

The evolution of human normativity: the role of prosociality and conformity

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Abstract

Normative behavior is a human universal that is intimately linked to morality. Morality is an adaptation to the specifically human subsistence niche of hunting and gathering, which is skill-intensive and therefore relies on transmission of opaque knowledge and involves critical interdependence, reliance on coordinated division of labor, and synchronized collective action. This lifestyle requires the presence of a variety of emotions that coevolved with it as the proximate mechanisms enabling this adaptive function. The high-urgency feel to many of these emotions reflect their functional importance: it serves to give them priority over other motivations. It is also what, to us, and makes them recognizable as moral. The key components of human morality are (1) prosocial emotions, and (2) an urge to conform. Together, they produce the urge to comply with moral norms. Normativity is thus an integral part of human morality. It evolved when two preferences came together. Strong informational conformity, needed to enable the transmission of opaque knowledge, was already present in the anthropoid primate ancestors of hominids and hominins. The added component evolved with the evolution of strong interdependence: a strong concern for one's reputation and fear of punishment, and thus strongly prosocial emotions. Thus, the emergence of normativity in our ancestors does not require a special explanation: it was an automatic byproduct of the emergence of moral behavior in our ancestors.

Introduction

An evolutionary biologist confronted with any persistent behavior, for instance food choice and diet selection, would develop the working hypothesis that it represents an adaptation molded by natural selection. The evolutionary approach, moreover, presupposes that function and mechanism fit together (Tinbergen 1963): natural selection for a particular adaptive function automatically implies selection on particular mechanisms. Thus, the presence of particular emotions must reflect the presence of evolved functions.

This evolutionary approach is not necessarily incompatible with the presence of major cultural variation in this behavior (for instance, diet, processing techniques), because one major adaptive strategy is phenotypic plasticity, which in the case of behavior can be called flexibility. This flexibility is culturally supported in various primates (Whiten 2012; van Schaik 2013). In the case of food selection and diet, for instance, we see major cultural variation in food processing techniques, including technologically supported techniques (Sanz et al. 2013) and geographic variation in diet (Bastian et al. 2010).

Obviously, such cultural elaborations of adaptive human behavior are especially pronounced in humans (Richerson & Boyd 2005).

In the case of human moral behavior, this approach leads to the hypothesis that morality is an adaptive behavior that is regulated by a set of preferences (predispositions to action with emotional overtones) for prosociality and conformity, and functions to support the uniquely derived form of human cooperation (esp. *coordinated activities, synchronized collective action* and *indirect reciprocity*). Extensive cultural variation in the content of moral norms and of realized moral preferences is entirely compatible with this hypothesis (cf. Hauser 2006; Monroe et al. 2009). Below, we sketch this hypothesis to arrive at an explanation of normativity; a full account of this hypothesis and its empirical basis can be found van Schaik et al. (2014).

The non-biologist reader may wonder why this obvious idea is not much better known, especially because Darwin (1871) himself had already proposed the basic outline of this hypothesis. Instead, most scientists, including eminent biologists have traditionally subscribed to what de Waal (2006) has called veneer theory, namely that human morality is “a cultural overlay, a thin veneer hiding an otherwise selfish and brutish nature,” in other words a recent innovation that is maintained purely culturally (and in the absence of the civilizing influence of culture would expose our brutal nature). Perhaps the main reason for this neglect of a biological foundation was that the functional context in which morality evolved – cooperative foraging, i.e. hunting and gathering – is hardly known today, and also quite different from the presumed ancestral state, as exemplified by the extant great apes, especially chimpanzees.

Understanding the hypothesis requires that we briefly summarize the lifestyle of mobile foragers, which is most representative for the conditions for which human sociality has evolved (Hill 2002; Hill et al. 2011; Johnson & Earle 2000; Kaplan et al. 2009; Marlowe 2005, 2010; Moffett 2013). Mobile foragers live in bands of about 25-50 people of all ages and both sexes who share a camp. Camps are moved multiple times per year. Camps of the same macro-band, also called community, regularly exchange members. Total community size ranges in the hundreds or at most a few thousand. All foragers form pair bonds that are socially recognized (i.e. marriage); they are freely formed or dissolved. Polygyny is allowed but rare.

Men hunt, fish or obtain honey, whereas women gather: the sexual division of labor. For both sexes, their foraging activities may be coordinated or synchronized, but most of the time they are cooperative in at least some sense. Depending on their technology and the prey species, men may hunt in groups or alone. The food obtained by men, in particular the meat from larger animals, is shared widely with other families in a camp. Gathered food is generally only shared within families.

Parents, but also many others, and prominently including grandmothers, look after babies and young children. Children are free to play and roam, and gradually learn their skills. The foraging niche is so skill-intensive that women reach peak foraging efficiencies (yields per unit time) in their mid-20s, whereas men do so about a decade or even more later. Major decisions are made collectively, sometimes after long discussions. The social system is egalitarian, with the majority of men jealously preventing one among them to emerge as leader, except transiently in times of war. Men gain status by being generous.

The following section will briefly present the main outline of the adaptive hypothesis, focusing especially on the internal emotional drivers of moral behavior. In the next section, we will focus on the function and evolutionary origins of the normative aspects of morality.

Before we do so, however, we must state clearly what our aim is and also what it is not. Our aim is naturalistic, and thus entirely descriptive. We intend to explain the origins of the behavioral expression of morality (moral action) and its underlying moral emotions and intuitions, and more specifically the origin of the moral norms in which moral action is embedded. It is expressly not our aim to argue that all the other aspects of morality – among others, moral reasoning and moral judgment, or the concept of moral agency – can be directly reduced to this biological foundation. However, our account may help to identify the fundamental building blocks (the moral axioms, as it were) of moral reasoning, and explain why moral norms almost inevitably contain compromises. This extension may have implications for the discussion surrounding the evolutionary debunking of morality (e.g. Joyce 2007; Street 2006).

Morality as a biological adaptation

Folk morality, i.e. the actual behavior considered moral by the average human being, is often seen as the key ingredient of social life: it is what makes social life possible. It can be regarded as the behavioral outcome of two basic underlying preferences: (1) a preference for prosocial behaviors, both proactive and reactive, especially toward in-group members, and (2) a preference to conform to a society's norms. This dichotomy corresponds closely to the two moral domains proposed by Haidt (2007, 2012), which he calls “contractual” and “beehive,” respectively. An exception is the latter's purity or cleanliness element, which we suspect to be of more recent origin, following the adoption of sedentary life.

Both preferences emanate from strong emotions, which have a feeling of urgency or priority, as if they are privileged over other feelings. Emotions can be regarded as the subjectively experienced side of what can be more objectively described (in ethological terms) as motivations, or more colloquially as drives. Morality thus refers to all behaviors that have a strong emotional feel to them, which serve to give them a higher priority than competing motivations. As a result, the contents of folk morality may be broader than the content considered by philosophers. In particular, the need to care for relatives, while avoiding inbreeding with them, is clearly accompanied by strong emotions, yet is not necessarily considered part of morality by contemporary moral philosophers.

The relevant players can be directly involved as actor (first party, or A in Figure 1) or as recipient or responder, B (second-party), but also as a third party, i.e. a non-involved bystander from the same group, C, with a social bond to A, or without any bond to A (E-G), or even more generally, as a completely non-involved, out-group third party (K-Q). The role of third parties is clearly strongest in humans, and is linked to the importance of indirect reciprocity, and its mechanism: reputation (and although reputation is uniquely important in humans, it may rely on older mechanisms: Anderson et al. 2013; Kawai et al. 2014). In indirect reciprocity, in-group third parties, C, observe interactions between others and decide, based on their evaluation of these interactions,

whether or not to engage in cooperative interactions with A in the future. If the role of C is important, we must expect that selection included the responses of C into the behavioral decisions by A. As a result, even the emotions that at the proximate level are internally generated and directed at second parties, may have ultimately (over evolutionary time) been co-shaped by third parties.

Because third-party responses may have affected the evolution of first-party preferences, we will have to discuss moral preferences more generally before we can focus on the normative aspects. This second part will therefore inevitably be somewhat redundant with the first.

The prosocial element

Table 1 lists the major functional contexts in which the major moral emotions evolved, the corresponding behaviors and their underlying motivational and emotional mechanisms. These moral emotions, and the adaptive behaviors that they enable, are a mix of old (ancestral) and new (derived). Human-specific morality, as defined here, is proposed to be an adaptation undergirding the unusual and highly derived subsistence niche into which our ancestors gradually evolved over the past 2 million years: interdependent hunting and gathering, together called foraging. Thus, the first two functional contexts are derived in humans relative to great apes. They contain moral emotions linked to cooperative breeding (proactive prosocial motivations, empathy) and those linked to coordinated and synchronous collective action (shared intentionality, and a preference of conformity). The importance of food sharing is reflected in emotions like concern with reputation and allocentric inequity aversion.

This straightforward reverse-engineering analysis explains why prosocial preferences are at the core of human-specific morality. The function is to maintain the unique form of direct and indirect reciprocity that evolved in human foragers and so enabled their interdependent lifestyle. Individuals help (provision, care for) immatures and those adults who have established and maintained a good reputation. Being cared for in case of need is a key requirement in an ecological niche characterized by interdependence on a variety of time scales (Hill & Hurtado 2009). A good reputation is essential for this, as shown in many sources (review: Hrdy 2009; Marlowe 2010). Reputation is enhanced by both prosocial preference and group-level norm compliance: people are nice to those with good reputation (Milinski 2006).

The function of establishing and maintaining one's reputation is partly represented by the actor in the form of a psychological goal. People are generally explicitly concerned about their reputation, and in modern state societies this concern is generally seen as legitimate, as shown by laws allowing individuals to sue others for slander. Indeed, reputation management already starts at an early age in humans (Rochat 2012).

But much of the concern for reputation is also subconscious, as shown by a variety of experiments in which humans show a high sensitivity to the perceived presence of an audience, which elicits greater proactive and reactive prosociality (Bateson et al. 2006; Burnham & Hare 2007; Haley & Fessler 2005). Incidentally, such audience effects on prosociality are not found among chimpanzees (Engelmann et al. 2012; Nettle et al. 2013), and are thus almost certainly derived in humans.

It can be argued that the safest tactic to maintain a good reputation is to have a strong intrinsic motivation to engage in proactive prosociality. If the costs of discovery are unacceptably high, one does better to avoid temptations altogether than by weighing the risks each time, and perhaps making a mistake. Selection has therefore assigned a high priority to these prosocial moral emotions, experienced as a sense of high urgency or sense of duty.

Privileging these motivations over others is especially important because they often occur in situations of low situational urgency, where signals of need may not be present whereas other competing selfish stimuli (the opportunity, also known as temptation) are immediately and clearly present. As a result, we generally do the right thing, except in cases of unusual hardship (and thus a strong motivation toward the selfish goal) or where the situation is perceived as carrying an unusually low risk of detection. The latter is achieved by our high subconscious sensitivity to the possible presence of an audience.

Another important motivation to uphold the fair sharing of large food items, e.g. a mammalian carcass that is acquired to be divided among group members, is allocentric inequity aversion. Among animals, we tend to see some form of so-called advantageous (egocentric) inequity aversion especially in those species where individuals form social bonds with non-relatives (Brosnan 2013; but see Bräuer & Hanus 2012). However, the disadvantageous (allocentric) version, where ego protests when alter receives a smaller share than seems fair, is unique to humans (Fehr & Schmidt 1999).

The conformity element

Turning now to the collective element, we see two distinct behavior patterns: coordination and synchrony. They are both intrinsically cooperative, but differ in the details of the behavior and thus their regulation. In coordination, two or more individuals perform different but complementary actions, and thus share a common goal; these individuals may, but need not be, in close proximity. Coordination makes the sexual division of labor possible. It also underlies the specialization and trade seen among more recent sedentary human societies. Coordination requires trust and basically the same underlying mechanisms as reciprocity and indirect reciprocity discussed above.

Synchrony refers to the simultaneous performance of the same or complementary actions in close proximity, and is thus a key requirement for collective action during some forms of hunting, gathering, processing, shelter production, raiding, etc. Motivating synchronous behavior is homophily, the preference for being behaviorally similar to dyad partners (Haun & Over 2013), which in the dyadic context may also be expressed as over-imitation and reflects (but perhaps also contributes to) the strength of the social bond. Homophily probably also underlies the chameleon effect or mimicry, which refers to the tendency to adopt the postures and gestures used of a partner during social interaction (Chartrand & van Baaren 2009), and which has a mutually enforcing effect on social bond strength (people who show mutual mimicry like each other more, and people who like each other show more mimicry).

Empirical evidence abundantly shows that synchronized action, such as marching or joint dancing, singing or music making, produces mutual trust and thus the feeling that one is a member of a supportive alliance (Fessler & Holbrook 2014). It therefore elicits a willingness to engage in joint tasks

(synchronized or coordinated), including joint aggression toward out-groups (Wiltermuth & Heath 2009). Thus, homophily and its behavioral product, synchrony, interact and mutually reinforce each other.

Both synchrony and coordinated action require as an underlying motivation the active preference for having a common goal, or shared intentionality (Tomasello 2009; Tomasello et al. 2005). There is no evidence for anything like it in nonhuman animals, although a satisfactory operational definition that would allow us to definitively rule it in or out among nonhumans is still lacking (see Schmidt & Rakoczy, this volume).

A more basic underlying motivation for both coordination and synchrony is the preference for conformity (in a more narrow sense), the tendency to forego personal information in favor of the cultural variant used by the majority. This leads the individual to perform particular actions in the same way as the majority does (producing similarity in behavioral repertoires) or to dress and act similarly. Conformity is therefore an independent but complementary influence on synchrony and coordination. An individual's urge to conform is thus another important underlying emotion. (We will discuss conformity in more detail when we examine the evolution of normativity below.)

We can also speak more broadly of conformity when we refer to all these elements together (synchrony, coordination, conformity), because they together make coordinated and collective cooperation possible. Normative conformity is subject to the internal regulators (homophily, shared intentionality, the urge to conform) mentioned above, but also to external proximate controls (Table 2), which are exactly the ones that make it normative.

On the external control side, people are expected to be forever alert to the presence of free riders or cheaters (Cosmides et al. 2005). We may therefore have a tendency to stress cheater detection more than praising the prosocial contributors: gossip is more often malicious than positive. This tendency may be adaptive as well. The cost of missing beneficial acts by a person with a good reputation may be negligible compared to not noticing inappropriate selfish acts by someone with an otherwise good reputation. In fact, one would expect people to be especially keen on identifying norm transgressions when there is a suspicion that someone's good reputation may be undeserved.

The second major component of the external control of normative conformity is punishment by either damaged second parties or third parties (extensively discussed in Kappeler et al., this volume). People experience anger when witnessing norm violations and have an urge to punish the transgressors if they can do so without incurring too high a cost, in second-party roles, but also in third-party roles. Indeed, we tend to derive satisfaction from it (de Quervain et al. 2004).

Punishment shows a striking difference between small-scale and large-scale societies. In foragers and perhaps other small-scale (face-to-face) societies, most punishment is in the form of dyadic (second-party) shunning and gossip (Marlowe 2009), perhaps to leave the door open for restorative behaviors. When punishment goes beyond this, it is often collective, reserved for the rare cases where particularly bad (violent) repeat norm violators are expelled or even killed (Boehm 1999; 2012). Regular third-party punishment is only common in large-scale societies (Fehr & Fischbacher 2004). Its absence in chimpanzees (Riedl et al. 2012) nonetheless indicates it is derived relative to great apes.

Many consider third-party punishment to be altruistic in both the psychological and the biological sense in that it apparently lowers the fitness of the punisher. Indeed, “altruistic punishment” is often considered the key explanandum in models of group selection or cultural group selection (Boyd et al. 2003). However, third-party policing of any kind can evolve only under very restrictive conditions, especially in large groups (El Mouden et al. 2010). Nonetheless, it is possible that those who seemingly unselfishly uphold the society’s moral norms actually are those who stand significantly from this activity, either directly due to disproportional benefits and/or negligible costs, as in punishing animals (Raihani et al. 2012), or indirectly, through reputation enhancement (dos Santos et al. 2010). At present, the jury is still out on which of these two explanations is best supported empirically. The group affiliation of third parties may also be relevant. In humans, uninvolved third parties that belong to a different group (K-Q in Figure 1) also tend to have evaluative judgments of A’s action toward B, especially if they involve serious harm.

The between-group hostility element

The third entry in Table 1, for the functional context of raiding (an opportunistic form of warfare: Wrangham & Glowacki 2012), is probably more pronounced in humans than in all other primates, with the possible exception of chimpanzee males. Such strong between-community hostility requires a strong within-group bias in all relevant moral emotions. There is extensive evidence for our moral parochialism in everyday interaction, as vividly confirmed by a formal study in a tribal society (Bernhard et al. 2006). This bias corresponds to Haidt’s (2012) loyalty domain.

The presence of within-group bias produces interesting interactions among the components of the moral system. For instance, people are forced to suppress their empathy with suffering when the signals of need come from an individual labeled ‘enemy.’ Our ability to suppress empathy may well be facilitated by the presence of ethnic marks (Bell et al. 2009), because these marks strongly affect the response to unfamiliar people. Ethnic marking probably evolved to maintain the trust needed for direct and indirect reciprocity in societies that had become so large that not all members knew each other directly or through reputation. But as an unanticipated byproduct, the presence of these homophily-inducing markers also made it easier to suppress empathetic responses to strangers.

Additional, shared components of human morality

Lest one believes this is all there is to human morality, we also add other entries into Table 1, which illustrate some aspects of morality that are probably more widely shared with other species, and thus phylogenetically older. Thus, they are also part of human morality, but not of the human-specific morality that is the main topic of this chapter and of philosophical argument.

The fourth set, linked to social bonding, is patchily distributed among primates (Silk 2012). In humans, within-sex social bonds are strongly expressed among adult males, which is a feature shared with chimpanzees. Pair bonds are found in various taxa (Dunbar & Shultz 2007), but not in great apes. The motivational mechanisms linked to maintaining social bonds, including pair

bonds, have been described in detail for primates (de Waal 2006), and much work is still being invested in describing them (Silk 2012). Given that they have an emotional overtone in humans (our obligations to our friends are part of everyday morality), parsimony suggests that they also have this in at least some nonhuman animals, especially our relatives the great apes and probably monkeys.

The fifth functional context, inbreeding avoidance, is even more widespread. It is especially useful to include it here because the aversion to mate with relatives is well documented among many primates, and also seen in humans (Pusey & Wolf 1996; van den Berghe 1983). It is known to develop automatically based on experience-expectant inputs during early immaturity (the so-called Westermarck effect), and is therefore close to what one might call innate. Most importantly, in humans it is accompanied by strong emotions, both on the side of individuals who are directly involved and on the side of outside observers (Fessler & Navarrete, 2004).

The final context refers to an even more basic aspect of folk morality: obligations to protect and care for close relatives. People generally feel that parents have an obligation to care for their children, that adult children should care for their aging parents, and that siblings should support each other. As a result, there is a kin bias in many moral emotions, such as empathy or proactive prosocial motivations, or greater forgiveness of norm violators, etc. Kin bias belongs in the category of moral behaviors in humans as well, because it is accompanied by strong feelings of duty and obligation, and society also expects this (a normative element).

The plausible presence of moral preferences shared with other animal species is a strong argument in favor of evolutionary continuity. Indeed, there may well be additional moral emotions that are shared, for instance an aversion to infanticide (van Schaik et al. 2014; Rudolf von Rohr et al. 2011). At the same time, evolutionary continuity inevitably also suggests that each species will have a unique subset of high-priority motivations (and the range of individuals to which they are applied) of the kind subjectively experienced as moral in humans, as a result of the adaptive fit between social organization and subsistence. Thus, the top entries in Table 1 are almost certainly unique to humans, at least in their strong expression, not to mention the cognitive elaborations in the form of moral reflection and attempts to build moral codes.

Although nonhuman animals may well have similar emotions as the ones we consider moral when it comes to the first- and second-party perspectives (thus including those involved in social interactions), the evolutionary continuity may well break down in the third-party perspective. At this stage, it is totally unclear whether any animal would, for instance, disapprove of inbreeding involving within-group third parties, as humans are wont to do, let alone inbreeding involving total strangers, as humans also tend to do. One way to approach this would be to examine a difference in putative norm violations that involve others in the same social group or total strangers (cf. Figure 1). If the emotional response is limited to violations by fellow group members, this would suggest the absence of a preference for abiding by the general rule, without regard to the individuals involved. This distinction can be exploited to study the presence of moral norms in non-human animals. (Note that similar responses to in-group and out-group norm violations do not allow any conclusion).

Conclusion

The cooperative foraging lifestyle of our ancestors installed a set of psychological motivations (preferences and response predispositions) that act to directly regulate this cooperation and are accompanied by subjectively experienced emotions. The latter have acquired a semi-privileged status commensurate with their high impact on fitness. The moral intuitions of lay people and most moral philosophers alike formed the foundation for our moral reflection and shaped moral codes.

The major elements of morality can seamlessly be fitted into this adaptive-foundation hypothesis. First, it explains the prosocial core of humanity's moral preferences. Second, this idea explains the feelings of 'ought' surrounding both major components of moral behaviors (the prosocial core and the conformity element). In the next section, we will show that the hypothesis can also explain two further features: our susceptibility to cultural influences when it comes to the content of our moral intuitions, as well as the important role of abiding by the society's norms.

Normativity

Directly or indirectly, third-party influences have been critical to the evolution of morality. Several important questions thus need to be resolved. First, why this is so: why is the conformity component normative rather than merely informational and thus more variable? Second, how can we reconcile the presence of moral norms with the extensive cultural variation in moral norms reported by ethnography? And finally, how could such a highly derived shaping force of behavior have evolved?

Before discussing these questions, we briefly clarify terminological distinctions (following Glock, this volume). Moral norms are defined as prescriptive rules of conduct, the upholding of which is seen as a duty surrounded by strong emotions. Moreover, norm violations are subject to shame by the perpetrator and sanctions by the community. Moral norms are felt to have a stronger social force than regular social norms, linguistic norms, or conventions (see below). The existence of such norms is demonstrated most convincingly by the presence of clear responses of non-involved bystanders: third parties. The actual contents of moral norms can be deduced from the kinds of situations and events that induce third-party punishment. Indeed, in non-linguistic organisms, third-party responses to norm violations are the only plausible way to demonstrate the existence of such norms.

The function of normativity

A functional approach asks under what conditions normativity in the moral domain is needed. If social life were merely about cooperation, no norms would be needed. However, social life inevitably contains element of both cooperation and competition. Morality is therefore essentially about restraint: not reaping benefits even though they are within reach. This analysis indicates that a moral system based entirely on prosocial motivations is unlikely to be stable without some pressures to refrain from harvesting immediate selfish

benefits that end up harming society. Thus, moral norms are needed when two conditions are met simultaneously: (1) *interdependence*: societies in which reliable food sharing or coordinated collective action is essential for fitness, and thus individuals, including dominants, need each other; and (2) *conflicts of interest*: there is an incentive to exploit others or free-ride on their efforts.

This analysis also helps to clarify the function of moral norms. It is to protect the weak against exploitation by the strong and the prosocial against the social parasitism of opportunists (free riding). Moral norms are needed because humans have a psychology with both selfish and prosocial tendencies, and have incentives to violate norms if they can do so undetected. In other words, although moral norms have social force, there are inevitably situations where an individual would benefit from breaking the rules. Indeed, non-adherence to norms is expected when large discrepancies in payoff accrue and when damage to reputation is minimal. For example, one should eat all of a valuable food when one is extremely hungry and unlikely to be detected. Consequently, one might naively expect those individuals who would benefit from violating a norm, not to truly subscribe to it, but merely comply with it because they are driven by an external (social) force: punishment. Such a conditional compliance should in fact be the evolutionarily stable strategy (ESS) because undiscovered transgressions should be highly beneficial.

This argument leads to the expectation that norm adherence is largely driven by external social forces. Thus, people should be keen on identifying norm violations, be interested in updating reputational information on all interaction partners (gossip) and be willing to punish norm violators. All of these predictions are actually met, underscoring the tendency of people to cheat on moral norms when they have a strong incentive to do so.

Yet, surprisingly, going against this naïve expectation, we already noted the presence of a strong internal element, suggesting a strong preference to adhere to the norms. The existence such an internalized preference for norm compliance thus requires an explanation. Functionally, the internal driver may be directly linked to the avoidance of social sanctions (although this function need not be mentally represented). Thus, its function may reflect the damage due to loss of reputation, which is extremely high, because a good reputation to a forager is vitally important and regaining it may require inordinately more effort than gaining it in the first place. The potential loss of reputation usually far outweighs the opportunity cost (and thus fitness loss) of not violating the norm. This asymmetry may make it adaptive to possess strong internal drivers and not rely too much on external drivers. Moreover, it is likely that those who adhere to norms gain in reputation, providing an incentive to internalize norms. Ultimately, then, these internal motivations were installed by external social forces, in particular the consequences of losing one's reputation.

It is perhaps ironic that this position is similar to the one reached by a reflective moral agent, who would feel compelled by his or her own logic to prefer adhering to moral norms. In any case, when couched in terms of external drivers, avoiding shame may thus be more important as a motivational factor than fear of punishment, because the direct loss due to one-off punishment may be far more limited than that due to losing one's reputation.

Cultural variation and normativity

Normative conformity is also what makes cultural variation in moral codes possible. Among modern societies, moral norms show remarkable variation, as do the underlying moral intuitions (where intuitions are realized emotions, as modified by experience). Historically, however, this may not always have been the case. Among foragers the content of morality is fairly uniform (Hill 2009), as predicted by the evolutionary hypothesis: the social problems are largely the same everywhere. Even so, even among foragers, social organization changes dramatically upon adopting a more sedentary lifestyle (Keeley 1988), and one can postulate similar changes in the underlying moral intuitions. The even more massive social changes following the invention of food production and the consequent changes in the nature and size of human societies (Diamond 1997) must have led to even more culturally induced variation in moral intuitions, in tune with the nature of the societies produced.

The evolutionary approach must be able to account for this variation, because the alternative hypothesis, that morality is the product of purely cultural processes, is on the face of it a more plausible explanation of this variation (Prinz 2012). In fact, as argued earlier, the presence of high flexibility in the behavioral expression of certain basic abilities is not incompatible with an evolutionary approach.

Cultural variation is strongly enhanced by the presence of the urge to conform to local moral norms. Thus, moral emotions, although they historically have a core context and are elicited by a core set of stimuli, are malleable and may expand (or perhaps even shift) their content. Figure 2 tries to capture this process. It shows how innate moral preferences (the primary emotions) are modified into realized moral preferences (the moral intuitions people have) under the influence of a variety of internal and external (social) processes.

In the end, moral norms owe this malleability to each individual's urge to conform to local moral norms. Such malleability is clearly adaptive because different subsistence styles have different adaptive peaks in terms of the moral codes, but it is obviously also susceptible to political processes, including coercion, leading it toward subverted equilibria that serve the interests of a powerful elite rather than society as a whole.

The tension between innate moral preferences and the preference toward conformity means that fully culturally universal moral norms may not exist. This outcome is relevant to the debate that we should expect such universal moral norms (Turiel, this volume). Interestingly, even moral norms that are more locally distributed often still involve strong emotions, as shown by the strictly policed rule of some religions.

Indeed, these considerations suggest that we must expect gradual transitions between statistical regularities, conventions, social norms and moral norms, because of the malleability of the content of moral emotions (Figure 2). This gradient is sketched in Figure 3, where we also indicate a few other factors that probably vary along with cultural variability.

One main reason for the diversity of our norms is that the normative element most likely evolved in the context of the transmission of complex, opaque skills. We now therefore turn to the evolution of normativity.

The evolution of normativity

Normative conformity is both a cultural universal (van Leeuwen & Haun 2013) and derived relative to apes, provided it remains uniquely reported for humans only (Asch 1956). It is therefore valid to ask how the various elements listed in table 2 could have come together. In evolution, it is highly unlikely that the various elements that make up a new, i.e. derived, function all evolved *de novo*. Much more commonly, these elements were somewhat modified or were combined with other preexisting elements to form new combinations that are functional in a new context. In these cases, we can speak of an exaptation process, where new functions arise out of pre-existing ones.

Norm compliance is a form of conformity. Conformity is a group-level phenomenon. When animals simply have a tendency to adopt whichever behavioral variant they see the most, this may gradually produce conformity. However, local homogeneity in any behavior, and thus in norms too, arises most reliably when animals actually have a preference for, and thus disproportionately adopt the majority's behavior (Efferson et al. 2008). The adaptive significance of such an explicit preference for the majority's variant (informational conformity) almost certainly is that it allows the individual to tap more effectively into the wisdom of the crowd. Recent experiments with nonhuman primates are beginning to provide solid evidence for it. Chimpanzees preferentially copied the actions demonstrated by the greater number of experts rather than merely the variant most commonly seen (Haun et al. 2012).

The preference for conformity may be even stronger than this. We can speak of strong informational conformity if an individual abandons a pre-existing preference for an alternative one shown by the majority. Although previous experiments with captive chimpanzees suggested it, an experiment on wild vervet monkeys has now convincingly confirmed it. Males that dispersed into a group with a contrasting color preference of dyed food items (corn), with no differences in taste, immediately switched to the new color once in the new group (van de Waal et al. 2013). Systematic inter-community differences among chimpanzees in the use stone versus wooden hammers for nut cracking provide another example of this, since maturing females who move into new groups apparently adopt the new preference (Luncz & Boesch 2014). The fact that both weak and strong informational conformity have now been reported for primate species as distinct as vervet monkeys and chimpanzees suggests that it is quite widespread, although clearly more work on more species is needed. These demonstrations, incidentally, underscore the importance of cultural variation, even among neighboring groups, in nonhuman primates.

It is important to stress that in nonhuman primates, there is no evidence so far that the conforming goes beyond the utilitarian, i.e. is truly normative. This is nicely illustrated by the experiment of van Leeuwen et al. (2013), which showed that individual chimpanzees readily abandoned the behavior shown by the majority if they found out that an alternative produced a much higher yield. When the crowd does not have more wisdom, there is no reason to follow it.

Strong informational conformity becomes normative the moment the preference for conformity takes on an intrinsic sense of high urgency, i.e. acquires an 'ought' feel to it. Given that the moral norms are always strongly prosocial (provided they concern in-group members), it is plausible to assume that normativity arose when the preexisting informational conformity was paired with moral prosocial emotions and especially the reputation-guarding

element that led to great concern with audience responses (Figure 4). Moral normativity, then, is an automatic byproduct of strong informational conformity and concern for reputation.

Strong informational conformity often involves the copying of opaque behaviors, i.e. behaviors whose goal is not immediately evident, especially to naïve immatures. Faithful copying of opaque, non-obvious behaviors requires trust, and has been linked to the phenomenon of over-imitation, a uniquely human form of social learning (Whiten et al. 2009). This feature of informational conformity must have also made it easier to adhere to social norms, which may equally seem intuitively non-obvious for naïve youngsters. The 'trust' part of strong informational conformity may thus have made the transition toward normative conformity even easier. In fact, over-imitation likewise serves the function of norm learning in human children (Kenward et al. 2010).

Discussion

The evolutionary approach to morality is currently in ascendancy. This is so because moral psychology has shown the critical role played by moral emotions in reaching moral judgment (Prinz 2007), even when it appears that moral reflection was involved (Haidt 2012). These findings should toll the death knell for any approach that assumed morality was a recent cultural invention, entirely built upon reason and passed on to the subsequent generations by patient conditioning. Furthermore, studies of the ontogeny of these preferences and biases show they often arise before one can reasonably assume a major effect of cultural influences on behavior (Bloom 2013). The evolutionary account can also accommodate cultural influences.

What is still missing from the evolutionary approach is a description of the innate core of morality, basically a list of moral intuitions that are most resistant to cultural modifications of their content. For the integrative evolutionary-cultural approach to have more explanatory power than the culture-only approach, such a core must exist, or at least there must be major variation in susceptibility to cultural influences on their content.

Most important from the perspective of this volume, however, is that the evolutionary approach can also provide a plausible account for both the adaptive function and the origin of normativity. This function is closely linked to the advantages of informational conformity, which turns normative if second parties begin to punish deviations. Avoiding punishment alone may already lead to higher priorities, especially if reputation also becomes relevant. Normativity can thus be seen as an inevitable byproduct of the combination of informational conformity and moral emotions.

Another important question remains. How would one recognize that individuals prefer moral norms to be a general rule, applied impartially to all (collective social norms, as defined by Rudolf von Rohr et al. 2011), rather than merely a certain rule (proto social norms in their terminology)? In principle, both proto- and collective moral norms are consistent with the presence of emotional responses and punishment by non-involved third parties (bystanders). Most punishment in non-humans is by individuals who are directly involved and thus stand to gain from correcting the behavior of their partners (see Kappeler et al., this volume), and third-party punishment is probably absent. Both kinds of

norms are also consistent with the presence of strong emotional responses by out-group bystanders.

Demonstrating the presence of collective social norms in non-linguistic organisms may be next to impossible. However, earlier we did suggest that we can recognize its absence, when in-group and out-group third parties respond differently to the same norm violation. Rudolf von Rohr et al. (in press) noted that chimpanzees, though clearly interested, did not respond emotionally to infanticidal scenes among unfamiliar chimps, in sharp contrast to infanticidal events in their own group. This suggests that chimpanzees do not have collective moral norms.

In fact, it could be argued that we should expect collective norms exclusively in linguistic organisms. It is very likely that language automatically triggers something like a moral dialogue in an egalitarian society, in a process of mutual challenges and justifications, which then inevitably favors the formulation of norms from an impartial perspective. The same process can also produce cultural variation in the content of social and moral norms (cf. Figure 2).

If individuals have an explicit preference for the impartial rule, this is an expression of justice. Justice is the normative (third-party) version of the individual-level preference for fairness. The prediction therefore is that non-linguistic species will necessarily lack aspects of justice, such as desert (Christen & Glock 2012).

Can we decide which of the various kinds of norms (moral, social, linguistic) and weaker versions such as conventions was ancestral to the others? In principle, each could be ancestral to the others, but our reconstruction of the evolutionary history of moral norms may help to distinguish between possible scenarios. Adherence to conformity may have been adaptive in many contexts and for a long time, well before hominins roamed the earth. Depending on one's definitions, the resulting kind of within-group uniformity, probably not accompanied by strong emotions of right and wrong, could be seen as a social norm. Thus, social norms of some sort are ancestral to all other forms.

Once the high-priority element evolved, moral norms were born. The emergence of the modern lifestyle of hunting and presumably gathering around 2 million years ago suggested that these moral norms emerged around that time as well.

A good guess would be that linguistic norms arose most recently, because the most plausible estimates put the emergence of modern language at approximately 0.5 -1 million years ago (Dediu & Levinson 2013). The question is whether linguistic norms arose from moral or from social norms. Because the social force of linguistic norms is clearly more limited than that of moral norms (Glock, this volume), it seems plausible to argue that linguistic norms arose automatically with language itself as an expression of preexisting preference for conformity, as seen in the presence of social norms more generally. Note, however, that linguistic norms differ fundamentally from social and moral norms in that there is normally no incentive to deviate from them, because it tends to lead to less effective communication (except in deliberate deviations, as in irony). Thus, linguistic norms are probably best seen as conventions. The normative element may be an artifact of the teaching of language rules to children; during teaching, active correction may then be interpreted as normative.

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Figures and Tables van Schaik & Burkart

Figure 1.

The role of third parties (C-G) in human morality. A's actions toward B may provoke responses from various parties: B, who is directly involved; C-F, who are un-involved, in-group bystanders, and K-Q, who are un-involved out-group bystanders. The response of in-group bystanders may also depend on their bond with A: thus, C may respond differently than D-F.

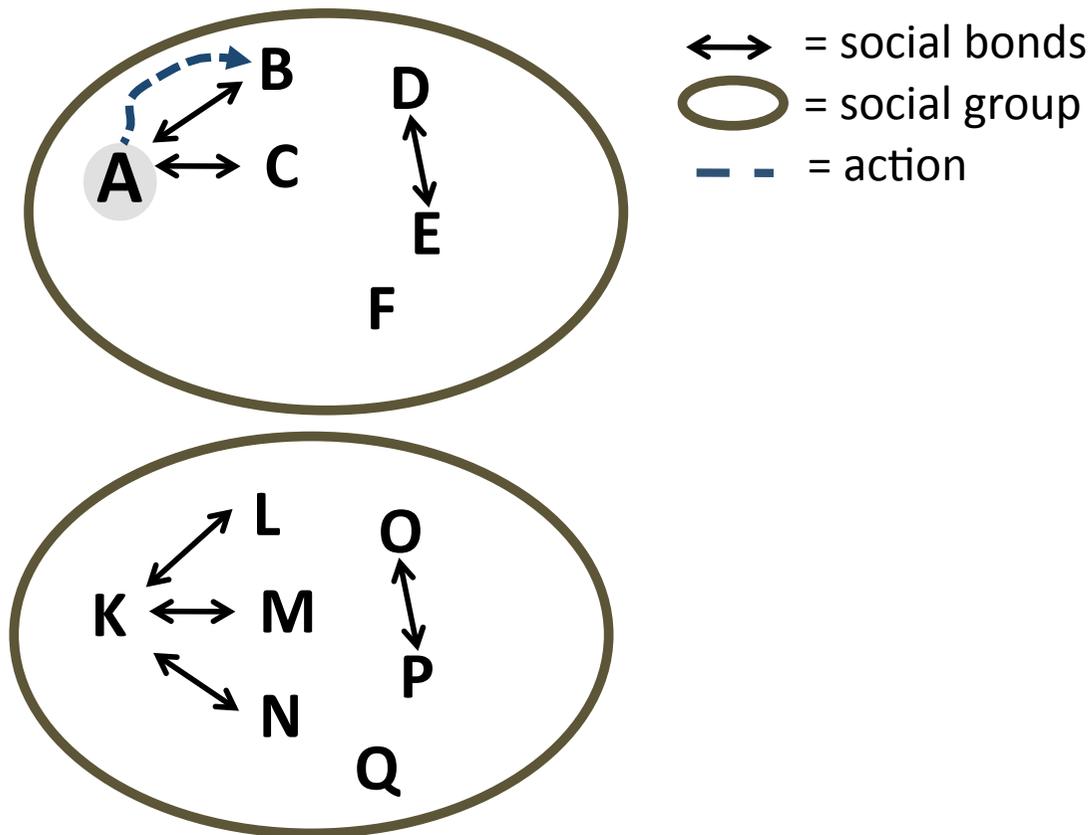


Table 1. The functional contexts in which major moral emotions evolved

Functional context	Behaviors	Mechanisms (+emotions)
Cooperative breeding	provisioning mother and offspring	proactive prosocial motivations steep reactive prosocial motivation (empathy)
	babysitting	
	teaching	
Cooperative hunting and gathering	adult food sharing	allocentric inequity aversion
	receiving help when needy	concern with reputation (sensitivity to audience)
	coordinated collective action (hunting, gathering)	shared intentionality (→ coordination, synchrony); preference for conformity, homophily (→ synchrony) ¹
Raiding (warfare)	Raids on other groups, defense against them	various above + within-group bias in relevant emotions
Social bonds (pair bonds, male-male bonds)	reciprocal exchanges	gratitude, guilt, shame, as well as cheater detection
Incest avoidance	No mating with relatives	sexual aversion toward relatives
Parenting and family support	Protect and support biological kin	strong kin-bias in relevant emotions

1: see Table 2 for more detail.

Table 2.

The components of normative conformity, and their underlying motivations

Internal drivers (→ collective norm)			External drivers (→ majority norm)	
<u>Prox. Mech.</u>	<u>Behavior</u>	<i>normative conformity</i>	<u>Behavior</u>	<u>Prox. Mech.</u>
preference for conformity (& similarity: homophily)	synchronized action		punishment of norm violators	cheater detection; urge to punish
shared intentionality	coordinated action			
felt duty to conform	actively conforming to majority			