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The nature of human aggression

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ABSTRACT

Human aggression is viewed from four explanatory perspectives, derived from the ethological tradition. The first consists of its adaptive value, which can be seen throughout the animal kingdom, involving resource competition and protection of the self and offspring, which has been viewed from a cost–benefit perspective. The second concerns the phylogenetic origin of aggression, which in humans involves brain mechanisms that are associated with anger and inhibition, the emotional expression of anger, and how aggressive actions are manifest. The third concerns the origin of aggression in development and its subsequent modification through experience. An evolutionary approach to development yields conclusions that are contrary to the influential social learning perspective, notably that physical aggression occurs early in life, and its subsequent development is characterized by learned inhibition. The fourth explanation concerns the motivational mechanisms controlling aggression: approached from an evolutionary background, these mechanisms range from the inflexible reflex-like responses to those incorporating rational decision-making.

"The nature of human aggression" refers to its place in the natural world. It concerns where aggression originated, and the implications of those origins for the form, development, and organization of human aggression. These issues are covered by the ethological approach to animal behavior, which is best-known as involving naturalistic observational studies of animal (and later human) behavior, to distinguish it from the laboratory experimental approach of behaviorism. In addition, ethology is distinguished from standard psychological and social science approaches by its broader theoretical orientation, which was described by Tinbergen (1963) in terms of four different types of questions that are asked in ethological studies. The nature of human aggression can be addressed by considering together these four explanations.

The first one is a functional explanation that views behavior in terms of its adaptive value, its contribution to an individual's survival and reproductive chances. The functional analysis of animal behavior involved a variety of theoretical models, notably those by Fisher, Hamilton, Maynard Smith, Trivers and Williams, which were summarized by Dawkins (1976) in *The Selfish Gene*. For example, Hamilton (1964) extended the concept of biological fitness to take account of the indirect effects genes have on aiding relatives, which explained many of the instances where animals helped others of their own kind to the apparent detriment of individual fitness. As Dawkins (1976) recognized in his book, the gene-centered approach proved to be a fundamental principle for understanding the evolution of behavior. Most of the other important functional analyses of animal behavior are based on assessments of the benefits of behavior in relation to its costs, and this approach has been extended to humans in the form of several approaches to human behavior, the best-known being evolutionary psychology (e.g., Barrett, Dunbar, & Lycett, 2001; Buss, 2004).

The second explanation concerns the phylogenetic origin of the behavior, its antecedents in evolutionary history. Ethologists used the comparative method to trace commonalities and differences among the courtship displays of related species, so as to infer the origins of present-day forms (Archer, 1992, pp. 149–156). A similar approach has been applied to the evolutionary origins of human facial expressions, such as laughing and smiling (e.g., Jolly, 1972; van Hooff, 1972). The concept of homology is important in this context, referring to structures or behavior that are similar owing to common origins (Eibl-Eibesfeldt, 1975, p. 219–224). These are distinguished from analogies, which are similarities produced by functional similarity, not past ancestry, for example in the wings of birds and insects.

The other two explanations shift the focus to the individual's lifetime. One concerns the developmental origin of behavior and its subsequent modification through experience, which is similar to the explanations sought by developmental psychologists and those concerned with the developmental origins of criminal and other antisocial behavior (e.g., Tremblay et al., 1999). The ethological approach to development has a different starting point from most psychological perspectives, which tend to adopt a non-evolutionary, cultural learning, view of social development (Pinker, 2002). Developmental issues covered by the ethological perspective concern the typical course of the development of behavior, the nature of individual differences, and how experiences during development can change its course and outcome.

The fourth explanation concerns the immediate causes of behavior. Ethologists used the term causation to refer to the immediate causes

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of behavior, its internal and internal causal influences, and this broadly corresponds to the area covered by the term motivation in psychology, although again the ethological approach views motivation from the perspective of an evolutionary background. In this article, I outline the application of these four explanations to human aggression, and consider ways in which they are linked.

1. Functional explanations of human aggression

Most considerations of animal aggression concentrate on the forms that occur in response to resource competition, although protective aggression–responses to attack by members of the same species or predators–is just as important (Archer, 1988). Protective aggression often involves less restrained actions, reflecting the high costs involved if such an encounter were lost (Archer, 1988). Similarly, forms of aggression whose function it is to protect offspring are often unrestrained, reflecting the importance of offspring survival for perpetuation of the parents' genes.

The principle underlying an evolutionary functional analysis of aggression is a cost–benefit analysis. This has been applied to competitive aggression, for example in studies of the conditions under which animals show territorial aggression. J.L. Brown (1964) put forward the principle of "economic defendability", that territorial defense would only occur when the benefits (e.g., access to food sources and mates) exceed the costs (e.g., those associated with fighting and patrolling an area). An example of one of the subsequent empirical studies demonstrating Brown's principle is that of Gill and Wolf (1975) on the nectar-feeding Kenyan golden-winged sunbird. These birds only defend a territory with flowers containing nectar when the nectar levels in undefended flowers are low. When these are high, and no additional benefit is obtained from defending nectar sources, the birds abandon territorial defense. This study neatly demonstrates that animals can monitor the cost–benefit contingencies in the environment, and modify their behavior accordingly.

Important resources are not confined to the physical environment. W.D. Brown, Chimenti, and Siebert (2007) manipulated the value of mating access to females in male house crickets, by either giving them daily access for 4 days, or no access. The mating-deprived group, for whom the value of access to a female was higher, showed more aggression toward other males in subsequent staged encounters.

These examples show variability in aggression in response to either a variable food supply or the availability or scarcity of a mating resource. A series of theoretical models based on cost–benefit principles were applied to the more complex case of adaptive responses to the behavior of other animals. In this case, what is adaptive will depend on the nature of these other responses. In order to simulate the likely adaptive outcomes under such circumstances, Maynard Smith (1974, 1982) modeled the evolution of fighting strategies in animals using game theory. The interaction of different strategies can be calculated by presenting them in a payoff matrix as players in a game, and simulating the change in their relative frequencies through succeeding generations. Maynard Smith transferred the principle of Nash equilibrium to game theory models of animal conflicts in the form of an Evolutionarily Stable Strategy (ESS), which is a strategy that cannot be replaced by alternatives given the costs and benefits of the strategies in that population.

Game theory models of the evolution of animal fighting were first used to explain why natural selection can produce strategies that stop short of damaging attacks on opponents. Rather than being the consequence of adaptations for the good of the whole group, or species, as had been argued by Lorenz (1966), they were shown to be the consequence of individual-level selection when the costs of escalated fighting were high in relation to the benefits (Maynard Smith, 1982), usually because of the presence of potentially damaging natural weapons, as occurs in the males of many large mammals (Clutton-Brock & Albon, 1979; Geist, 1966).

An important principle derived from one of the earlier game theory models of animal fighting was Resource Holding Power (RHP). Parker (1974) showed that when animals can assess the fighting ability (RHP) of opponents before fighting with them, and use this assessment to decide whether or not to fight, this is selectively more advantageous than simply fighting regardless. The strategy of making an assessment before fighting is an ESS, and is expected to have evolved widely in the animal kingdom. This is the case, with cues to fighting ability, such as larger size, predicting which of two opponents withdraw prior to an aggressive encounter, and which is likely to win an encounter, in many diverse species (Archer, 1988, pp. 166–171).

In humans, size and strength have been found to be positively correlated with physical aggression and dominance in boys (Pellegrini et al., 2007), adolescents (Tremblay et al., 1998), and adults (Archer & Thanzami, 2007; Felson, 1996; Sell, Tooby, & Cosmides, 2005). Many vertebrate species use vocalizations as cues to RHP (e.g., Clutton-Brock & Albon, 1979; Davies & Halliday, 1978; Mager, Walcott, & Piper, 2007; McElliott, O'Neill, & Hayden, 1999), and in humans two aspects of pitch which together produce deepening of the voice, lowering of fundamental frequency and smaller formant dispersal, provide accurate indications of a man's shoulder-to-hip ratio and his body size (Evans, Neave, & Wakelin, 2006). Artificially slowing the pitch of a man's voice increased ratings of his fighting ability by other men, and men who perceived themselves to be physically dominant lowered their voice pitch in a competitive situation (Puts, Gaulin, & Verdolini, 2006). These studies show that the study of physical individual difference variables, such as size and strength and vocal pitch, enable links to be made between functional analyses of animal and human aggression.

Daly and Wilson (1988) viewed homicide in terms of principles derived from natural selection. They were careful to make it clear that homicide itself is not as an adaptation but the result of mechanisms shaped by natural selection for dealing with evolutionarily important conflicts, such as inter-male competition and sexual jealousy. They proposed (from the principle of inclusive fitness: Hamilton, 1964) that genetic relatedness would be an important predictor of patterns of homicide, and they showed this to be so in two different cases. The first involved homicide records from thirteenth century England, where many homicides were collaborative: collaborators were six times more likely to be related than were victims and offender. The second involved evidence from modern Canada and the US: this showed the much greater risk of stepparents killing stepchildren than was the case with their natural children.

The importance of cost–benefit principles comes out in several of Daly and Wilson's other analyses. When brothers do kill one another, this tends to occur where there is patrilineal descent, in which all the inheritance goes to one sibling, producing a high degree of resource conflict. Daly and Wilson (1988) used a game theory simulation to show that selection favors increasingly risky violent strategies as fitness differentials increase. This is because those who are unlikely to reproduce (through having no resources) will at least stand some chance of doing so if they adopt a risky strategy, despite high individual mortality costs, if the benefit of winning is sufficiently high, and the fitness consequences of not competing are low. Daly and Wilson (1988) applied this analysis to the finding that homicidal perpetrators and victims are more likely to be unemployed and unmarried, i.e. to have relatively few resources, and therefore little to lose by dangerous competition. Support for this view, rather than a gradual decline in criminal tendencies with age, comes from an analysis by Laub, Nagin, and Sampson (1998) of the age–crime curve, showing that desistance is facilitated by good-quality marital bonds. Similarly, Daly and Wilson (2001) found that the homicide rates against unrelated individuals among divorced and widowed men were more like those among single men than those among currently married men.

Human sex differences can also be understood from an evolutionary cost–benefit perspective. Humans show a moderate sex difference in size, muscular development and longevity, which are all consistent with the operation of some degree of sexual selection (Darwin, 1871, 1959) not as much as in markedly polygynous species such as baboons, but more than in monogamous ones, such as gibbons. These sex differences in size and strength are accompanied by a sex difference in direct forms of aggression, which increases in magnitude as the aggression becomes more escalated and potentially dangerous (Archer, 2004). Escalated forms of aggression, notably homicide (Daly & Wilson, 1990), show the largest sex difference.

The key to understanding these sex differences is that sexual selection affects the value of the potential benefit to be obtained by reproductive competition so that it is higher for males than females. This occurs as a consequence of differences in the reproductive rates of males and females (Clutton-Brock & Vincent, 1991), associated with inequalities in parental investment that are ultimately the result of specialization in gamete formation, eggs being more costly to produce than sperm (Trivers, 1972). This leads to females being a resource to be competed over by males. This situation can even out to some extent when male parental care is necessary for offspring survival (and reversed in cases where males specialise in parental care). In humans, this has occurred to some extent, but males still show many of the typical characteristics of sexually selected attributes, such as larger size and strength, a shorter life-span and higher variability in reproductive success than human females (Archer, in press).

Nevertheless, it is still the case that the magnitude of the sex difference can be affected by environmental variables that alter local cost–benefit contingencies. For example where females are subjected to high reproductive competition, for example by the absence of suitable men, they show more physical aggression (Campbell 1995). Where there are high costs of physical aggression for men, as in modern professional life, direct physical aggression will be replaced by more indirect forms that have fewer direct costs (Bjorkqvist, Osterman, & Lagerspetz, 1994). These two examples will lead to a reduction in the magnitude of sex differences. Other circumstances, for example, the presence of a high proportion of uneducated men without resources or status or families, and relatively few women (Courtwright, 1996), will lead to higher rates of inter-male violence and therefore will accentuate the sex differences.

These few examples show how the evolutionary principles of kin selection and cost–benefit analyses can be applied to the study of human aggression, to reveal meaningful patterns that are consistent with forms of behavior resulting from natural selection. Important as it is, the functional approach can be further enriched by other ways of explaining behavior.

2. Phylogenetic origins of human aggression

The second of Tinbergen's four explanations, phylogenetic origins, is closely tied to evolutionary function. In a wide variety of species, whenever the benefits of engaging in physical aggression have outweighed the costs, some form of aggression has independently evolved. Aggression can therefore be observed throughout the animal kingdom (Archer, 1988; Huntingford & Turner, 1987). Several aspects of human aggression are noteworthy from a comparative zoological perspective. One concerns the brain mechanisms underlying the expression and inhibition of human aggression. A second involves the emotions associated with direct aggression, and their expression. A third is the absence of natural weapons, and the variety of ways in which aggressive actions are manifest.

Aggressive behavior occurs in animals with very simple levels of neural organization, such as sea anemones, chitons (sedentary mollusks) and corals (Archer, 1988, p.18–19). It is clear that having a brain is not a requirement for physical aggression. But in humans, aggression is controlled by a complex interplay of brain mechanisms that are phylogenetically ancient. The sympathetic nervous system, a part of the autonomic nervous system that controls the internal state of the body, is located throughout the spinal cord and the brain, and it regulates the body's preparation for situations requiring muscular exertion and vigilance. This was termed the “flight or flight response” by Cannon (1929), the pioneering physiologist, thus recognizing its link to the outward expression of preparations for aggression and fear, and hence to the precursors of human emotions.

The brain mechanisms underlying human aggression are complex and evolutionarily ancient. MacLean (1990) explained the origins in the human forebrain in terms of a three-part “triune brain”, consisting of three interconnecting structures: the lower part, the reptilian brain (or R-complex), is phylogenetically older and is shared with most land vertebrates; the middle part, the paleomammalian brain, arose with the early mammals; and the most recent part, the neomammalian brain, arose later in the evolution of mammals. Of course, this refers only to the forebrain, which is built around the midbrain and hindbrain, which are shared with fish and amphibians, in which the forebrain is much smaller.

The neural circuits that underlie aggressive behavior lie in all three parts of the forebrain, with connections to the mid and hindbrains and the autonomic nervous system. Basic action patterns for aggression are controlled by the basal ganglia (reptilian brain), and the limbic system, located in the paleomammalian brain, which controls emotional behavior. The neomammalian brain consists of the neocortex, which of course is greatly enlarged in the course of human evolution. In relation to aggression, this forms the basis of self-control, the neural mechanisms that regulate and potentially inhibit the more immediate responses to events.

A number of studies involving electrical stimulation of the brain, carried out since the 1930s, have located common neural circuits underlying the control of aggression in mammals, including humans (Panksepp, 1998). The so-called rage circuits are to be found in the medial areas of the amygdala, through to the hypothalamus (both are parts of the limbic system), and down to a midbrain structure termed the periaqueductal grey. These structures are hierarchically arranged so that higher level structures control those lower down. This also applies to cortical regulation, which exerts an inhibiting influence in many circumstances when the circuits are activated.

Blair (2004) suggested that the amygdala regulates subcortical systems that respond to stress, so that the response can be upgraded or downgraded according to context. Studies of humans, and of other mammals, have shown that the frontal cortex regulates subcortical structures that control anger-induced aggression (so-called “reactive” aggression). The orbitofrontal cortex (OFC) plays a particularly important part in this process. Lesions to the OFC result in impulsive behavior, and Blair (2004) presented a model of the part played by this and other processes in the regulation of aggression. The OFC is viewed as integrating information from competing cortical and sub-cortical inputs.

An example of a modern study of the activation of the brain circuits underlying aggression is that of Hermans, Ramsey, and van Honk (2008), who used functional MRI (magnetic resonance imaging) to measure activity in cortical and subcortical brain areas of female volunteers in response to a presentation of an angry face, involving a masking technique used in previous work (e.g., Putman, Hermans, & van Honk, 2004). Activity was found in a range of cortical and subcortical structures referred to in previous paragraphs, the orbitofrontal cortex, the amygdala, the hypothalamus, and areas in the midbrain, such as the periaqueductal grey. This study showed extensive activation in the brain areas familiar from many decades of animal research using techniques such as electrical stimulation of the brain, and lesions. Hermans et al. (2008) also found that raising the circulating testosterone concentrations of young women to levels similar to those of young men, affected responses in these areas, primarily involving increasing excitability of the subcortical structures involved in regulating aggression.

The human emotion of anger is based on a phylogenetically ancient set of neural, endocrine and behavioural mechanisms. Although anger is the emotion that is typically associated with aggression, similar circumstances produce both anger and fear (Archer, 1976; Berkowitz, 1962), and aggression, particularly protective forms, is often fear-motivated (Archer, 1988). In many animals there is a clear separation, both in form, emotional expression, and in neural bases, between anger-induced and fear-induced aggression (Blanchard & Blanchard, 1984). Typically, anger-induced aggression occurs in conflicts involving resource competition, and attack is more restrained than in the case of fear-motivated aggression (Blanchard & Blanchard, 1981; Blanchard & Blanchard, 1984). D.C. Blanchard (1984) applied these principles to human aggression, where provocations to anger typically involve disputed resources or status. Insults were viewed as explicit challenges to status, developing out of the more direct dominance disputes of animals.

Although the basic neural and behavioral mechanisms underlying anger can be viewed as derived from the phylogenetically ancient fight–flight system, in humans anger is communicated to others mainly via facial expressions and gestures associated with anger. Darwin (1872) described the expressions of anger in a range of monkey and ape species, indicating that in some species the teeth are shown whereas in others the mouth is closed, as it is in humans. Jolly (1972) described the primate homologies of human facial expressions. For example, the open-mouthed threat display, which is shown in humans as an angry shout, is characteristic of a wide range of primates, including prosimians and new-world monkeys, which are more distantly related to humans than are old-world monkeys and apes. However, the tense-mouth face, shown in humans as a silent glare, is characteristic of old-world monkeys and apes, although humans seem to share the contraction of the brows, originally described by Darwin (1872), only with their closest relatives, the great apes.

Sell (2006) has argued that the prominence of both the brows and the jaw are exaggerated in angry faces. He analyzed the facial action units associated with the closed-mouth angry face, and found that seven out of ten of these increased the size of the brow-ridge or jaw. He also showed that these features were more pronounced in men than women, and that they formed the basis of accurate estimations of a man's strength based on facial features alone (Sell et al., 2009).

Throughout the animal kingdom, animals–particularly males–show a range of organs that are used in fighting others of their own species. In some cases, these are maintained in the mating season, to be shed thereafter. In some groups of animals, the evolution of these natural weapons can be traced through a comparison of present-day related species. Geist (1966, 1978) used this method to infer the evolution of horn-like organs in several mammalian groups, including ungulates, notable sheep and goats, putting them in the context of the relative size and longevity of these animals. These natural weapons serve both defensive and offensive functions, defense being necessary in relatively long-lived animals possessing dangerous offensive weapons.

In humans, there are no organs specialized for fighting. Human males do not have the enlarged canines found in the males of many other primate species, including our closest relative, the chimpanzee. Humans are left to use a range of body parts to inflict damage on an opponent, fists and feet being the usual ones. However, early in human evolution it is likely that there was compensation for these deficiencies by the use of external weapons, beginning with sticks and stones, and developing into sophisticated instruments designed to kill an opponent. One feature of the evolution of fighting strategies is that animals possessing dangerous natural weapons, such as deer (Bartoš et al., 2007; Clutton-Brock & Albon, 1979) tend to show restraint when fighting one another and only gradually escalate from threat postures at a distance to escalated dangerous moves involving their weapons. This can be understood in terms of game theory cost–benefit models. The probability of an escalated encounter for any given benefit decreases as the likely costs of such an encounter increase. Animals, such as humans, that do not possess harmful natural weapons are on this basis likely to attack with a shorter initial phase of display. However, it is likely that the effectiveness of artificial weapons is readily learned by potential victims, although restraint by the perpetrator is likely to depend on the opponent's weapons. Thus cost–benefit considerations may be operating in humans, but are complicated by the use of external weapons and individual learning.

I have so far placed human aggression in the contexts of evolutionary functional principles, and the brain mechanisms, emotions, and acts of behavior found in mammals and in vertebrates generally. The following two sections switch the level of explanation from this broader evolutionary background to what happens within a single individual, first considering the developmental time-scale and then the shorter time-scale surrounding an act of aggression.

3. The developmental origins of human aggression

Acceptance that aggression is the consequence of natural selection, and is deeply embedded in our animal past, will have implications for how its development is considered. Conventional psychology has a long tradition of interest in development, but largely from a non-evolutionary perspective. The emphasis has been on the impact of social learning in explaining social development (Pinker, 2002). Thus, aggression is viewed as behavior that is learned throughout childhood from a variety of influences, including parents, peers, and the media (e.g., Bandura, 1973; Lefkowitz, Eron, Walder, & Huesmann, 1977).

In contrast, an evolutionary perspective on development is primarily concerned with regularities in the developmental process underlying a form of behavior that is the result of natural selection. Although the environment clearly plays an important part in this process (Archer & Côté, 2005; Bjorklund & Pellegrini, 2002; Stamps, 2003), the emphasis shifts from the impact of the social environment on the individual to the interaction between an evolved genetic program and the local environment. This can produce wide variations in outcome, through processes more diverse than social learning.

In general, evolved forms of behavior vary in the extent to which they can be modified by their developmental environments. The onset of physical aggression early in life appears to be relatively consistent despite variations in the local social environment. Typically, unfocussed actions and angry expressions begin during the first year of life, and there is evidence of using force against peers by 14 or 15 months of age (Hay, 2005; Tremblay & Nagin, 2005). Several longitudinal studies inform us about its developmental progression. Contrary to what we might expect from the social learning perspective, physical aggression is found at a high level in the second year of postnatal life, and its subsequent development is characterized by learning to inhibit this form of aggression, replacing it with alternative forms of aggression or other ways of achieving social goals. Using mothers' reports of 11 acts of physical aggression, in a large nationally representative sample of Canadian children, Tremblay et al. (1999) found that physical aggression increased from 12 to 17 months of age, so that by 17 months, almost 80% of the children in the population sample used were reported to have shown physical aggression. From ages 2 to 11 years, there was an overall decline in levels of physical aggression, although this overall trend hides considerable individual variation (Côté, Vaillancourt, Leblanc, Nagin, & Tremblay, 2006): around one sixth of children followed a continuing path of a high level of physical aggression.

Although the regularity in the early onset of aggression suggests that it arises from a program for development that has been molded by natural selection in ancestral environments to serve adaptive outcomes, the range of outcomes that can arise from this program is varied. The scope for different environmental influences increasing or decreasing the level of aggression is wide. It is beyond the scope of this article to cover the range of environmental influences on the development of individual differences in aggressive behavior. I shall just note that early in life they include the presence of young siblings, early age of motherhood, antisocial behavior by the mother, smoking during pregnancy, postpartum depression, and low parental income (Tremblay et al., 2004).

Thus environmental influences that operate early on, and throughout later periods of life, clearly provide a source of variation in the level of aggression shown by individuals. The large-sample longitudinal studies of Tremblay and his group (e.g., Côté et al., 2006; Tremblay & Nagin, 2005) show that there is a wide variation, some of which is a consequence of the interaction of temperamental differences with the environment. The importance of genotype-environment interaction in relation to the development of aggression has been emphasized in recent years (e.g., Caspi et al., 2002; Raine, Brennan, & Farrington, 1997). For example, in a study of rhesus monkeys, Suomi (2005) identified a specific genetic variation that produced low levels of 5-hydroxyindoleacetic acid (5-HIAA), a metabolite of the neurotransmitter serotonin, in the cerebrospinal fluid, and which was reliably associated with impulsive aggression, but only in monkeys who were peer-reared (i.e. without their mothers). Mother-rearing seemed to buffer the expression of this genetic variation, resulting in an absence of the lowering of 5-HIAA and no impulsive aggression. Caspi et al. (2002) found a comparable interaction in humans for a gene that affects neurotransmitter catabolism (degradation) and encodes the enzyme monoamine oxidase A. They found that young adults who possessed this gene were more likely to show criminal activities than those who did not, but only when they had been abused as children.

A further complication in the study of gene–environment interactions is that an individual's behavior will contribute to their local environment (Scarr & McCartney, 1983). Thus a person's temperament will affect the sort of environment they evoke and select for themselves. Perhaps the best-known example of this in relation to aggression is the study by Caspi, Elder, and Bem (1987). They examined data from a longitudinal study that began in 1928, taking measures of temper-tantrums at 8–10 years and adult characteristics when the people were 30–40 years old. They found that those who were anger-prone at 10 years tended to be more under-controlled and irritable as adults. There was also a direct link between being anger-prone at 10 years and lower educational achievement, having an erratic work life and a failed marriage in adulthood.

Another important principle to arise from an evolutionary approach to development stems from the consideration that selection may favor diversity in phenotypes rather than there being a single adaptive form. This is well known in studies of animal behavior, where in some species males may show morphological differences in accordance with their adaptive specialization. Thus in some species there are those who are larger, and specialized for fighting other males, and those who are smaller and are adapted to sneaking up on females unnoticed by the fighters. This example introduces the principle that there are likely to be a group of interlinked characteristics that are associated together in the same person. Thus an aggression-prone individual may show a number of other features, such as being impulsive, risk-taking, extravert, and also having high testosterone levels (Archer, 2006) compared with a less aggressive individual. These characteristics all represent adaptations for different reproductive (or life history) strategies (Archer & Mehdikhani, 2003).

The concept of alternative reproductive strategies applied to human aggression would seem to indicate that a pattern of behavior regarded as antisocial is just another way of getting by in the world. However, a further consideration is that impulsive forms of aggression may well be considered to be maladaptive, if they are very disruptive to the social life of the group (which is, after all, the environment into which a social animal must fit). An example from Suomi's (2005) studies of rhesus monkeys illustrates this point. About 5–10% of rhesus monkeys of Indian origin, living in conditions in the US that simulate those in the wild, showed impulsive behavioral tendencies, manifest as fewer positive and more aggressive interactions with their peers. These individuals showed evidence of low cerebrospinal fluid 5-HIAA (a serotonin metabolite: see above). The same pattern was found in an island free-living sample of rhesus monkeys, where these impulsive males were mostly driven from their troop before they could breed. Suomi (2005) speculated that the gene for impulsive behavior is maintained by females, who are not driven out, and do breed. In this instance, therefore, aggression that is viewed as pathological is highly disruptive to social relations, and hence to survival and reproductive chances. Of course, there are many other cases among both humans and animals where aggressive individuals do successfully use aggression to obtain resources and access to mates.

Although evolutionary psychology typically concerns instances where genes underlying adaptive characters are expressed in a species-typical environment, adding a developmental perspective can broaden this scope by recognizing that the genetic underpinning of adaptive characteristics interacts with the environment to produce a range of different outcomes (Bjorklund & Pellegrini, 2002). Genes may or may not be expressed depending on the early and later environment; differences from the evolutionary environment may produce novel outcomes; individuals create different local environments through their own behavior; there may be different adaptive pathways in development; and non-adaptive features may be maintained indirectly by natural selection.

4. The motivation of human aggression

If aggressive motivation is approached from a functional evolutionary viewpoint, the first question to ask is what problem is the system designed to solve, and a second concerns the possible ways in which this can be achieved. One approach used by North American evolutionary psychologists is to list the specific adaptive functions that aggression fulfills, and then to suggest specific mental modules for each of these different functions (Buss & Shackelford, 1997). This can be viewed as a reaction to the general-purpose models of aggressive motivation in psychology, such as the frustration–aggression hypothesis (Berkowitz, 1962, 1989, 1993; Dollard, Doob, Miller, Mowrer, & Sears, 1939). Here, I offer a different approach to moving from function to mechanism, one where the mechanisms underlying aggressive motivation are viewed as existing on a continuum from the inflexible to the flexible. There is both generality and specificity built into the mechanisms suggested.

As indicated in the first section, the general functions of aggression fall into two main categories, reacting to localized danger, and resource competition (Archer, 1988). Inflexible mechanisms are simple reflex-like responses to specific stimuli. These include the initiation of territorial aggression by specific simple stimuli, termed social releasers, such as the red breast of a robin (Lack, 1939). Although later controlled experiments showed that these were often more complex reactions than were originally thought, there are sufficient examples (Archer, 1988, pp.130–134) to show that specific stimuli can elicit attack. Lest we think that such automatic responses have no relevance to humans, it is clear that human parental responses are readily elicited by a very simple set of facial stimuli (Lorenz, 1943, 1971). In relation to aggression, sudden localized pain is perhaps the nearest humans show to an aggressive reaction to a specific stimulus (Archer, 1989–90). This is a phylogenetically ancient reaction that has its roots in a reflex-like response to events that had already endangered the animal's bodily integrity (Archer, 1976, 1988). Hence it functions as a form of protective aggression.

Mid-way between flexible reflex-like responses and rational actions are responses involving the emotions. As Johnson-Laird and Oatley (1992, p. 206) put it: “The function of emotions is to fill the gap between fixed action patterns and impeccable rationality”. They do this by representing similar behavioral and physiological responses to a class of events: these responses are generally likely to be adaptive without being fine-tuned to the details of each specific set of circumstances. Anger, the emotion most commonly associated with aggression, can be linked with an aversively-generated motivational system that underlies most forms of aggression, and, at higher levels of activation, fear responses. A model of this system was proposed for animal aggression by Archer (1976), entailing a two-stage process, first the registering of a discrepancy from some important expectation in the current input, which generates an affective state, and a second decision-process that evaluates the specific situation in relation to stored associations and expectancies. The end-product of activation of the system is removal of the source of the discrepancy from the animal's environment, or in the case of a fear response, removal of the animal from the situation. It therefore clearly establishes aggressive motivation as primarily a reaction to aversive events, and in this respect it is similar to the frustration–aggression model.

Thus discrepancies from a range of internal representations of desired external events will evoke the aggression–fear system (Archer, 1976, 1988). Inputs from specific internal and external events will then narrow down the response to one associated with either aggression or fear. The consequences of these responses will be to respond appropriately when another animal invades a territory, or when a previous reward ceases to occur. In human terms, discrepancies that challenge a person's self-image (an internal model of the person's place in their social world) will evoke aggressive actions in a similar manner (Baumeister, Smart, & Boden, 1996).

These anger-generated aggressive reactions provide responses that are generally adaptive, but they do not in themselves take account of specific aspects of each situation that evokes them. In order to fine-tune specific responses so that they are adaptive in a range of circumstances, the emotional–motivational system has to incorporate some aspects of rational analysis of specific situations. The ability to do this is not restricted to humans. In fact, aspects of a cost–benefit analysis of situations involving conflict are apparent in animals, as the game theory models showed in relation to the assessment of fighting ability. Such rational decision-making enables fine-tuning of a general emotionally-driven reaction, which according to Johnson-Laird and Oatley (1992), provides rapid decision-making about what is appropriate on the basis of a class of events, rather than a detailed and specific analysis of each new situation.

From this perspective, the view of D.C. Blanchard and Blanchard (1984), that anger represents a link between evolutionary cost–benefit analysis and fighting is only partially correct. They regarded anger as representing the pooled values of a number of diverse variables, such as the internal state of the animal, the provoking situation, and the properties of the opponent. It is certainly the case that specific information about, for example, the benefits to be obtained by aggression towards a particular opponent, and the dangers involved in fighting specific opponents, are incorporated into the motivational system underlying anger (Archer, 1988). However, the anger-system represents a crude approximation of the specific cost–benefit considerations relating to a specific situation. Especially in the human case, decisions based on rational choice, and involving neocortical mechanisms, assume considerable importance. In this way, a rational decision-making mechanism can overlay the operation of the anger-motivational system. In social psychology, approaches emphasizing either the role of anger (e.g., Berkowitz, 1989) or rational decision-making (e.g., Tedeschi & Felson, 1994) have tended to be seen as alternatives. It seems more realistic to view them as complementary, and inter-related, in a manner similar to the brain mechanisms underlying aggression (Blair, 2004; MacLean, 1990).

From this perspective, the costs and benefits that have been considered in evolutionary analyses of animal aggression are incorporated at various stages of the decision-making process. At the most general level, the fact that aggression is a response to aversively-motivated events means that it is likely to occur in a range of situations that pose threats or challenges to the animal, i.e. situations which are likely to impose fitness costs if action is not taken. This is why it generally makes functional sense for an aggressive motivational system to be based on an aversion-generated rather than an appetite-generated principle (Toates & Archer, 1978), as was once suggested by Lorenz (1966).

Beyond this incorporation of general cost–benefit principles into the underlying motivational system, specific cost–benefit considerations may be incorporated into the main system for anger, or form part of the secondary appraisals that analyze situation-specific contingencies. An example of the first would be the impact of a large formidable opponent, which is likely to bias the basic reaction towards fear rather than anger, and hence escape rather than attack. An example of the second is when a person is aroused to anger and shows the intention to strike another person, but reasons that the reputation costs of doing so in that situation would be high, and hence withdraws.

5. Conclusions

I have approached the nature of human aggression from four perspectives that characterize a biological approach to any form of behavior, and I have shown that development and motivation, which overlap with standard social sciences approaches to human behavior, can be enriched by considering them in relation to an evolutionary background. This enables us to move away from one-dimensional accounts that emphasize, for example, self-control, or social learning, or genetic inheritance, or evolved modules, towards a multidimensional integrated account. According to this account, aggression has its origins in evolved adaptations, and is characteristic of humans, as it is of many other animals. We should not therefore categorize it as abnormal or pathological behavior. Yet at the same time, some variations associated with its underlying genetic basis, or brain function, or environmental influences, may well represent forms of aggression that are abnormal in an adaptive sense, in that they are counter-productive for the individuals concerned. In other cases, forms of aggression that are disruptive, to other individuals and to society as a whole, may be based on rational decision-making processes. The approach taken by legal and medical authorities to the two cases may well be very different, the first involving predominantly medical and psychiatric facilities and the second involving legal sanctions. However, both types of aggression are rooted in phylogenetically ancient mechanisms evolved to solve a range of adaptive problems.

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