

# Evolutionary Origins of Morality: Insights from Nonhuman Primates

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## Abstract

The aim of this contribution is to explore the origins of moral behavior and its underlying moral preferences and intuitions from an evolutionary perspective. Such a perspective encompasses both the ultimate, adaptive function of morality in our own species, as well as the phylogenetic distribution of morality and its key elements across primates. First, with regard to the ultimate function, we argue that human moral preferences are best construed as adaptations to the affordances of the fundamentally interdependent hunter-gatherer lifestyle of our hominin ancestors. Second, with regard to the phylogenetic origin, we show that even though full-blown human morality is unique to humans, several of its key elements are not. Furthermore, a review of evidence from nonhuman primates regarding prosocial concern, conformity, and the potential presence of universal, biologically anchored and arbitrary cultural norms shows that these elements of morality are not distributed evenly across primate species. This suggests that they have evolved along separate evolutionary trajectories. In particular, the element of prosocial concern most likely evolved in the context of shared infant care, which can be found in humans and some New World monkeys. Strikingly, many if not all of the elements of morality found in nonhuman primates are only evident in individualistic or dyadic contexts, but not as third-party reactions by truly uninvolved bystanders. We discuss several potential explanations for the unique presence of a systematic third-party perspective in humans, but focus particularly on mentalizing ability and language. Whereas both play an important role in present day, full-blown human morality, it appears unlikely that they played a causal role for the original emergence of morality. Rather, we suggest that the most plausible scenario to date is that human morality emerged because our hominin ancestors, equipped on the one hand with large and powerful brains inherited from their ape-like ancestor, and on the other hand with strong prosocial concern as a result of cooperative breeding, could evolve into an ever more interdependent social niche.

## Key words

Evolution, morality, hunter-gatherers, prosociality, normativity, norm violations, conformity, concern for reputation, cooperative breeding, nonhuman primates

## 42 **1 Introduction**

43

44 Contemplation of law as a natural social phenomenon quickly reveals that it cannot be reduced to  
45 purely rational processes and explicit reasoning. It is fundamentally built on (albeit not identical  
46 with) our sense for morality, the propensity to differentiate actions, decisions and intentions  
47 between those that are proper and right and those that are improper or wrong (Long and Sedley,  
48 1987). This evaluation can be the result of deliberation, but also of automatic proximate  
49 mechanisms such as intuitions that are expressed by a variety of moral emotions, motivations,  
50 and preferences which often have a high-urgency feel (Weaver et al., 2014).

51

52 Social scientists have traditionally considered morality as a recent, purely cultural innovation,  
53 seemingly necessary to keep our otherwise brutish nature under control (e.g. reviewed in Long  
54 and Sedley, 1987; de Waal, 2006; Haidt, 2013). In support of this conjecture, what is considered  
55 moral in a given culture or society, or what the corresponding systems of laws prescribe, can  
56 indeed be quite variable. However, despite this variability in the content of what counts as moral  
57 among cultures, there are also elements that seem universal, both with regard to the proximate  
58 mechanisms that regulate moral behavior and the content of moral norms. For instance, Barrett et  
59 al. (2016) found that across societies, including small-scale societies, humans take an agent's  
60 reason for action into account for moral judgments, but they also found independent variation  
61 when looking at specific contents, e.g. harm vs. theft, or in how the content influences the role of  
62 intentionality. Furthermore, even if conformist transmission could in principle stabilize a variety  
63 of behaviors and norms (Chudek and Henrich, 2011), there appears strong canalization in that  
64 some kinds of content (such as for instance not to harm others, or engage in parental investment)  
65 are more readily considered moral than others (van Schaik 2016).

66

67 Ubiquitous key elements of human morality discussed in this paper are prosocial concern and  
68 conformity, as well as the moral contents of doing good, not harming others, or avoiding inequity  
69 and incest (van Schaik, 2016). Importantly, these elements are not only expressed when the  
70 individual is personally involved, i.e. in individualistic or dyadic contexts, but also in the absence  
71 of personal involvement, i.e. in third-party contexts. For instance, moral behavior not only  
72 includes the urge to conform to the rules and norms of one's own community, but also evokes  
73 strong feelings that others ought to do so as well. The universal presence of these elements of  
74 morality across human societies suggests there is an evolved core to morality, which should  
75 therefore be amenable to a functional and comparative evolutionary analysis *sensu* Tinbergen  
76 (Tinbergen, 1963; Bateson and Laland, 2013).

77

78 Such an evolutionary analysis claims that whenever universal, proximate mechanisms have  
79 evolved, they must have done so to fulfill a specific adaptive function. In the first section of this  
80 contribution we will argue that the adaptive function of our evolved morality was to enable the  
81 highly interdependent life-style of Pleistocene hunter-gathers.

82

83 An evolutionary analysis of human morality also includes the examination of its phylogenetic  
84 origin, to which we will turn in the second section. Whereas full-blown human morality, which

85 includes explicit moral reasoning and evaluation, may well be unique to humans, some of its  
86 elements or building blocks are not, and we can use data from nonhuman primates to trace the  
87 evolutionary history of each of them separately. An obvious first, and very popular, step is to  
88 look at the great apes, and in particular the chimpanzees and bonobos (e.g. de Waal, 2006), to  
89 investigate the possible presence of a specific building block in our closest relatives. However, a  
90 broader and more informative comparative approach consists in mapping the presence or absence  
91 of each of these building blocks or traits in a broader set of species, to then test which factor best  
92 predicts this pattern of distribution (MacLean, 2016). If the specific case of humans fits such an  
93 identified pattern, this allows us to identify the evolutionary context of the emergence of this  
94 trait. This approach thus ideally allows not only to identify *that* a trait is or is not unique to  
95 humans, but also *why* it is present in a given set of species, including humans.

96  
97

## 98 **2. Hunter-gatherers: the evolutionary context of the emergence of human morality**

99

100 As a species, humans have spent 95% of their evolutionary past as Pleistocene hunter-gatherers  
101 (Hill et al., 2011). Even though we cannot travel back in time and observe how these people  
102 lived, the few remaining hunter-gatherer societies across the globe allow us a glimpse into our  
103 evolutionary past, by providing useful models for the reconstruction of ancestral selection  
104 pressures. Intriguingly, despite often considerable geographical distance and principled variation,  
105 these societies are rather homogeneous (Marlowe, 2005), and the communalities between them  
106 therefore are likely representative for the evolutionary context in which human sociality in  
107 general, and thus morality, has evolved.

108

109 Nomadic hunter-gatherers live in highly interdependent, egalitarian societies (Marlowe, 2005).  
110 Even though some individuals can be more influential than others, major decisions are usually  
111 made collectively. In fact, if some individual tries to rise to a leader position through coercive  
112 leadership in order to dominate the rest of the group, the majority will try to prevent this  
113 (Boehm, 2012). Hunter-gatherers form socially recognized pair bonds (i.e. marriages), and show  
114 a marked sexual division of labor: women gather and men hunt cooperatively, fish, or collect  
115 honey (Marlowe, 2007). The foraging niche is skill-intensive and often requires intense  
116 cooperation. The skills are socially transmitted and shaped by cumulative cultural evolution  
117 (Dean et al., 2014; Hill et al., 2014), and it takes women until their mid-twenties, and men even  
118 longer, to become fully efficient foragers. The social structure and networks of hunter-gatherers  
119 in fact appears to optimize efficient transmission of cultural knowledge. Either sex may disperse,  
120 but adult brothers and sisters often co-reside. Most individuals in the group are unrelated, and  
121 strong ties with non-kin play an important role for the spread of skills and knowledge (Hill et al.,  
122 2011; Migliano et al., 2017).

123

124 Hunter-gatherer lives are characterized by high levels of interdependence in almost all contexts  
125 and at different time-scales. Food sharing is vital, at the time scale of days (hunters, but also  
126 foragers, may return empty-handed), weeks to months (in case of sickness or injury), and years  
127 to decades (families with growing children do not produce enough and rely on younger and older

128 camp members: Sugiyama and Chacon, 2005; Kaplan et al., 2009; Hill et al., 2011). Gathered  
129 food is generally shared within families, but honey and meat, in particular from large animals,  
130 which are hunted cooperatively, are shared with all other families in a camp (Wood and  
131 Marlowe, 2013). In general, food is shared with those who are needy, but also preferentially with  
132 those who have shared in the past. It is thus crucial that someone build a good reputation and  
133 support others without being solicited, to ensure receiving support when needy themselves. A  
134 good reputation is thus vital, because sooner or later this need will arrive. Men can gain status by  
135 being generous (Gurven et al., 2000; Marlowe, 2010), and by participating in coordinated  
136 collective action, as during warfare, cooperative hunting, gathering, or moving camp.

137  
138 Not only subsistence and foraging activities are fundamentally cooperative, but also child  
139 rearing. For a mother, it is almost impossible to rear a child successfully by herself, and she  
140 receives ample support from others, in particular fathers, grandmothers and older siblings, but  
141 also from other camp members (Hrady, 2009). In fact, humans qualify as *cooperative breeders*, a  
142 reproductive system also known in several other animals, such as many bird species, but also  
143 wolves, or callitrichid monkeys. In all these species, including humans (Sear and Mace, 2008),  
144 parents obtain a significant amount of help in rearing their offspring, and both growth and  
145 survival of the offspring depends on the availability of helpers. Cooperative breeding typically  
146 evolves when conditions are harsh, which makes it increasingly difficult for mothers to raise  
147 their offspring alone (Burkart, van Schaik, & Griesser 2017b). When our hominin ancestors  
148 moved into the savanna, food was more often dispersed and hidden underground than before.  
149 This required not only more cooperation during foraging and more elaborate food processing  
150 techniques (e.g. cooking: Wrangham 2009), but also made it more difficult for mothers to rear  
151 their offspring independently, unlike the practice in all the other great apes. Furthermore, large  
152 brains require large amounts of energy, in particular during ontogeny (Kuzawa et al. 2014). It is  
153 thus parsimonious to assume that our ancestors had already started to engage in systematic  
154 allomaternal care rather early since otherwise the evolution of our big brains would not have  
155 been possible (Isler & van Schaik 2012).

156  
157 Human morality can be understood as a straight-forward adaptation to this hunter-gatherer life-  
158 style, in that it enables and stabilizes interdependence (see also van Schaik et al., 2014).  
159 According to this hypothesis, one key element of morality, a prosocial predisposition, is crucial  
160 to maintain food sharing with immatures and adults. Having a good reputation serves as  
161 insurance to being cared for when in need, and also for being chosen as a mate or cooperation  
162 partner. A strong concern for one's reputation, including reputation management, thus ensues.  
163 The second element, an urge to conform, is crucial in a niche where coordinated or synchronized  
164 action is vital for survival. In addition, the urge to conform serves to acquire the many complex  
165 skills that make up our ecological niche via social learning. When skills and knowledge are  
166 opaque, i.e. when it is not obvious how separate steps involved in an activity lead to an overall  
167 goal, trustful copying even of seemingly useless elements is mandatory (Henrich and Broesch,  
168 2011; Dean et al., 2014).

169

170 The ultimate function of human morality and its key elements can thus readily be understood as  
171 an adaptation to the hunter-gatherer lifestyle. But are these elements unique to humans, or can  
172 some of them, or perhaps their precursors, also be found in other primates, and if so, why? These  
173 questions are important because a better understanding of the phylogenetic origins of elements of  
174 morality in nonhuman species can help evaluate the functional hypothesis that human morality  
175 has evolved to solve problems inherent to a fundamentally interdependent lifestyle.

176  
177

### 178 **3. Evolutionary origins of the building blocks of morality**

179

180 Building blocks of morality include both mechanisms and contents. For clarity, we discuss them  
181 separately (mechanisms: prosocial concern, section 3.1 and conformity, section 3.2; contents:  
182 universal, biologically anchored norms, section 3.3 and arbitrary, culturally variable norms,  
183 section 3.4). However, links between them exist and will be addressed in the corresponding  
184 sections. An important issue for full-blown morality that applies to all building blocks is whether  
185 they are expressed in individualistic or dyadic contexts only, or whether they are also present in  
186 third-party contexts. For instance, can a prosocial concern in a given species be found between  
187 an actor and a recipient only, or do non-involved third parties (i.e. non-involved bystanders) also  
188 evaluate the prosocial interaction between an actor and a recipient as morally appropriate? This  
189 third-party perspective is an overarching hallmark of human morality in general and we will  
190 therefore also focus on this particular aspect when reviewing the evidence from nonhuman  
191 animals.

192

#### 193 **3.1 Prosocial concern**

194

195 One key element of human morality is prosocial concern, i.e. a concern not only with one's own  
196 but also with others' well-being, also referred to as other-regarding preferences by behavioral  
197 economists (Fehr and Fischbacher, 2003). In the primatological literature, it is often referred to  
198 as proactive prosociality, to stress that the corresponding behaviors, such as for instance food  
199 sharing, are not the result of solicitation by recipients, begging or even harassment, but that they  
200 are initiated spontaneously by the actor without triggering by other individuals (Jaeggi et al.,  
201 2010).

202

203 Over the last decade, proactive prosociality has been extensively studied in a number of primate  
204 species. Early studies found it was absent in chimpanzees, who are independent breeders, but  
205 present in the small marmoset monkeys, who like humans, are cooperative breeders (Cronin,  
206 2012; Marshall-Pescini et al., 2016). Importantly, even though the evolution of cooperative  
207 breeding is based on inclusive fitness benefits (Burkart et al., 2017b), kin selection and  
208 relatedness per se cannot explain why some primates show proactive prosociality but others  
209 don't. First, marmosets can show proactive prosociality toward non-related group members as  
210 well, and even strangers who are potential group members (Burkart et al., 2007). Second, highly  
211 related mother-offspring dyads in independently breeding primates, including chimpanzees  
212 (Ueno and Matsuzawa, 2004), fail to show proactive prosociality.

213  
214 Later prosociality studies produced more mixed results, also because different methodologies  
215 make it difficult to compare between studies and species (Burkart and Rueth, 2013). A large  
216 comparative study therefore compared proactive prosociality across 15 primate species, using  
217 exactly the same methodology and thus providing directly comparable data. Phylogenetic  
218 analyses revealed that the extent of allomaternal care, (i.e. the amount of help that mothers  
219 receive from others when rearing infants, with cooperative breeding found in the higher range of  
220 values) is indeed the best predictor for proactive prosociality in a group service paradigm,  
221 whereas brain size or other socio-ecological factors cannot explain a significant amount of inter-  
222 specific variation (Burkart et al., 2014).

223  
224 Accordingly, chimpanzees, our closest relatives, scored low on prosociality. Nevertheless, their  
225 score was not zero, which corresponds to reports of occasional targeted helping in this species  
226 (Warneken and Tomasello, 2015; but see Tennie et al., 2016), as well as occasional food sharing  
227 or alerting others of danger. In addition to prosociality, targeted helping also has an important  
228 cognitive component, which is particularly strong in the large-brained apes (Burkart et al.,  
229 2017a). A highly relevant test case are bonobos, for which evidence for proactive prosociality is  
230 quite mixed (Tan and Hare, 2013; Tan et al., 2015; Tan et al., 2017), but who unfortunately were  
231 not in the cross-species sample of the group service study.

232  
233 In sum, among primates, proactive prosociality increases with the amount of allomaternal care  
234 found in a species and culminates in cooperative breeders. Since humans also qualify as  
235 cooperative breeders, it is most parsimonious to conclude that our prosociality is simply the  
236 result of cooperative breeding too, i.e. that the same regularity applies to nonhuman and human  
237 primates alike (Burkart et al., 2014).

238  
239 So far, primate proactive prosociality has mostly been studied from the dyadic perspective.  
240 However, in humans, it also encompasses the third-party context. Social evaluation studies  
241 address whether subjects, after observing how target individuals interact with others, avoid  
242 antisocial target individuals (and thus show a negativity bias) or prefer prosocial and cooperative  
243 target individuals (positivity bias). For instance, babies already have a preference for agents who  
244 help, rather than hinder others (Hamlin et al., 2007). Such studies are also increasingly done with  
245 non-human animals, as reviewed in Abdai and Miklosi (2016). For instance, in a study modeled  
246 after Hamlin et al. (2007), bonobos unexpectedly showed a preference for hinderers, rather than  
247 helpers (Krupenye and Hare, 2018). Abdai and Miklosi (2016) point out that there are still  
248 considerable conceptual and procedural issues in animal social evaluation studies, in particular to  
249 clearly demonstrate positivity biases. Negativity biases may be taxonomically far more  
250 widespread than positivity biases, since the need to avoid harm is universal whereas the need to  
251 cooperate is less common. Evidence for positivity biases (which correspond to the third-party  
252 perspective on prosociality) appears present too in several nonhuman primate species but is more  
253 elusive due to methodological issues, including the use of humans rather than conspecifics as  
254 target individuals (see Abdai & Miklosi 2016).

255

256 An important aspect of human prosociality directly follows from the fact that we evaluate people  
257 based on their prosocial behavior toward others. When deciding whether to behave prosocially or  
258 not, we are highly sensitive to a potential audience. We thus strongly care not only about to what  
259 extent others behave prosocially, but also about whether others perceive *us* as prosocial and thus  
260 reliable partners (Goffman 1959). In dictator games, which are used by behavioral economists to  
261 quantify other-regarding preferences, humans typically contribute a non-zero amount of money  
262 even if they could keep this money for themselves without any negative consequences, consistent  
263 with proactive other-regarding preferences (Fehr and Fischbacher, 2003). However, when the  
264 same game is played and stylized eye-cues are added on the answer sheet, these “watching eyes”  
265 elicit increased prosocial donations in such games, which reflects our strong concern for  
266 reputation (Nettle et al., 2013b). In corresponding experiments with chimpanzees, the same  
267 effect was not found, and the authors concluded that the extreme human sensitivity to cues of  
268 potential conspecific observation appears absent in chimpanzees (Nettle et al., 2013a, see also  
269 Engelmann et al., 2012).

270  
271 These findings suggest that chimpanzees are perhaps not the best species to look for such effects.  
272 Rather, these effects would arguably be most likely in habitually prosocial species, such as the  
273 cooperatively breeding marmoset monkeys. We therefore studied audience effects on prosocial  
274 behavior in this species in a naturalistic context, i.e. proactive food sharing with immatures  
275 (Brügger et al., 2018). Marmosets live in family groups, and all members contribute to infant  
276 rearing. When the infants are small, they are carried by all group members, and in big and well-  
277 established groups they sometimes are only handed back to the mother for breastfeeding. When  
278 the infants are older and ingest solid food, all group members share food with the immatures.  
279 This food sharing can take the form of proactive food sharing, i.e. food is offered to the  
280 immatures without previous begging, even when immatures are not even aware that a valuable  
281 food item has been found. To test for an audience effect on proactive food sharing, we quantified  
282 food sharing by helpers with immatures, either when they were alone with the offspring in a  
283 separate room or when the rest of the family was present. If they were sharing food to increase  
284 their reputation of being a good helper, one would expect them to share more when an audience  
285 was present than when they were alone with the offspring. The marmosets were sensitive to the  
286 audience, but in the opposite direction than expected: they showed *more* proactive food sharing  
287 in the absence of an audience. This effect is in fact consistent with the well-established bystander  
288 apathy (Latané & Darley 1969) or diffusion of responsibility (Bierhoff & Rohmann 2017) effect  
289 in humans. Thus, the marmosets perhaps shared more because they felt more “responsible” to  
290 fulfill the immatures’ needs when no one else was around, but in any case, these results show  
291 that they did not take advantage of this situation to engage in reputation management.

292  
293 To summarize, a genuine proactive prosocial concern is not unique to humans but we also see it  
294 in other primates, in particular in those who like humans engage in cooperative breeding.  
295 Nevertheless, to date there is no solid evidence that primates would take into account whether  
296 others behave prosocially or not. Thus, a third-party perspective on prosociality appears largely  
297 lacking in primates.

298  
299

### 300 **3.2 Conformity**

301  
302 A second key element of human morality is conformity. Conformity can be conceptualized in  
303 different ways (Van Leeuwen et al., 2015; Whiten and van de Waal, 2016a), from copying the  
304 majority, to copying a new behavioral variant while abandoning a personal preference for a  
305 previously acquired behavioral variant, to not only copying the majority but doing so with a  
306 disproportionate probability. Empirical evidence for such a disproportionate tendency is scarce in  
307 humans (Acerbi et al., 2016) and also among animals (Aplin et al., 2017). However, there is  
308 increasing evidence in primates for the other forms of conformity.

309  
310 Even though chimpanzees may sometimes be reluctant to give up their personal preferences for  
311 learned behaviors (Hrubesch et al., 2009), other studies have shown that a specific foraging  
312 technique seeded in a group will spread within this group. Intriguingly, even individuals who  
313 independently discovered an alternative solution would tend to stick to the seeded solution that  
314 was most prevalent in the group (Whiten et al., 2005; Whiten et al., 2007). A similar pattern was  
315 also found for capuchin monkeys (Dindo et al., 2009). Thus, depending on the specific context,  
316 primates can be either conservative (i.e. stick to their personal solution) or conformist (Hopper et  
317 al., 2011).

318  
319 Perhaps the most striking evidence for conformity in nonhuman primates comes from vervet  
320 monkeys. Immigrating males, who in their origin group developed a strong preference for one  
321 type of novel food (artificially colored blue or pink maize of identical taste), immediately  
322 changed their preference after immigrating in a group where the majority of individuals preferred  
323 the other color (van de Waal et al., 2013; Whiten and van de Waal, 2016a). The function of this  
324 kind of informational conformity is most likely to quickly adapt to the local knowledge of the  
325 new group. Strong informational conformity also enables naïve individuals to socially learn  
326 cognitively opaque skills where the causal role of each single step in achieving the overall goal is  
327 not obvious. Thus, a preference for social knowledge over private knowledge, or an urge to  
328 conform can be understood in the service of self-interest, i.e. to acquire reliable information  
329 about the world.

330  
331 An interesting phenomenon, which questions whether all primate conformity is informational,  
332 has recently been reported from the same vervet monkey population. In one of the study groups,  
333 a small number of subordinate females split off to form its own group. In the original parent  
334 group, the individuals preferred blue maize. However, since the females from the future splinter  
335 group were subordinate, they had not always had access to the preferred food, and therefore also  
336 had repeatedly sampled the pink maize, with some having eaten even more pink than blue maize  
337 in the parent group. After group fission, all these previously subordinate females could now  
338 freely express their preference in the new splinter group, and continued to show a strong  
339 preference for blue maize (even after 4 month, they ate 100% of the time blue maize). They thus  
340 still conformed to the preference of the parent group even though they were no longer  
341 surrounded by individuals from the parent group, and even though there was no difference in the  
342 taste between the blue and the pink maize (in fact, some never even knew that one or the other  
343 color was unpalatable). There can thus be remarkable resilience in preferences established

344 through social learning, at least in vervet monkeys, and the authors propose the notion of social  
345 conformity, i.e. that individuals act like others to achieve a social function and simply be “like  
346 others”, rather than to achieve an informational benefit (van de Waal et al., 2017). In fact, being  
347 more similar to others may facilitate group integration, and increasing evidence suggests that  
348 primates indeed prefer others who are more similar to themselves as social partners (Paukner et  
349 al., 2009; Massen and Koski, 2014; Capitanio et al., 2017; Ruch et al., 2018).

350  
351 In sum, at the individual level, several instances of conformity can be found in primates, which  
352 can result in informational but perhaps also social benefits. But what about the third-party  
353 perspective? The third-party perspective becomes obvious in normative conformity, which  
354 consists not only of an individual’s urge to conform (the individual perspective), but also of the  
355 expectation of others that the individual converges to their group’s norms (the third party  
356 perspective). In general, as we will review below, normative conformity is absent in nonhuman  
357 primates, but the situation may be slightly more differentiated, depending on the specific norm  
358 that is at stake. In the following sections, we therefore turn to specific contents of potential  
359 norms in primates, making the fundamental distinction between (putative) social norms that have  
360 a universal and presumably biologically anchored vs. an arbitrary and culturally variable content.

361

362

### 363 **3.3 Social norms I: universal, biologically anchored contents**

364

365 The contents of morality are norms, which permeate every aspect of human life and  
366 systematically guide our behavior (Gelfand and Jackson, 2016). Social norms are notoriously  
367 difficult to define. They broadly refer to implicit or explicit rules that prescribe behavior, whose  
368 violation elicits social sanctions. They range from being more or less compulsory (e.g. not to  
369 murder vs. to eat with chop-sticks), to being just common sense, as in conventions. Their content  
370 can be arbitrary and therefore culturally variable, or universal and biologically anchored. The  
371 two distinctions often overlap, but not always. For instance, not to commit murder is most likely  
372 compulsory and universal in most societies, but also more arbitrary norms such as taking off  
373 one’s shoes before entering a house can be compulsory in a given society. Universal norms,  
374 however, tend to be compulsory in most societies (for a more detailed discussion of the nature of  
375 norms, see also Rudolf von Rohr et al., 2011).

376

377 Identifying universal moral norms in humans is still an ongoing endeavor (e. g. Barrett et al.,  
378 2016) but they minimally include the contents of *not harming infants*, *avoiding inequity*, *caring*  
379 *for one’s own offspring*, and *avoiding incest*. Some evidence suggests that they may be present at  
380 least in dyadic, but sometimes even in third-party contexts in nonhuman primates too. In dyadic  
381 contexts, they are observed when interaction partners expect each other to behave in a specific  
382 way consistent with a potential norm, whereas in third-party contexts, uninvolved bystanders  
383 who observe interactions between other dyads would expect these dyad partners to interact in  
384 this way, and experience disapproval or even show moralistic aggression upon violations of this  
385 expectation.

386

387 Among chimpanzees, for instance (but also among many other primates), infants usually enjoy  
388 high levels of tolerance and are hardly ever harmed by others. However, exceptions exist, which  
389 eventually even include infanticide (Townsend et al., 2007). Naturalistic observations show that  
390 bystanders who observe harmful behaviors often show strong reactions (Goodall, 1971; de Waal,  
391 1991), such as waa barks (protest vocalizations: Clay et al., 2016), and even direct interventions  
392 in the form of policing (Rudolf von Rohr et al., 2012). Harmful behaviors toward infants elicit  
393 particularly strong reactions (Goodall, 1977; Townsend et al., 2007), such as interventions and  
394 defense of the mother-infant pair by multiple group members, sometimes culminating in highly  
395 dramatic situations. These behaviors are consistent with a strong third-party bystander reaction  
396 toward infanticide. However, it is important to note that these bystanders are not completely  
397 uninvolved, since they (e.g. other mothers with dependent offspring) may still have a very strong  
398 individual stake in discouraging infanticide by group males. We therefore presented captive  
399 chimpanzees with video clips of infanticide committed by completely unaffected third parties  
400 (conspecifics in the wild). The chimpanzees indeed clearly reacted to this norm violation: they  
401 paid far more attention to these clips compared with control videos depicting hunting scenes  
402 (lethal aggression against small hetero-specific monkeys), grooming and nut cracking, or  
403 displays and aggression between adult chimpanzees. However, this expectation violation as  
404 evident in looking times did not also translate in higher levels of arousal. Together, these results  
405 suggest that chimpanzees do indeed react strongly toward the violation of the putative norm “do  
406 not harm infants”, including indignation-like expressions, but only if this happens in the within-  
407 group context. As truly non-involved bystanders, they still appear to detect such a putative norm  
408 violation, but this is not accompanied by overt disapproval (e.g. no arousal, and no waa-barks  
409 (Rudolf von Rohr et al., 2015). It is worth pointing out that in humans too, morality tends to be  
410 parochial in that we feel stronger about norm violations within the group (Fessler et al., 2015, but  
411 see Piazza and Sousa, 2016), and that punishment of norm violations is often not altruistic  
412 (Guala, 2012).

413  
414 Vervet monkey mothers too appear to expect that others don't harm their infants, and adult males  
415 behave accordingly (Hector et al., 1989). In an experiment, vervet males showed less aggression  
416 toward an infant if the infant's mother could see them compared to when not. Furthermore,  
417 mothers were more aggressive towards males after separation when they had observed the male  
418 behaving aggressively to the infant through a one-way mirror. Thus, vervet mothers appear to  
419 evaluate the males based on their behavior towards infants (and can act accordingly, because of  
420 minor sexual size dimorphism), and males adjust their behavior toward infants depending on  
421 whether they could be seen by the mothers. But again, mothers don't count as truly non-involved  
422 bystanders because they have high stakes in the wellbeing of their infants.

423  
424 Inequity aversion is another content particularly closely related to morality (Decety and Yoder,  
425 2017). It can take the form of disadvantageous inequity aversion, i.e. an aversion against being  
426 treated unfairly, such as receiving a *lower* reward for the same amount of work compared to a  
427 partner, which is egocentric. Alternatively, it can be advantageous inequity aversion, i.e. an  
428 aversion against obtaining a reward that is *higher* than that of a partner, which is therefore

429 allocentric. In humans, both forms can already be observed in 3 year old toddlers (Ulber et al.,  
430 2017). Inequity aversion has also been reported in a variety of primate species (reviewed in  
431 Talbot et al., 2016; but see Engelmann et al., 2017; Ulber et al., 2017), but only in the egocentric  
432 form (but see Brosnan et al., 2010).

433  
434 Disadvantageous inequity aversion is consistent with an individualistic perspective on one's own  
435 benefit, whereas advantageous inequity aversion includes a prominent prosocial element and is a  
436 particularly strong indicator for a concern with equity per se. However, both types of inequity  
437 aversion include personal involvement, which can automatically trigger a self-serving bias that  
438 may overshadow equity preferences. This methodological problem can be overcome by  
439 quantifying inequity aversion in third-party contexts. In third-party contexts, the question is  
440 whether individuals have a preference for the fairness between third parties, and self-serving  
441 biases therefore no longer interfere. This can be a preference for a fair distribution of rewards  
442 (i.e. fifty-fifty in dyads), but also a preference for distributions that take into account merit and  
443 wealth, which has been shown to be already present in young children (Kanngiesser and  
444 Warneken, 2012; Paulus, 2014). We are not aware of any work on this among nonhuman  
445 primates.

446  
447 A final universal and biologically determined content of human social norms is incest avoidance.  
448 Incest avoidance is often construed as a cultural taboo (Turner and Maryanski, 2015), and we  
449 have strong third-party attitudes toward it, for instance including indignation and disgust in the  
450 case of sibling sex (Fessler and Navarrete, 2004). Nevertheless, incest avoidance is also practiced  
451 by nonhuman primates (Bischof, 1975; Pusey and Wolf, 1996), and is particularly strong in  
452 callitrichid monkeys (marmosets and tamarins: Saltzman, 2003; Saltzman et al., 2004). For  
453 instance, opposite-sex callitrichid siblings can be kept for years without them engaging in  
454 reproduction or sexual behavior, and also fathers show no sexual interest in their reproductively  
455 mature daughters. These preferences are especially adaptive in the callitrichid social system  
456 because offspring of both sexes often remain in their natal group for extended periods of time  
457 and help raise their younger siblings. But again, unlike in humans (Fessler and Navarrete, 2004),  
458 there is no evidence that other group members or even non-involved third parties would object to  
459 close kin having sexual relationships (although we are not aware of any direct test of this idea).

460  
461 Taken together, non-human primates often have clear expectations about how others should  
462 interact with them. In fact, we can readily add other examples, such as the expectation of  
463 dominants regarding how subordinates should behave towards them, or how a partner should  
464 behave during playful interactions. Thus, natural social rules appear ubiquitous in primates and  
465 in fact in other gregarious species too, but a crucial limitation in most cases is that these rules are  
466 applied only to actual or potential partners but not in third-party contexts when uninvolved  
467 bystanders are concerned. Exceptions may be found in some specific contexts, such as shown in  
468 the case of infanticide in chimpanzees, who show strong bystander reactions, as long as norm  
469 violations occur within their social group but not when they occur in complete stranger  
470 conspecifics. Similar reactions are not unlikely in other primate species susceptible to male  
471 infanticide (van Schaik and Janson, 2000).

472

473

### 474 **3.4 Social norms II: arbitrary, culturally variable contents**

475

476 Arbitrary, culturally variable norms are particularly salient elements of human morality, and at  
477 least in part responsible for the traditional view that morality is a purely cultural innovation (de  
478 Waal, 2006; Haidt, 2013). Nevertheless, cultural behavioral variation has also been described for  
479 nonhuman primates and other animals (Whiten and van de Waal, 2016b). Behavioral innovations  
480 can spread via social learning within populations, which leads to cultural differences in  
481 behavioral repertoires, and these are particularly large in great ape species such as chimpanzees  
482 (Whiten et al., 2017) and orangutans (van Schaik et al., 2009). These cultures differ from human  
483 cultures in that they are not cumulative and also not symbolic (Gruber et al., 2015).

484

485 As discussed in detail in 3.2, such primate cultures can be supported by strong informational and  
486 perhaps social conformity. Nevertheless, they are not supported by normative conformity. In  
487 other words, individuals may be eager to conform to other group members even in the case of  
488 arbitrary, culturally variable behaviors (e.g. eating pink instead of blue corn in vervet monkeys:  
489 van de Waal et al., 2013, or specific tool use techniques in chimpanzees: Luncz and Boesch,  
490 2014), but the group members who are performing the majority behavior appear to have no stake  
491 in whether others conform or not, let alone show signs of indignation or even punishment of non-  
492 conformers. This might also explain why conformity can also be absent in cultural behaviors, as  
493 for instance in high-arm grooming among chimpanzees (Wrangham et al., 2016).

494

495

## 496 **4. Conclusions**

497

498 Our goal was to provide an overview over the current state of the art on research into the  
499 evolutionary origin of morality (see also van Schaik et al., 2014). We did so by analyzing both its  
500 ultimate function in our own species, and investigating the phylogenetic origin of elements of  
501 human morality in nonhuman primates.

502

503 We propose that the ultimate function of human morality is best understood as a straightforward  
504 adaptation that enabled the fundamentally interdependent lifestyle of our hunter-gatherer  
505 ancestors. Even though full-blown morality is most likely unique to humans, several of its key  
506 elements can be found in nonhuman primates and some other animals. Our goal was to provide  
507 an overview of the occurrence of such elements in nonhuman primates, to understand under what  
508 conditions they emerged during evolution, and to better delineate in which ways human morality  
509 is unique (Figure 1). We therefore focused on two key components of morality, i.e. a prosocial  
510 concern and conformity, and the contents of natural and arbitrary, cultural norms. These  
511 elements are arguably necessary and crucial for the emergence of morality, but not sufficient.  
512 Additional elements include language (discussed below), parochialism (Baumgartner et al.,  
513 2012; Fessler et al., 2015), and perhaps coalitional psychology (DeScioli and Kurzban, 2013).  
514 For the elements discussed in this paper, there is evidence from nonhuman primates and

515 sometimes from other animals as well. The contents can be highly species-specific, adapted to  
 516 the social requirements of a given species. An evolutionary perspective on moral behavior  
 517 therefore suggests that with regard to content, it may be useful to distinguish between human  
 518 morality, chimpanzee morality, marmoset morality, and so on.

519  
 520  
 521  
 522

		<i>Individualistic or 2<sup>nd</sup> party perspective</i>	<i>3<sup>rd</sup> party perspective</i>
		<b>Elements of morality</b>	<b>Mechanisms</b>
Present, linked to cooperative breeding	Absent, no concern for reputation, no reputation management		
<b><i>Conformity</i></b>			
Present, informational (and perhaps social) conformity in at least some primates	Absent, no normative conformity		
<b>Contents</b>	<b><i>Social norms I: universal, biologically determined contents e.g. “do not harm infants”, “avoid inequity”, or “avoid incest”</i></b>		
	Present, high tolerance toward infants and egocentric inequity aversion in most primates, incest avoidance in callitrichids and others	Present for infanticide in chimpanzees, and perhaps other primates, but only in within-group context	
	<b><i>Social norms II: arbitrary, culturally variable contents</i></b>		
	Present, behavioral traditions resulting from informational and social conformity	Absent, no normative conformity, no concern for reputation, reputation management	

523  
 524 **Figure 1:** The presence of elements of morality in non-human primates.

525  
 526  
 527 Intriguingly, some of these elements of morality are not necessarily most prevalent in our closest  
 528 relatives, the great apes. In particular the key element of prosocial concern is stronger in primates  
 529 that show more similarities in social structure with humans, namely the cooperatively breeding  
 530 callitrichid monkeys. The lives of humans are very much different from that of other great apes,  
 531 in modern societies as in hunter-gatherers. Compared to nonhuman great apes, every domain of

532 our lives is built on high levels of interdependence (van Schaik and Burkart, 2010b; Tomasello,  
533 2016), from subsistence (foraging) and institutionalized activities to rearing children.  
534 Nevertheless, a high degree of interdependence is not unique to humans, but also present in other  
535 primates, in particular in cooperatively breeding callitrichid monkeys who also raise their  
536 offspring with the help of all group members (Hrdy, 2009). It thus appears that some of the  
537 elements of morality evolved convergently in highly cooperative, interdependent species (such as  
538 humans and callitrichid monkeys) but not in more individualistic ones (such as chimpanzees).  
539 Based on comparative studies, we have argued that interdependence during infant rearing is key,  
540 but others place greater emphasis on the role of interdependence during foraging (Tomasello et  
541 al., 2012; Tomasello and Gonzalez-Cabrera, 2017). Note, however, that arguably, the latter could  
542 only emerge once some basic proactive prosociality that facilitates cooperation and sharing had  
543 evolved in the context of shared offspring care (van Schaik and Burkart, 2010a).

544  
545 Obviously, cooperatively breeding callitrichid monkeys don't have full-blown human morality,  
546 perhaps because more cognitively demanding elements of morality appear well beyond the  
547 capacities of these small brained monkeys. Systematic comparative analyses confirm that  
548 cognitive abilities across nonhuman primates are correlated with brain size, and humans fit this  
549 pattern too (Burkart et al., 2017a). Accordingly, the very big brained great apes have many  
550 remarkable cognitive abilities, and a valid working hypothesis is that it was the unique  
551 coincidence in our ancestors of two elements that enabled full-blown morality: the strong  
552 cognitive abilities, supported by big brains and inherited from our common ancestors with the  
553 other great apes on the one hand, and on the other hand our strong prosocial concern, which was  
554 added convergently because our ancestors started to engage in cooperative infant care sometime  
555 after they had diverged from the other great ape lineage (Burkart et al., 2009; Burkart and van  
556 Schaik, 2016). For instance, great apes, but not callitrichids, appear to show disadvantageous  
557 inequity aversion in that they are upset when they receive a lower-value reward compared to a  
558 social partner (Talbot et al., 2016). This suggests that they are accurately keeping track of each  
559 other's efforts and the amount of reward obtained for it. However, only when this cognitive  
560 precondition is coupled with a stable prosocial concern for others (as it is the case in our own  
561 species only) may we also see disadvantageous inequity aversion, or an aversion from the  
562 perspective of an uninvolved bystander towards inequity between two social partners.

563  
564 A striking pattern for all these elements is that even though they are present in at least some  
565 primate species, they are fundamentally restricted to the individual perspective in nonhuman  
566 primates (Figure 1). We can imagine three possible, non-exclusive explanations for the  
567 emergence of the third-party perspective in human morality. First, the third-party perspective  
568 may simply require even more sophisticated mentalizing abilities and perhaps language.  
569 However, a third-party perspective is not even taken systematically by chimpanzees, for whom  
570 increasing evidence for quite impressive mentalizing abilities is available (Krupenye et al.,  
571 2016). Likewise, the case of human psychopaths suggests that language per se is at least not a  
572 sufficient condition for full-blown human morality (Hare, 1999).

573

574 A second possible explanation for the origin of the third-party perspective, in particular in the  
575 case of conformity, emerges in the face of increasing evidence for assortative preferences in  
576 primates (see also Haun and Over, 2015 for a similar argument). This body of evidence suggests  
577 that primates have a general preference for partners that are like themselves (Paukner et al.,  
578 2009; Massen and Koski, 2014; Capitanio et al., 2017; Ruch et al., 2018). In situations of high  
579 interdependence at the group level, it is important for individuals to have reliable relationships  
580 with all group members, which can result in a preference for ego to conform to the behaviors of  
581 the group. However, it may also mean that the group members themselves now have a stake in  
582 newcomers to conform, i.e. normative expectations. In other words, similarity, for instance in  
583 vocal communication, may turn into a tag for affiliation and cooperation (Cohen et al., 2012;  
584 Ruch et al., 2018) and signal an individuals' readiness to be a reliable member of the group,  
585 which is important for all group members. For the individual, this will lead to an increasing urge  
586 to conform not only for informational, but also for social reasons (van de Waal et al., 2017). In  
587 other group members, it will lead to the normative expectation that a specific individual indeed  
588 conform. This explanation is also consistent with studies that find only weak evidence for the  
589 idea that group norms are the only or principal explanation for third-party moral judgments in  
590 humans (Krasnow et al., 2012; Delton and Krasnow, 2017), or that norm-based punishment is  
591 not necessarily altruistic (Guala, 2012).

592  
593 Finally, the third-party perspective may simply have emerged as a byproduct of the increasing  
594 importance of indirect reciprocity, which is an essential element of the ecological  
595 interdependence of human foragers. Indirect reciprocity critically involves the observation and  
596 evaluation of interactions between third parties, so as to assess the suitability of each participant  
597 as recipient of prosocial actions and thus as a partner in exchanges. Once such evaluations of  
598 third parties are shared with others in the cooperation network through language, they can easily  
599 acquire the same emotional status as judgments about direct partners, i.e. second parties.

600  
601 Language may thus have played a crucial role for the evolution of full-blown human morality.  
602 First, as just argued, it amplifies the importance of reputation effects, because misbehavior can  
603 be made public via gossip to the entire group. Language thus likely is the key driver for our  
604 obsession with reputation (see also van Schaik & Burkart, in press), and that even most subtle  
605 cues of being observed can significantly influence our behavior (Nettle et al., 2013b). Second,  
606 language enables negotiation and therefore the formation of formal, explicit and institutionalized  
607 rules, and thus can lead to culturally modified contents of social and moral norms. Linked to this,  
608 language and language-based moral reflection may well be responsible for the finding that the  
609 truly independent third-party perspective (i.e. also including out-group contexts) is only found in  
610 humans. Unreflected moral judgments, emotions and preferences are typically highly parochial:  
611 humans spontaneously care most about their in-group, in particular when we are under duress  
612 (Baumgartner et al., 2012; De Dreu et al., 2015; Fessler et al., 2015). This in-group bias can be  
613 overcome when we manage to view out-group individuals at least as potential in-group members,  
614 but also via explicit, language-based moral reasoning.

615

616 Finally, through language, spontaneous behavioral predispositions themselves can secondarily  
617 become the content of a norm, via representational redescription of pre-existing behavioral  
618 tendencies (Karmiloff-Smith, 1992). Above, we have exemplified this for the case of incest  
619 avoidance, a behavioral predisposition present in animals that in humans also takes the form of a  
620 cultural taboo (Turner and Maryanski, 2015). However, representational redescription also  
621 occurs in the case of the behavioral mechanisms of morality per se, such as prosocial concern. In  
622 this case, our prosocial concern may appear the result of purely cultural processes linked to  
623 language, whereas prosociality tests with primates have shown that it is more likely the simple  
624 convergent result of cooperative breeding, a general pattern that applies broadly.

625  
626 In sum, we find that human morality had an important adaptive function in our hunter-gatherer  
627 ancestors in that it undergirded the extraordinarily interdependent lifestyle. Nevertheless, human  
628 morality was not invented from scratch in our hominin ancestors but could build on a rich set of  
629 pre-adaptations. A critical transition was the transformation of these elements to appear not only  
630 in individualistic and second-party contexts, but also in true third-party constellations. Based on  
631 evidence from the primate behavior and cognition literature, we are just beginning to understand  
632 how this transition and thus normativity emerged. Many new hypotheses emerge from this  
633 endeavor and will need to be tested in the future.

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