



Two types of aggression in human evolution

Richard W. Wrangham^{a,1}

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Two major types of aggression, proactive and reactive, are associated with contrasting expression, eliciting factors, neural pathways, development, and function. The distinction is useful for understanding the nature and evolution of human aggression. Compared with many primates, humans have a high propensity for proactive aggression, a trait shared with chimpanzees but not bonobos. By contrast, humans have a low propensity for reactive aggression compared with chimpanzees, and in this respect humans are more bonobo-like. The bimodal classification of human aggression helps solve two important puzzles. First, a long-standing debate about the significance of aggression in human nature is misconceived, because both positions are partly correct. The Hobbes–Huxley position rightly recognizes the high potential for proactive violence, while the Rousseau–Kropotkin position correctly notes the low frequency of reactive aggression. Second, the occurrence of two major types of human aggression solves the execution paradox, concerned with the hypothesized effects of capital punishment on self-domestication in the Pleistocene. The puzzle is that the propensity for aggressive behavior was supposedly reduced as a result of being selected against by capital punishment, but capital punishment is itself an aggressive behavior. Since the aggression used by executioners is proactive, the execution paradox is solved to the extent that the aggressive behavior of which victims were accused was frequently reactive, as has been reported. Both types of killing are important in humans, although proactive killing appears to be typically more frequent in war. The biology of proactive aggression is less well known and merits increased attention.

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Much human aggression is either currently adaptive or derived from adaptive strategies (1–7). Patterns of violence therefore appear to have been shaped by natural selection. However, an unresolved question is whether human propensities for aggression have evolved to be relatively low or high.

Two opposed positions predominate. Before Darwin they are often considered to have been represented by the contrasting stances of Jean-Jacques Rousseau and Thomas Hobbes, and afterward by those of evolutionists Peter Kropotkin and Thomas Henry Huxley (8). The “Rousseau–Kropotkin paradigm” sees humans as a naturally benign and unaggressive species, comparable to primates that have a consistently low frequency of conflict (e.g., *Callitrichidae* or muriqui, *Brachyteles arachnoides*) (9, 10). This position therefore considers violence to be promoted mainly by recent cultural novelties, such as settled living, patriarchal ideology, or lethal technology (9, 11, 12). The “Hobbes–Huxley paradigm,” in contrast, rejects the

idea of the noble savage and holds violence in the evolutionary past to have been frequent and adaptive. By this view human tendencies are more like those of primates with steep dominance hierarchies and relatively frequent deaths from aggression, such as chacma baboons, *Papio ursinus*, and chimpanzees, *Pan troglodytes* (13, 14). Accordingly, cultural constraints on violence, such as social controls exerted by a powerful leader, are considered to be responsible for human societies’ being relatively peaceful (15, 16). In short, Rousseau–Kropotkin sees humans as a naturally peaceful species corrupted by society, while Hobbes–Huxley sees humans as a naturally aggressive species civilized by society.

In this paper I argue that the two opposed perspectives are both inadequate because they suffer from the same problem: They wrongly treat aggression as a single behavioral category. Their implication that aggression is “unimodal” forces an erroneous choice because it requires the human propensity for aggression

^aDepartment of Human Evolutionary Biology, Harvard University, Cambridge, MA 02138

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¹Email: wrangham@fas.harvard.edu.

to be either low (as per Rousseau–Kropotkin) or high (as per Hobbes–Huxley). However, researchers in sciences other than evolutionary anthropology have long claimed that aggression falls into two types, here called proactive and reactive (17–26). The classification of aggression as bimodal is well supported by psychological and biological data. It solves the traditional debate by seeing the human species as having a low propensity for reactive aggression and a high propensity for proactive aggression.

The distinction between the two types is centered on the aims of aggression. Proactive aggression involves a purposeful planned attack with an external or internal reward as a goal. It is characterized by attention to a consistent target, and often by a lack of emotional arousal. Aggressors normally initiate action only when they perceive that they are likely to achieve their goals at an appropriately low cost (19, 23, 27, 28). Examples include bullying, stalking, ambushes, and premeditated homicides, whether by a single killer or a group.

By contrast, reactive aggression is a response to a threat or frustrating event, with the goal being only to remove the provoking stimulus. It is always associated with anger, as well as with a sudden increase in sympathetic activation, a failure of cortical regulation, and an easy switching among targets (20, 24, 29). Examples are bar fights arising from mutual insults and crimes of passion immediately after the discovery of infidelity. Note that the term “reactive aggression” refers to the nature of the aggressive act rather than the reason for acting aggressively. According to this definition acts of revenge are not necessarily reactive and in fact are unlikely to be so, given that revenge typically involves planning.

The two types are sometimes easy to distinguish. For example, when two animals compete with steadily escalating intensity, as frequently occurs in fights over food or mates, aggression is typically reactive without any proactive elements. In most species proactive aggression is rarer than reactive aggression but a common form in some primate taxa is sexually selected infanticide, which can be carried out by a male targeting, stalking, and deliberately killing a specific unrelated infant (30, 31). Human aggression likewise varies from purely reactive cases with unplanned fighting rich in emotional arousal to purely proactive, premeditated, and deliberate efforts to harm a particular victim.

Versions of the proactive–reactive distinction have long been discussed in relation to potential explanations for aggression. Proactive (instrumental) aggression was argued by Bandura (32) to be a learned behavior acquired during development in response to rewards. Reactive aggression, by contrast, was viewed by Berkowitz (33) as an innate response to frustration.

The terms “proactive aggression” and “reactive aggression” were proposed to unify concepts of aggression types in children, adults, and animals (27) and have been used widely (17, 28, 34–36). Several parallel dichotomies are also employed (35). Proactive aggression is similar to what some researchers call instrumental, predatory, offensive, controlled, or cold aggression. Likewise, reactive aggression is similar to impulsive, affective, hostile, defensive, emotional, or hot aggression. The terms “predatory” and “affective” (or “defensive”) are more common in psychiatry and animal behavior, while “premeditated” and “impulsive” are typical in legal systems (37).

The various dichotomies are not identical. For instance, the proactive–reactive distinction applies more to individual traits, whereas the premeditated–impulsive distinction tends to reflect the aggressive act itself. This means that although such classifications are often used interchangeably they should not be treated as if they are fully equivalent to each other (23, 38). Furthermore, a

more elaborate categorization is sometimes employed (35). For example, the National Institute of Mental Health (NIMH) Research Domain Criteria are designed to promote research on the mechanisms underlying psychopathology. The NIMH Research Domain Criteria categorize three types of aggression, namely, frustrative nonreward, defensive aggression, and offensive (or proactive) aggression (39). In this case the first two types are both reactive. While more discriminating classifications such as used by NIMH can be useful they do not undermine the value of the bimodal distinction.

The bimodal concept was questioned by Bushman and Anderson (40) because both in nonhumans and humans episodes of aggression vary in how completely the proactive and reactive types are separated. Sometimes an individual can express proactive and reactive aggression in the same act, such as when a premeditated act is met with an effective defense and the initiator is forced into a reactive fight. The two types can also be hard to separate when an individual frustrated by a conflict becomes angry (reactively) and later coolly plots revenge (proactively). However, although proactive and reactive elements can indeed be combined, much evidence finds that the neural systems mediating reactive and proactive aggression are different (41, 42). Furthermore, aggression results primarily from one or the other motivation (43), and within individuals either proactive or reactive aggression tends to be the predominant form (23, 38). In practice researchers and clinicians find the bimodal concept of aggression useful whether applied to children (19, 27, 28), adolescents (44), or adults (36), including both normal individuals and psychopaths (43, 45). It helps with understanding the dynamics of various antisocial offenses including bullying (44, 46), domestic violence (22), criminality (36), homicides (29), and mass murder (47, 48). The value of the dichotomy comes partly from its predictive power. For instance, proactive aggressors are more likely to be recidivists (49, 50), are less likely to respond to pharmacological interventions (19, 51), are more often diagnosed with psychopathy (52), and are less likely to experience a decline in aggressiveness during adulthood (53, 54).

The proactive–reactive distinction contributes to evolutionary theory because it raises the possibility that selection has influenced the two types of aggression independently. To justify its evolutionary significance I first review its biological basis. I then compare the expression of proactive and reactive aggression in humans with other species and argue that the Rousseau–Kropotkin and Hobbes–Huxley positions are, in different ways, each importantly correct. Finally, I consider how the bimodal model can help explain the evolution of contrasting propensities for proactive and reactive aggression in *Homo sapiens*.

Proactive vs. Reactive Aggression

The bimodal classification of aggression based on behavioral criteria suggests that the two types are supported by different physiological mechanisms. For ethical reasons most of the work on this problem has been carried out with nonhuman animals.

Neural studies of aggression began during the mid-20th century. Cats whose hypothalamus was stimulated in different locations were found to produce different behaviors. Electrodes placed in the lateral hypothalamus elicited a “quiet biting attack,” whereas those placed more medially led to “affective defensive behavior” (55). The distinction led to a detailed understanding of underlying neural pathways (56, 57). Since quiet biting attacks by cats were feeding behaviors directed in these experiments toward laboratory rats, the two behaviors were not initially regarded as challenging a unimodal concept of aggression (19). In studies of

rodents a similar conceptual separation was at first assumed between feeding attacks and intermale aggression (58).

However, in 2010 Tulogdi et al. (59) showed that feeding attacks on prey were innervated in similar ways to proactive aggression on conspecifics. They used male laboratory rats to compare feeding attacks (on mice and cockroaches) with proactive aggression toward other males. Proactive aggression was characterized by low physiological arousal, a lack of social communication, and targeting of vulnerable body parts. By contrast, reactive aggression was associated with high physiological arousal and communication of intent including threats. The two types of rat aggression thus conformed to the human distinction.

A key finding was that feeding attacks and within-species aggression were not only ethologically similar but were also controlled by overlapping neural mechanisms, distinct from those supporting reactive aggression (59, 60). In rats, as in other mammals, aggression is importantly modulated by a neural circuit that links the amygdala, hypothalamus, and periaqueductal gray (61). Tulogdi et al. (59) found that both feeding attacks and proactive aggression were associated with innervation of the central and basolateral amygdala, the lateral hypothalamus, and the ventrolateral periaqueductal gray. By contrast, reactive aggression among rats was associated with the medial amygdala, the mediobasal hypothalamus, and the dorsal periaqueductal gray (59, 60, 62). These differences in rat innervation between proactive and reactive aggression were the same as those found in cats between quiet biting attacks and affective defensive behavior. In male mice selected for aggressiveness the same essential differences in neurobiology were found between more proactive or reactive forms of attack (63). Tulogdi et al. (ref. 60, p. 114) concluded that the "neural underpinnings of predatory aggression show remarkable cross-species similarities."

The results of Tulogdi et al. (59, 60) indicate the existence of two different pathways in a key neural circuit underlying aggression. They thereby conform to much other evidence of differential innervation for the two types of aggression in humans. Although the neural basis of human proactive aggression is not well understood, the critical result is that it is different from reactive aggression (42, 64). Thus, according to the well-supported serotonin-deficiency hypothesis, reactive aggression is suppressed by high concentrations of brain serotonin. Disruption of serotonergic projections to the prefrontal or anterior cingulate cortex accordingly enhances reactive aggression, whereas serotonin selective reuptake inhibitors and other agents that elevate serotonin levels can contribute to control of reactive aggression in both humans and nonhuman models (18, 65–67). Proactive aggression, by contrast, is unaffected by such interventions. In line with the implications of the serotonin-deficiency hypothesis, deficits in frontocortical function arising from lesions, low blood flow, or reduced glucose metabolism are associated with elevated reactive aggression (43). For example Raine et al. (29) used PET scans to show that in men accused of murder reduced prefrontal control was associated with homicides for which aggression was reportedly reactive. Prefrontal function in predatory (proactive) killers, however, was unexceptional. Recent experiments also suggest that testosterone facilitates reactive aggression by reducing prefrontal activity (68). A different kind of evidence comes from tumors. Tumors in the human mediobasal hypothalamus have been observed to promote reactive, but not proactive, aggression (21).

Differences in innervation between the two types of aggression are also supported by reactive aggression's being generally more sensitive to therapeutic interventions and neuroanatomical

changes (19, 21). Thus, lithium carbonate given to prison inmates reduced impulsive aggressive acts to low levels but did not affect proactive aggression (67). Similar results come from use of phenytoin (69). Pharmacological impacts on androgen levels could in theory also impact reactive aggression, because testosterone concentrations respond to competition in ways that appear to increase an individual's potential to react aggressively (17).

Less is known about the brain circuitry underlying proactive aggression in humans but, as with reactive aggression, multiple mechanisms are engaged (70). One model, the integrated emotion system (IES), explains how it might develop during ontogeny (71, 72). The IES suggests a role for hypoactivity in the amygdala, leading to low responsiveness to emotionally salient stimuli such as others' fear expressions (as seen in psychopathy) (41, 73). Glucocorticoid deficiency has also been found to shift aggression toward being more proactive (59). Cortical activity is likewise important. Proactive aggression, but not reactive aggression, was reduced in men by the induction of neural activity in the right frontal hemisphere (using transcranial direct current stimulation) (42).

Tendencies for both proactive and reactive aggression are strongly influenced by developmental experience (74). Nevertheless, studies of twins up to puberty, using questionnaire ratings by parents or teachers, indicate that propensities for proactive and reactive aggression tend to be stable over time and are mediated by partly different genes (54, 75). In a recent example with 254 monozygotic and 413 dizygotic pairs of twins, variation between children in aggressiveness ratings by teachers was unrelated to the extent of shared environment. Genetic factors that overlapped between proactive and reactive aggression accounted for 39–45% of the variance in proactive aggression scores and for 27–42% of the variance in reactive aggression scores. Aggression scores were also associated with unique genetic factors, stronger for reactive than proactive aggression (37).

Evidence thus indicates that proactive and reactive aggression are innervated, hormonally influenced, and genetically supported in partly different ways, whereas proactive aggression and feeding attacks on prey share overlapping neural mechanisms. Limited breeding experiments reinforce those conclusions. Mice selected for a proactive type of increased intermale aggression also increased their propensity to attack prey (crickets) (58). Predatory aggression by rats (toward mice) showed no reduction in a line selected for reduced reactive aggression (76).

In sum, the bimodal concept of aggression is based on differences in behavior found in multiple contexts, parallel neurobiological differences between proactive and reactive aggression in rats, mice, and cats, and much evidence for differences in the innervation of proactive vs. reactive aggression in humans. A plausible inference, therefore, is that the mechanisms underlying proactive aggression are evolutionarily conservative, as they are with reactive aggression, such that in humans proactive aggression is innervated in a similar manner to rats and (with respect to feeding attacks) cats. In other words, human proactive aggression will be found to engage the lateral hypothalamus, the ventrolateral periaqueductal gray, and the central and basolateral amygdala (60). While that hypothesis remains speculative, it is already clear that different pathways underlie proactive aggression compared with those that underlie reactive aggression. This means that we can reject unimodal hypotheses that would envisage proactive aggression as merely combining a single category of aggression with enhanced prefrontal control.

Resolving the Rousseau–Kropotkin vs. Hobbes–Huxley Debate

Recognition of proactive and reactive aggression as separate biological categories raises the possibility that the two types could have followed separate evolutionary trajectories. Comparison of aggressive patterns in humans with those of our closest relatives, chimpanzees (*P. troglodytes*) and bonobos (*Pan paniscus*), indicates that this has indeed happened, because the three species show varying combinations of proactive and reactive aggression. Nomadic hunter-gatherers provide relevant reference points for evolutionary comparison of human behavior with apes (77, 78).

Chimpanzees express proactive aggression when coalitions of males travel to the border areas of their community territories without feeding and make surprise attacks on members of neighboring social communities (13). The frequency of this behavior varies depending on factors such as the number of males in the community and the population density, but overall it results in significant death rates, higher than those reported in intergroup aggression among any other nonhuman primates, in most of which such behavior is unknown (79). Humans are the only other primate species in which similarly high (or higher) rates of death have been recorded in intergroup aggression (80). Notably, in hunter-gatherers, hostile intergroup encounters are principally planned raids and ambushes rather than escalated battles. Lethal violence in those societies is therefore frequently a result of proactive aggression (81–84). By contrast, in bonobos (*P. paniscus*) no proactive aggression leading to intergroup killings has been observed, despite ample opportunity to make relevant observations, and no other evidence of proactive aggression toward conspecifics has been reported (13). Unlike in chimpanzees, there are no reports of violent infanticide in bonobos (13). Proactive aggression toward conspecifics is accordingly much more common in chimpanzees and humans than in bonobos, where it is infrequent or absent.

Reactive aggression presents a different distribution. In this case chimpanzees and bonobos both show more aggression than humans. In chimpanzees reactive aggression is routinely expressed in dyadic fights prompted by spontaneous competition over mates, food, or dominance status (85, 86). Rates of contact fighting and/or chasing within two wild social communities have been found to be similar to those in captivity, in every context averaging around one to three cases per 100 h of individual observation of both sexes (80). In bonobos the severity of aggression is greatly reduced compared with chimpanzees (87). However, the species difference in frequency of aggression, as opposed to its severity, is less pronounced. A long-term field study found that wild male bonobos were aggressive at about half the rate of male chimpanzees, while female bonobos were aggressive at higher rates than female chimpanzees (88).

In comparison with both chimpanzees and bonobos, frequencies of fighting in small-scale human societies are very low (89). For example, Hill and Hurtado (90) reported that in 17 y of working with the Aché foragers of Paraguay they never observed a scuffle. At the opposite extreme, a study of Australian aborigines in difficult circumstances (due to poverty and alcohol) revealed an unusually high rate of physical aggression (91). However, compared with *Pan* even this supposedly high rate was trivial. The frequency of attack among the Australians was estimated as 0.005–0.006 per 100 h, that is, two to three orders of magnitude less than in chimpanzees and bonobos (80). This rare example of quantitative data on rates of human fighting conforms to the conclusions of ethnographers who uniformly stress the peaceful tenor of daily life within small-scale societies (9, 92–94).

Even violence between the sexes, which occurs often in humans, suggests humans are relatively low on the scale of reactive aggression. Unfortunately, it is uncertain how much of intersexual violence is proactive or reactive. However, if human intersexual aggression were all reactive, which is clearly an exaggeration (95), it would still be less frequent than in chimpanzees. Thus, a survey of 79 countries and two territories found that the lifetime prevalence of intimate partner violence among ever-partnered women was 30% (96). In a similarly global study 7.2% of women had experienced sexual violence by men other than partners (97). By contrast, in chimpanzees the lifetime prevalence of males physically beating and sexually coercing females is 100% given that every adult female is regularly attacked by every young male as he moves into the adult hierarchy, and his attacks on females continue routinely throughout his life partly in the context of sexual intimidation (86, 98). In bonobos females initiate and win more conflicts than males, who are mostly subordinate to females and do not regularly attack them (87, 99, 100).

Humans thus have a low frequency of within-group fighting compared with chimpanzees, and in the generally peaceful quality of daily life humans are more similar to bonobos. Accordingly, the two *Pan* species provide reference points for scaling human propensities for aggression. Humans share with chimpanzees a higher propensity for proactive aggression than is found in bonobos. However, humans share with bonobos a lower propensity for severe reactive aggression than is found in chimpanzees. The distribution of these patterns means that during the evolution of *Pan* and *Homo* from a common ancestor ~6–10 million y ago (101) propensities for both proactive and reactive aggression changed.

The polarity of the changes is a matter of debate because the phenotype of the last common ancestor is uncertain. If chimpanzees provide a valid model of the last common ancestor (102, 103), there was a minimum of two changes: Reactive aggression declined in humans while proactive aggression declined in bonobos. If the three relatives descended from a species unlike any living species (104) other kinds of change are possible. However, regardless of the evolutionary route, compared with *Pan* species humans fall into the “high” category for proactive aggression and into the “low” category for frequency of reactive aggression.

This asymmetric combination offers a resolution of the debate between Rousseau–Kropotkin and Hobbes–Huxley. First, humans’ relatively low propensity for reactive aggression fits the Rousseau–Kropotkin view. In accord with Rousseau–Kropotkin, human emotional reactivity is clearly strongly influenced by biology. For example an increased risk for reactive aggression (such as in patients with Intermittent Explosive Disorder) is associated with elevated amygdala responsiveness and/or decreased prefrontal cortex activity (19, 41). Compared with our closest relatives such mechanisms are clearly set at a relatively unresponsive level in humans. Thus, although humans show cultural variation in the frequency of reactive aggression (105), the rate of fighting is always lower than among chimpanzees and bonobos. Furthermore fossil evidence from human crania during the last 200,000 y shows a reduction in anatomical features associated with aggression (106). These points suggest that the unusually low human propensity for reactive aggression results at least partly from an evolved down-regulation that occurred in the second half of the Pleistocene.

By contrast humans’ high propensity for proactive aggression does not fit Rousseau–Kropotkin, but it does fit Hobbes–Huxley. Assessing the role of biology in proactive aggression is complicated by the fact that extensive societal variation occurs in the

frequency of premeditated violence (such as war). Such variation could in theory be due entirely to cultural influences, but it is also predicted by a biological perspective, given that proactive aggression is expected to be expressed only when it is likely to be successful (107). Biological influences on humans' high propensity for proactive aggression are indicated by the contrasts to reactive aggression, including the almost complete suppression of sympathetic arousal and any awareness of emotion, and similarities to nonhumans. Psychopathy is a risk factor for proactive aggression, indicating that selection could adjust the frequency of proactive aggression by favoring more psychopathy (19).

Thus, the bimodal concept of aggression suggests that humans have evolved to combine a low propensity for reactive aggression with a high propensity for proactive aggression. Rousseau–Kropotkin and Hobbes–Huxley were accordingly each right in complementary ways.

Evolution of Proactive and Reactive Aggression in *H. sapiens*

What adaptive reasons might explain why humans combine a high propensity for proactive aggression with a low propensity for reactive aggression? There are various possibilities. Consider proactive aggression first.

Behavioral similarities between small-scale war and chimpanzee intergroup attacks suggest that proactive aggression toward members of other groups was favored in a similar way in the two species. In chimpanzees, as in many animals, community members win conflicts against neighboring communities by fighting cooperatively and have higher fitness if their community territory increases in size (108). An unusual feature of chimpanzees is a highly dynamic fission–fusion grouping pattern, which means that subgroup size varies unpredictably from day to day or hour to hour. The result is that larger subgroups can sometimes locate much smaller subgroups of rivals in neighboring territories. Those in the larger subgroup can then have an overwhelming imbalance of power in their favor, such that they can attack, wound, and/or kill without suffering serious costs (13). Since there are long-term benefits from killing members of neighboring groups, natural selection has putatively favored this style of proactive aggression (13, 108–110). Essentially the same explanation applies to chimpanzees and hunter-gatherers, except that humans have cultural systems of reward and coercion that promote more risk taking (82, 111, 112). As a result, compared with chimpanzees, during intergroup aggression human attackers are more likely to be wounded or die (82).

An alternative explanation for proactive aggression in intergroup attacks suggests that group selection favors risk-prone altruism if it increases the probability of a group winning conflicts with its neighbors (113, 114). In favor of the hypothesis, rates of war mortality and genetic differentiation among hunter-gatherer groups have been estimated to be sufficiently high for group selection to favor costly intergroup aggression (114). Against it, levels of intergroup migration among chimpanzees are too high to allow group selection to operate (111), yet estimated rates of war mortality and degree of genetic differentiation among groups are similar between chimpanzees and hunter-gatherers, indicating a problem with the group selection model (115).

Proactive aggression occurs within groups also, both in humans and chimpanzees. Examples include capital punishment (discussed below) and homicide in humans and coalitionary aggression and infanticide in chimpanzees (116). Whether selection

first favored a propensity for proactive aggression in within-group or between-group contexts is unknown.

Humans' low propensity for reactive aggression requires entirely different kinds of explanation. Reduced reactive aggressiveness is closely tied to high tolerance and extensive cooperation. Explanations for reduced aggressiveness are therefore allied to ideas for the evolution of within-group tolerance, such as individual selection for cooperative breeding (9, 117, 118), group selection for parochial altruism (114, 119), and cultural group selection for prosocial norms (120). Reduction in (reactive) aggression has also been proposed to decline in response to socioecological influences such as high population density (106, 121, 122), sedentariness (122), and social preferences for cooperators (123–125). However, all these proposals suffer from their inability to explain how human societies would prevent a determined individual from winning conflicts by the use of force. So long as a bully could predictably win conflicts his aggressive behavior would be favored by selection.

In the case of bonobos, a reduction in the propensity for male reactive aggression compared with chimpanzees is proposed to have resulted from an ecology that permitted the evolution of relatively stable female subgroups. These led to strong female coalitions that were able to control aggressive males (87). There is no indication of any equivalent dynamic in humans.

The explanation that most explicitly addresses why domineering human males with high individual fighting ability would not have achieved high reproductive success is the theory of coordinated punishment by other males (78, 119, 126–131). In nonhuman primates high male rank comes from the ability to win fights, and the highest-ranking males tend to have high fitness (132, 133). By contrast, in nomadic hunter-gatherers the closest equivalent to high male rank in nonhuman primates is high respect coming from prestige, alliance formation, and negotiation ability. The problem for individual hunter-gatherers who attempt to use fighting prowess to achieve their goals is that they are vulnerable to the actions of male coalitions who can jointly intimidate, expel, or kill the offending individual (77, 78, 127, 131, 134). The occurrence of coordinated aggression against domineering males, including socially approved execution, is apparently responsible for relationships among married men being egalitarian. This system of control, called a "reverse dominance hierarchy" (131) or a "counterdominance hierarchy" (134), is universal in nomadic hunter-gatherers including the gerontocratic and polygynous societies of northern Australia (131, 135).

The potency of sociopolitical leveling mechanisms in hunter-gatherers inspired Boehm's proposal that social control was responsible for the evolutionary reduction of aggression (127). According to Boehm's "execution hypothesis," communally approved killings of group members emerged in the Pleistocene as a cultural adaptation for suppressing domineering bullies and norm violators (120, 127). Killings were facilitated by the evolution of shared intentionality (136), and possibly by weapons (137). The evolution of a reduced propensity for reactive aggressiveness followed as an incidental genetic consequence.

In support of the execution hypothesis, traditionally capital punishment appears to have been a cultural universal (138), which suggests that it was adopted before the dispersal of *H. sapiens* from Africa at ~60,000 y ago (127); in nomadic hunter-gatherers antisocial males with a history of selfish aggression form a high proportion of the victims of capital punishment (127), and evidence of increasing craniofacial feminization in *H. sapiens* from at least 200,000 y ago onward parallels morphological changes in dogs resulting from selection against reactive aggression (106).

Theoretical models support the evolutionary validity of coordinated punishment as a mechanism for promoting cooperation (139), suggesting that the death penalty could have been readily adopted as a social tactic after human ancestors had acquired sufficient cognitive and linguistic ability to collaborate effectively against aggressive norm violators (136). These points indicate that socially approved executions have been widespread since before *H. sapiens*. They can therefore be expected to have led to selection against aggressive tendencies.

The inference that aggression among *H. sapiens* has declined as a result of selection is supported by comparisons with other species. Domesticated mammals that have been selected for reduced aggression tend to exhibit a suite of morphological, physiological, and cognitive characteristics unrelated to aggression (i.e., a domestication syndrome) (122, 140). *H. sapiens* has been argued to exhibit many features of the domestication syndrome, including in morphology (e.g., craniofacial feminization) (106, 122), behavior (e.g., play and food sharing) (125, 127), life history (e.g., expanded developmental period) (141), and cognition (e.g., cooperative communication) (120, 141).

However, to date the execution hypothesis has treated aggression unimodally, which is problematic: The hypothesis argues that a propensity for aggression became down-regulated as a result of aggressors' being killed by capital punishment, yet those who carried out the killings were by definition exhibiting a high level of aggression. Fitness benefits that the killers received by executing aggressive victims would undermine selection against aggression.

The bimodal view of aggression readily solves the problem. Among hunter-gatherers and universally, aggression exhibited by the executioners is proactive: It is carefully planned so as to minimize the risk of a victim fighting back (127). According to Boehm (127) the victims of capital punishment were frequently men with a history of aggression. When the victims had high propensities for reactive aggression, the long-term effect would be a reduction in reactive aggression. When the victims killed because of their proactive aggression, there would have been no long-term effect since executioners and victims were displaying similar tendencies.

Discussion

The idea that aggression consists of two main types has long been widely adopted in biology, psychology, and related social sciences, but it has been largely missing from discussions of the extent to which human propensities for aggression have evolved to be low or high. The omission is surprising since behavioral, neurophysiological, and genetic data richly justify the division of human aggression into proactive and reactive forms. However, much remains to be learned about the dichotomy, particularly with regard to proactive aggression.

The fact that the underlying neurobiology is understood less well for proactive than for reactive aggression is unfortunate because proactive aggression has large impacts on society. Pre-meditated attacks predominate in war, a significant proportion of within-group homicides is considered to be proactive [e.g., >25% in the United States (142)], and proactive aggressors are more predictably dangerous than reactive aggressors. No drugs are known that reduce tendencies for proactive aggression. The discovery of a rat model of proactive aggression should help advance work on such problems.

Among other consequences, further animal studies could help elucidate sex differences by extending research on proactive aggression to females. Whether sex differences in humans take different forms between proactive and reactive aggression appears

to be unstudied. Levels of anger show no difference between men and women and there is little evidence of sex differences in reactive aggression when the conflict is mild, whereas in contexts risking serious physical harm males are more aggressive (2). Proactive aggression has been predicted to be associated with equivalent or larger sex differences, consistent with the greater prevalence of psychopathy among males (143). Sex differences in participation in aggression are also larger in between-group contexts, in both humans and chimpanzees, than they are in within-group contexts (2, 82), again suggesting a relatively greater propensity for proactive aggression in males.

The hypothesis that humans have experienced a recently evolved reduction in the propensity for reactive aggression should be testable partly by an increased understanding of its genetic basis. For example, a mechanism proposed to be responsible for down-regulating reactive aggression is a reduction in the rate of neural crest cell production and migration (144, 145). One test, therefore, is whether human neural crest cell biology exhibits similarities to patterns in domesticated animals. Preliminary evidence from genetic comparisons of *H. sapiens* with Neandertals and Denisovans supports that idea (146).

Such evidence suggests that the bimodal view of aggression will be helpful not only in resolving an old debate about human nature but also in pointing the way toward new understandings of our evolution. The putative reduction in reactive aggression is closely tied to the concept of self-domestication, for which there is growing behavioral and cognitive evidence (122, 127, 141). The self-domestication hypothesis has been criticized on the grounds that some heterochronic differences between humans and apes are not, as expected, paedomorphic (147, 148). For example, compared with chimpanzees and bonobos humans have accelerated, rather than delayed, development of social skills (147), and the large size of the human brain is achieved by peramorphism, not paedomorphism (148). Such critiques indicate that various evolutionary processes in addition to self-domestication are needed to explain the evolution of human traits over the last 6–8 million y. However, the hypothesis for human self-domestication based on morphological evidence refers to the evolution of *H. sapiens* from a mid- to late-Pleistocene *Homo*, rather than to the differences between *H. sapiens* and apes (106). While comparisons between humans and apes show that self-domestication may have played little part in the evolution of the genus *Homo*, they are silent on the role of self-domestication in the evolution of *H. sapiens* from its immediate ancestor.

Recognition that there are two main types of aggression provides an answer to the old question of whether humans are aggressive by nature. Humans have a high propensity for proactive aggression and a low propensity for reactive aggression. Appreciation of this point has both theoretical and practical implications. With regard to theory, the combination appears to be unusual among primates, so it should not surprise us to find that the suggested evolutionary dynamics depend on unique aspects of human ancestral adaptations. The imbalance-of-power hypothesis and the execution hypothesis discussed here will benefit from being tested against other ideas. With regard to practical applications, Weinschenker and Siegel (ref. 19, p. 243) noted that "the vast majority of studies that have been conducted in humans have concerned forms of aggressive behavior most closely linked with affective defense." More attention to proactive aggression is overdue.

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- 1 Shackelford TK, Hansen RD, eds (2016) *The Evolution of Violence* (Springer, New York).
- 2 Archer J (2009) Does sexual selection explain human sex differences in aggression? *Behav Brain Sci* 32:249–266, discussion 266–311.
- 3 Daly M (2015) Interpersonal conflict and violence. *The Handbook of Evolutionary Psychology* (Wiley, New York), Vol 26, pp 1–15.
- 4 Gat A (2000) The human motivational complex: Evolutionary theory and the causes of hunter-gatherer fighting. Part I. Primary somatic and reproductive causes. *Anthropol Q* 73:20–34.
- 5 Macfarlan SJ, Walker RS, Flinn MV, Chagnon NA (2014) Lethal coalitionary aggression and long-term alliance formation among Yanomamö men. *Proc Natl Acad Sci USA* 111:16662–16669.
- 6 Glowacki L, Wrangham R (2015) Warfare and reproductive success in a tribal population. *Proc Natl Acad Sci USA* 112:348–353.
- 7 de Almeida RMM, Cabral JCC, Narvaes R (2015) Behavioural, hormonal and neurobiological mechanisms of aggressive behaviour in human and nonhuman primates. *Physiol Behav* 143:121–135.
- 8 Crook DP (1994) *Darwinism, War and History: The Debate over the Biology of War from the 'Origin of Species' to the First World War* (Cambridge Univ Press, Cambridge, UK).
- 9 Hrdy SB (2009) *Mothers and Others: The Evolutionary Origins of Mutual Understanding* (Harvard Univ Press, Cambridge, MA).
- 10 van Schaik CP (2016) *The Primate Origins of Human Nature* (Wiley, Hoboken, NJ).
- 11 Fry DP (2006) *The Human Potential for Peace: An Anthropological Challenge to Assumptions About War and Violence* (Oxford Univ Press, New York).
- 12 Kelly RC (2005) The evolution of lethal intergroup violence. *Proc Natl Acad Sci USA* 102:15294–15298.
- 13 Wilson ML, et al. (2014) Lethal aggression in Pan is better explained by adaptive strategies than human impacts. *Nature* 513:414–417.
- 14 Henzi P, Barrett L (2003) Evolutionary ecology, sexual conflict, and behavioral differentiation among baboon populations. *Evol Anthropol* 12:217–230.
- 15 Pinker S (2011) *The Better Angels of Our Nature: Why Violence Has Declined* (Penguin, New York).
- 16 LeBlanc SA (2003) *Constant Battles* (St. Martin's, New York).
- 17 Carré JM, McCormick CM, Hariri AR (2011) The social neuroendocrinology of human aggression. *Psychoneuroendocrinology* 36:935–944.
- 18 Nelson RJ, Trainor BC (2007) Neural mechanisms of aggression. *Nat Rev Neurosci* 8:536–546.
- 19 Weinschenker NJ, Siegel A (2002) Bimodal classification of aggression: Affective defense and predatory attack. *Aggress Violent Behav* 7:237–250.
- 20 Siegel A, Victoroff J (2009) Understanding human aggression: New insights from neuroscience. *Int J Law Psychiatry* 32:209–215.
- 21 McEllistrem JE (2004) Affective and predatory violence: A bimodal classification system of human aggression and violence. *Aggress Violent Behav* 10:1–30.
- 22 Meloy JR (2006) Empirical basis and forensic application of affective and predatory violence. *Aust N Z J Psychiatry* 40:539–547.
- 23 Babcock JC, Tharp ALT, Sharp C, Heppner W, Stanford MS (2014) Similarities and differences in impulsive/premeditated and reactive/proactive bimodal classifications of aggression. *Aggress Violent Behav* 19:251–262.
- 24 Craig IW, Halton KE (2009) Genetics of human aggressive behaviour. *Hum Genet* 126:101–113.
- 25 Vitaro F, Brendgen M (2005) *Developmental Origins of Aggression*, eds Tremblay R, Hartup WW, Archer J (Guilford, New York), pp 178–201.
- 26 Poulin F, Boivin M (2000) Reactive and proactive aggression: evidence of a two-factor model. *Psychol Assess* 12:115–122.
- 27 Dodge KA, Coie JD (1987) Social-information-processing factors in reactive and proactive aggression in children's peer groups. *J Pers Soc Psychol* 53:1146–1158.
- 28 Crick NR, Dodge KA (1996) Social information-processing mechanisms in reactive and proactive aggression. *Child Dev* 67:993–1002.
- 29 Raine A, et al. (1998) Reduced prefrontal and increased subcortical brain functioning assessed using positron emission tomography in predatory and affective murderers. *Behav Sci Law* 16:319–332.
- 30 Hrdy SB (1977) *The Langurs of Abu* (Harvard Univ Press, Cambridge, MA).
- 31 Lukas D, Huchard E (2014) Sexual conflict. The evolution of infanticide by males in mammalian societies. *Science* 346:841–844.
- 32 Bandura A (1973) *Aggression: A Social Learning Theory Analysis* (Prentice-Hall, New York).
- 33 Berkowitz L (1993) *Aggression: Its Causes, Consequences and Control* (Temple Univ Press, Philadelphia).
- 34 Card NA, Little TD (2006) Proactive and reactive aggression in childhood and adolescence: A meta-analysis of differential relations with psychosocial adjustment. *Int J Behav Dev* 30:466–480.
- 35 Chichinadze K, Chichinadze N, Lazarashvili A (2011) Hormonal and neurochemical mechanisms of aggression and a new classification of aggressive behavior. *Aggress Violent Behav* 16:461–471.
- 36 Cima M, Raine A, Meesters C, Popma A (2013) Validation of the Dutch Reactive Proactive Questionnaire (RPQ): Differential correlates of reactive and proactive aggression from childhood to adulthood. *Aggress Behav* 39:99–113.
- 37 Paquin S, et al. (2014) The genetic-environmental architecture of proactive and reactive aggression throughout childhood. *Monatsschr Kriminol* 97:398–420.
- 38 Teten Tharp AL, et al. (2011) Correspondence of aggressive behavior classifications among young adults using the Impulsive Premeditated Aggression Scale and the Reactive Proactive Questionnaire. *Pers Individ Dif* 50:279–285.
- 39 Veroude K, et al. (2016) Genetics of aggressive behavior: An overview. *Am J Med Genet B Neuropsychiatr Genet* 171B:3–43.
- 40 Bushman BJ, Anderson CA (2001) Is it time to pull the plug on the hostile versus instrumental aggression dichotomy? *Psychol Rev* 108:273–279.
- 41 Blair RJR (2016) The neurobiology of impulsive aggression. *J Child Adolesc Psychopharmacol* 26:4–9.
- 42 Dambacher F, et al. (2015) Reducing proactive aggression through non-invasive brain stimulation. *Soc Cogn Affect Neurosci* 10:1303–1309.
- 43 Reidy DE, Shelley-Tremblay JF, Lilienfeld SO (2011) Psychopathy, reactive aggression, and precarious proclamations: A review of behavioral, cognitive, and biological research. *Aggress Violent Behav* 16:512–524.
- 44 Book A, Volk AA, Hosker A (2012) Adolescent bullying and personality: An adaptive approach. *Pers Individ Dif* 52:218–223.
- 45 Raine A, et al. (2006) The reactive-proactive aggression questionnaire: Differential correlates of reactive and proactive aggression in adolescent boys. *Aggress Behav* 32:159–171.
- 46 Roland E, Idsøe T (2001) Aggression and bullying. *Aggress Behav* 27:446–462.
- 47 Declercq F, Audenaert K (2011) Predatory violence aiming at relief in a case of mass murder: Meloy's criteria for applied forensic practice. *Behav Sci Law* 29:578–591.
- 48 Meloy JR (1997) Predatory violence during mass murder. *J Forensic Sci* 42:326–329.
- 49 Swogger MT, Walsh Z, Christie M, Priddy BM, Conner KR (2015) Impulsive versus premeditated aggression in the prediction of violent criminal recidivism. *Aggress Behav* 41:346–352.
- 50 Stanford MS, Houston RJ, Baldrige RM (2008) Comparison of impulsive and premeditated perpetrators of intimate partner violence. *Behav Sci Law* 26:709–722.
- 51 Kockler TR, Stanford MS, Nelson CE, Meloy JR, Sanford K (2006) Characterizing aggressive behavior in a forensic population. *Am J Orthopsychiatry* 76:80–85.
- 52 Glenn AL, Raine A (2009) Psychopathy and instrumental aggression: Evolutionary, neurobiological, and legal perspectives. *Int J Law Psychiatry* 32:253–258.
- 53 Brugman S, et al. (2015) Identifying cognitive predictors of reactive and proactive aggression. *Aggress Behav* 41:51–64.
- 54 Tuvblad C, Raine A, Zheng M, Baker LA (2009) Genetic and environmental stability differs in reactive and proactive aggression. *Aggress Behav* 35:437–452.
- 55 Wasman M, Flynn JP (1962) Directed attack elicited from hypothalamus. *Arch Neurol* 6:220–227.
- 56 Flynn JP (1967) *Neurophysiology and Emotion*, ed Glass DC (Rockefeller Univ Press, New York), pp 40–60.
- 57 Shaikh MB, Barrett JA, Siegel A (1987) The pathways mediating affective defense and quiet biting attack behavior from the midbrain central gray of the cat: An autoradiographic study. *Brain Res* 437:9–25.

- 58 Sandnabba NK (1995) Predatory aggression in male mice selectively bred for isolation-induced intermale aggression. *Behav Genet* 25:361–366.
- 59 Tulogdi A, et al. (2010) Brain mechanisms involved in predatory aggression are activated in a laboratory model of violent intra-specific aggression. *Eur J Neurosci* 32:1744–1753.
- 60 Tulogdi A, et al. (2015) Neural mechanisms of predatory aggression in rats—Implications for abnormal intraspecific aggression. *Behav Brain Res* 283:108–115.
- 61 Siegel A, Bhatt S, Bhatt R, Zalcman SS (2007) The neurobiological bases for development of pharmacological treatments of aggressive disorders. *Curr Neuropharmacol* 5:135–147.
- 62 Toth M, et al. (2012) The neural background of hyper-emotional aggression induced by post-weaning social isolation. *Behav Brain Res* 233:120–129.
- 63 Haller J, Tóth M, Halasz J, De Boer SF (2006) Patterns of violent aggression-induced brain c-fos expression in male mice selected for aggressiveness. *Physiol Behav* 88:173–182.
- 64 Dambacher F, et al. (2015) Out of control: Evidence for anterior insula involvement in motor impulsivity and reactive aggression. *Soc Cogn Affect Neurosci* 10:508–516.
- 65 Siever LJ (2008) Neurobiology of aggression and violence. *Am J Psychiatry* 165:429–442.
- 66 Davidson RJ, Putnam KM, Larson CL (2000) Dysfunction in the neural circuitry of emotion regulation—a possible prelude to violence. *Science* 289:591–594.
- 67 Umukoro S, Aladeokin AC, Eduviere AT (2013) Aggressive behavior: A comprehensive review of its neurochemical mechanisms and management. *Aggress Violent Behav* 18:195–203.
- 68 Nave G, Nadler A, Zava D, Camerer C (2017) Single-dose testosterone administration impairs cognitive reflection in men. *Psychol Sci* 28:1398–1407.
- 69 Barratt ES, Stanford MS, Felthous AR, Kent TA (1997) The effects of phenytoin on impulsive and premeditated aggression: a controlled study. *J Clin Psychopharmacol* 17:341–349.
- 70 Haller J (2013) The neurobiology of abnormal manifestations of aggression—A review of hypothalamic mechanisms in cats, rodents, and humans. *Brain Res Bull* 93:97–109.
- 71 Blair RJR (2005) Applying a cognitive neuroscience perspective to the disorder of psychopathy. *Dev Psychopathol* 17:865–891.
- 72 Blair RJR (2004) *Neurobiology of Mental Illness*, eds Charney DS, Nestler EJ (Oxford Univ Press, New York), 2nd Ed, pp 1076–1085.
- 73 Umbach R, Berryessa CM, Raine A (2015) Brain imaging research on psychopathy: Implications for punishment, prediction, and treatment in youth and adults. *J Crim Justice* 43:295–306.
- 74 Sandi C, Haller J (2015) Stress and the social brain: Behavioural effects and neurobiological mechanisms. *Nat Rev Neurosci* 16:290–304.
- 75 Tuvblad C, Baker LA (2011) Human aggression across the lifespan: Genetic propensities and environmental moderators. *Adv Genet* 75:171–214.
- 76 Nikulina EM (1991) Neural control of predatory aggression in wild and domesticated animals. *Neurosci Biobehav Rev* 15:545–547.
- 77 Knauft B (1991) Violence and sociality in human evolution. *Curr Anthropol* 32:391–428.
- 78 Boehm C (1999) *Hierarchy in the Forest: The Evolution of Egalitarian Behavior* (Harvard Univ Press, Cambridge, MA).
- 79 Crofoot MC, Wrangham RW (2009) *Mind the Gap*, eds Kappeler PM, Silk J (Springer, Berlin), pp 171–197.
- 80 Wrangham RW, Wilson ML, Muller MN (2006) Comparative rates of violence in chimpanzees and humans. *Primates* 47:14–26.
- 81 Turney-High HH (1949) *Primitive War: Its Practice and Concepts* (Univ of South Carolina Press, Columbia, SC).
- 82 Wrangham RW, Glowacki L (2012) Intergroup aggression in chimpanzees and war in nomadic hunter-gatherers: Evaluating the chimpanzee model. *Hum Nat* 23:5–29.
- 83 Allen MW, Jones TL, eds (2014) *Violence and Warfare Among Hunter-Gatherers* (Left Coast, Walnut Creek, CA).
- 84 Gat A (2015) Proving communal warfare among hunter-gatherers: The quasi-Rousseauian error. *Evol Anthropol* 24:111–126.
- 85 Muller MN (2002) *Behavioural Diversity in Chimpanzees and Bonobos*, eds Boesch C, Hohmann G, Marchant L (Cambridge Univ Press, Cambridge, UK), pp 112–124.
- 86 Goodall J (1986) *The Chimpanzees of Gombe: Patterns of Behavior* (Harvard Univ Press, Cambridge, MA).
- 87 Hare B, Wobber V, Wrangham RW (2012) The self-domestication hypothesis: Bonobos evolved due to selection against male aggression. *Anim Behav* 83:573–585.
- 88 Surbeck M, Deschner T, Schubert G, Weltring A, Hohmann G (2012) Mate competition, testosterone and intersexual relationships in bonobos, *Pan paniscus*. *Anim Behav* 83:659–669.
- 89 Hess N, Helfrecht C, Hagen E, Sell A, Hewlett B (2010) Interpersonal aggression among Aka Hunter-Gatherers of the Central African Republic: Assessing the effects of sex, strength, and anger. *Hum Nat* 21:330–354.
- 90 Hill K, Hurtado MA (1996) *Aché Life History: The Ecology and Demography of a Foraging People* (Aldine de Gruyter, New York).
- 91 Burbank VK (1992) Sex, gender, and difference: Dimensions of aggression in an Australian aboriginal community. *Hum Nat* 3:251–277.
- 92 Thomas EM (1959) *The Harmless People* (Vintage, New York).
- 93 Heider KG (1997) *Grand Valley Dani: Peaceful Warriors* (Holt, Rinehart, and Winston, New York).
- 94 Turnbull C (1965) *Wayward Servants: The Two Worlds of the African Pygmies* (Greenwood, Westport, CT).
- 95 Tweed RG, Dutton DG (1998) A comparison of impulsive and instrumental subgroups of batterers. *Violence Vict* 13:217–230.
- 96 Devries KM, et al. (2013) Global health. The global prevalence of intimate partner violence against women. *Science* 340:1527–1528.
- 97 Abrahams N, et al. (2014) Worldwide prevalence of non-partner sexual violence: A systematic review. *Lancet* 383:1648–1654.
- 98 Muller MN, Emery Thompson M, Kahlenberg SM, Wrangham RW (2011) Sexual coercion by male chimpanzees shows that female choice may be more apparent than real. *Behav Ecol Sociobiol* 65:921–933.
- 99 Tokuyama N, Furuichi T (2016) Do friends help each other? Patterns of female coalition formation in wild bonobos at Wamba. *Anim Behav* 119:27–35.
- 100 Surbeck M, Hohmann G (2013) Intersexual dominance relationships and the influence of leverage on the outcome of conflicts in wild bonobos (*Pan paniscus*). *Behav Ecol Sociobiol* 67:1767–1780.
- 101 Moorjani P, Amorim CEG, Arndt PF, Przeworski M (2016) Variation in the molecular clock of primates. *Proc Natl Acad Sci USA* 113:10607–10612.
- 102 Wrangham RW, Pilbeam D (2001) African apes as time machines. *All Apes Great and Small. Volume 1: Chimpanzees, Bonobos, and Gorillas*, eds Galdikas BMF, Briggs N, Sheeran LK, Shapiro GL, Goodall J (Kluwer Academic/Plenum, New York), pp 5–18.
- 103 Stanford CB (2012) Chimpanzees and the behavior of *Ardipithecus ramidus*. *Annu Rev Anthropol* 41:139–149.
- 104 Sayers K, Raghanti MA, Lovejoy CO (2012) Human evolution and the chimpanzee referential doctrine. *Annu Rev Anthropol* 41:119–138.
- 105 Nisbett RE, Cohen D (1996) *Culture of Honor: The Psychology of Violence in the South* (Westview, Boulder, CO).
- 106 Cieri RL, Churchill SE, Franciscus RG, Tan J, Hare B (2014) Craniofacial feminization, social tolerance, and the origins of behavioral modernity. *Curr Anthropol* 55:419–443.
- 107 Brookman F (2015) Killer decisions: The role of cognition, affect and ‘expertise’ in homicide. *Aggress Violent Behav* 20:42–52.
- 108 Williams J, Oehlert G, Carlis J, Pusey A (2004) Why do male chimpanzees defend a group range? *Anim Behav* 68:523–532.
- 109 Wrangham RW (1999) Evolution of coalitional killing. *Am J Phys Anthropol* 42:1–30.
- 110 Gavrillets S, Fortunato L (2014) A solution to the collective action problem in between-group conflict with within-group inequality. *Nat Commun* 5:3526.
- 111 Glowacki L, Wrangham RW (2013) The role of rewards in motivating participation in simple warfare. *Hum Nat* 24:444–460.
- 112 Mathew S, Boyd R (2011) Punishment sustains large-scale cooperation in prestate warfare. *Proc Natl Acad Sci USA* 108:11375–11380.
- 113 Choi J-K, Bowles S (2007) The coevolution of parochial altruism and war. *Science* 318:636–640.
- 114 Bowles S (2009) Did warfare among ancestral hunter-gatherers affect the evolution of human social behaviors? *Science* 324:1293–1298.
- 115 Langergraber K, et al. (2011) Genetic differentiation and the evolution of cooperation in chimpanzees and humans. *Proc Biol Sci* 278:2546–2552.

- 116 Gilby IC, et al. (2013) Fitness benefits of coalitional aggression in male chimpanzees. *Behav Ecol Sociobiol* 67:373–381.
- 117 Burkart JM, Hrdy SB, van Schaik CP (2009) Cooperative breeding and human cognitive evolution. *Evol Anthropol* 18:175–186.
- 118 Nesse RM (2010) *Evolution, Culture, and the Mind*, eds Schaller M, Norenzayan A, Heine SJ, Yamagishi T, Kameda T (Psychology, New York), pp 137–150.
- 119 Gintis H, van Schaik C, Boehm C (2015) Zoon Politikon: The evolutionary origins of human political systems. *Curr Anthropol* 56:327–353.
- 120 Henrich J (2016) *The Secret of Our Success: How Culture Is Driving Human Evolution, Domesticating Our Species, and Making Us Smarter* (Princeton Univ Press, Princeton).
- 121 Payne K (2015) *The Psychology of Modern Conflict: Evolutionary Theory, Human Nature and a Liberal Approach to War* (Palgrave Macmillan, New York).
- 122 Leach H (2003) Human domestication reconsidered. *Curr Anthropol* 44:349–368.
- 123 Hood B (2014) *The Domesticated Brain* (Penguin, London).
- 124 Nesse RM (2007) Runaway social selection for displays of partner value and altruism. *Biol Theory* 2:143–155.
- 125 Tomasello M (2016) *A Natural History of Human Morality* (Harvard Univ Press, Cambridge, MA).
- 126 Boehm C (2008) Purposive social selection and the evolution of human altruism. *Cross-Cultural Res* 42:319–352.
- 127 Boehm C (2012) *Moral Origins: The Evolution of Virtue, Altruism, and Shame* (Basic Books, New York).
- 128 Wrangham R (2014) Comment on Cieri et al. Craniofacial feminization, social tolerance, and the origins of behavioral modernity. *Curr Anthropol* 55:435–436.
- 129 Darwin C (2006) *From So Simple a Beginning: The Four Great Books of Charles Darwin*, ed Wilson EO (Norton, New York).
- 130 Bednarik RG (2014) Doing with less: Hominin brain atrophy. *Homo* 65:433–449.
- 131 Boehm C (1993) Egalitarian behavior and reverse dominance hierarchy. *Curr Anthropol* 34:227–240.
- 132 Ostner J, Schülke O (2014) The evolution of social bonds in primate males. *Behaviour* 151:871–906.
- 133 Wroblewski EE, et al. (2009) Male dominance rank and reproductive success in chimpanzees, *Pan troglodytes schweinfurthii*. *Anim Behav* 77:873–885.
- 134 Erdal D, Whiten A (1994) On human egalitarianism: An evolutionary product of Machiavellian status escalation? *Curr Anthropol* 35:175–178.
- 135 Flanagan JG (1989) Hierarchy in simple “egalitarian” societies. *Annu Rev Anthropol* 18:245–266.
- 136 Gavrilets S, Duenez-Guzman EA, Vose MD (2008) Dynamics of alliance formation and the egalitarian revolution. *PLoS One* 3:e3293.
- 137 Chapais B (2015) Competence and the evolutionary origins of status and power in humans. *Hum Nat* 26:161–183.
- 138 Otterbein KF (1986) *The Ultimate Coercive Sanction: A Cross-Cultural Study of Capital Punishment* (Human Relations Area Files, New Haven, CT).
- 139 Boyd R, Gintis H, Bowles S (2010) Coordinated punishment of defectors sustains cooperation and can proliferate when rare. *Science* 328:617–620.
- 140 Trut LN (1999) Early canid domestication: The farm-fox experiment. *Am Sci* 87:160–169.
- 141 Hare B (2017) Survival of the friendliest: *Homo sapiens* evolved via selection for prosociality. *Ann Rev Psychol* 68:155–186.
- 142 Felson RB, Massoglia M (2012) When is violence planned? *J Interpers Violence* 27:753–774.
- 143 Corr PJ, Perkins AM (2009) Differentiating defensive and predatory aggression: Neuropsychological systems and personality in sex differences. *Behav Brain Sci* 32:274–275.
- 144 Wilkins AS, Wrangham RW, Fitch WT (2014) The “domestication syndrome” in mammals: A unified explanation based on neural crest cell behavior and genetics. *Genetics* 197:795–808.
- 145 Sánchez-Villagra MR, Geiger M, Schneider RA (2016) The taming of the neural crest: A developmental perspective on the origins of morphological covariation in domesticated mammals. *R Soc Open Sci* 3:160107.
- 146 Theofanopoulou C, et al. (2017) Comparative genomic evidence for self-domestication in *Homo sapiens*. *PLoS One* 10:e0185306.
- 147 Hawkes K (2014) Primate sociality to human cooperation. Why us and not them? *Hum Nat* 25:28–48.
- 148 Francis R (2015) *Domesticated: Evolution in a Man-Made World* (Norton, New York).