
25
26 140 cortex [16–18]. Work on rodents and humans suggest that, at least when socially learning about
27
28 141 threats, both social and non-social information are processed in a common value-representation
29
30 142 circuits [19]. Similarly, in *Drosophila*, the neurotransmitters [20] and functions of neural
31
32 143 structures [21] involved in social learning are the same as those involved in non-social learning.
33
34 144 Research indicates that these structures play a role in learning, memory, and reward in
35
36 145 vertebrates, suggesting a phylogenetically ancient origin [20,22]. Although social learning also
37
38 146 incorporates information that non-social learning does not [19,23], the capacity to learn from
39
40 147 others emerges from mechanisms designed for learning more generally [19].
41
42

43
44 148 Among the neural mechanisms of learning, those underlying long-term memory are
45
46 149 critical because they allow social information to be encoded [24]. Despite their importance,
47
48 150 however, such mechanisms remain largely overlooked in the study of cultural transmission. As
49
50 151 biologists recognize, long-term memory must involve the fine-tuning of gene expression, which
51
52
53
54
55
56
57
58
59
60

1
2
3 152 can in turn involve epigenetic change, making it a promising direction of future study [25,26].
4
5
6 153 Although the mechanistic understanding of memory formation remains superficial, research has
7
8 154 shown that blocking major epigenetic routes interferes with memory formation. In rats, for
9
10 155 instance, the inhibition of the DNA methyltransferases fully blocks contextual fear conditioning,
11
12 156 as well as memory formation, following the rapid methylation of memory suppressor genes and
13
14 157 demethylation of memory promoting genes in a highly dynamic way in the hippocampus [27].
15
16
17 158 Studying the epigenetic basis of memory will help clarify its mechanistic basis and provide
18
19 159 insight into the foundations of learning and culture more broadly.

20
21
22 160 In short, the striking similarities of mechanistic pathways among vertebrates and
23
24 161 invertebrates suggest that the basic mechanisms of culture are ancestral, and that culture may be
25
26 162 far more common in animals than previously suspected. Insofar as non-cultural species have
27
28 163 general-purpose learning mechanisms, and therefore some form of social learning, explaining the
29
30 164 emergence of culture will require examining capacities aside from social learning.
31
32
33 165

34 35 166 **2.2. Cognitive-behavioural**

36
37
38 167 Research on cognitive-behavioural mechanisms further demonstrates that social learning can
39
40 168 emerge from general capacities serving to acquire information, regardless of whether that
41
42 169 information comes from a social source [28]. Consider bumblebees, which copy the foraging
43
44 170 preferences of other hive members [29]. Researchers studying this behaviour have found
45
46 171 evidence that bumblebees engage in second-order associative learning. In the same way that
47
48 172 Pavlov's dog associated a metronome tick with food, bumblebees seem to learn to associate the
49
50 173 presence of conspecifics with rewards. And just as Pavlov's dog could then learn secondary
51
52 174 associations (e.g., salivating at a black box associated with a metronome tick), bumblebees may
53
54
55
56
57
58
59
60

1
2
3 175 learn stimuli associated with conspecifics because they are reliable indicators of rewards [30].
4
5 176 Researchers have provided support for this explanation using a series of ingenious experiments.
6
7
8 177 They have shown that naïve individuals do not yet treat conspecifics as indications of rewards
9
10 178 [31], and that reducing the reliability of social information [32] and associating conspecifics with
11
12 179 bitter substances [31] lead bumblebees to no longer use social information and to avoid stimuli
13
14
15 180 associated with conspecifics, respectively. Moreover, there is no difference between how trained
16
17 181 bumblebees use information from heterospecifics and how they use information from
18
19 182 conspecifics [33]. Bumblebees socially learn by using general learning mechanisms that are
20
21
22 183 likely widely shared among animals.

23
24 184 If social learning can occur with widespread, general learning mechanisms, then which
25
26 185 additional capacities are needed for culture? One potentially crucial enabler of culture is the
27
28 186 capacity to innovate, which generates cultural variation [34,35]. Although scholars have
29
30
31 187 considered innovation when explaining cumulative cultural evolution [36,37], the capacities
32
33 188 underlying innovation have gone largely overlooked in explaining why some species have
34
35 189 traditions. The importance of innovation has been demonstrated again with bumblebees. Alem et
36
37
38 190 al. [38] found that a technique on a string-pulling task could diffuse from a knowledgeable
39
40 191 bumblebee to the majority of a colony's foragers. Yet they also found that virtually no
41
42 192 individuals could innovate the technique on their own. Bumblebees, like *Drosophila* [24], have
43
44 193 the abilities necessary to maintain and transmit culture, but it remains unclear whether
45
46
47 194 bumblebees can generate enough cultural variation. An animal's capacity to innovate seems to
48
49 195 hinge on factors such as motor variability, persistence, exploration, analogical reasoning,
50
51
52 196 neophilia, and learning speed [39–42]. Given that species vary greatly in their tendency to
53
54
55
56
57
58
59
60

1
2
3 197 innovate [43,44], the underlying capacities for innovation may be critical for determining
4
5 198 whether a species has culture.
6
7

8 199

10 200 **2.3. Populational**

11
12 201 Population-level variables are usually invoked to explain cultural complexity and aspects of
13
14 202 cultural form (see sections 3 and 4). But they are also likely key for whether a species has culture
15
16 203 in the first place. The capacity to learn socially has been observed in supposedly solitary species
17
18 204 such as the common octopus [45] and the red-footed tortoise [46]. If, as Heyes [12] suspects,
19
20 205 conspecifics interact infrequently in these species, it is unlikely that they have culture. For a
21
22 206 cultural tradition to persist, individuals need to interact frequently enough for cultural traits to
23
24 207 transmit. Individuals should be tolerant and sufficiently gregarious, both cognitive-behavioural
25
26 208 tendencies that, in turn, have population-level effects [47]. In many cases, interaction alone does
27
28 209 not appear sufficient. Experiments with humans suggest that multiple exposures are necessary
29
30 210 for a trait to remain stable [48,49], while theoretical work suggests that, under many conditions,
31
32 211 uniparental transmission is not sufficient to maintain culture [50]. Moreover, given that many, if
33
34 212 not all, cultural traits are only expressed in particular circumstances, such as foraging, mate
35
36 213 choice, and food processing [51], the likelihood that a species exhibits cultural traditions should
37
38 214 vary with the number of contexts in which conspecifics interact.
39
40
41
42
43
44

45 215

47 216 **3. Factors contributing to cumulative cultural evolution**

48
49 217 While the capacity for culture is present across a broad taxonomic range, the capacity for
50
51 218 cumulative culture (i.e. the repeated modification and social learning of cultural traits over
52
53 219 successive generations [52]) seems to be absent, or at least uncommon, in non-human species.
54
55
56
57
58
59
60

1
2
3 220 Recent research suggests that some non-human animals may exhibit simple forms of cumulative
4
5 221 cultural evolution (CCE) [53–55], but the diversity and complexity of human cumulative culture
6
7
8 222 remain unparalleled [10].
9

10 223 Despite attempts to identify the mechanisms responsible for cumulative culture (e.g.,
11
12 224 [56–58]), there is still no consensus on what makes human culture so distinctive. Because CCE
13
14 225 only operates when information is passed socially, scholarly attention has focused on **capacities**
15
16 226 that promote informational stability. At the individual level, these include social learning abilities
17
18 227 that support high-fidelity transmission, such as imitation and teaching [59,60]. At the group
19
20 228 level, scholars have stressed the role of the size of the population that shares social information
21
22 229 in buffering the risk of losing cultural traits [61]. Still, theoretical work shows that **factors** that
23
24 230 support the production of new traits are no less important than **factors** that promote their
25
26 231 maintenance to explain CCE [37]. Furthermore, mechanisms that support high-fidelity
27
28 232 transmission only become important when individuals are willing to abandon previous
29
30 233 behaviours. Explaining CCE requires recognizing the explanatory role of **factors** that contribute
31
32 234 not only to the maintenance of cultural traits but to their production and spread, as well.
33
34
35
36
37
38
39

40 236 **3.1. Neural**

41
42 237 Evolutionary neuroscience can help explain cumulative cultural evolution by uncovering the
43
44 238 human neural mechanisms that promote the production, spread and maintenance of cumulative
45
46 239 culture [62]. Davis et al., for instance, attributed the existence of CCE partly to humans' unique
47
48 240 behavioural flexibility, which allows individuals to relinquish existing behaviours to adopt more
49
50 241 efficient ones [63]. The neural underpinnings of this flexibility are still unclear [13], but recent
51
52 242 research has identified one potential mechanism. Cross-species investigations tracking the
53
54
55
56
57
58
59
60

1
2
3 243 activity of single neurons indicate that human brains trade off robustness (in terms of higher
4
5 244 speed of response and increased reliability) for greater efficiency in information processing. This
6
7
8 245 lower robustness promotes the flexible learning of new tasks and adaptation to new conditions
9
10 246 although at the cost of slower and less reliable production of behavioural responses [64].

11
12 247 Cultural evolutionary researchers have also suggested that creativity and innovation
13
14 248 might enable cumulative cultural evolution ([36,37]; see also [34]). Indeed, the modification of
15
16
17 249 cultural traits includes what researchers call “guided variation”, wherein human intention and
18
19 250 intelligence produce cultural variants that are on average culturally more successful than would
20
21 251 be expected by chance [7]. Evolutionary neuroscience research allows us to pinpoint the precise
22
23
24 252 faculties that might underpin the production of guided variation. For instance, comparative
25
26 253 studies have revealed that humans possess unusually large brains (both in terms of absolute and
27
28 254 relative size) and that absolute and relative brain sizes correlate with innovation frequency in
29
30
31 255 primates [44]. Furthermore, human brains contain more cortical neurons than those of any other
32
33 256 mammals, which allows more neuronal specialization and increases the number of computational
34
35 257 levels involved in information processing, decision-making, and information storage [65,66].

36
37
38 258 **These examples demonstrate how considering the neural basis of human uniqueness might help**
39
40 259 **explain our capacity for elaborate cumulative cultural evolution.**

41
42 260

43 44 261 **3.2. Cognitive-behavioural**

45
46
47 262 Humans exhibit several cognitive-behavioural capacities aside from social learning that allow the
48
49 263 propagation of complex cultural traits. One example is the capacity for future thinking and
50
51 264 mental time travel [57], which may be limited to humans [67]. Mental time travel is potentially
52
53
54 265 important because acquiring complex culture can be costly. Stout [68] observed that an

1
2
3 266 apprenticeship in adze-making in the New Guinean village of Langda began at the age of 12-13
4
5 267 and lasted for several years, although “it might take ten years or more for the highest level of
6
7 268 skill to be achieved.” Ache hunter-gatherers do not peak in their marksmanship skills until the
8
9 269 age of 40 [69]. A sensitivity to short-term self-interest might prevent individuals from investing
10
11 270 in learning behaviours that confer benefits later in life. By making salient the long-term benefits,
12
13 271 mentally travelling forward in time might make individuals more tolerant of learning costs and
14
15 272 more willing to adopt unfamiliar behaviours.
16
17
18

19 273 The propagation of cultural traits that are not immediately beneficial might be further
20
21 274 supported by our comparatively greater motivation to attend to sources of social information
22
23 275 (e.g., [70]). Indeed, social learning abilities only become important when individuals are
24
25 276 motivated to pay attention to what other are doing. Evidence for the role of this tendency in the
26
27 277 propagation of cultural traits comes from comparative experiments conducted with humans and
28
29 278 other apes. Compared to chimpanzees, for instance, children are more likely to solve problems
30
31 279 which they have failed to solve for themselves upon exposure to social information
32
33 280 demonstrating the solution [71–73]. Thus, human motivation towards social information may
34
35 281 have the effect of allowing rapid acquisition of effective techniques that are difficult to innovate
36
37 282 from scratch. Importantly, this tendency might be connected to other well-developed human
38
39 283 capacities, such as theory of mind and metacognition, which allow humans to recognize intention
40
41 284 behind another’s behaviour and infer utility from social demonstration [74].
42
43
44
45
46

47 285 Finally, cumulative cultural evolution should be favored by humans’ communication, a
48
49 286 capacity that remains understudied in the cultural evolutionary literature. Humans communicate
50
51 287 in a way that is, if not unique to our species, certainly distinctive [75,76]: Human communication
52
53 288 is not just intentional, it is *overtly* intentional. Through behaviours such as eye contact,
54
55
56
57
58
59
60

1
2
3 289 motherese, stylization, and exaggeration, communicators show audiences that an action is done
4
5 290 *for* the audience—and this ‘for-ness’ helps audiences interpret the stimuli [77,78]. Human infants
6
7 291 can differentiate among behaviours produced (i) accidentally, (ii) intentionally but not
8
9 292 communicatively (i.e. without overt intentionality), and (iii) communicatively (i.e. in an overtly
10
11 293 intentional way) [79–84]. Overtly intentional communication (and particularly language) allows
12
13 294 potential learners to query what they do not understand, and allows experienced individuals to
14
15 295 explain, justify, and instruct, as appropriate to the needs of the learner [85,86]. **Communication,**
16
17 296 **like attention towards social stimuli, may enable cumulative cultural evolution by promoting the**
18
19 297 **opportunity for social learning, as well as the fidelity of transmission.**
20
21
22
23
24 298

25 299 **3.3. Populational**

26
27 300 The population-level variables most often invoked to explain cumulative cultural evolution are
28
29 301 population size and structure. According to experimental and theoretical work, population size is
30
31 302 important because the risk of losing cultural information varies with the number of potential
32
33 303 demonstrators [87]. As the number of demonstrators declines, the risk of losing cultural
34
35 304 information increases. Meanwhile, population structure is important because individuals’
36
37 305 opportunity for innovation varies with the cultural diversity they encounter [88–90]. In studying
38
39 306 these mechanisms, researchers typically assume that individuals have unconstrained access to
40
41 307 others’ solutions. Yet in more realistic situations, skilled demonstrators might have no interest in
42
43 308 providing useful information to unrelated individuals [91]. This limitation suggests that more
44
45 309 attention should be paid to the formation of social links that are conducive to cultural
46
47 310 transmission. A recent study in hunter-gatherer populations revealed that individuals invest early
48
49 311 in their childhood in a few close friends and that friendship facilitates the sharing of social
50
51
52
53
54
55
56
57
58
59
60

1
2
3 312 information during adulthood [92]. Other studies have reported that social links are more likely
4
5 313 to form between people who share similar traits [93,94]. Group-level traits, such as stylistic
6
7 314 markers of group identity, might thus promote CCE by extending the size of the social network
8
9 315 through which cultural information can flow. Finally, group-level factors, such as the intensity of
10
11 316 group-level competition, might influence individuals' propensity to share information. Indeed,
12
13 317 experimental work shows that demonstrators set lower informational access costs (the costs that
14
15 318 potential learners must pay in order to access the demonstrators' information) when their groups
16
17 319 engage in between-group competition [95]. In these examples, population-level mechanisms
18
19 320 shaping cumulative cultural evolution stem from individuals' propensities to connect and share
20
21 321 information. A better understanding of these mechanisms will help clarify how individual-level
22
23 322 interactions produce population-level dynamics, resulting in the emergence of cumulative
24
25 323 cultural evolution.
26
27
28
29
30
31
32

33 325 **4. Factors contributing to the design of cultural traits**

34
35 326 **Why do cultural traits exhibit the features that they do?** As with research on culture and
36
37 327 cumulative cultural evolution, research on the **factors** responsible for **the design of cultural traits**
38
39 328 grew out of a focus on social learning. Researchers interested in explaining adaptive culture—
40
41 329 variants that allow individuals to better exploit their environments—began a fruitful tradition of
42
43 330 building theoretical models in which iterated social learning gives rise to emergent cultural
44
45 331 evolutionary processes [7,96]. These include models in which success- and prestige-biased
46
47 332 learning drives the selection of variants that promote prestige, health, and other indicators of
48
49 333 success, and in which conformity and other learning biases create enduring group-level
50
51 334 differences, allowing for selection among equilibria (cultural group selection). Of course,
52
53
54
55
56
57
58
59
60

1
2
3 335 researchers appreciate that other forces shape cultural form. Boyd and Richerson acknowledged
4
5 336 the role of content biases, while proponents of Cultural Attraction Theory have long advocated
6
7
8 337 that features of our cognitive architecture favor some variants over others [97,98]. Nevertheless,
9
10 338 we here propose that research on cultural form will benefit from **considering factors** beyond the
11
12 339 most commonly cited cultural evolutionary processes. We highlight the value of a multilevel
13
14
15 340 approach and the advantages of incorporating insights from fields such as economics and
16
17 341 political science, which have long aimed to explain the form of institutions specifically [99–101].
18
19
20 342

21 343 **4.1. Neural**

22 344 **Examining neural underpinnings can help explain why cultural traits exhibit the features that**
23
24 345 **they do in at least two ways. First, basic neural mechanics constrain the design of cultural traits.**
25
26 346 **For instance, Nieder [102] argues that neuronal mechanisms of estimating number, which are**
27
28 347 **products of a phylogenetic heritage, contribute to the relative ease of discriminating numbers of**
29
30 348 **low values (e.g., 1 and 2) over discriminating numbers of higher values (e.g., 783 and 784). This,**
31
32 349 **in turn, seems to shape numbering systems, biasing them to discriminate among low numbers but**
33
34 350 **not high ones (e.g., low-limit number systems such as “one”, “two”, “many”) [103].**

35
36
37
38 351 Studying neural **underpinnings** can also illuminate the structure of cognitive systems,
39
40 352 helping explain how our mental computational systems bias which representations we adopt. An
41
42 353 example is mind-body dualism. Researchers hypothesize that mind-body dualism, manifesting as
43
44 354 beliefs in souls, ghosts, zombies, and possession, results from a computational division between
45
46 355 processing mental information and processing physical information [104]. Although
47
48 356 psychological experiments can indirectly indicate whether information of the two kinds is
49
50
51
52
53 357 processed separately [105,106], another test involves examining where in the brain that

1
2
3 358 information is represented. In that vein, research now suggests a division between those brain
4
5 359 areas or networks specialized for social cognition and those specialized for physical cognition
6
7
8 360 [107]. Notably, the value here of **examining neural activity** is that it sheds light on the
9
10 361 functioning of **cognitive** mechanisms. **Studying a cognitive mechanism at the neural level** allows
11
12 362 us to better characterize the mechanism's behaviour and its effects on cultural **design** (**see a**
13
14
15 363 **similar approach in the field of neuroaesthetics: [108]**).

16 17 364 18 19 365 **4.2. Cognitive-behavioural**

20
21 366 Researchers have made major progress applying cognitive science to explain the design of
22
23 367 cultural traits. Many cognitive and social scientists, for instance, ask how reliably developing
24
25 368 features of human psychology predispose people to find certain variants more memorable,
26
27 369 believable, entertaining, attention-grabbing, or apparently useful [97,98,109–112]. Such
28
29 370 researchers have used attentional biases to explain portraits [113], epistemological mechanisms
30
31 371 to explain divination [114], mechanisms for representing agents to explain gods [115], suites of
32
33 372 automatic inferential systems to explain economic beliefs [116], the mechanics of emotion to
34
35 373 explain story [117–119], the psychology of outrage and paranoia to explain witchcraft [120], and
36
37 374 systems for identifying causality and conceptualizing humanness to explain shamanism [121].
38
39
40 375 Researchers have also found that people preferentially remember and transmit negative
41
42 376 information [122], threat-related information [123], elements eliciting disgust [124], and
43
44 377 information about social interactions and relationships [125,126], helping explain the form of
45
46 378 news [127,128], fiction [129,130] (although see [131]), urban legends [126], and online
47
48 379 misinformation [132].
49
50
51
52
53
54
55
56
57
58
59
60

1
2
3 380 As this diversity demonstrates, studying psychological systems is potent for
4
5
6 381 understanding how features of human cognition fashion culture. But scholars have overlooked at
7
8 382 least one additional set of capacities: the subjective psychological criteria involved in evaluations
9
10 383 [133,134]. Evaluation crucially contributes to the development of much of culture. People often
11
12 384 selectively copy and retain variants they evaluate as serving their goals, over time resulting in
13
14 385 increasingly compelling cultural traditions. Still, mechanisms for evaluating causal relationships
15
16 386 can be erroneous, resulting in ineffective practices. In a well-known example, scouts and
17
18 387 managers of baseball teams evaluated players on the basis of easy-to-observe traits, while
19
20 388 undervaluing traits that seemed out of a player's control (e.g., whether a pitcher threw bad
21
22 389 pitches at them) [135]. This, in turn, led to systematic inefficiencies in the design of teams.
23
24 390 Similarly, humans are endowed with cognitive mechanisms for evaluating whether some
25
26 391 technology produces a desired end. However, biases in these mechanisms predispose us to note
27
28 392 erroneous causal relationships, such that acting on one object (such as a voodoo doll) is thought
29
30 393 to affect the target it resembles (a rival) [136]. Magical practices seem to evolve because they are
31
32 394 subjectively evaluated as producing a desired end, even though they are ultimately ineffective
33
34 395 [137]. Characterizing the psychological mechanisms involved in evaluating efficacy will help
35
36 396 explain the evolution of functional complexity, systematic inefficiencies, and elaborate but
37
38 397 ineffective technologies.
39
40
41
42
43
44
45
46

47 399 4.3. Populational

48
49 400 There are many population-level properties aside from population size or structure that shape
50
51 401 culture yet remain underexplored in the cultural evolution literature. Perhaps the two most
52
53 402 important are power and competition.
54
55
56
57
58
59
60

1
2
3 403 Power is the capacity of a party to change other parties' behaviour [138]. There are many
4
5 404 ways in which distributions of power can shape culture, but the most important is when
6
7
8 405 individuals compete to institute and maintain self-serving rules [139,140]. The form of these
9
10 406 rules is frequently determined by the parties' relative abilities to enforce their preferences.
11
12 407 Distributions of power explain, among many other outcomes, food taboos in small-scale
13
14 408 societies, rules for how children should treat fathers, institutions of redistribution throughout
15
16
17 409 Polynesia, and the political institutions of colonial powers and their local inheritors around the
18
19 410 world [139,141,142]. Of course, just as distributions of power shape institutions, institutions can
20
21 411 shape distributions of power [142]. Still, power leaves such defining marks on institutions and
22
23 412 practices that it has become the primary lens through which scholars in fields such as Marxist
24
25 413 and feminist anthropology analyze culture. Although cultural evolutionary scholars have begun
26
27 414 to consider power when explaining practices such as religion [143] and human sacrifice [144],
28
29 415 and although some have considered it as an *outcome* of interest [145], it should be considered
30
31 416 when explaining any tradition that involves conflicts of interest among competing parties.
32
33

34
35 417 Another population-level characteristic that partly determines cultural form is the
36
37 418 intensity of competition, whether between individuals or groups. Competition determines how
38
39 419 much competing parties invest in services or signals, driving variation in the elaborateness of
40
41 420 culture. In markets, higher competition among service providers drives up the quality of services,
42
43 421 transforming products including cars, supermarkets, and even the trance performances of
44
45 422 shamans [121,146,147]. Increased status competition, which may be driven by rising inequality,
46
47 423 is correlated with higher investments in signaling, presumably as individuals want to
48
49 424 discriminate themselves from competitors [148]. This manifests in increasingly showy signs of
50
51
52
53
54
55
56
57
58
59
60

1
2
3 425 wealth and status, transforming practices ranging from potlatches [149] to female adornment on
4
5
6 426 social media [148].

7
8 427 Population-level mechanisms aside from power and competition shape culture, as well.

9
10 428 One example is what researchers call “common knowledge”—roughly, recursive, shared beliefs

11
12 429 that enable coordination [150]. Without channels facilitating widespread coordination,

13
14
15 430 populations often sustain suboptimal practices, even when the majority of individuals prefer to

16
17 431 change them. Social scientists posit that such “pluralistic ignorance” has maintained suboptimal

18
19 432 norms and institutions including drinking behaviour on US college campuses [151] and restricted

20
21 433 female labor force participation in Saudi Arabia [152].

22
23
24 434

25 26 435 **5. Conclusion**

27
28
29 436 Explanations for the existence, accumulation, and design of cultural traditions benefit from a

30
31 437 perspective that is both broad and deep, that both considers interactions among a web of factors

32
33 438 and clarifies their contribution by probing their deeper workings. Not only does such a

34
35 439 perspective reveal that a more diverse set of factors shapes culture, but it also suggests that

36
37 440 explanations currently regarded as alternatives are, in fact, complimentary.

38
39
40 441 We reviewed potential factors at the neural, cognitive-behavioural, and populational

41
42 442 levels. But other levels are relevant too, including the genetic, epigenetic, and inter-populational

43
44 443 levels. Moreover, cultural evolution can be influenced and constrained by physiology and

45
46 444 existing cultural traditions, as well as the biotic and abiotic environment. For instance, explaining

47
48 445 cumulative culture may require not only specifying behavioural differences but anatomical ones,

49
50 446 as well. Since Darwin, theorists have hypothesized that unique features of human anatomy,

51
52 447 especially bipedalism, were key for setting the evolutionary stage for our greater reliance on

1
2
3 448 tools and cultural knowledge [153]; cultural evolutionists may benefit from considering such
4
5 449 anatomical pre-adaptations. Similarly, explaining a cultural artifact like a spear demands
6
7
8 450 considering not only the transmission processes allowing manufacturing knowledge to evolve,
9
10 451 but also the anatomy of the primate hand, existing tools and techniques for procuring spear-
11
12 452 materials, and the animals spear-makers intend to hunt.

13
14
15 453 We have proposed many directions of future research in this paper; among the most
16
17 454 important is the development of studies on culture in non-human animals. The lack of data on
18
19 455 culture in animals likely stems from researchers only recently expanding investigations beyond
20
21 456 charismatic and supposedly intelligent vertebrates. After all, we now have surprising evidence
22
23 457 that even insects may have culture [24,38], suggesting that culture is phylogenetically ancient,
24
25
26 458 present among ancestors that lived hundreds of millions of years ago. This constitutes a
27
28 459 stimulating challenge for the study of the foundations of cultural evolution.
29
30

31 460

32 33 461 **Acknowledgements**

34
35
36 462 M.S. and M.D. acknowledge IAST funding from ANR under grant ANR-17-EURE-0010
37
38 463 (Investissements d'Avenir program). C.C. was supported by a European Research Council
39
40 464 (ERC) Consolidator Grant (No. 648841 RATCHETCOG). T.S.P. was supported by the European
41
42 465 Research Council, under the European Union's Seventh Framework Programme (FP7/2007-
43
44 466 2013)/ERC grant agreement no. 609819 (Somics project). M.D. received funding from the
45
46 467 European Union's Horizon 2020 Research and Innovation Programme (under Marie
47
48 468 Sklodowska-Curie grant agreement number 748310).
49
50

51
52 469

53
54 470

471 **References**

- 472 1. Mesoudi A. 2011 *Cultural Evolution: How Darwinian Theory Can Explain Human*
473 *Culture and Synthesize the Social Sciences*. University of Chicago Press.
- 474 2. Richerson PJ, Boyd R. 2008 *Not by genes alone: How culture transformed human*
475 *evolution*. Chicago: University of Chicago Press.
- 476 3. Rendell L, Whitehead H. 2001 Culture in whales and dolphins. *Behav. Brain Sci.* **24**, 309–
477 382. (doi:10.1016/B978-0-12-373553-9.00068-7)
- 478 4. Tomasello M, Kruger AC, Ratner HH. 1993 Cultural learning. *Behav. Brain Sci.* **16**, 495–
479 511.
- 480 5. Whiten A, McGuigan N, Marshall-Pescini S, Hopper LM. 2009 Emulation, imitation,
481 over-imitation and the scope of culture for child and chimpanzee. *Philos. Trans. R. Soc.*
482 *Lond. B. Biol. Sci.* **364**, 2417–28. (doi:10.1098/rstb.2009.0069)
- 483 6. Whiten A. 2017 Social learning and culture in child and chimpanzee. *Annu. Rev. Psychol.*
484 **68**, 129–154. (doi:10.1146/annurev-psych-010416-044108)
- 485 7. Boyd R, Richerson PJ. 1985 *Culture and the evolutionary process*. Chicago: University of
486 Chicago Press.
- 487 8. Cavalli-Sforza LL, Feldman MW. 1981 *Cultural transmission and evolution: A*
488 *quantitative approach*. Princeton University Press.
- 489 9. Kendal RL, Boogert NJ, Rendell L, Laland KN, Webster M, Jones PL. 2018 Social
490 Learning Strategies: Bridge-Building between Fields. *Trends Cogn. Sci.* **22**, 651–665.
491 (doi:10.1016/j.tics.2018.04.003)
- 492 10. Henrich J. 2015 *The secret of our success: How culture is driving human evolution,*
493 *domesticating our species, and making us smarter*. Princeton, NJ: Princeton University

1
2
3 494 Press.

4
5 495 11. Heyes C. 2016 Blackboxing: Social learning strategies and cultural evolution. *Philos.*

6
7
8 496 *Trans. R. Soc. B Biol. Sci.* **371**. (doi:10.1098/rstb.2015.0369)

9
10 497 12. Heyes C. 2012 What's social about social learning? *J. Comp. Psychol.* **126**, 193–202.

11
12
13 498 (doi:10.1037/a0025180)

14
15 499 13. Rosati AG. 2017 Chimpanzee cognition and the roots of the human mind. In *Chimpanzees*

16
17 500 *and human evolution*, pp. 703–745. Harvard University Press.

18
19 501 14. Laland K, Evans C. 2017 Animal social learning, culture, and tradition. In *APA Handbook*

20
21
22 502 *of Comparative Psychology*, pp. 441–460.

23
24 503 15. Whiten A, Hinde R a, Laland KN, Stringer CB. 2011 Culture evolves. *Philos. Trans. R.*

25
26 504 *Soc. Lond. B. Biol. Sci.* **366**, 938–48. (doi:10.1098/rstb.2010.0372)

27
28 505 16. Dölen G, Darvishzadeh A, Huang KW, Malenka RC. 2013 Social reward requires

29
30
31 506 coordinated activity of nucleus accumbens oxytocin and serotonin. *Nature* **501**, 179–184.

32
33 507 (doi:10.1038/nature12518)

34
35 508 17. Klein JT, Platt ML. 2013 Social information signaling by neurons in primate striatum.

36
37
38 509 *Curr. Biol.* **23**, 691–696. (doi:10.1016/j.cub.2013.03.022)

39
40 510 18. Noritake A, Ninomiya T, Isoda M. 2018 Social reward monitoring and valuation in the

41
42 511 macaque brain. *Nat. Neurosci.* **21**, 1452–1462. (doi:10.1038/s41593-018-0229-7)

43
44 512 19. Olsson A, Knapska E, Lindström B. 2020 The neural and computational systems of social

45
46
47 513 learning. *Nat. Rev. Neurosci.* **21**, 197–212. (doi:10.1038/s41583-020-0276-4)

48
49 514 20. Monier M, Nöbel S, Danchin E, Isabel G. 2019 Dopamine and serotonin are both required

50
51 515 for mate-copying in *Drosophila melanogaster*. *Front. Behav. Neurosci.* **12**, 1–5.

52
53
54 516 (doi:10.3389/fnbeh.2018.00334)

- 1
2
3 517 21. Kacsoh BZ, Bozler J, Ramaswami M, Bosco G. 2015 Social communication of predator-
4 induced changes in *Drosophila* behavior and germ line physiology. *Elife* **4**, e07423.
5
6 518
7
8 519 (doi:10.7554/eLife.07423)
9
10 520 22. Carcea I, Froemke RC. 2019 Biological mechanisms for observational learning. *Curr.*
11
12 521 *Opin. Neurobiol.* **54**, 178–185. (doi:10.1016/j.conb.2018.11.008)
13
14 522 23. Lindström B, Haaker J, Olsson A. 2018 A common neural network differentially mediates
15 direct and social fear learning. *Neuroimage* **167**, 121–129.
16
17 523
18
19 524 (doi:10.1016/j.neuroimage.2017.11.039)
20
21 525 24. Danchin É *et al.* 2019 Cultural flies: Conformist social learning in fruitflies predicts long-
22 lasting mate-choice traditions. *Science* (80-.). **362**, 1025–1030.
23
24 526
25
26 527 25. Fischer A. 2014 Epigenetic memory: The Lamarckian brain. *EMBO J.* **33**, 945–967.
27
28 528 (doi:10.1002/embj.201387637)
29
30 529 26. Campanelli SE, da Rocha JM, Oliveira JIN. 2019 Molecular and epigenetic mechanisms
31 associated with extinction of fear memory: A systematic review. *eNeurobiología* **10**.
32
33 530
34
35 531 27. Miller CA, Sweatt JD. 2007 Covalent modification of DNA regulates memory formation.
36
37 532 *Neuron* **53**, 857–869. (doi:10.1016/j.neuron.2007.02.022)
38
39 533 28. Lind J, Ghirlanda S, Enquist M. 2019 Social learning through associative processes: A
40 computational theory. *R. Soc. Open Sci.* **6**. (doi:10.1098/rsos.181777)
41
42 534
43
44 535 29. Worden BD, Papaj DR. 2005 Flower choice copying in bumblebees. *Biol. Lett.* **1**, 504–
45
46 536 507. (doi:10.1098/rsbl.2005.0368)
47
48 537 30. Leadbeater E, Dawson EH. 2017 A social insect perspective on the evolution of social
49 learning mechanisms. *Proc. Natl. Acad. Sci. U. S. A.* **114**, 7838–7845.
50
51 538
52
53 539 (doi:10.1073/pnas.1620744114)
54
55
56
57
58
59
60

- 1
2
3 540 31. Dawson EH, Avarguès-Weber A, Chittka L, Leadbeater E. 2013 Learning by observation
4 emerges from simple associations in an insect model. *Curr. Biol.* **23**, 727–730.
5
6 541
7
8 542 (doi:10.1016/j.cub.2013.03.035)
9
10 543 32. Dunlap AS, Nielsen ME, Dornhaus A, Papaj DR. 2016 Foraging Bumble Bees Weigh the
11 Reliability of Personal and Social Information. *Curr. Biol.* **26**, 1195–1199.
12
13 544
14
15 545 (doi:10.1016/j.cub.2016.03.009)
16
17 546 33. Dawson EH, Chittka L. 2012 Conspecific and heterospecific information use in
18 bumblebees. *PLoS One* **7**, 1–6. (doi:10.1371/journal.pone.0031444)
19
20 547
21
22 548 34. Fogarty L, Creanza N, Feldman MW. 2015 Cultural Evolutionary Perspectives on
23 Creativity and Human Innovation. *Trends Ecol. Evol.* **30**, 736–754.
24
25 549
26
27 550 (doi:10.1016/j.tree.2015.10.004)
28
29 551 35. Reader SM, Laland KN, editors. 2003 *Animal innovation*. Oxford University Press.
30
31 552 36. Dean LG, Vale GL, Laland KN, Flynn E, Kendal RL. 2014 Human cumulative culture: A
32 comparative perspective. *Biol. Rev.* **89**, 284–301. (doi:10.1111/brv.12053)
33
34 553
35
36 554 37. Enquist M, Ghirlanda S, Jarrick A, Wachtmeister CA. 2008 Why does human culture
37 increase exponentially? *Theor. Popul. Biol.* **74**, 46–55. (doi:10.1016/j.tpb.2008.04.007)
38
39 555
40 556 38. Alem S, Perry CJ, Zhu X, Loukola OJ, Ingraham T, Søvik E, Chittka L. 2016 Associative
41 Mechanisms Allow for Social Learning and Cultural Transmission of String Pulling in an
42
43 557
44
45 558 Insect. *PLoS Biol.* **14**, 1–28. (doi:10.1371/journal.pbio.1002564)
46
47 559 39. Griffin AS, Guez D. 2014 Innovation and problem solving: A review of common
48 mechanisms. *Behav. Processes* **109**, 121–134. (doi:10.1016/j.beproc.2014.08.027)
49
50 560
51
52 561 40. Griffin AS, Diquelou M, Perea M. 2014 Innovative problem solving in birds: A key role
53 of motor diversity. *Anim. Behav.* **92**, 221–227. (doi:10.1016/j.anbehav.2014.04.009)
54
55 562
56
57
58
59
60

- 1
2
3 563 41. Day RL, Coe RL, Kendal JR, Laland KN. 2003 Neophilia, innovation and social learning:
4
5 564 A study of intergeneric differences in callitrichid monkeys. *Anim. Behav.* **65**, 559–571.
6
7
8 565 (doi:10.1006/anbe.2003.2074)
9
10 566 42. Reader SM, Morand-Ferron J, Flynn E. 2016 Animal and human innovation: Novel
11
12 567 problems and novel solutions. *Philos. Trans. R. Soc. B Biol. Sci.* **371**.
13
14 568 (doi:10.1098/rstb.2015.0182)
15
16
17 569 43. Lefebvre L, Whittle P, Lascaris E, Finkelstein A. 1997 Feeding innovations and forebrain
18
19 570 size in birds. *Anim. Behavior* , 549–560.
20
21
22 571 44. Reader SM, Laland KN. 2002 Social intelligence, innovation, and enhanced brain size in
23
24 572 primates. *Proc. Natl. Acad. Sci. U. S. A.* **99**, 4436–4441. (doi:10.1073/pnas.062041299)
25
26 573 45. Fiorito G, Scotto P. 1992 Observational learning in *Octopus vulgaris*. *Science (80-.)*. **256**,
27
28 574 545–547.
29
30
31 575 46. Wilkinson A, Kuenstner K, Mueller J, Huber L. 2010 Social learning in a non-social
32
33 576 reptile (*Geochelone carbonaria*). *Biol. Lett.* **6**, 614–616. (doi:10.1098/rsbl.2010.0092)
34
35
36 577 47. Van Schaik CP, Deaner RO, Merrill MY. 1999 The conditions for tool use in primates:
37
38 578 Implications for the evolution of material culture. *J. Hum. Evol.* **36**, 719–741.
39
40 579 (doi:10.1006/jhev.1999.0304)
41
42 580 48. Flynn E, Whiten A. 2010 Studying children’s social learning experimentally ‘in the wild’.
43
44 581 *Learn. Behav.* **38**, 284–296. (doi:10.3758/LB.38.3.284)
45
46
47 582 49. Derex M, Beugin MP, Godelle B, Raymond M. 2013 Experimental evidence for the
48
49 583 influence of group size on cultural complexity. *Nature* **503**, 389–391.
50
51 584 (doi:10.1038/nature12774)
52
53
54 585 50. Enquist M, Strimling P, Eriksson K, Laland K, Sjostrand J. 2010 One cultural parent
55
56
57
58
59
60

- 1
2
3 586 makes no culture. *Anim. Behav.* **79**, 1353–1362. (doi:10.1016/j.anbehav.2010.03.009)
4
5
6 587 51. Whiten A. 2019 Cultural evolution in animals. *Annu. Rev. Ecol. Evol. Syst.* **50**, 27–48.
7
8 588 (doi:10.1146/annurev-ecolsys-110218-025040)
9
10 589 52. Mesoudi A, Thornton A. 2018 What is cumulative cultural evolution? *Proc. R. Soc. B-*
11
12 *Biological Sci.* **285**, 20180712.
13 590
14
15 591 53. Claidière N, Smith K, Kirby S, Fagot J. 2014 Cultural evolution of systematically
16
17 592 structured behaviour in a non-human primate. *Proc. R. Soc. B Biol. Sci.* **281**, 1–9.
18
19 593 (doi:10.1098/rspb.2014.1541)
20
21 594 54. Sasaki T, Biro D. 2017 Cumulative culture can emerge from collective intelligence in
22
23 595 animal groups. *Nat. Commun.* **8**, 1–6. (doi:10.1038/ncomms15049)
24
25
26 596 55. Jesmer BR *et al.* 2018 Is ungulate migration culturally transmitted? Evidence of social
27
28 597 learning from translocated animals. *Science (80-.)*. **361**, 1023–1025.
29
30 598 (doi:10.1126/science.aat0985)
31
32
33 599 56. Tennie C, Call J, Tomasello M. 2009 Ratcheting up the ratchet: On the evolution of
34
35 600 cumulative culture. *Philos. Trans. R. Soc. B Biol. Sci.* **364**, 2405–2415.
36
37 601 (doi:10.1098/rstb.2009.0052)
38
39
40 602 57. Vale GL, Flynn EG, Kendal RL. 2012 Cumulative culture and future thinking: Is mental
41
42 603 time travel a prerequisite to cumulative cultural evolution? *Learn. Motiv.* **43**, 220–230.
43
44 604 (doi:10.1016/j.lmot.2012.05.010)
45
46
47 605 58. Shea N, Boldt A, Bang D, Yeung N, Heyes C, Frith CD. 2014 Supra-personal cognitive
48
49 606 control and metacognition. *Trends Cogn. Sci.* **18**, 186–193.
50
51 607 (doi:10.1016/j.tics.2014.01.006)
52
53
54 608 59. Dean LG, Kendal RL, Schapiro SJ, Thierry B, Laland KN. 2012 Identification of the
55
56
57
58
59
60

- 1
2
3 609 social and cognitive processes underlying human cumulative culture. *Science* (80-.). **335**,
4
5 610 1114–1118. (doi:10.1126/science.1213969)
6
7
8 611 60. Lewis HM, Laland KN. 2012 Transmission fidelity is the key to the build-up of
9
10 612 cumulative culture. *Philos. Trans. R. Soc. B Biol. Sci.* **367**, 2171–2180.
11
12 613 (doi:10.1098/rstb.2012.0119)
13
14
15 614 61. Muthukrishna M, Shulman BW, Vasilescu V, Henrich J. 2014 Sociality influences
16
17 615 cultural complexity. *Proc. R. Soc. B* **281**, 20132511.
18
19 616 62. Stout D, Hecht EE. 2017 Evolutionary neuroscience of cumulative culture. *Proc. Natl.*
20
21 617 *Acad. Sci. U. S. A.* **114**, 7861–7868. (doi:10.1073/pnas.1620738114)
22
23
24 618 63. Davis SJ, Vale GL, Schapiro SJ, Lambeth SP, Whiten A. 2016 Foundations of cumulative
25
26 619 culture in apes: Improved foraging efficiency through relinquishing and combining
27
28 620 witnessed behaviours in chimpanzees (*Pan troglodytes*). *Sci. Rep.* **6**, 1–12.
29
30 621 (doi:10.1038/srep35953)
31
32
33 622 64. Pryluk R, Kfir Y, Gelbard-Sagiv H, Fried I, Paz R. 2019 A Tradeoff in the Neural Code
34
35 623 across Regions and Species. *Cell* **176**, 597-609.e18. (doi:10.1016/j.cell.2018.12.032)
36
37
38 624 65. Herculano-Houzel S. 2016 *The human advantage: A new understanding of how our brain*
39
40 625 *became remarkable*. MIT Press.
41
42 626 66. Kaas JH, Herculano-Houzel S. 2017 What Makes the Human Brain Special: Key Features
43
44 627 of Brain and Neocortex. In *The physics of the mind and brain disorders* (eds I Opris, MF
45
46 628 Casanova), pp. 3–22. Springer International Publishing. (doi:10.1007/978-3-319-29674-
47
48 629 6_1)
49
50
51 630 67. Roberts WA. 2002 Are animals stuck in time? *Psychol. Bull.* **128**, 473–489.
52
53 631 (doi:10.1037/0033-2909.128.3.473)
54
55
56
57
58
59
60

- 1
2
3 632 68. Stout D. 2005 The social and cultural context of stone-knapping skill acquisition. In *Stone*
4
5 633 *knapping: the necessary conditions for a uniquely hominin behaviour* (eds B Brill, V
6
7 634 Roux), pp. 331–340. McDonald Institute for Archaeological Research.
- 8
9
10 635 69. Walker R, Hill K, Kaplan H, McMillan G. 2002 Age-dependency in hunting ability
11
12 636 among the Ache of eastern Paraguay. *J. Hum. Evol.* **42**, 639–657.
13
14 637 (doi:10.1006/jhev.2001.0541)
- 15
16
17 638 70. Van Leeuwen EJC, Call J, Haun DBM. 2014 Human children rely more on social
18
19 639 information than chimpanzees do. *Biol. Lett.* **10**. (doi:10.1098/rsbl.2014.0487)
- 20
21 640 71. Tennie C, Call J, Tomasello M. 2010 Evidence for emulation in chimpanzees in social
22
23 641 settings using the floating peanut task. *PLoS One* **5**. (doi:10.1371/journal.pone.0010544)
- 24
25
26 642 72. Nielsen M. 2013 Young children’s imitative and innovative behaviour on the floating
27
28 643 object task. *Infant Child Dev.* **22**, 44–52.
- 29
30
31 644 73. Beck SR, Apperly IA, Chappell J, Guthrie C, Cutting N. 2011 Making tools isn’t child’s
32
33 645 play. *Cognition* **119**, 301–306. (doi:10.1016/j.cognition.2011.01.003)
- 34
35
36 646 74. Dunstone J, Caldwell CA. 2018 Cumulative culture and explicit metacognition: A review
37
38 647 of theories, evidence and key predictions. *Palgrave Commun.* **4**, 1–11.
39
40 648 (doi:10.1057/s41599-018-0200-y)
- 41
42
43 649 75. Scott-Phillips TC. 2015 Meaning in animal and human communication. *Anim. Cogn.* **18**,
44
45 650 801–805. (doi:10.1007/s10071-015-0845-5)
- 46
47 651 76. Scott-Phillips T. 2015 *Speaking our minds*. Palgrave Macmillan.
- 48
49 652 77. Csibra G. 2009 Natural pedagogy. *Trends Cogn. Sci.* **13**, 148–153.
50
51 653 (doi:10.1016/j.tics.2009.01.005)
- 52
53
54 654 78. Sperber D, Wilson D. 2002 Pragmatics, modularity and mind-reading. *Mind Lang.* **17**, 3–

- 1
2
3 655 23.
4
5
6 656 79. Senju A, Csibra G. 2008 Gaze Following in Human Infants Depends on Communicative
7
8 657 Signals. *Curr. Biol.* **18**, 668–671. (doi:10.1016/j.cub.2008.03.059)
9
10 658 80. Behne T, Carpenter M, Tomasello M. 2005 One-year-olds comprehend the
11
12 659 communicative intentions behind gestures in a hiding game. *Dev. Sci.* **8**, 492–499.
13
14 660 (doi:10.1111/j.1467-7687.2005.00440.x)
15
16
17 661 81. Grosse G, Moll H, Tomasello M. 2010 21-Month-olds understand the cooperative logic of
18
19 662 requests. *J. Pragmat.* **42**, 3377–3383. (doi:10.1016/j.pragma.2010.05.005)
20
21
22 663 82. Schulze C, Tomasello M. 2015 18-month-olds comprehend indirect communicative acts.
23
24 664 *Cognition* **136**, 91–98. (doi:10.1016/j.cognition.2014.11.036)
25
26 665 83. Tauzin T, Gergely G. 2018 Communicative mind-reading in preverbal infants. *Sci. Rep.* **8**.
27
28 666 (doi:10.1038/s41598-018-27804-4)
29
30
31 667 84. Grosse G, Behne T, Carpenter M, Tomasello M. 2014 Infants communicate in order to be
32
33 668 understood. *Dev. Psychol.* **46**, 1710–1722. (doi:10.1037/a0020727)
34
35
36 669 85. Dingemans M *et al.* 2015 Universal principles in the repair of communication problems.
37
38 670 *PLoS One* **10**, 1–15. (doi:10.1371/journal.pone.0136100)
39
40 671 86. Morin O. 2013 What does communication contribute to cultural transmission? *Soc.*
41
42 672 *Anthropol.* **21**, 230–235. (doi:10.1111/1469-8676.12014)
43
44
45 673 87. Henrich J. 2004 Demography and cultural evolution: How adaptive cultural processes can
46
47 674 produce maladaptive losses - the Tasmania case. *Am. Antiq.* **69**, 197–214.
48
49 675 88. Derex M, Boyd R. 2016 Partial connectivity increases cultural accumulation within
50
51 676 groups. *Proc. Natl. Acad. Sci.* , 201518798. (doi:10.1073/pnas.1518798113)
52
53
54 677 89. Creanza N, Kolodny O, Feldman MW. 2017 Greater than the sum of its parts? Modelling
55
56
57
58
59
60

- 1
2
3 678 population contact and interaction of cultural repertoires. *J. R. Soc. Interface* **14**.
4
5
6 679 (doi:10.1098/rsif.2017.0171)
7
8 680 90. Derex M, Mesoudi A. 2020 Cumulative cultural evolution within evolving population
9
10 681 structures. *Trends Cogn. Sci.* **24**, 654–667. (doi:10.1016/j.tics.2020.04.005)
11
12 682 91. Henrich J. 2009 The Evolution of Innovation-Enhancing Institutions. In *Innovation in*
13
14 683 *Cultural Systems: Contributions in Evolution Anthropology* (eds SJ Shennan, MJ O’
15
16 684 Brien), Cambridge: MIT Press.
17
18
19 685 92. Migliano AB *et al.* 2017 Characterization of hunter-gatherer networks and implications
20
21 686 for cumulative culture. *Nat. Hum. Behav.* **1**, 1–6. (doi:10.1038/s41562-016-0043)
22
23
24 687 93. Centola D, Gonzalez-Avella JC, Eguíluz VM, San Miguel M. 2007 Homophily, cultural
25
26 688 drift, and the co-evolution of cultural groups. *J. Conflict Resolut.* **51**, 905–929.
27
28 689 (doi:10.1177/0022002707307632)
29
30
31 690 94. Apicella CL, Marlowe FW, Fowler JH, Christakis NA. 2012 Social networks and
32
33 691 cooperation in hunter-gatherers. *Nature* **481**, 497–501. (doi:10.1038/nature10736)
34
35
36 692 95. Derex M, Godelle B, Raymond M. 2014 How does competition affect the transmission of
37
38 693 information? *Evol. Hum. Behav.* **35**, 89–95. (doi:10.1016/j.evolhumbehav.2013.11.001)
39
40 694 96. Henrich J. 2004 Cultural group selection, coevolutionary processes and large-scale
41
42 695 cooperation. *J. Econ. Behav. Organ.* **53**, 3–35. (doi:10.1016/S0167-2681(03)00094-5)
43
44
45 696 97. Sperber D. 1996 *Explaining culture: A naturalistic approach*. Oxford, UK: Blackwell
46
47 697 Publishers Ltd.
48
49 698 98. Morin O. 2016 *How traditions live and die*. New York: Oxford University Press.
50
51 699 99. Knight J. 1992 *Institutions and social conflict*. Cambridge, UK: Cambridge University
52
53 700 Press.
54
55
56
57
58
59
60

- 1
2
3 701 100. North DC. 1990 *Institutions, institutional change, and economic performance*. New York,
4
5 702 NY: Cambridge University Press.
6
7
8 703 101. Ostrom E. 1990 *Governing the commons: The evolution of institutions for collective*
9
10 704 *action*. Cambridge, UK: Cambridge University Press.
11
12 705 102. Nieder A. 2020 Neural constraints on human number concepts. *Curr. Opin. Neurobiol.* **60**,
13
14 706 28–36. (doi:10.1016/j.conb.2019.10.003)
15
16
17 707 103. Epps P, Bowern C, Hansen CA, Hill JH, Zentz J. 2013 On numeral complexity in hunter-
18
19 708 gatherer languages. *Linguist. Typology* **16**. (doi:10.1515/lity-2012-0002)
20
21 709 104. Bloom P. 2004 *Descartes' baby: How the science of child development explains what*
22
23 710 *makes us human*. New York, NY: Basic Books.
24
25
26 711 105. Kuhlmeier VA, Bloom P, Wynn K. 2004 Do 5-month-old infants see humans as material
27
28 712 objects? *Cognition* **94**, 95–103. (doi:10.1016/j.cognition.2004.02.007)
29
30
31 713 106. Chudek M, McNamara R, Birch S, Bloom P, Henrich J. 2013 Developmental and cross-
32
33 714 cultural evidence for intuitive dualism. *Psychol. Sci.*
34
35 715 107. Jack AI. 2014 A scientific case for conceptual dualism: The problem of consciousness and
36
37 716 the opposing domains hypothesis. In *Oxford Studies in Experimental Philosophy (Vol. 1)*,
38
39 717 108. Pearce MT, Zaidel DW, Vartanian O, Skov M, Leder H, Chatterjee A, Nadal M. 2016
40
41 718 Neuroaesthetics: The Cognitive Neuroscience of Aesthetic Experience. *Perspect. Psychol.*
42
43 719 *Sci.* **11**, 265–279. (doi:10.1177/1745691615621274)
44
45
46 720 109. Sperber D, Hirschfeld LA. 2004 The cognitive foundations of cultural stability and
47
48 721 diversity. *Trends Cogn. Sci.* **8**, 40–46. (doi:10.1016/j.tics.2003.11.002)
49
50
51 722 110. Boyer P. 2001 *Religion explained: The evolutionary origins of religious thought*. New
52
53 723 York: Basic Books.
54
55
56
57
58
59
60

- 1
2
3 724 111. Acerbi A. 2020 *Cultural evolution in the digital age*. Oxford University Press.
4
5 725 112. Miton H, Claidière N, Mercier H. 2015 Universal cognitive mechanisms explain the
6
7
8 726 cultural success of bloodletting. *Evol. Hum. Behav.* **36**, 303–312.
9
10 727 (doi:10.1016/j.evolhumbehav.2015.01.003)
11
12 728 113. Morin O. 2013 How portraits turned their eyes upon us: Visual preferences and
13
14
15 729 demographic change in cultural evolution. *Evol. Hum. Behav.* **34**, 222–229.
16
17 730 (doi:10.1016/j.evolhumbehav.2013.01.004)
18
19 731 114. Boyer P. 2020 Why divination? Evolved psychology and strategic interaction in the
20
21
22 732 production of truth. *Curr. Anthropol.* **61**, 100–123. (doi:10.1086/706879)
23
24 733 115. Barrett JL. 2000 Exploring the natural foundations of religion. *Trends Cogn. Sci.* **4**, 29–
25
26 734 34.
27
28 735 116. Boyer P, Petersen MB. 2018 Folk-Economic Beliefs: An Evolutionary Cognitive Model.
29
30
31 736 *Behav. Brain Sci.* , e158. (doi:10.1017/S0140525X17001960)
32
33 737 117. Singh M. 2019 The sympathetic plot, its psychological origins, and implications for the
34
35
36 738 evolution of fiction. *PsyArxiv* , 1–28. (doi:10.31219/osf.io/p8q7a)
37
38 739 118. Tan ES. 1996 *Emotion and the structure of narrative film: Film as an emotion machine*.
39
40 740 Mahwah, NJ: Lawrence Erlbaum Associates.
41
42 741 119. Hogan PC. 2003 *The mind and its stories: Narrative universals and human emotion*. New
43
44
45 742 York: Cambridge University Press.
46
47 743 120. Singh M. In press. Magic, explanations, and evil: On the origins and design of witches and
48
49
50 744 sorcerers. *Curr. Anthropol.*
51
52 745 121. Singh M. 2018 The cultural evolution of shamanism. *Behav. Brain Sci.* **41**, e66.
53
54 746 (doi:10.1017/S0140525X17001893)
55
56
57
58
59
60

- 1
2
3 747 122. Bebbington K, MacLeod C, Ellison TM, Fay N. 2017 The sky is falling: evidence of a
4
5 748 negativity bias in the social transmission of information. *Evol. Hum. Behav.* **38**, 92–101.
6
7
8 749 (doi:10.1016/j.evolhumbehav.2016.07.004)
9
10 750 123. Blaine T, Boyer P. 2018 Origins of sinister rumors: A preference for threat-related
11
12 751 material in the supply and demand of information. *Evol. Hum. Behav.* **39**, 67–75.
13
14 752 (doi:10.1016/j.evolhumbehav.2017.10.001)
15
16
17 753 124. Eriksson K, Coultas JC. 2014 Corpses, maggots, poodles and rats: Emotional selection
18
19 754 operating in three phases of cultural transmission of urban legends. *J. Cogn. Cult.* **14**, 1–
20
21 755 26. (doi:10.1163/15685373-12342107)
22
23
24 756 125. Mesoudi A, Whiten A, Dunbar R. 2006 A bias for social information in human cultural
25
26 757 transmission. *Br. J. Psychol.* **97**, 405–431. (doi:10.1348/000712605X85871)
27
28
29 758 126. Stubbersfield JM, Tehrani JJ, Flynn EG. 2015 Serial killers, spiders and cybersex: Social
30
31 759 and survival information bias in the transmission of urban legends. *Br. J. Psychol.* **106**,
32
33 760 288–307. (doi:10.1111/bjop.12073)
34
35
36 761 127. Hester JB, Gibson R. 2003 The economy and second-level agenda setting: A time-series
37
38 762 analysis of econom... *Journal. Mass Commun. Q.* **80**.
39
40
41 763 128. Niven D. 2001 Bias in the news: Partisanship and negativity in media coverage of
42
43 764 presidents George Bush and Bill Clinton. *Harvard Int. J. Press.* **6**, 31–46.
44
45 765 129. Morin O, Acerbi A. 2017 Birth of the cool: a two-centuries decline in emotional
46
47 766 expression in Anglophone fiction. *Cogn. Emot.* **31**, 1663–1675.
48
49 767 (doi:10.1080/02699931.2016.1260528)
50
51
52 768 130. Clasen M. 2017 *Why horror seduces*. Oxford University Press.
53
54 769 131. Morin O, Acerbi A, Sobchuk O. 2019 Why people die in novels: testing the ordeal
55
56
57
58
59
60

- 1
2
3 770 simulation hypothesis. *Palgrave Commun.* **5**, 1–10. (doi:10.1057/s41599-019-0267-0)
4
5
6 771 132. Acerbi A. 2019 Cognitive attraction and online misinformation. *Palgrave Commun.* **5**, 1–
7
8 772 7. (doi:10.1057/s41599-019-0224-y)
9
10 773 133. Rogers E. 2003 *The diffusion of innovations*. New York: The Free Press.
11
12 774 134. Singh M. 2020 Subjective selection and the evolution of complex culture. *PsyArxiv*
13
14 775 (doi:10.31234/osf.io/4t2ud)
15
16
17 776 135. Thaler R, Sunstein C. 2004 Market efficiency and rationality: The peculiar case of
18
19 777 baseball. *Mich. Law Rev.* **102**, 1390–1403. (doi:10.2307/4141950)
20
21
22 778 136. Nemeroff C, Rozin P. 2000 The makings of the magical mind: The nature and function of
23
24 779 sympathetic magical thinking. In *Imagining the impossible: Magical, scientific, and*
25
26 780 *religious thinking in children*, pp. 1–34. (doi:10.1017/CBO9780511571381.002)
27
28
29 781 137. Vyse S. 2014 *Believing in magic: The psychology of superstition*. Oxford and New York:
30
31 782 Oxford University Press.
32
33 783 138. Keltner D, Gruenfeld DH, Anderson C. 2003 Power, approach, and inhibition. *Psychol.*
34
35 784 *Rev.* **110**, 265–284. (doi:10.1037/0033-295X.110.2.265)
36
37
38 785 139. Singh M, Wrangham RW, Glowacki L. 2017 Self-interest and the design of rules. *Hum.*
39
40 786 *Nat.* **28**, 457–480. (doi:10.1007/s12110-017-9298-7)
41
42
43 787 140. Singh M, Glowacki L, Wrangham RW. 2016 Self-interested agents create, maintain, and
44
45 788 modify group-functional culture. *Behav. Brain Sci.* **39**, e30, 40–41.
46
47 789 (doi:10.1017/S0140525X15000242)
48
49 790 141. Goldman I. 1955 Status rivalry and cultural evolution in Polynesia. *Am. Anthropol.* **57**,
50
51 791 680–697. (doi:10.1525/aa.1955.57.4.02a00030)
52
53
54 792 142. Acemoglu D, Robinson JA. 2012 *Why nations fail: The origins of power, prosperity, and*
55
56
57
58
59
60

- 1
2
3 793 *poverty*. New York, NY: Random House.
- 4
5 794 143. Baumard N, Chevallier C. 2015 The nature and dynamics of world religions: a life-history
6
7 approach. *Proc. R. Soc. B Biol. Sci.* **282**, 20151593. (doi:10.1098/rspb.2015.1593)
8 795
9
- 10 796 144. Watts J, Sheehan O, Atkinson QD, Bulbulia J, Gray RD. 2016 Ritual human sacrifice
11
12 promoted and sustained the evolution of stratified societies. *Nature* , 1–7.
13 797
14 (doi:10.1038/nature17159)
15 798
- 16
17 799 145. Henrich J, Boyd R. 2008 Division of labor, economic specialization, and the evolution of
18
19 social stratification. *Curr. Anthropol.* **49**, 715–724. (doi:10.1086/587889)
20 800
- 21 801 146. Matsa DA. 2011 Competition and product quality in the supermarket industry. *Q. J. Econ.*
22
23 **126**, 1539–1591. (doi:10.1093/qje/qjr031)
24 802
- 25
26 803 147. Olivares M, Cachon GP. 2009 Competing retailers and inventory: An empirical
27
28 investigation of General Motors' dealerships in isolated U.S. markets. *Manage. Sci.* **9**,
29 804
30 1586–1604. (doi:10.1287/mnsc.1090.1050)
31 805
- 32
33 806 148. Blake KR, Bastian B, Denson TF, Grosjean P, Brooks RC. 2018 Income inequality not
34
35 gender inequality positively covaries with female sexualization on social media. *Proc.*
36 807
37 *Natl. Acad. Sci.* **115**, 8722–8727. (doi:10.1073/pnas.1717959115)
38 808
- 39
40 809 149. Piddocke S. 1965 The potlatch system of the southern Kwakiutl: A new perspective.
41
42 *Southwest. J. Anthropol.* **21**, 244–264.
43 810
- 44
45 811 150. De Freitas J, Thomas K, DeScioli P, Pinker S. 2019 Common knowledge, coordination,
46
47 and strategic mentalizing in human social life. *Proc. Natl. Acad. Sci. U. S. A.* **116**, 13751–
48 812
49 13758. (doi:10.1073/pnas.1905518116)
50 813
- 51 814 151. Prentice DA, Miller DT. 1993 Pluralistic ignorance and alcohol use on campus: Some
52
53 consequences of misperceiving the social norm. *J. Pers. Soc. Psychol.* **64**, 243–256.
54 815
55
56
57
58
59
60

1
2
3 816 (doi:10.1037/0022-3514.64.2.243)
4

5 817 152. Bursztyn L, Gonzzlez A, Yanagizawa-Drott D. 2018 Misperceived Social Norms: Female
6
7 Labor Force Participation in Saudi Arabia. *SSRN Electron. J.* (doi:10.2139/ssrn.3202392)
8 818
9

10 819 153. Lieberman DE. 2013 *The story of the human body: Evolution, health, and disease*. New
11
12 York: Pantheon Books.
13 820
14

15 821

16
17 822
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

For Review Only