



Review

Behavioural, hormonal and neurobiological mechanisms of aggressive behaviour in human and nonhuman primates



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HIGHLIGHTS

- Sex plays an essential role in agonistic behaviours in human and nonhuman primates.
- Testosterone, progesterone, cortisol and vasopressin affect sex-specific aggression.
- Neurotransmitters, mainly GABA and 5-HT, are crucial for sex-specific aggression.
- Positive allosteric modulator of GABA_A-R influences sexually dimorphic aggression.
- Neurotransmitter, neuromodulator and hormone relations are the future direction of the field.

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ABSTRACT

Aggression is a key component for social behaviour and can have an adaptive value or deleterious consequences. Here, we review the role of sex-related differences in aggressive behaviour in both human and nonhuman primates. First, we address aggression in primates, which varies deeply between species, both in intensity and in display, ranging from animals that are very aggressive, such as chimpanzees, to the nonaggressive bonobos. Aggression also influences the hierarchical structure of gorillas and chimpanzees, and is used as the main tool for dealing with other groups. With regard to human aggression, it can be considered a relevant adaptation for survival or can have negative impacts on social interaction for both sexes. Gender plays a critical role in aggressive and competitive behaviours, which are determined by a cascade of physiological changes, including GABAergic and serotonergic systems, and sex neurosteroids. The understanding of the neurobiological bases and behavioural determinants of different types of aggression is fundamental for minimising these negative impacts.

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1. Introduction

Aggression is an individual or collective social behaviour that has a highly adaptive value [1,2]. It may be defined in general terms as a hostile behaviour with the intention of inflicting damage or harm [3]. The display of agonistic behaviour has evolved in the context of defending or obtaining resources for almost all species of primates and other presocial mammals [4–7]. However, among humans, aggression and violent crimes are considered one of the most serious urban problems currently faced [8,9]. The remarkable sex differences in aggressive behaviour in primates may be explained by natural determinants. The knowledge on biological and behavioural aspects of this significant sexual dimorphism is essential to be able to not only manage and predict more accurately the social consequences of aggression, but also for guidance of public and judicial policies.

Hence, ethological analyses have helped to elucidate the differences and similarities between human and nonhuman primates, as well as the phylogenetic origins of social behaviours. The comparative behavioural sciences have indicated that primates, especially those belonging to the Hominidae family, present a significant sexually dimorphic pattern of aggressive behaviour [10]. These data, along with physiological analyses, may clarify the role of sex and gender on aggressive behaviour. Nevertheless, the interdisciplinary nature of the field, and the wide and continuous effort of the scientific community to deepen understanding of aggressive behaviour, make the task of synthesising these data a major challenge, which must constantly be overcome. Here, we propose the integration of the behavioural, hormonal and neural bases of sex differences in aggressive behaviour in both human and nonhuman primates, along with future directions for aggression research.

2. Aggression in nonhuman primates

Aggressive behaviour is well known as a key element of primate social behaviour [6]. There are some main contexts in which aggression is important in primates, e.g. intergroup resource defence, antipredator behaviour, predation, and intragroup social contexts such as dominance contests (for food, mates, status etc.) and reproduction [11]. However, primates also show pathological self-directed aggression as self-injurious behaviour [11]. Displays of aggression are common in all species of primates, and male–male competition associated with physical aggression is prevalent in all great apes [12].

2.1. Species differences

It is important to differentiate the great apes from the other primates due to evolutionary differences of the first that might favour aggressive behaviour – for example, short legs might not only be associated with better climbing, but also with better stability and stronger impulses in a fight [13]. Moreover, there are many different social structures among primates. For example, while chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*) usually live in large groups [14], male orangutans (*Pongo pygmaeus*) are extremely intolerant of each other [15]. Similarly, most encounters involving male gorillas result in displays of aggression. Among the groups of chimpanzees, aggressive encounters are frequent, but the tension inside the group is usually mended by the reconciliatory behaviour these animals show [14].

Whereas intragroup aggression is stressful, intergroup aggression poses a much bigger threat to chimpanzees than social stress from hierarchical ranks. Chimpanzees are known to attack and kill males in other groups to expand their territories [16,17]. Nonlethal intergroup fights are widespread in primates, but the pattern of killing males in other groups is, to this point, recorded only in humans and chimpanzees [17]. These lethal attacks usually happen when the risk of physical harm is minimal to the aggressors and where the balance of power between the groups is extremely asymmetrical. Wrangham and colleagues [18] calculated the median risk of violent death in chimpanzees

due to intergroup violence and found that it ranges from 69 to 287 per 100,000 per year, and the victims were mostly adult males (42.4%) and infants (51.5%). Watts and colleagues [19] report that, while the injuries on the aggressors were minimal, the attacked males were reported to have broken bones, wounds covering a considerable part of the exposed surfaces of the victim, castration and torn thoraxes, despite resisting intensely [20].

More astonishingly, chimpanzees can also attack humans for various reasons [21]; these attacks may be due to food deprivation or surprise encounters between humans and chimpanzees in areas of common use, such as paths. Most of these attacks were predatory, having children as the main targets of the primates. The children were between 18 months and 12 years old, and 7 out of 10 attacks happened when the children were alone; one happened when a man was present, but the man had a physical disability. However, once they were pursued by a human, the attacking chimpanzees would immediately cease the attack. While the occurrences were rare, Hockings and colleagues [21] reported that chimpanzees have demonstrated bold behaviour by moving up to 182 m away from the edge of the forest to capture human prey; and, on two occasions, a baby was removed from the doorway of a house.

Unlike chimpanzees, bonobos show extremely low levels of intragroup aggressive behaviour. Even between groups, they rarely engage in physical aggression, which their phenotype reflects. They have much smaller canines when compared to their body sizes than those of chimpanzees and gorillas, and they rarely obtain bone fractures from interspecific confrontation [13]. There are no known cases of male–female aggression in bonobos, since females show feeding priority over males; contrarily from what happens with chimpanzees, the females always occupy higher ranks in the bonobo hierarchy [22]. Hare and colleagues [22] proposed that this strong reduction in the expression of the aggressive behaviour in bonobos is due to a natural domestication process that occurred in the species, describing many phenotypical traits that bonobos share when compared to other domesticated animals that have a “wild counterpart” (i.e., dogs and wolves), such as reduced cranial size and diminished sexual dimorphism in the brains and crania when compared to chimpanzees.

While chimpanzees and bonobos usually live in large groups, gorillas' groups are much smaller (sometimes even living as lone males) and have periods of sub- and super-grouping. Lowland, sometimes called western, gorillas (*Gorilla gorilla gorilla*) are more frugivorous and use larger home ranges than the closely-related mountain gorilla (*Gorilla beringei beringei*) [23]. Lowland gorillas are also more tolerant than mountain gorillas to adult males in other groups, even though it is unusual to have more than one silverback (adult males). In a study on home-ranges of lowland gorillas, Bermejo [23] found that 50% of the encounters between his focal group of gorillas and lone males resulted in avoidance, while the other 50% involved aggressive displays. However, encounters between his focal groups and other groups showed different results: 64% of the time, the focal group showed tolerance, and 14% of the time, the focal group avoided the other groups. The aggressive encounters corresponded to approximately 21%, with 7% involving physical aggression. Therefore, only a small portion of the encounters resulted in aggression, and the silverback gorilla of the focal group sometimes tolerated other males to the point where they conested, showing a much different behaviour than the more aggressive mountain gorilla [23]. Mountain gorillas form groups that contain one or more silverbacks [24], and approximately 40% of the mountain gorilla groups contain more than one male; however, one single male is likely to monopolise the reproduction in his group, which is similar to what happens in the lowland gorilla. Mountain gorillas are not only much less tolerant than lowland gorillas to males in other groups [23], but they also perform aggressive displays to females [25]. Interestingly, the silverbacks from lowland gorilla groups also control the aggression between the younger members of the group by physically intervening in conflicts [26], especially in captive groups, where resources, such as

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