
Evolution

1.1 The Social Brain

The human brain is among the largest relative to body size in mammals (Herculano-Houzel, 2009), but more surprising is that in the evolutionary time scale, the brain has recently (in the last million years or so) shown rapid increases in size (Adolphs, 2009). This poses a puzzle: Why such a massive increase in such a relatively short time? One widely accepted answer to this puzzle is the social brain hypothesis (Adolphs, 2009; Byrne & Whiten, 1988; Whiten & van Schaik, 2007). This is the idea that the rapid development of the brain was in response to¹ increases in the complexity of the *social problems* that were necessary for early hominids to solve. These problems include many of those we will review in this chapter: various forms of cooperation, deception, status hierarchy negotiation, altruistic punishment, and anticipatory fear of punishment. It is during this rapid spate of development that humans became a species able to enact a complex (im)morality.

Philosophers as early as Aristotle (1941) recognized the importance of the social nature of humans. His discussion of humans as *zōon politikon*² in the early chapters of the *Politics* makes it clear that our social nature (as opposed to that of bees or cranes) is intimately related to our concern for justice. For Aristotle and many thinkers that followed, the connection between our social nature and our moral nature is intimate and inextricable. We will find this to be true in our evolutionary history as well.

We know today that moral judgment and action involve a rich, complex interaction of emotion, inference, automatic and controlled processing, strategic planning, etc. A core assumption of evolutionary psychology is that the capacities for these activities evolved under the pressure of selection from the social environment and together constitute our distinct form of moral/social organization as the human species (Krebs, 2008).

¹Or at least in coevolutionary tandem with, see Section 2.4.

²Perhaps best translated as *political beings*. Aristotle's *Politics* is about the role that the community and its lawgivers should play in bringing about the virtuous life in the citizens. Thus, morality is closely linked to our social nature.

To understand how these capacities might have evolved, we first need to understand some basic concepts and terminology in evolution. That will give us the vocabulary to describe how difficult it is to build a strong case that some particular psychological characteristic has been evolutionarily selected. After we see what a good evolutionary argument looks like, we will then review a set of six basic building blocks out of which our complex moral nature might be constructed, and review the evidence for them. Finally, we will look at a set of eleven ways that human morality is distinct from the proto-morality of other species, and ask how one might build an evolutionary argument for these aspects. We conclude that there is strong evidence that much of human morality has evolved and a long (but possible) way to go to build evidence for how a uniquely human morality might have evolved. One offshoot of this grounding of morality in evolution is that it highlights the intimate links between the development and expression of morality and immorality, a theme that will be woven throughout the book.

1.2 Basic Evolutionary Processes (With an Eye Toward Morality)

“Survival of the fittest” is a phrase that Darwin first uses in his fifth edition of *The Origin of Species* (Darwin, 1869 p. 92). He uses it as a synonym for natural selection. The many misunderstandings of this phrase over time have come to haunt those who would talk about evolution, and particularly evolution and morality. Herbert Spencer originated the “survival of the fittest” phrase (Spencer, 1866, pp. 444–445) and, among other burdens the phrase carries, it has come to be associated with Social Darwinism, a much maligned attempt to derive a kind of “might makes right” ethical principle.³ The phrase has also been misunderstood to suggest that it is the most physically fit, or aggressive, or selfishly competitive individual who survives. This is a mistake on multiple fronts. Natural selection is not about individual survival, but about the ability to reproduce (and thus propagate one’s genome). And since it is about reproduction, it need not be about physical fitness or aggressiveness, but also about cooperation or camouflage or cleverness or compassion that allows the production and continuation of the genome. As we will see later, it is also a mistake in terms of the level at which one can speak of selfishness. Genes may metaphorically be selfish (Dawkins, 1976), but individuals do not have to be (de Waal, 2006).

However, to understand Darwin’s approach to “natural” selection, one must first understand the material on which it works. Darwin begins his *Origin of Species* (Darwin, 1859) not by talking about natural selection but about variation. Any population (of sheep, pigeons, or insect-eating plants) has some natural variation in the characteristics of individuals in that population. Darwin begins his argument by noting that breeders (of pigeons or of strawberries, etc.) take advantage of this variation and selectively breed individuals with characteristics they desire. Darwin calls this “selection by man.” Natural selection is a similar process operating without (usually) human intervention. Some individuals with particular characteristics survive long

³See Weinstein (2009) for a balanced discussion of Spencer’s role in Social Darwinism.

enough to pass on those characteristics to their offspring. To the extent that those characteristics have played a role in the propagation of characteristics in further individuals, then one can say those characteristics have been “naturally” selected or that they are evolutionary “adaptations.” This, then, is the basic idea of selection.

Scholars of evolution list many and various varieties of selection (see Sober, 2006 for an overview of these and other issues). Because the moral is so closely associated with the social, the kind of selection that will particularly concern us here is *social selection*. This is natural selection driven by social interaction within a species, selection of the sort that may have resulted in the rapid increases in brain size mentioned earlier. There are four versions of social selection we will deal with here: sexual, kin, and group selection and gene–culture coevolution.

1.2.1 Sexual Selection

Though it may certainly have other functions, a primary evolutionary function of sexual interaction is the continuation of the species and the genome. In animals, sexual selection occurs during mating choice, with the choice based on some characteristic among the available partners (Krebs, 2008). The classic example in the literature is the mating selection among peacocks, with the female basing her choice in part on the characteristics of the splendid tail of the male.⁴

Can we construct a story of how this might account for moral characteristics among humans? It is at least the case that, across many cultures, moral qualities are preferred in mates (Buss et al., 1990), with dependability and kindness/understanding appearing near the top in lists of preferences for both sexes from thirty-three different countries. In addition, there is evidence that humans can reliably identify moral dispositions in others based on short observations (Fetchenhauer, Groothuis, & Pradel, 2010), making it possible that selection could be based on this identification. Miller (2007) has marshaled the evidence for a theoretical account of sexual selection of virtues and suggested a set of testable theses based on this account. Others (Goetz, Keltner, & Simon-Thomas, 2010) have included sexual selection among the kinds of selection pressure that can support an evolutionary account of the virtue of compassion in both sexes.

Thus, one can construct a case for the evolutionary sexual selection of virtues. We expect this is often overlooked because of the unfortunate connotations of “survival of the fittest.”

1.2.2 Kin (Family) Selection

The idea of kin selection is implicit in the phrase *inclusive fitness* (Krebs, 2008). Inclusive fitness is based on the number of genes an individual can contribute to succeeding generations both directly (by producing offspring) and indirectly (by supporting family relatives who share genetic material). This concept makes it

⁴The empirical story is somewhat more complicated by the search to determine just what it is about the splendid tale that the peahen responds to (Loyau, Petrie, Saint Jalme, & Sorci, 2008). This cannot, of course, be immediately applied to the human species.

possible to understand how compassion toward one's immediate and extended relatives might evolve (Goetz et al., 2010) since care for relatives increases one's inclusive fitness. This pattern of closer care for closer relatives has been documented in a wide variety of cultures (Essock-Vitale & McGuire, 1980). If compassion for kin already exists it can be adapted or generalized to compassion for a wider group (Goetz et al., 2010).⁵

1.2.3 Group Selection

One can extend the idea of selection based on one's relatives to selection based on one's group. Wilson and Sober (1994, 1998) revived the idea of group selection and embedded it in a model of multi-level selection. One can think of selection occurring at the level of the gene, the cell, the individual, the kin group, or of larger, arbitrary groups. Group selection was originally proposed by Darwin (1859). It seemed to later researchers (see Richerson & Boyd, 2005 for a review) that selfish individuals in an arbitrary group would take advantage of cooperation, without themselves helping, increasing their fitness with no cost to themselves. It was thought that mathematical models easily predicted that in this case, the selfish defectors would eventually take over in any group (see Thompson, 1998 for some of the complexities in this claim). This "free riding" seemed to make it impossible for cooperative behavior to evolve based on its adaptive value for a group of unrelated individuals. In response to these concerns, Sober and Wilson (1999) identified the conditions that must obtain for group selection to work.

To make group selection viable, variation on the characteristic (e.g. compassion) *between* competing groups would need to be larger than variation *within* each group. Simply put, the groups must differ on the characteristic. Equally important is that *selection pressure between* the groups would also need to be greater than any *within group selection* that might be caused by free riding. Sufficient selection pressure between groups could be produced by things like intergroup conflict, foraging for a common but scarce resource, or the founding of new groups (Sober & Wilson, 1999).

If group selection is going to work to increase some moral attribute that is favorable to the group, it needs to be the case that individuals can recognize the group and establish an attraction to it. This makes immediate sense in terms of kin groups, and such attraction can develop from already existing attractions associated with parenting (Goetz et al., 2010). But how might this attraction establish itself with arbitrary groups? Lewis and Bates (2010) used a twin study and mathematical modeling to provide evidence for genetically based preferences for particular groups (in this case, ethnicity, religion, and race). In addition to these basic preferences for each of the groupings, they also found evidence for a *central affiliation mechanism* (CAM) that

⁵The technical term for this is *exapted*, the selection of an already existing characteristic to serve another purpose. The existing characteristic need not have been naturally selected before, but it might simply have been a necessary byproduct of an already selected characteristic (e.g. a biologically affective experience like compassion for kin that is available to be exapted for non-kin). It might then play a role in group selection to produce a broader characteristic (Goetz et al., 2010).

allows for affiliation or attachment to arbitrary groupings (like a sports team). This preference to be loyal to groups that develop out of local culture might be naturally selected (in a similar way that sexual selection might select virtues). Thus, there is some support for the idea that loyalty to groups of individuals is a characteristic that might be selected for by evolutionary processes (see also Krebs, 2008).

1.2.4 Gene–Culture Coevolution

One more complication must be added to the ways that evolution is socially shaped. Human culture can itself create new selection pressures on individuals in a population, and thus influence genetic characteristics of the population over time. Culture creates an environment that produces selection pressure on the individuals in that culture. One example of this is the widespread change to agriculture. Richerson and Boyd (2010) provide examples of this sort of coevolution with the change in the enzymes that allow adults to digest milk occurring among those populations that had adopted herding of livestock and also the coevolution of enzymes that help with the digestion of plant starch among those adopting agriculture. Gene–culture coevolution is at the center of debates about the evolution of cooperation and altruism,⁶ since this process involves cultural processes like altruistic punishment⁷ that would “deselect” individuals who violate group norms (Boyd et al., 2003; Boyd, Richerson, & Henrich, 2011).

We are only beginning to understand the complexity of the pathways that might lead to the current variety in human culture and genome. Genes do not code for specific behaviors, but they can influence systems that make some behaviors more likely to be expressed or some things easier or harder to learn (see Schmitt & Pilcher, 2004 for examples). The processes of development in the organism that move from a genetic encoding to a phenotypic (body, behavior, etc.) outcome of that encoding (a process called expression) can interact with an organism’s experience in the world. For instance, careful maternal care can support the expression of genes that make the giving of maternal care more likely when the offspring grows up (Goetz et al., 2010).

1.2.5 Evolution vs. Culture

One of the standard critiques of evolutionary accounts of morality (and indeed one of the standard critiques of evolutionary psychology) is that these accounts ignore the overwhelming influence of culture on the complexity of human behavior (McKinnon, 2005). The dichotomous structure of this argument should immediately make one suspicious, since it mirrors many other sometimes overzealous debates in the social sciences like that between nature or nurture, personality or situation, reason or emotion, altruism or selfishness, etc.

⁶See the section on Selfishness for selection for altruism.

⁷This is punishment of an offender of a norm that is costly to the punisher (thus altruistic).

But before looking at an integrative response to this dichotomy, we should note the difficulties that the “culture alone” camp has with explaining some aspects of morality. Two of the most well-documented psychological accounts of moral judgment and action are the social learning (Bandura & Walters, 1963) and cognitive developmental ones (Boyd et al., 2011; Kohlberg, 1963; Turiel, 2006). Both have difficulties explaining some aspects of morality in comparison to evolutionary accounts. Social learning accounts have trouble explaining how moral rules emerged in culture, why people are motivated to preach them, and why children resist induction of moral rules. Cognitive developmental accounts struggle to explain the centrality of affect in moral judgment, the continuing presence of “childish” moral thinking in adults, and the connection (or lack thereof) between moral reasoning and behavior (Krebs, 2008). In addition, both approaches have difficulty in explaining the pattern of data that surround some effects (such as the incest taboo) that have been extensively investigated from an evolutionary perspective (Schmitt & Pilcher, 2004). Finally, both cultural approaches find it hard to explain (or even finding relevant) the extensive list of cultural universals that have moral content (Brown, 1991; Curry, Mullins, & Whitehouse, 2019). This is not an argument that cultural or purely psychological approaches are wrong but simply that they are incomplete, as the evolutionary approach itself is incomplete. This is the reason we try to bring together multiple narratives of moral behavior in this text.

In Section 1.2.4, we covered the process of coevolution. This is the idea that culturally valued, socialized, and transmitted behaviors can influence the evolutionary path of groups, making things like cooperation an evolutionary advantage for a group. This suggests that culture may influence evolutionary paths more than evolutionary paths may influence the expression of culture. The idea of coevolution has emerged from decades of theoretical and empirical confrontation in the evolution–culture debate (Durham, 1991; McElreath, 2010; Richerson et al., 2010).

This understanding of culture–evolution interaction helps to bring some resolution to the voluminous literature on altruism (de Waal, 2008) as we will see in the A Note on Selfishness and Altruism section. And it also helps us understand the many different ways one might find culture–evolution interaction underlying moral judgment and behavior. Some authors (e.g. Mikhail, 2007) have proposed that much of our moral judgment is innate and pre-packaged into independently operating modules.⁸ But it is more likely that the wide range of moral things in our lives is, from the perspective of evolution, a kludge (Stich, 2006) and is constructed from a range of abilities and predispositions (Cushman & Young, 2011; Cushman, Young, & Hauser, 2006; Heyes, 2020). For instance, moral emotions can channel our reactions (e.g. anger against defectors can provoke us to punish them) in ways that help to enforce group norms and make the group more successful (and in ways that pass on this capacity for altruistic punishment). This is an approach adopted by Haidt and Joseph (2004, 2007), who propose sets of moral emotions linked to dimensions of how actions are morally judged.

⁸See Chapter 7 for more detail.

1.2.6 A Note on Selfishness and Altruism

One of the conceptual oddities of the debate in evolution for the past thirty years has been confusion about the word “selfish.” This is in part because Dawkins (1976) published a book using the “selfish gene” as a metaphor for evolution at about the same time that economic models of the rational and self-interested “Homo economicus” were widely discussed. Dawkins’s argument was that natural selection occurs at the level of the gene, and that genes were metaphorically “selfish” when their “strategies” to replicate themselves were analyzed at this level. The idea received wide acceptance in biology and for some time formed the orthodox view of the level at which selection was operating: the level of the gene. More recently, multi-level approaches to selection (see the discussion in Section 1.2.3) have been proposed and favorably evaluated (Wilson & Sober, 1994, 1998).

However, the confluence of Homo economicus and the selfish gene in the 1970s, along with some unfortunate language that Dawkins used toward the end of his influential book, have served to support the idea that because genes are *metaphorically* “selfish,” then human psychological motivations must be selfish too. There are a variety of problems here. First, the idea simply assumes an identity across these levels of explanation. The word selfish is rooted in a description of one kind of human motivation and action, and it works as a metaphor for the point Dawkins wants to make about genes. But to then take that metaphorical use and deduce a psychological motivation or even a pattern of behavior is at best a stretch requiring good evidence. Genetically selfish is simply different from psychologically selfish. And the case for the psychologically selfish Homo economicus is not as strong as it used to be, and may well be suffering the death of a thousand limiting factors (Aktipis & Kurzban, 2004). An additional difficulty is that a simple “always be selfish” strategy is an implausible one in a shifting environment and may be less successful across different environments (Krebs, 2008).

There is clear evidence for a wide range of cooperative, non-prototypically selfish activities in humans and other animals including: mutualism (e.g. group hunting), simple reciprocity (e.g. exchanging meals), cooperation with cooperators (requiring keeping track of “defectors”), “community concern” (de Waal, 2006), and long-term social investment (e.g. care for infants, family, friends). Work in the laboratory (Aktipis & Kurzban, 2004; Van de Vondervoort & Hamlin, 2018) and in the field across many societies (Curry et al., 2019; Henrich et al., 2005) supports these sorts of cooperative motivations in human action against the simple self-interest model. And work by de Waal and colleagues (2006, 2008) shows similar behavior among other species. The renewal of research on cooperative and compassionate behavior across cultures and species seems to be leading to the “extinction” of the selfish Homo economicus model (Aktipis & Kurzban, 2004).

Even though cooperation, nurturance, and compassion are important and natural human motivations, we should not assume a uniformly bright picture. There is a range of motivations and behavioral strategies in our moral interaction that involves selfishness, deception, taking advantage of others, and outright aggression. Indeed, a profound irony is likely built into the group selection mechanism that may be operating to produce cooperation and caretaking. Effective group selection for cooperation *within* the group requires some level of competition *between* groups

(Sober & Wilson, 1999; Wilson & Sober, 1994, 1998). This competition can be created by warfare, but also other more peaceful means, like competition for a scarce resource. In addition, most models of group selection to produce cooperation assume what is called *vicarious punishment* for in-group members, that is, aggression against those who deviate from the cooperative norm of the group. Both of these mechanisms underpin what has been called the dark side of altruism (Graham & Haidt, 2012; Skitka & Mullen, 2002).

Now that we have a sense of the basic terms of how evolutionary processes might work, we will look into ways they might be combined together to produce evidence for how some aspect of morality might have evolved.

1.3 How to Argue That Behavior Was Selected Because It Was Adaptive

Evolutionary psychology has frequently been accused of consisting of too many “just so” stories⁹ about how some psychological characteristic might have been selected in a hypothetical past (Gould & Lewontin, 1979) – but having only that hypothetical possibility and little evidence. Having a “just so” story is a fine place to begin when that story points to where one might collect evidence. Given the relatively recent state of evolutionary psychology, we might expect for evidence about most proposed psychological adaptations to be fairly sparse, but these networks should become denser as more work is done. How might this happen?

Much of evolutionary psychology is an argument for how some trait, or constellation of traits, might have been selected 100,000–300,000 or more years ago. How does one collect evidence and make an empirical argument for something that happened this long ago? In part, one does it by changing the question. For example, if in fact incest avoidance, a common ethical norm, is an evolutionary adaptation, what pattern of evidence would we expect to find today in incest avoidance’s distribution across cultures, its relationship with genetics, its physiology, etc.? To answer this question requires several different kinds of evidence. Schmitt and Pilcher (2004) provide us with a useful map of eight different areas of evidence that are needed to give a convincing, valid case that some item of interest is an evolutionary adaptation:

1. *Theoretical coherence*: The extent to which the adaptation connects to one or more theories or theoretical networks about evolution. This can involve some of the classical theoretical accounts in biology or psychology or game-theoretic or mathematical modeling theory. This is a central piece of evidence in the network: lacking a coherent theoretical explanation means we would not have information about why or how the item is related to an evolutionary history or even the pattern of data we should expect in the other seven categories. In the case of incest, this consists of evidence that genetic problems arise in offspring of incest (Schmitt & Pilcher, 2004).

⁹This is a reference to Rudyard Kipling’s *Just So Stories* (1912) for children. These are fantastic stories of how, for instance, the camel got its hump or the whale got its throat. The narrative logic in the stories is that it is a pleasing tale, and therefore must be true, just so.

2. *Cross-cultural evidence*: If an adaptation occurs with regularity across cultures, or interacts across cultures in interesting ways (e.g. being less prevalent when cultural norms are strong, or occurring in reaction to specified cultural stimuli), then one may have evidence that the characteristic is influenced, at least in part, by some factor in common across all the cultures. There are almost universal prohibitions against incest across cultures (though what counts as incest varies), and there is cross-cultural evidence that being raised with other-sex peers before age six produces a diminishment of attraction to those peers (Schmitt & Pilcher, 2004).
3. *Hunter-gatherer evidence*: There are still cultures today that inhabit environments much like that of our pre-agricultural forebears. This gives us (somewhat tenuous, but nevertheless helpful) evidence of the likely environmental and cultural pressures for selection that may have been operating at the time the theory says the adaptation should have been adaptive. Ethnographies of these cultures show, again, almost universal absence of incest (Schmitt & Pilcher, 2004).
4. *Psychological evidence*: A particular attribute like incest avoidance may follow a developmental path that seems linked with the function our theory says it should have. Or it might relate to other psychological characteristics (or *not* correlate with them), or serve similar functions in modern societies. All these are part of the network of evidence that the characteristic is playing the adaptive role the theory says it should. Being raised with other-sex peers before age six reduces attraction, and this provides developmental psychological evidence (Schmitt & Pilcher, 2004).
5. *Physiological evidence*: If one can find a physiological substrate for the characteristic in question (e.g. oxytocin and empathy: Rodrigues, Saslow, Garcia, John, & Keltner, 2009), then one has established a physical mechanism by which a characteristic might be heritable. The interaction of this physical mechanism with culture and situational stimuli can enrich the evidence network to provide more detail about how the adapted characteristic functions in society. There is evidence for the sense of smell as a mechanism that produces sexual aversion to close kin, thus incest avoidance (Weisfeld, Czilli, Phillips, Gall, & Lichtman, 2003)
6. *Medical evidence*: This is similar to the physiological evidence but based in medical cases of the supposed physiological mechanism going wrong. When the physiology is upset, are the functional relationships of the characteristics also upset (see e.g. the use of brain damage cases in Chapter 2)? Schmitt and Pilcher (2004) do not list any medical evidence for incest avoidance.
7. *Phylogenetic evidence*: Finding similar patterns in other species, where the theory leads one to expect the patterns, is another set of nodes in the network of evidence. For some characteristics (e.g. the effects of oxytocin on social behavior) one might expect to see a range of species across all mammals (Rodrigues et al., 2009), while for other characteristics (like a sense of fairness) one may expect only similarities among other primates (de Waal, 2006; Preston & de Waal, 2002). In terms of incest, animals rarely mate with parents or siblings (Schmitt & Pilcher, 2004).
8. *Genetic evidence*: We are increasingly able to use genomic evidence to trace the timing of events in human evolution (Richerson et al., 2010) and this will become a rich source of data that can connect with the others in this list. Schmitt and Pilcher (2004) do not list any genetic evidence for incest avoidance.

Schmitt and Pilcher (2004) use this framework to survey the evidence for four psychologically relevant characteristics as evolutionary adaptations. Profet (1988) has followed the possibility that pregnancy sickness and its associated food aversions are an adaptation that allows for the fetus to be protected against toxins in plants that would cause birth defects. This story suggests that pregnancy sickness will follow a particular pattern (certain food avoidances, a particular timeline, the relationship of sickness to miscarriage, similarity across cultures, etc.) and there is much evidence for this rich network of relationships (Schmitt & Pilcher, 2004). Schmitt and Pilcher (2004) find less extensive, but still “exemplary,” evidence for incest avoidance. They find only “extensive” evidence for men’s greater desire for short-term sexual variety than that of women, and “moderate” levels of evidence that we have evolved a mechanism that makes it easier to learn fear of snakes.

1.4 Evolutionary Building Blocks for a Robust Morality

So, what can we learn about our moral nature by seeing it through the lens of evolutionary adaptation? At the most complex level, this might mean we have inherited a distinct and structured universal moral grammar, much like what has been claimed for the deep structure of a universal linguistic grammar (Huebner, Dwyer, & Hauser, 2009; Mikhail, 2007). We will evaluate this claim in a moment, but the picture of morality we provide in this book attempts a much wider claim. Moral action certainly involves a kind of structure of moral intuition, but the full picture includes far more: emotional intuitions, strategic planning, self-regulation, self-concept and group identity, and much more. Each of these might have an evolutionary underpinning. But it seems unlikely that they would have all evolved together as one piece. The usual pattern of evolutionary adaptation that moves toward complexity is more one of building that complexity slowly based on some existing variation.¹⁰ Given that many of these aspects, such as opposing values, are often at odds with one another (and that self-regulation is, in one sense, a mechanism to help adjudicate these conflicts), an evolutionary story would expect the complexity of moral action in humans to have been built up slowly across many species and a great deal of time. For instance, maternal care for the young is common to all mammals, but it plays an important part in human morality (Preston & de Waal, 2002).

For an overview of how these building blocks might come together, we will follow the proposal by Krebs (2008) of the various psychological building blocks that likely came together to constitute what we now call morality. This overview itself will suggest additional pieces that remain to be covered, and we address them in Section 1.5.

1.4.1 Adaptive Sociality

The first and fundamental building block that Krebs lists is that of sociality – or living in groups. Group living is built out of interdependence among animals and the

¹⁰Evolution does not always build toward complexity. Even “build” is a metaphor that contains intention. “Natural” selection has no intention. An organism may evolve toward less complexity if that makes it fit better in an environment.

complexities of how that interdependence is negotiated. This sociality is the basic background for the development of all the other building blocks. One thing to note: in Krebs's phrase, social life is built of both confluence *and* conflict of interest. For organisms to work in a group there must be some attachment to the group, some confluence of interest, and this attachment can be elaborated in many directions. As de Waal (2002) and Goetz et al. (2010) have documented, one origin (at least in mammals) of this social attraction must have been the giving and receiving of care between parents and offspring, which became more crucial as the time for complete maturation of offspring increased. And there is of course conflict of interest that must also be managed. This conflict and confluence is the arena in which moral action and judgment evolved.

1.4.2 Pro-social Behavior Strategies Based in Social Emotions

Emotions are not simply “feelings” but are instead a complexity of: (1) *cognitive appraisal* (that arouses and shapes the emotion); (2) *directed arousal* (that provides the “feel” of the emotion and signals its urgency); and (3) *action tendency* (that links action to the reaction of the emotion). (See Oatley, Keltner, & Jenkins, 2006 or Chapter 8 for an overview). How this complex itself has evolved is a fine puzzle; but for social animals, it certainly evolved in connection with socially relevant behavior. Krebs (2008) lists three relevant sets of emotions tied to pro-social behaviors: (1) *deference* in dominance hierarchies based in fear and respect; (2) *cooperation* among individuals based in gratitude, anger, and indignation; and (3) *altruism* based in love, sympathy, and empathy. We suggest some more in Chapter 8.

1.4.3 Strategic Interaction

Simply having social emotions and reacting based on them produces a sort of mechanical social order. But, once sociality is established, cheating is possible when one can take the other's perspective in order to deceive. A basic requirement for strategic social interaction is *theory of mind*, recognizing and ascribing mental states to ourselves and others (Wellman, 2018). There is evidence that even infants have basic aspects of theory of mind (Hudac & Sommerville, 2020) though its developmental trajectory looks similar to that of reading (Heyes, 2020), suggesting that the full capacity is some mix of built-in capability and cultural shaping.

The capacity to take perspective can then produce an “arms race” (Krebs, 2008) when it makes it possible to detect cheating and punish free riders. It can become even more complex when we keep track not only of cheaters but also those among us who do not punish the cheaters. (Boyd, Gintis, & Bowles, 2010; Boyd et al., 2003). This strategic level of interaction can apply to areas as abstract as what de Waal has called “community concern,” the strategic intervention in group processes to produce desired outcomes at the group level (de Waal, 2006).

1.4.4 Conscience

Krebs (2008), citing Darwin (1859), lists the linking of emotional responses with anticipatory fear of punishment from others (and later the internalized other) as a potential origin for what we call conscience. There is some evidence for this linkage.

For instance, physical responses associated with negative self-emotions (like shame and guilt) mirror behavior shown in appeasement displays in humans and other primates (Keltner & Buswell, 1997; Leary, 2007). Leary (2007) provides an overview of the research that makes this link between what we might call conscience and anticipatory reactions of real or imagined others. But one need not assume that this effect runs on anticipatory punishment alone. One can find evidence of an evolved capacity for compassion that can motivate behavior, not merely of avoiding the bad but also approaching the good (Goetz et al., 2010).

1.4.5 Moral Judgment and Reasoning

Krebs (2008) proposes that the origin of moral reasoning lies in moral communication—in verbal influence attempts to get others to behave in morally prescribed ways. But this is surely starting too late in the process. Tse (2008) looks back even further to a proposed delinking of attention from concrete objects in the world that allows arbitrary symbols to be associated with each other.¹¹ This is likely a basis for the flexibility of human reasoning, and the basis of things like metaphor, allowing for the association of arbitrary symbols and ideas in metaphor (a poem as lovely as a tree) but also the association of actions with abstract classes of good and bad. There is currently a vigorous debate about whether something as structured as a moral “grammar” is an evolutionary heritage of humans. This idea is an analogy from what seems to be an evolved grammar in language. There is currently only suggestive evidence for this hypothesis (Beller, 2010) and nothing like the strong networks of evidence we have reviewed for other adaptations (see Greene, 2008; Mikhail, 2007 for some idea of the controversy).

1.4.6 Moral Norms

Earlier we reviewed at least one moral norm (the incest taboo) that seems to have an evolutionary basis (Schmitt & Pilcher, 2004). But we clearly have a large store of moral norms that are in regular use, and that vary widely from culture to culture. In Chapters 7 and 8, we review the evidence that there is a structure to these norms that is cross-culturally consistent, with the same value sets showing up across all cultures but differently emphasized by each culture (Haidt & Joseph, 2004; Haidt, Koller, & Dias, 1993; Schwartz, 2006). This cross-cultural evidence of a universal structure might argue for an evolutionary origin (see Haidt & Joseph, 2007 for an evolutionary argument). Managing these norms involves a complex cultural process of protecting against deviance while promoting diversity (Wright, 2021).

We already have a long list of building blocks, and Krebs (2008) provides some idea of how these might come together to support what we call moral judgment and action. However, the chapters in this text suggest we need to add even more complexity to this picture. There must be some accounting of the development and

¹¹There is currently little evidence for this interesting proposal. Whether one calls this an interesting theoretical proposal or a “just so story” depends on one’s attitude toward the likelihood that such evidence will turn up (Dietrich, 2008).

integration of short- and long-term self-regulation. How and why might willpower (and variations in willpower) have evolved (Heatherton, 2011)? While it is merely difficult to assemble the network of evidence for short-term self-regulation as an evolutionary adaptation, work on the evolutionary underpinnings of longer-term self-regulation seems quite thin (Heatherton, 2011); though Miller (2007) suggests the sexual selection of moral virtues like dependability might play a role.

We know that storytelling (McAdams, 2009) and religion (Graham & Haidt, 2010; Kirkpatrick, 1999) play a role in moral judgment and action. For many of these more complex and higher-level aspects of morality it may well be that the relatively new approaches to culture and coevolution (Wilson & Sober, 1998) will provide us with a way to understand their construction. We will now look at a list of many of these additional aspects of morality that may (or may not) find some evolutionary underpinning.

1.5 Human Distinctiveness: How Large is the Gap?

We have spent most of this chapter looking at the processes of evolution and the building blocks of human morality. The goal has been to see how we can ground human morality in, or derive it from, various aspects of the capacities and behavior of our ancestors. An older version of this approach, disparagingly called “vener theory” by de Waal (2006), proposes that humans have only a veneer of politeness and hypocrisy overlaying the motivation of brute selfishness. Higgins and Pittman (2008) suggest that this version of human moral evolution is mirrored in the historical split in evolutionary approaches in different sub-fields of psychology. In cognition, we are said to have “developed from” prior species, while in motivation, we have been presented as merely “deriving” our animal motivations from prior species. This results in an image, they claim, of “humans as having the mind of a god and the motives of a brute” (Higgins & Pittman, 2008, p. 363). In the realm of morality, this image of the supremacy of reason is aided and abetted by philosophical approaches to ethics (e.g. Kant, 1999; Rawls, 1971/1999) that portray reason as both the foundation and the limit of real (that is, human) morality.

But current approaches to human morality that we review in this book suggest that: (1) human morality is constituted of more complex stuff than pure reason; and (2) the differences with other animals and our primate ancestors lie in a *range* of distinctly human abilities and motivations (Higgins & Pittman, 2008) and not just differences in reason alone. There is unanimity in recognizing that there are deep differences between humans and other animals in morality but the nature, structure, and meaning of those differences is still in dispute.¹²

¹²Some claims might underestimate these differences (Adolphs, 2009) in the way veneer theory does. Other claims may underestimate the unique abilities of other animals by making human morality the criterion, and missing uniquely adapted, species-specific capacities of other animals (Emery & Clayton, 2009). Crows, for example, do not have a full-blown theory of mind like humans, but they are remarkably good at hiding food from other crows (Emery & Clayton, 2009). De Waal (2006, 2009), Emery and Clayton (2009), and Adolphs (2009) provide some insight into the debates about these differences.

The dimensions associated with morality on which humans differ from other animals include at least the eleven categories noted in Sections 1.5.1–1.5.11. We have constructed this incomplete list from the literature in evolutionary psychology. The effort to build coherent networks of evidence for the origins of human ability in each of these categories may, of course, suggest additional categories or the merging of some. The list makes it clear that we are, indeed, at the very beginning of an evolutionary understanding of the structure and development of a truly human morality.

1.5.1 Symbolizing and Reasoning

The beginning of the ability to reason lies, perhaps, in the ability to take any particular representation of an object and link it arbitrarily to some other mental representation, e.g. a poem is like a tree (Tse, 2008). This may provide the basis for human ability to represent things symbolically (think of early cave paintings and whether any animal other than humans would “get” them). The empirical evidence for an evolutionary basis for moral reasoning and judgment remains unclear (Beller, 2010). Some researchers claim that regularities in the way people ignore logical structure and reason in specific content areas (e.g. cheating, incest) show the primacy of evolutionary modules for content-specific reasoning (Cosmides & Tooby, 2008; Cushman et al., 2006).¹³ But this claim is disputed by both philosophers (Prinz, 2008) and psychologists (Chater & Oaksford, 1996; Pietraszewski & Wertz, 2021). This is a disagreement about *how* ought-based (or deontic) reasoning might have evolved in humans. But it is also a dispute anchored in an agreement that human capabilities for deontic reasoning are vastly more complex than that of other animals.

1.5.2 Time Perspective

Time perspective underlies the ability to think about the moral consequences of an action or to make plans to achieve moral goals. In order to support some conception of a past or a future time, or of an alternative present, one must construct a mental representation and distinguish it from one’s own current experience (Higgins & Pittman, 2008). Thus, a conception of time requires the symbolizing abilities mentioned in Section 1.5.1. It remains unclear whether any animals other than humans can experience an imagined point of view (Adolphs, 2009) and thus have some sense of time. The sense of the future and past allows humans to construct moral stories about the past and about the future, and compare the self to them (Higgins & Pittman, 2008). This adoption of another point of view than that of immediate consciousness is likely one that underlies the ability to recognize other minds (Adolphs, 2009).

¹³For an example of this content-specific reasoning, see the discussion on moral dumbfounding in Chapter 7. In short, careful experimentation can find instances where people will simply say “I know it is wrong, but I do not know why.” Such moral intuition suggests that these particular moral judgments do not derive from a general reasoning mechanism. But this does not mean that no moral judgments derive from a general reasoning mechanism.

1.5.3 Cognitive Control and Self-Regulation

As we argue in Chapters 6 and 9, self-regulation is central to moral action. It is certainly the case that other animals can exert cognitive control over immediate desire, both to deceive other animals (de Waal, 2006) and in response to training by humans (H. C. Miller et al., 2010). This sort of immediate willpower of response suppression seems to share similar biological substrates in humans and other mammals (e.g. it uses glucose-based energy: Baumeister, Bratslavsky, Muraven, & Tice, 1998; H. C. Miller et al., 2010). But the extent, complexity, and flexibility of human self-control mechanisms far outpaces those of other animals (Heatherston, 2011). It extends to what the philosopher Frankfurt (1971) has called “second order desires,” or the desire to have a particular desire and to the planning of outside influences that will help one attain future states (for example, by going to school: Cohen, 2005). It also requires directed planning and practice to achieve long-term goals (Baumeister, Masicampo, & Vohs, 2011; Cervone, Shadel, Smith, & Fiori, 2006; Lord, Diefendorff, Schmidt, & Hall, 2009; McRae, Ochsner, & Gross, 2011).

1.5.4 Extensive Integration of Reason and Emotion

Moll and colleagues (de Oliveira-Souza, Zahn, & Moll, 2016; Moll, de Oliveira-Souza, & Eslinger, 2003; Moll, De Oliveira-Souza, & Zahn, 2009) have hypothesized that the most important thing about human reason may well be its *integration* with rather than its opposition to emotion.¹⁴ Even philosophical champions of reason as a marker of human morality (Korsgaard, 2006) have suggested that the integration of reason and emotion is a central puzzle in the evolution of morality (Korsgaard, 2010). It is not simply the *addition* of rationality to an “emotional animal” that makes humans special and human morality possible. It is the extensive integration of that rationality with emotion that allows them to influence and “tune” each other. Emotions influence our implicit and explicit moral reasoning by guiding intuition (Haidt, 2001) and reasoning (Goldin et al., 2008; McRae et al., 2011). And rationality influences emotion through the multifaceted self-regulation processes mentioned in Section 1.5.3, through the appraisal and re-appraisal process (Lazarus, 1991; Ochsner et al., 2010), and through the planned construction of culture (Cohen, 2005).

1.5.5 Extensive Culture

Humans have complex, stable, and constantly adapting cultural systems with enduring artifacts, language, artistic expression, economies, ritual, values, social structures, and extensive bodies of knowledge and practice (McElreath, 2010; Richerson & Boyd, 2005). These cultural achievements are clearly one of the major differences between humans and other animals. There is some evidence for social transmission of information among other primates (Adolphs, 2009) and thus some rudimentary socially shared culture. Understanding the linkages among evolution, neuroscience, and cultural processes will be a crucial undertaking for a complete understanding of moral action (Kitayama, Varnum, & Salvador, 2019; Wright, 2021).

¹⁴We review evidence for this integration in Chapters 2 and 8.

1.5.6 Self-Consciousness and Self-Awareness

The classic experimental demonstration of self-consciousness in children and in non-humans is the body awareness test. This involves placing some marker on the body in a place that is difficult to see without a mirror and then measuring the attempts to examine the new decoration. Evidence for such awareness has been found in chimpanzees, bonobos, dolphins, elephants, and monkeys (Adolphs, 2009). This seems adequate to demonstrate body awareness but its evidential status for awareness of one's own mind is unclear (Adolphs, 2009; Gallup & Anderson, 2020). For normally functioning adolescent and adult humans, there is unanimity that a complex, multidimensional, and morally relevant self-awareness is present (Byrne & Whiten, 1988; Robins, 2021).

1.5.7 Social Consciousness

Dogs and some other domesticated animals, perhaps because they have been shaped by human intervention over many generations, are skilled at interpreting gestures (e.g. pointing) and in responding correctly in the guesser–knower paradigm (in which they must choose a person based on that person's knowledge of where some food is hidden) (Emery & Clayton, 2009). But dogs do not appear to have some basic theory of mind characteristics that human infants share, like preferring helpers over hinderers in an attention task (Hamlin, 2013; McAuliffe et al., 2019; Van de Vondervoort & Hamlin, 2018). Primates are particularly skilled at tracking kinship and dominance relationships over time (Adolphs, 2009). However, if one asks for a full-fledged human theory of mind in other primates, it appears to be lacking (Emery & Clayton, 2009) – although one can likely find components of it. For example, there is evidence that other primates know that others know something but probably cannot grasp the complexity that the other's knowledge may be false (Emery & Clayton, 2009). Waytz and colleagues (Waytz, Cacioppo, & Epley, 2010; Waytz et al., 2010) have shown that humans' perception of agency (even the anthropomorphic perception of agency in inanimate objects) includes a moral dimension allowing for blame and suggesting that the roots of moral perception go quite deep into basic perception. And though other primates form coalitions (de Waal, 2007) the complexity of human tribalism is much greater (Clark et al., 2019).

1.5.8 Manipulation of Others' Perception

There is evidence that other primates understand and practice deception (Adolphs, 2009; Emery & Clayton, 2009). There is even evidence that crows and other corvids cache food in ways that make it difficult for other crows to find it, but only if other crows who might take it are present (Emery & Clayton, 2009). But again, even in young children, human manipulation of others' perception is vastly more complex, multidimensional, and subtle (Higgins & Pittman, 2008). Humans are deeply concerned about what others think (Higgins & Pittman, 2008) and particularly what others think about them (Leary, 2007).

1.5.9 Sharing Reality With Other People

Humans have a deep need to share their understanding of the world with others (Higgins & Pittman, 2008). All mammals have some abilities at social coordination and signaling (Goetz et al., 2010) and some have components of a theory of mind (Emery & Clayton, 2009). But even human children are competent in communicating shared social knowledge, sharing joint attention, and explicit teaching. Language is a primary achievement of this need (Byrne & Whiten, 1988).

1.5.10 Universalized Normative Evaluations

People's concern about what others think of them has been included in models of the "generalized other" (Heatherton, 2011; Mead & Morris, 1934) as one source of how humans universalize normative evaluations. The philosopher Korsgaard (2006) argues that this concern is more than simply worrying about how others might think of us, it involves seeing a moral reason as a reason for behavior, and using that reason to guide planning and action. In short, it involves some version of moral autonomy where the desires associated with moral reason become dominant over other desires or appetites.¹⁵ Managing these norms in a society involves a complex cultural process of protecting against deviance while promoting diversity (Wright, 2021).

Psychologically, these reasons are experienced as "natural law," as a moral imperative that trumps any social convention or personal preference (Shweder, 2012; Shweder, Mahapatra, & Miller, 1987); and this experience is one of the aspects of human morality that is a cultural universal. Despite clear evidence that other primates have some expectation about the nature of their social world, and show clear distress and attempts at punishment or repair when they are violated, it seems unlikely that one would find evidence for this aspect of moral expectation in non-human primates (Kitcher, 2006; Korsgaard, 2006). Indeed, it is unclear how one could even collect such evidence.

1.5.11 Self-Actualization, Religious Experience, and Self-Transcendence

Although some evolutionary theorists would prefer to dismiss self-actualization since it is not "clearly linked to reproductive fitness" (Schaller et al., 2010, p. 336), others find it both compatible with evolutionary theory and essential in understanding human experience (Peterson & Park, 2010). Both sides in the controversy agree that they do not expect to find it in other animals. A similar pattern emerges with another human universal: religion (Brown, 1991). Though there is disagreement about the status of religion and its relationship to evolutionary theory (Dawkins, 2006; Kirkpatrick, 1999), any suggestion that one might find something like human religion in other animals is conspicuous by its absence. Self-transcendence goes beyond the fulfillment of the self, and invests the self in some purpose beyond the self (Maslow, 1969). It seems to be both a natural product of adult development and a

¹⁵Note how desire and reason are integrated in this account.

process that can lead to extraordinary moral commitment (Walker & Frimer, 2015). This commitment has a dark side, depending in part on the cause one chooses (Koltko-Rivera, 2006; Skitka & Mullen, 2002).

1.6 Discussion

1.6.1 Conclusion

An evolutionary understanding of morality can primarily help us in understanding our capacities for taking moral action. How those capacities are shaped, influenced, and directed is the subject of the other chapters of this book. However, an understanding of capacity, its structures, and its limitations can help to articulate the structure and limits of our morality, help us see how good and evil are linked, and allow us to grasp the precarious human condition that is balanced in the gray zone between those two:

1. *Moral action is deeply tied to the social nature of being human.*

Much philosophy and psychology have presented morality as the achievement of reason and will alone. Evolutionary theory confronts us with how our human morality is deeply rooted in the social nature of our species. The need to negotiate a complex social hierarchy within groups and to compete between groups has produced a set of capacities that we list in Section 1.4. These capacities are densely interwoven and help us to see how moral action results from the complex interplay among social emotions, planning, and rationality. Any understanding of morality that does not take this interplay into account will be inadequate.

2. *The dark side of morality is, ironically, enabled by our desire to do good.*

An evolutionary approach to morality also helps us to understand the peculiar dual-sided interaction of morality with social motives and structures. Social status in social hierarchies and in between groups is based in respect but also anger and fear. Cooperation among individuals and groups is based in gratitude and respect but also vicarious anger and indignation. Compassion for others is based in love and empathy but also vicarious anger and revenge against those who hurt loved ones.

This complex set of social emotions can be harnessed by our rationality and culture in the service of a range of goals, producing both international aid organizations and organized ethnic cleansing and self-giving care for a partner and abuse for a partner. In this way, the psychology of being moral is also the psychology of evil.

1.6.2 Application

In the Introduction, we presented the story of Rick Munson and his wife.¹⁶ The Munsons began by hosting foster children, then went on to host disabled foster children. Eventually, they founded a charitable organization and a facility that provided

¹⁶Rick Munson is a pseudonym for a participant in a study of volunteerism (Hart & Atkins, 2006). The report of the study does not give a pseudonym for his wife, though it makes it clear they made decisions together.

integrated services to children with physical challenges. One can chart this as a move from the pro-social integration of the two individuals into a committed couple, followed by the expression of their concern for others in caring for children, followed by the extension of that concern to community action. Their taking in of foster children already stretches our conception of a narrow evolutionary basis for pro-social action, as it was likely an extension of the desire to have children to those who were clearly outside their genetic family. But their actions were surely due to a capacity for compassion that is a part of their evolutionary heritage and was shaped and supported by their religious culture. It was also made possible by an organized cultural practice of finding homes for children without any. The empathy the Munsons had for other disabled children and their parents and the couple's capacity for planning and rationality led them to a more general community concern, which was expressed by volunteering in charitable organizations. This in turn led to their founding of organizations to meet community needs.

One can see in this example the integration of evolutionarily shaped emotional and rational capacities with culturally constructed social structures to produce good. This provides an example of the fit of these capacities (rationality, planning, compassion, empathy) to the local ecology in which the Munsons were embedded. But it is also an example of the shaping of those capacities by the wider moral ecology (e.g. religious practice) and the local ecology (the lack of integrated service for disabled children and the practice of founding organizations to meet needs). An understanding of the evolutionary basis of morality will require this sort of complexity.

1.6.3 Open Questions

1. *We have an excellent beginning of a model of the evolution of morality and a long way to go in developing it.*

The review of building blocks (Section 1.4) suggests that we are beginning to accumulate an evidential network of the underpinning of the moral ability in humans. But a comparison of the standards for making an evolutionary argument (Section 1.3) with the evidence for each building block suggests we still have a long way to go to fill in the argument.

2. *There is a significant collection of capacities that underlie moral action for which we so far have no viable evolutionary explanations.*

Section 1.5 gives a list of eleven areas in which there is an easily discernable distinction between the moral capacities of humans and other animals. There is clearly a vast field of opportunity for good research and theory here. But doing this work will require changing the way the question is asked. Instead of asking *whether* humans are different from other animals in their morality, we should begin asking *how* they are different, and how those differences have come about. It is some combination of these morally relevant differences in *how* that differentiates human morality from what might be called the proto-morality of other species.

3. *Exploring the fit of the evolved moral capacities of humans with their social and physical ecology will provide for a more complete evolutionary understanding of human morality.*

A central mistake in work on theory of mind is the tendency to measure other animals by their differences from human theory of mind, rather than by the

ecologically valid fit of the abilities of the particular species with that species' social and physical ecology. The field of moral psychology should take a clue from this mistake and insist on an ecologically valid explanation of human morality. Thus, rather than simply looking for universals, we should look for a more complete understanding of human morality in the fit of the moral capacities of humans with their varied social and physical ecologies. This will necessarily include an evolutionary perspective, but is unlikely to be reducible to only that perspective.

4. *The evolution of morality and immorality are closely linked and interdependent.*

Neither morality nor immorality is more “basic.” Aggression against outsiders and norm-violators is integral to our understanding of how moral commitment to a group evolved. We can regulate this, and even balance it with compassion, but altruistic punishment based in revenge motives will likely remain central to doing so. Empirical and theoretical work might help us find ways to motivate pro-social behavior and discourage anti-social behavior that work within the limits of our evolutionary heritage and are still acceptable to ethical norms.

1.7 Further Readings

These suggested readings are designed to lead the reader further into the literature that forms the main themes of this chapter. They combine some classic pieces and recent work. Complete citations are provided in the references section.

- Aktipis and Kurzban (2004). “Is Homo economicus extinct? Vernon Smith, Daniel Kahneman and the Evolutionary Perspective.” An historical overview of the idea of the selfish “economic human” and its diminishing psychological appeal in the face of a wave of research suggesting its falsity (or at least incompleteness).
- Curry et al. (2019). “Is it good to cooperate?” An excellent example of cross-cultural work to establish an evolutionary basis for morality.
- de Waal (2008). “Putting the altruism back into altruism: The evolution of empathy.” Primatologist Franz de Waal provides a useful presentation of the evidence for the evolution of empathy and its role in altruism.
- Gallup and Anderson (2020). “Self-Recognition in animals.” A review of a half-century of research on animal consciousness that argues that the gap between great apes/humans and other species is larger than usually acknowledged.
- Krebs (2008). “Morality: An evolutionary account.” A thoughtful presentation of the main issues in an evolutionary account of human morality.
- Schmitt and Pilcher (2004). “Evaluating evidence of psychological adaptation: How do we know one when we see one?” A readable and systematic overview of what it means to say that some psychological characteristic is an evolutionary adaptation.
- Sober (2006) *Conceptual Issues in Evolutionary Biology* (3rd ed.). Excellent volume edited by a philosopher deeply involved in the evolutionary debates within the biological disciplines. Every chapter is an example of how to think carefully about evolution. Essays on what fitness means, levels of selection, race, culture, ethics, etc.

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