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PERSPECTIVE

THE ANTIQUITY OF EMPATHY

Frans B. M. de Waal

The view of humans as violent war-prone apes is poorly supported by archaeological evidence and only partly supported by the behavior of our closest primate relatives, chimpanzees and bonobos. Whereas the first species is marked by xenophobia, the second is relatively peaceful and highly empathic in both behavior and brain organization. Animal empathy is best regarded as a multilayered phenomenon, built around motor mirroring and shared neural representations at basal levels, that develops into more advanced cognitive perspective-taking in large-brained species. As indicated by both observational and experimental studies on our closest relatives, empathy may be the main motivator of prosocial behavior.

After the devastations of World War II, humans were routinely depicted as "killer apes"—in contrast to the real apes, which were regarded as pacifists. Books by Konrad Lorenz, the Austrian ethologist, and Robert Ardrey, an American journalist, contributed to the idea that a hallmark of humanity is aggression. Until well into the 1980s, this remained the dominant theme of biological approaches to human behavior. This literature is now recognized as one-sided because it overlooked our species' capacity for cooperation, empathy, and prosocial behavior.

Species-typical tendencies normally come with built-in rewards. Nature has ensured that we find fulfillment in eating, sex, nursing, and socializing, all of which are necessary for survival and reproduction. If there were truly a genetic basis to our participation in lethal combat, we should willingly engage in it. Yet soldiers report a deep revulsion to killing and shoot at the enemy only under pressure (*1*). After these experiences, they often end up with substantial psychological damage. Far from being a recent phenomenon, haunting memories of combat were already known to the ancient Greeks, such as Sophocles, who described Ajax's "divine madness," now known as posttraumatic stress disorder (PTSD).

Even though evidence for individual murder goes back hundreds of thousands of years, comparable signs of warfare (such as graveyards with weapons embedded in a large number of skeletons) are lacking from before the Agricultural Revolution [about 12,000 years ago (*2*)]. This is not to imply that war was absent before then, but it does mean that the common assumption that our ancestors waged perpetual wars and knew peace only at "precarious interludes" (as Winston Churchill surmised) lacks solid archaeological backing. During most of our prehistory, we were nomadic hunter-gatherers, whose cultures are nowadays not particularly known for warfare (*3*). They do occasionally raid, ambush, and kill their neighbors (*4*), but more often trade with them, intermarry, and permit travel through their territories. Hunter-gatherers illustrate a robust potential for peace and cooperation.

Going back farther in time, we end up with *Ardipithecus ramidus*, a 4.4-million-year-old hominin that has been described as relatively peaceful, owing to its reduced canine teeth as compared to those of the chimpanzee (*Pan troglodytes*) (*5*), who can be lethally violent during territorial encounters between communities. However, the conclusion drawn from *Ardipithecus*' dentition that our ancestors were less war-prone than the apes is not rigorous unless the bonobo (*P. paniscus*), which also has relatively small canines (Fig. 1), is included. Despite being as closely related to us as chimpanzees, the behavior of bonobos fails to support traditional violence-based scenarios of human evolution. Deadly aggression among bonobos has thus far not been observed, neither in captivity nor in the wild, and xenophobia is only weakly developed. Bonobos sometimes mingle across territorial borders, where they engage in sex, grooming, and play. They are known as the "make love, not war" primates for solving dominance issues through sexual activity (*6*). Indeed, it has been suggested that these apes "may approach more closely to the common ancestor of chimpanzees and man than does any living chimpanzee" (*7*).

In addition, developments in psychology, neuroscience, behavioral economics, and animal behavior have begun to question the view, dominant until a decade ago, that animal life, and by extension human nature, is based on unmitigated competition. In primatology, the countermovement started with research into the survival value of friendships (*8*) and conflict resolution (*9*). After the discovery that chimpanzees often kiss and embrace shortly after a fight within their group, numerous studies have documented "reconciliations" in nonhuman primates. Methodologies comparing postconflict observations with baseline data to determine how species members behave in the presence versus absence of previous antagonism show that primates are generally attracted to former opponents, seeking friendly contact especially if they otherwise enjoy a mutually beneficial relationship. Relationship value appears to drive post-conflict repair (*10*). The behavioral expression of reconciliation varies, but its general effect is a rapid return to preexisting levels of tolerance and affiliation. This reunion process has been reported for macaques, gorillas, golden monkeys, capuchins, and many other primates, but also for nonprimates, such as wolves, dolphins, and hyenas. Reconciliation is a common social mechanism that would be superfluous if social life were ruled entirely by dominance and competition.

The level of cooperation among nonhuman primates tends to be underappreciated. In order to set it apart from human cooperation with nonrelatives, aid among primates is sometimes ascribed largely to kinship (*11*). This claim has not held up, however, on the basis of DNA extracted from chimpanzee feces in the wild. Males without genetic ties make up the majority of mutually supportive partnerships (*12*). The same seems to apply to bonobos. Female bonobos maintain a close social network that allows them to collectively dominate the majority of males despite the fact that females are also the migratory sex, which means that they are largely unrelated within each community (*6*). Both of our closest primate relatives are marked, therefore, by high levels of nonkin cooperation, probably explained by well-developed reciprocity.

Expressions of empathy are common in apes and resemble those of our own species. In child research, for example, a family member is typically instructed to feign distress or pain, upon which touching, stroking, and close-up eye-contact by the child is interpreted as a sign of sympathetic concern. In chimpanzees, bystanders at a fight go over to the loser and put an arm around his or her shoulders or provide other calming contact (Fig. 2). Data from several thousand postconflict observations in chimpanzees indicate that consolation reduces the recipient's arousal and follows the same sex difference as reported for sympathetic concern in children, with female apes providing comfort more often than males (*13*). Bonobos express the same tendency sociosexually by means

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of genital contacts. A comparison of chimpanzee and bonobo brains supports the general view of bonobos as more empathic (*6*). This species has more gray matter in brain regions involved in the perception of distress, including the right dorsal amygdala and right anterior insula, and a better developed circuitry for inhibiting aggression (*14*).

Human empathy has been described as taking the perspective of another or imagining oneself in another's position. Psychologists commonly apply this cognitively demanding explanation of empathy even if the immediacy of the response hints at simpler processes. If we see a child fall and scrape its knee, we flinch, and exclaim "ouch!" as if what happened to the child happened at the same instant to ourselves. Another way of looking at empathy is as a multilayered phenomenon that starts with automatic state-matching based on motor mimicry and shared neural representations (*15*). We should not be surprised, therefore, by unconscious empathy, such as when human study participants mimic observed facial expressions and report corresponding emotions even though the expressions were presented too briefly for conscious perception (*16*). In this view, which may map onto nested neural processing (*17*), cognitive perspective-taking is a secondary development built around more elementary mechanisms, such as state-matching and emotional contagion (Fig. 3).

The evolution of empathy is thought to go back to mammalian maternal care. Whether a mouse or an elephant, a mother needs to be exquisitely in tune with indications of hunger, danger, or discomfort in her young. Sensitivity to emotional signals confers clear adaptive value. This hypothetical origin of empathy would explain the observed sex differences as well as the stimulating effect of oxytocin (*18*). That empathy is rooted in bodily connections between individuals is reflected in pain contagion in mice (*19*) and yawn contagion in apes and humans (*20*). Mirror neurons are often mentioned in this context, even though their precise role remains a point of speculation. The fact that these neurons were discovered not in humans, but in monkeys, supports the idea of evolutionary continuity. Social animals need to coordinate travel, communicate about danger, and assist group mates in need. Bodily synchronization and sensitivity to the emotional states of others ranges from rapid spreading of alarm through an entire group to a mother ape returning to a whimpering youngster to help it from one tree to the next by draping her body between the two. The first is a reflex-like transmission of fear, whereas the mother ape is more discriminating because she needs to assess the reason for her offspring's distress in order to ameliorate its situation.

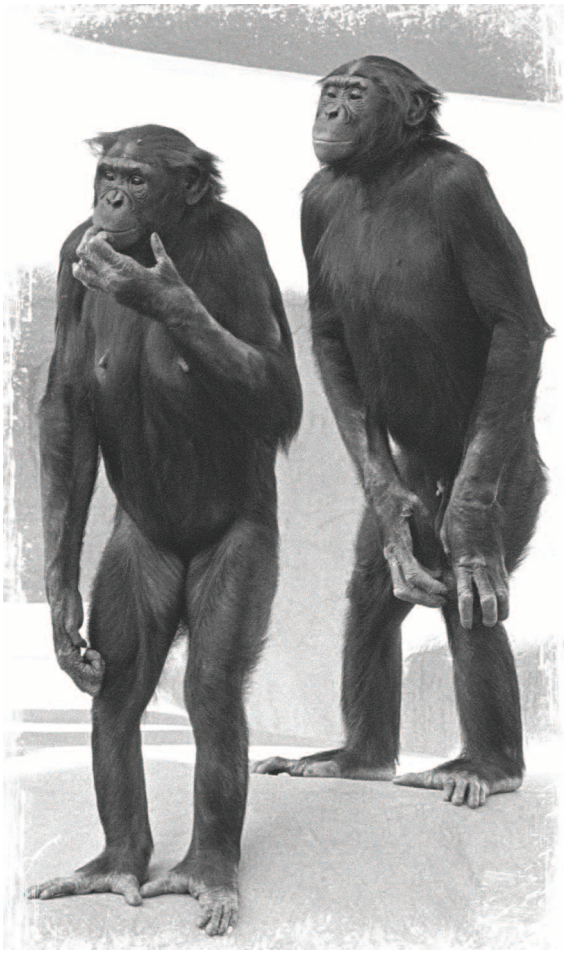

Fig. 1. Two bipedal bonobos, an adult female (left) and adolescent male (right), show the species' relatively long legs, which makes it anatomically more similar to early hominins than to the chimpanzee, with its longer arms and shorter legs (photograph by Frans de Waal). *Ardipithecus ramidus* may be the closest comparison to the bonobo in terms of its overall body proportions, grasping feet, and reduced canine teeth. *Ardipithecus* is thought to have been relatively peaceful, and bonobos are likewise marked by high sensitivity to others and low levels of violence.

Fig. 2. Contact comfort is critically important in the lives of apes, such as here between two chimpanzees watching a disturbance in their group (photograph by Frans de Waal). Apes go out of their way to console distressed parties, showing the same sex difference in this tendency as humans.

The idea that empathy translates into altruism and helping is widely assumed for humans and has also been proposed for other mammals (*21*). Reports of spontaneous assistance among primates are abundant and are also available for elephants and cetaceans. For example, a female chimpanzee may react to the screams of her closest associate by defending her against an aggressive male, thus taking great risk on her behalf. Such coalitions are among the most systematically studied forms of cooperation in primatology (*22*). One advantage of an empathy-based explanation is its ability to explain "unrepaid" altruism, such as that shown toward nonreciprocating nonkin. This type of behavior is well illustrated by the adoption of orphans by wild male chimpanzees, who may devote years of costly care to unrelated juveniles (*23*). Although empathy, such as between a mother and offspring or between cooperation partners, is likely to be adaptive, not each and every application of this capacity needs to be for it to retain overall adaptive value.

Increasingly, the importance of mammalian prosocial tendencies is backed by experiments that range from demonstrating that rats give priority to the liberation of a trapped companion over eating chocolate (*24*) to those showing that apes are prepared to assist others even in the absence of incentives, go out of their way to give others access to food, or choose shared benefits over selfish ones (*25, 26*). Studies have also demonstrated more complex expressions of empathy among apes, such as "targeted helping" (assistance based on an appreciation of the other's specific needs), both in their spontaneous behavior (*21*) and during controlled experiments (*27*). This increased knowledge suggests that nearly the full spectrum of empathy-based altruism may be represented among nonhuman primates, including the cognitive perspective-taking that marks human altruism.

Empathy automatically produces a stake in another's welfare; that is, the behavior comes with

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an intrinsic reward, known as the "warm glow" effect. Humans report feeling good when they do good and show activation of reward-related brain areas (*28*). It will be important to determine whether the same self-reward system extends to other primates. We do know from studies on rodents, apes, and humans that empathy is biased toward the ingroup. For example, while watching the yawns of videotaped conspecifics, chimpanzees frequently joined the yawns of their own group members but not those of unfamiliar individuals (*23*). This ingroup bias makes sense from an evolutionary perspective, because it is with the members of one's own group that apes cooperate. At the same time, however, it poses a profound challenge for the modern human world, which seeks to integrate a multitude of groups, ethnicities, and nations. The flip side of the ingroup bias in empathy is lack of empathy for the outgroup, as is typical of xenophobia.

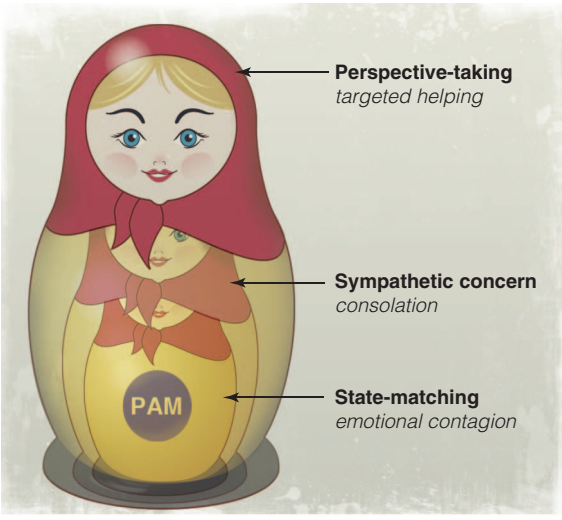

Fig. 3. The Russian doll model of multilayered empathy. The doll's inner core consists of the perception-action mechanism (PAM) that underlies state-matching and emotional contagion (*15*). Built around this hard-wired socioaffective basis, the doll's outer layers include sympathetic concern and targeted helping. The complexity of empathy grows with increasing perspective-taking capacities, which depend on prefrontal neural functioning, yet remain fundamentally connected to the PAM. A few large-brained species show all of the doll's layers, but most show only the inner ones.

Nevertheless, empathy may be our only hope to deal with these issues. We know that it can be activated by outsiders, even by members of a different species, such as when we empathize with a stranded whale and move it back into the ocean. This is not an outcome for which empathy evolved, yet once in existence, capacities are often emancipated from their evolutionary origin. If it weren't for empathy with all life forms, including enemy lives, soldiers would have no reluctance to kill nor would they return from the battlefield with PTSD. Although it is true that empathy has trouble reaching beyond the ingroup, it is an automated response that does not allow itself to be fully suppressed by rationalizations and political indoctrination. This is another lesson from World War II, with examples such as Oskar Schindler and the guardians of Anne Frank. To better understand the power of empathy requires investigation of its neurological basis as well as its evolutionary antiquity.

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PERSPECTIVE

WARRIORS, LEVELERS, AND THE ROLE OF CONFLICT IN HUMAN SOCIAL EVOLUTION

Samuel Bowles

The origins of such varied features of contemporary life as the national state and the desire to uphold generous and civic social norms are to be found in a combination of conflict between groups and attenuation of both inequalities and conflicts within groups. In contrast to the adoption of a better tool or a more productive crop, which can be adopted by a single individual, a new institution works only if most people adopt it. This explains why collective action against those benefitting from the status quo at the expense of others, as well as conflict between groups governed by different norms and institutions, figures so prominently in our capacity to adapt to changing circumstances and to harness new knowledge for human benefit.

Conflict has a bad name, one that it richly deserves for the suffering, tragedy, and waste of human and material resources that it brings about. But conflict—both violent and civil, both within and between societies—has also been a midwife for humanity's most cherished values and institutions: among them democracy, the rule of law, and a propensity to help others and to abhor injustice.

I will make the case that it was warfare that culled Europe's once-motley collection of governments to produce the modern national state, which, as a result of subsequent conflicts within nations, would become liberal and eventually democratic. This occurred because, not content to free ride on the sacrifices of others, people were willing to take mortal risks in pursuit of democratic and liberal values. And this, if I am right, is itself a result of millennia of conflict between groups of ancestral humans where, Charles Darwin wrote, the groups with large numbers of "courageous, sympathetic and faithful members, who were always ready to...aid and defend each

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