

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, 2013a), 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., 2013b). 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 Leuwen, 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, Buttellmann, 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 (Uzgoris, 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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