

1 Adaptive cultural transmission biases in children and nonhuman primates

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16 Abstract

17 Comparative and evolutionary developmental analyses seek to discover the similarities
18 and differences between humans and non-human species that illuminate both the
19 evolutionary foundations of our nature that we share with other animals, and the
20 distinctive characteristics that make human development unique. As our closest animal
21 relatives, with whom we last shared common ancestry, non-human primates have been
22 particularly important in this endeavour. Such studies that have focused on social
23 learning, traditions, and culture have discovered much about the ‘how’ of social learning,
24 concerned with key underlying processes such as imitation and emulation. One of the
25 core discoveries is that the adaptive adjustment of social learning options to different
26 contexts is not unique to human infants, therefore multiple new strands of research have
27 begun to focus on more subtle questions about when, from whom, and why such learning
28 occurs. Here we review illustrative studies on both human infants and young children and
29 on non-human primates to identify the similarities shared more broadly across the
30 primate order, and the apparent specialisms that distinguish human development.
31 Adaptive biases in social learning discussed include those modulated by task
32 comprehension, experience, conformity to majorities, and the age, skill, proficiency and
33 familiarity of potential alternative cultural models.

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39 Key words: cultural transmission; social learning; model biases; children; infants;

40 nonhuman primates

41 1. Introduction

42 The adaptive benefits of social learning are well-established and the ability is widespread
43 among a diverse range of vertebrate and invertebrate species. Social learning is
44 fundamental to the maintenance and spread of animal 'cultures' or behavioural traditions,
45 and we have extensive observational and experimental evidence for these in animals
46 (Price, Caldwell, & Whiten, 2010). However to date, there exists no strong evidence of
47 significant cumulative culture - cultures that become increasingly complex over time as
48 they do in humans - in other species (Dean, Vale, Laland, Flynn, & Kendal, 2014).

49 Comparative cultural cognition research typically focuses on differences in the
50 social learning mechanisms underlying culture in human and nonhuman animals. One
51 prominent theory suggests that differences in the specific means by which information is
52 spread between individuals might help explain the lack of cumulative culture in species
53 other than our own (Tennie, Call, & Tomasello, 2009; Tomasello, 1996). The suggestion
54 is that humans tend to copy or imitate with higher fidelity than other species, copying
55 actions, end results, and goals. In contrast, other animals are limited by a tendency to
56 copy only some aspects of a behaviour, or only the results of actions (emulation), and
57 precise information regarding actions is not so readily transmitted, leading to cultural
58 "slippage" effects (i.e. the loss of cultural information over time).

59 Whilst there is certainly evidence to support higher fidelity copying in human
60 children compared to other apes (most typically chimpanzees, e.g. Call, Carpenter, &
61 Tomasello, 2005; Nagell, Olguin, & Tomasello, 1993), both children and chimpanzees
62 have been shown to employ a suite of social learning mechanisms (Whiten, McGuigan,
63 Marshall-Pescini, & Hopper, 2009). Other animals sometimes exhibit imitation (e.g.

64 (Voelkl & Huber, 2000; Zentall, Sutton, & Sherburne, 1996), and children can be seen
65 both to selectively imitate in some contexts (e.g. Gergely, Bekkering, & Kiraly, 2002),
66 and ‘overimitate’, copying even causally irrelevant actions in others (e.g. Lyons, Young,
67 & Keil, 2007; McGuigan, Whiten, Flynn, & Horner, 2007).

68 Thus, a given individual (or species) does not always apply a single social
69 learning mechanism; rather, they may apply different psychological rules that govern
70 when and from whom to acquire information, and how much of the available information
71 to copy. Such processes have been labeled social learning strategies (Laland, 2004) or
72 cultural transmission biases (Boyd & Richerson, 1985), and may allow an individual to
73 counteract the risk of potentially outdated or maladaptive information (Kendal, Coolen,
74 van Bergen, & Laland, 2005). These biases also likely play a crucial role in determining
75 how behavioural variants are spread and maintained at population levels (Haun, van
76 Leeuwen, & Edelson, 2013).

77 Comparative research seeking to pinpoint differences underlying cultural
78 transmission biases in humans and other animals has thus risen in prominence. But while
79 transmission biases have been explored separately in both animals (Laland, 2004) and
80 children (Wood, Kendal, & Flynn, 2013), the comparative exploration of these factors,
81 employing similar procedures in humans and nonhumans, is lacking. Given the rapidly
82 growing scale of recent research, we cannot here provide a comprehensive review of
83 cultural transmission biases; rather, we highlight those that we believe to be particularly
84 good candidates for the exploration of similarities and differences between humans and
85 other primates. Although we note that comparisons between diverse species are essential
86 for a full understanding of how cognition evolves, here we focus on human infants and

87 nonhuman primates (hereafter primates) specifically, because of their central relevance in
88 illuminating the most recent phases of hominin cognitive and cultural evolution. We
89 examine how the context of the learning environment, coupled with the psychological
90 rules the observer is following, helps us better understand the different types of cultural
91 transmission processes observed in human children and primates. Now that we have a
92 substantial corpus of comparative studies focusing on the "how" of social learning with
93 regard to mechanisms, it is important to consider the social and psychological contexts
94 under which different mechanisms are employed, or the "when", "who", and "why" of
95 social learning.

96

97 2. When to copy

98 In some cases, it might not be the most adaptive option to learn from watching others,
99 particularly when information gained asocially by one's own efforts may be more
100 relevant or accurate. Information gleaned from others may be out of date or misleading
101 for a variety of reasons. Choosing between social and asocial learning in any one context
102 can be modulated by the observer's understanding of the problem, experience, or
103 proficiency. Alternatively, the perceived skill of the model or the number of models
104 displaying a particular behaviour may influence when an individual chooses to copy, as
105 outlined below.

106

107 2.1. Task comprehension and experience

108 A given task may be opaque with respect to the actions needed to complete it, for
109 example because the internal mechanisms are occluded. In such cases, it may be

110 beneficial to apply a "copy-everything" bias to reach a solution. Both preschool-aged
111 children and young chimpanzees have been found to copy all actions, including irrelevant
112 actions, from adult humans when the processes involved in task completion are opaque
113 (Horner & Whiten, 2005).

114 Children also seem to evaluate a task in relation to a model's particular actions
115 and efficacy with the task. When faced with a model who performs an action with an
116 unexpected body part without a plausible reason (e.g. turns a light switch on with her
117 head, rather than hand), both 14-month-old infants (Gergely, Bekkering, & Király, 2002)
118 and enculturated chimpanzees (Buttelmann, Carpenter, Call, & Tomasello, 2007) copy
119 the specific method used. When there is an evident reason for the seemingly odd action
120 (e.g. arms are wrapped up or hands occupied), both species copy 'rationally', achieving
121 the goal through the more regular means (i.e. manually, in this example). Similarly,
122 (Carr, Kendal, & Flynn, 2015) children are more likely to seek innovative solutions to a
123 task as the efficacy of a demonstration decreases (Carr et al., 2015) and older children are
124 more likely to reject a model's demonstration with a non-appropriate tool in favour of a
125 functional tool (diYanni & Kelemen, 2008); diYanni & Kelemen (2008) suggest that this
126 was due to older children's increased knowledge of artefact design.

127 The difficulty of the task and the cognitive savvy or experience of the observer
128 can both influence the type of social learning mechanism employed. For example, in
129 simpler tasks (e.g. breaking open a tube, or raking in a reward), chimpanzees tend to
130 perform equally well on witnessing information about actions or about end-results only,
131 whereas children require information about actions to perform best (Call et al., 2005;
132 Nagell et al., 1993). In more difficult tasks (e.g. tool construction), chimpanzees may

133 require action information to perform better than controls deprived of information (Price,
134 Lambeth, Schapiro, & Whiten, 2009).

135 Prior experience or familiarity with a given task also influences when or how
136 much information to copy. For example, if social information conflicts with personally-
137 gained information, preschool-aged children may favour personal information (Clément,
138 Koenig, & Harris, 2004; Ma & Ganea, 2010). When five-year-old children have
139 previously successfully solved a task on their own, they are motivated to copy subsequent
140 socially demonstrated solutions but are less likely to copy actions that appear causally
141 irrelevant (Wood et al., 2013). Similarly, if children have a difficult prior experience
142 achieving a goal, they are more likely to copy an adult demonstration precisely than those
143 with an easier prior experience (Williamson, Meltzoff, & Markman, 2008).

144 Primates' attention to social information can also be affected by prior experience,
145 with young callitrichid monkeys seeking social information about novel over familiar
146 food items (Kendal et al., 2005; Rapaport, 1999). Interestingly, in foraging tasks,
147 previous knowledge of one method can also lead to so-called 'conservatism', wherein a
148 given individual sticks to an individually learned method, even when an alternative, more
149 efficient or better rewarded, method is presented. This has been suggested to be a limiting
150 factor in cultural learning in chimpanzees, with individuals unable or unwilling to adopt
151 new methods, preferring to stick to their asocially learned techniques (Hopper, Schapiro,
152 Lambeth, & Brosnan, 2011; Hrubesch, Preuschof, & Van Schaik, 2008). To date,
153 experimental evidence that specifically explores how individual knowledge of a task
154 influences copying fidelity in primates is lacking and could help inform differences in
155 social learning mechanisms employed by children and chimpanzees, seen in earlier tests.

156

157 2.2. Majority-biased transmission and conformity

158 Comparative research into conformity must cope with somewhat differing definitions
159 deriving from different disciplinary origins (Claidière & Whiten, 2012). Comprehensive
160 reviews of the field can be found elsewhere (Claidière & Whiten, 2012; Haun et al.,
161 2013); for the purpose of this review we restrict ‘conformity’ to when a given individual
162 forgoes an existing behaviour in favour of the behaviour of a majority of others. The
163 broader phenomenon of majority-biased transmission occurs when individuals show an
164 exaggerated tendency to adopt behaviour they witness most frequently, or is
165 demonstrated by most other individuals (a distinction is sometimes made between these
166 two types of observations, (Haun, Rekers, & Tomasello, 2012), but for simplicity we treat
167 them together here).

168 Perry (2009) traced the development of food extraction techniques in capuchin
169 monkeys over seven years and found that after a period of exploring equally efficient
170 techniques, monkeys typically settled on the technique they had witnessed most often in
171 infancy. Experimental evidence for primates comes mainly from studies employing a
172 two-action methodology, wherein one of two equally beneficial solutions is seeded into a
173 social group via a trained demonstrator. The group members' subsequent adoption of the
174 technique is then traced. In some instances, group members will discover the alternative,
175 equally rewarding technique, but then revert back to the technique exhibited by the
176 majority of the group. Such behaviour has been seen in children (Flynn, 2008; Flynn &
177 Whiten, 2008), a range of captive primates (Bonnie, Horner, Whiten, & de Waal, 2007;
178 Dindo, De Waal, & Whiten, 2009; Price & Caldwell, 2007; Stoinski, Drayton, & Price,

179 2011) and in wild vervet monkeys (van de Waal, Borgeaud, & Whiten, 2013). Similar
180 results have been reported using an exchange paradigm in chimpanzees (i.e. chimpanzees
181 exchanged inedible tokens for varying food rewards, Hopper et al., 2011).

182 Without experimental manipulation it is difficult to determine if these animals are
183 eschewing minority information or are instead conservatively relying on the technique
184 they learned first, or that has been most frequently reinforced (Hrubesch et al., 2008;
185 Marshall-Pescini & Whiten, 2008; van Leeuwen & Haun, 2013). Haun et al. (2012)
186 directly tested preferences for majority over minority information and found that both
187 children and chimpanzees, but not orangutans, were more likely to copy an action
188 performed by three individuals than by one, controlling for the number of times the
189 action was seen. With reference to conformity specifically, defined as individuals
190 rejecting personal experience in favour of a majority bias, children as young as 4 years
191 have been found to reject correct personal information in favour of incorrect information
192 offered by a majority of adults (Corriveau & Harris, 2010; Ma & Ganea, 2010) and peers
193 (Haun & Tomasello, 2011), albeit only under certain conditions.

194 Differences between normative and informational conformity further complicate
195 interpretations. Normative conformity is socially motivated, whereas informational
196 conformity functions to gain more information about reality (Deutsch & Gerard, 1955).
197 In the above instances with children, conforming to incorrect information was either only
198 in the presence of those who modeled the behaviour, or was restricted to perceptual tasks
199 (Corriveau & Harris, 2010). When children were alone, or presented with a practical
200 problem, correct personal information was relied upon (Haun & Tomasello, 2011).

201 Recent use of experimental procedures in field settings has provided compelling
202 evidence of animal conformity (e.g. great tits, Aplin et al. 2015; vervet monkeys, van de
203 Waal et al. 2013, although see van Leuuwen, Kendal, Tennie, & Haun, 2015, for a
204 critique of this interpretation and Aplin et al. 2015 for an instructive response). More
205 probing experimental evidence is needed. Tests with primates where comparisons are
206 made between individuals operating a task both in the presence of and away from their
207 groupmates might help shed light on this, as has been done recently with children
208 (McGuigan & Robertson, 2015).

209

210 3. Whom to copy

211 This area has perhaps received the most attention in the literature, with a wealth of
212 information suggesting that children prefer and selectively attend to and copy certain
213 types of models, as outlined below. To date, we have less information pertaining to
214 primates, but emerging data from both wild and captive populations of primates suggest
215 that some similar preferences may be in place. We focus on the model attributes of
216 perceived skill/age/proficiency, social status, and familiarity or social bonding.

217

218 3.1. Model skill, age, and status

219 From a young age, infants are able to discriminate between competent and
220 incompetent models (Zmyj, Buttelmann, Carpenter, & Daum, 2010) and children will
221 preferentially copy proficient models in a variety of contexts (e.g. Birch, Vauthier, &
222 Bloom, 2008; Brooker & Poulin-Dubois, 2013; Koenig & Harris, 2005; Metzoff &
223 Moore, 1992, although see Wood, Kendal & Flynn, 2015) . Importantly, children's theory

224 of mind ability has recently been linked to their ability to copy accurate over inaccurate
225 speakers (Brosseau-Liard, Penney, & Poulin-Dubois, 2015).

226 Age is an indication of experience with the environment, so copying older
227 individuals is also a potentially beneficial strategy. From infancy, children are more
228 likely to copy actions presented by adults over children (Rakoczy, Hamann, Warneken, &
229 Tomasello, 2010; Seehagen & Herbert, 2011). Children are also more likely to copy
230 visibly, causally irrelevant actions if presented by an adult as opposed to a similarly-aged
231 peer (Flynn, 2008; McGuigan, 2012; Wood, Kendal, & Flynn, 2012). These copying
232 strategies also seem to depend on context, with children more likely to copy adults than
233 peers when information is novel (Zmyj, Daum, Prinz, Nielsen, & Aschersleben, 2012) or
234 related to motor skills (Kuczynski, Zahn-Waxler, & Radke-Yarrow, 1987) and to copy
235 peers when information is familiar or related to play (Ryalls, Gul, & Ryalls, 2000).

236 Copying high status individuals is another potentially adaptive strategy, since
237 those individuals might be more successful and thus better equipped to deal with the
238 social or physical environment. When a novel puzzle is presented to children to solve in
239 a group, dominant and popular children were attended to more often than their less
240 dominant and popular peers (Flynn & Whiten, 2012). Children also copy more irrelevant
241 actions made by a higher status adult (e.g. head teacher) as compared to a lower status
242 adult (McGuigan, 2013) .

243 In free-ranging primates, chimpanzees pay more attention to older individuals
244 than younger individuals (Biro et al., 2003; Lonsdorf, 2006) and capuchin monkeys
245 attend more to proficient individuals (Ottoni, de Resende, & Izar, 2005). Van de Waal,
246 Renevey, Favre, and Bshary (2010) found that vervet monkeys selectively attended to

247 female models over male models. The authors suggest that females, as the philopatric
248 sex, might be better sources of information than immigrant males.

249 Experimental evidence in captivity is limited, though there is some evidence to
250 suggest a preference in chimpanzees for older, dominant, and previously successful
251 individuals as models (Horner, Proctor, Bonnie, Whiten, & de Waal, 2010) and
252 alternative methods discovered by low ranking individuals do not spread through groups
253 (Bonnie et al., 2007). Similar trends have been found in capuchins on novel foraging
254 tasks (Dindo, Thierry, & Whiten, 2008); however, in a different study, infant capuchins
255 were not more likely to choose food preferred by older or more experienced individuals
256 (Fragaszy, Visalberghi, & Galloway, 1997). Given the nature of many captive tests,
257 dominant individuals are frequently used as models to limit opportunities for individual
258 learning prior to viewing model demonstrations. In the absence of relevant controls, it is
259 therefore difficult to distinguish whether individuals are relying on the first learned
260 method or preferentially attending to these individuals, although recent statistical
261 modeling suggests that chimpanzees operating a foraging device are biased to copy
262 knowledgeable individuals (Kendal et al., 2015).

263

264 3.2. Familiarity and social bonds

265 Copying individuals who are similar to yourself can serve two purposes: first it can be
266 instrumentally fruitful because those individuals are more likely to live in a similar
267 environment and have relevant experience, and second it can help you learn the social
268 customs necessary to integrate and live successfully in a social group (Over & Carpenter,
269 2014). Infants and children preferentially copy familiar over less familiar models

270 (Buttelmann, Zmyj, Daum, & Carpenter, 2013; Learmonth, Lamberth, & Rovee-Collier,
271 2005; Shutts, Kinzler, McKee, & Spelke, 2009).

272 Children also tend to copy more actions demonstrated by engaging, interactive
273 models, over televised or aloof models (McGuigan et al., 2007; Nielsen, Simcock, &
274 Jenkins, 2008). This ‘video deficit’ perhaps exists partly because children might have
275 difficulty understanding the correspondence between televised information and reality
276 (Anderson & Pempek, 2005; Troseth & DeLoache, 1998), but also because social cues
277 are reduced. When children have the opportunity to engage with a televised model prior
278 to a demonstration through a live video feed, the video deficit effect is reduced (Nielsen
279 et al., 2008). Children seem predisposed towards ostensive signals, such as eye contact,
280 and pointing, that indicate that the model is trying to communicate relevant information
281 (Csibra & Gergely, 2009). For example children copy a model more when s/he stoops to
282 the child’s level, leans in, makes eye contact and talks engagingly (Brugger, Lariviere,
283 Mumme, & Bushnell, 2007).

284 Learning techniques from others is facilitated by close proximity and some degree
285 of social tolerance (Coussi-Korbel & Fragaszy, 1995; van Schaik, 2003) and thus might
286 be expected to occur more frequently between close affiliates, typically defined as those
287 who spend the most time in close spatial proximity (Van Schaik & Aureli, 2000). In fact,
288 the way in which behaviours spread throughout wild populations of primates is often
289 used to infer whether social learning is occurring. For example, if a novel behaviour
290 spreads from an individual to his or her close associates first, it is deemed more likely to
291 be learned via observation than asocial learning, as has been described in several primate
292 species (Hobaiter, Poisot, Zuberbühler, Hoppitt, & Gruber, 2014; Huffman & Quiatt,

293 1986; Itani & Nishimura, 1973; Kawai, 1965; Kendal et al., 2010; Leca, Gunst, &
294 Huffman, 2007; Nishida, 1987). Similarly, the amount of time individuals spend in close
295 proximity with others is related to the number of cultural variants they display (van
296 Schaik et al. 2003), the similarity of the foraging techniques they use (Agostini &
297 Visalberghi, 2005; Panger et al., 2002) or the actions they copy (Claidière, Messer,
298 Hoppitt, & Whiten, 2013; Russon & Galdikas, 1995). New techniques, including social
299 network analysis can help determine how social bonds influence the spread of
300 information in both wild and captive populations (e.g. chimpanzees, Hobaiter et al., 2014;
301 Kendal et al., 2015).

302 Controlled experiments comparable to those in the developmental literature are
303 difficult to implement. For logistical reasons, models are typically selected from the
304 social group without the possibility of comparisons between familiar and unfamiliar
305 individuals, so such experiments are typically limited to species whose group
306 composition can be more easily manipulated (see Swaney, Kendal, Capon, Brown, &
307 Laland, 2001 for examples with guppies). Video demonstrations offer one avenue to
308 explore these potential biases in primates. For example, chimpanzees copied
309 demonstrated behaviour in video displays of an unfamiliar model on both a tool
310 modification task (Price et al., 2009) and a two-action task (Hopper, Lambeth, &
311 Schapiro, 2012). Colobus monkeys (*Colobus guereza kikuyuensis*) also copied the
312 modeled solution of a two-action task by watching video footage of a different species
313 (*Colobus polykomos*, Price & Caldwell, 2007) although in the latter instance the monkeys
314 had had previous visual contact with those animals. Mixed species groups are becoming

315 increasingly common in captivity and offer an excellent opportunity to test for
316 preferences to copy genetically similar individuals in a shared environment.

317 Considering the latter point, some comparative studies of social learning have
318 been criticized for using human demonstrators with both chimpanzees and children,
319 potentially putting chimpanzees at a disadvantage (De Waal, Boesch, Horner, & Whiten,
320 2008; Price & Whiten, 2012). Conspecific models are now used more frequently;
321 however, another, equally relevant point to consider is that in the majority of comparative
322 studies, children are presented with unfamiliar models, whereas primates are typically
323 presented with familiar group-mates as models. Given the known role of model type in
324 children's social learning, and the likely similar role in primates, this is an important
325 consideration.

326

327 4. Why copy?

328 Copying can help a naive observer learn new skills or deal with the physical
329 environment, but it can also serve a social function (Uzgiris, 1981). As discussed, cultural
330 transmission biases can vary based on the characteristics of the model, the observer, and
331 the context the learning occurs in. This then makes determining the motivation
332 underlying copying essential to understanding differences between species.

333 Copying precise actions, or imitation, may help reinforce similarity between the
334 imitator and the imitated, increasing social cohesion (Meltzoff, 2005; Over & Carpenter,
335 2012). Infants tend to prefer individuals who mimic them over those who do not
336 (Meltzoff & Beeghly, 1990) and will copy more actions of an experimenter who imitates
337 them over one who does not (Eckerman & Stein, 1990). Children given a goal to affiliate

338 with another will copy actions more precisely than those not given such a goal (Carpenter
339 & Call, 2009) and children also endorse the preferences of those who have previously
340 mimicked them, over those who have not (Over, Carpenter, Spears, & Gattis, 2013).

341 One of the most fascinating forms of social learning occurs when causally
342 irrelevant and even inefficient actions are copied: ‘overimitation’. Investigation of this
343 phenomenon in children has burgeoned in recent years, with some evidence to suggest
344 that the behaviour increases with age, even into adulthood (McGuigan, Makinson, &
345 Whiten, 2011), and is present in very different human cultures (Nielsen, Mushin,
346 Tomaselli, & Whiten, 2014; Nielsen & Tomaselli, 2010). Many hypotheses have been put
347 forward to explain overimitation. For example, children might automatically encode
348 actions as causally relevant, thus permitting them to negotiate causally opaque processes
349 or tasks before they have the cognitive savvy to work them out for themselves (Lyons et
350 al., 2007). Alternatively, children may realize that the actions are irrelevant, but copy
351 them because they interpret them as part of a larger cultural convention (Kenward, 2012;
352 Keupp, Behne, Zachow, Kasbohm, & Rakoczy, 2015).

353 One prominent view stresses the importance of social motivation, specifically that
354 overimitation might stem from a motivation to be seen to be like others and in
355 consequence be liked by them (Over & Carpenter, 2012). The apparent paradox that
356 exists between selective imitation and overimitation in children is thus explained by the
357 underlying goal the child has when performing the task (Over & Carpenter, 2013). For
358 example, if the information sought is purely functional, children may be more likely to
359 omit irrelevant actions (Carpenter, 2006), and there is some evidence to suggest that
360 children are more likely to copy irrelevant actions in the presence of the model who

361 originally demonstrated them (Nielsen & Blank, 2011). Disentangling social from
362 functional copying contexts is a difficult endeavor, however, particularly given that
363 copying is by its very nature a social activity, and children may be motivated by both
364 functional and social dynamics on a given task (Over & Carpenter, 2012).

365 Carpenter and Call (2009) argue that it is this social motivation, or the drive to be
366 like others, that distinguishes humans from other animals, yet attempting to study this
367 interaction from a comparative perspective is inherently difficult. Experimentally, there is
368 evidence to suggest that apes are aware when others are imitating them (Haun & Call,
369 2008; Nielsen, Collier-Baker, Davis, & Suddendorf, 2005) and capuchin monkeys show
370 more affiliative behaviours toward humans who have previously imitated them (Paukner,
371 Suomi, Visalberghi, & Ferrari, 2009). Deciphering the goals or motivations underlying
372 copying is more difficult. In free-ranging primates, some observed cultural traditions are
373 social by their nature, including social customs, games, and stone-handling behaviours
374 (Leca et al., 2007; Panger et al., 2002; Perry et al., 2003; van Leeuwen, Cronin, & Haun,
375 2014; van Schaik et al., 2003; Whiten et al., 2001). Given their social nature or lack of
376 immediate adaptive value, we can infer that motivations to copy these actions are social,
377 rather than instrumental, but in the absence of controlled experiments, it is difficult to
378 draw firm conclusions.

379 Experimental studies specifically seeking to isolate underlying motivations are
380 equally difficult. As previously discussed, some comparative studies suggest that
381 chimpanzees only copy irrelevant actions when their irrelevance is masked (by the object
382 being manipulated being opaque, for example; Horner and Whiten, 2005); in situations
383 where the function of an action seems readily determined, only children, and not apes,

384 persist in copying irrelevant actions (Call et al., 2005; Nagell et al., 1993). However,
385 there is some evidence that chimpanzees might overimitate. For example, after socially
386 learning a particular method of constructing a tool, only those chimpanzees who had seen
387 another chimpanzee construct the tool persisted in using this method after a delay of two-
388 weeks when it was no longer necessary (Price et al., 2009). The results cannot be
389 explained by conservatism, since chimpanzees that had learned via emulation or asocial
390 learning tended only to build tools when necessary.

391 Comparative research is further limited by tasks that focus specifically on
392 learning about the physical environment, typically achieving a food reward (Watson &
393 Caldwell, 2009) although see (Bonnie & de Waal, 2007). Gaining a preferred food in
394 your home environment (be that in captivity or in the wild) might be very different than
395 gaining a sticker or small toy (as is most frequently used with children) in a school or in a
396 laboratory. This difference alone may mean the child's testing environment is more (or
397 less) inherently social.

398

399 5. Conclusions and Future Directions

400 From an early age humans can moderate what to learn, whom to learn from, and when to
401 learn, in apparently adaptive ways. As understanding of knowledge states, memory,
402 physical cognition, language skills, and other key abilities develop throughout ontogeny,
403 these strategies progress, allowing individuals to optimize the combined knowledge of
404 their own individual problem-solving with that of the information that can be learned
405 from others. While many animals have been shown to exhibit cultural transmission
406 biases, to date, the adaptability and flexibility of these remain to be clarified, along with

407 the potential similarities and differences of these biases to our own. Are other primates
408 able to adapt their copying behaviour under as flexible a set of contexts as humans? Do
409 primates copy for purely instrumental purposes, or also to help affiliate with group
410 members? Do social relationships or understanding of a problem determine how much
411 information is copied? Do multiple biases interact or are some of higher priority and do
412 they over-ride others? Most fundamentally, what determines the relative roles of
413 individual versus social learning?

414 We anticipate that further, rigorous comparative studies will be conducted to
415 answer such questions, as has been achieved previously with social learning mechanisms.
416 We have highlighted several areas warranting further exploration, but comparative
417 psychologists face many challenges when designing experiments to be as similar as
418 possible between species. Meeting these challenges will require designing studies that do
419 not rely heavily on language and can be applied in an ecologically valid fashion across
420 species and contexts.

421

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423

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