The Role of Fear in the Agonistic Complex

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Although the term ‘agonistic behavior' was originally coined by Scott & Fredericson (1951) to incorporate both attack and defense/flight components, it has virtually become synonymous with the term ‘aggression'. The role of fear (i.e., the motivational construct hypothesized to underlie the defense/flight behaviors), has been relatively underilluminated in the theoretical literature, with the (partial) exception of the game-theoretical analyses of the evolution of agonistic behavior, where it appears as a factor in the cost/benefit calculus. In this paper I present a review of the literature concerning the role of fear in animal and human aggression and violence.

The Role of Fear in Animal Aggression

Leyhausen (1967) has argued that intraspecific fear is a genuine instinct having its own appetence. As the counterpart of intraspecific aggression, intraspecific fear is totally indispensable. The two propensities make ‘sense' only in conjunction with one another. Why should one fear a conspecific if he were never aggressive? And conversely, if the one attacked were not afraid, aggression would either be quite unsuccessful or would lead to uninhibited self-exterrmination of the species.

The counteraction between intraspecific fear and aggression is, according to Leyhausen, the foundation of all social hierarchy, whether absolute or relative, and thus of all social order whatsoever; for without the individual being prepared to accept a higher or lower social position according to circumstances, no vertebrate, and certainly no human, social community would be possible.

When its specific reaction - escape - is blocked, fear has a strong tendency to activate another very specific instinct: aggression. This mechanism is so common and so stereotyped that some authors have already put forward the view that aggression possesses absolutely no specific propensity of its own but is simply learned in fear. Leyhausen regards this hypothesis as quite untenable.

In a situation where there is no way out, such as in the example of the cornered cat, attack is initially only an appetitive act: By feigning attack the cat attempts to ‘bluff' its enemy, to cause it to withdraw and thus to drive it away altogether, or to open up an escape route for itself.

If this does not succeed, it is as first followed by 'limited' fighting in defense against the attacking enemy; and finally in an extreme case ‘genuine' attacking behavior can also be elicited, followed, if successful, by the pursuit of the opponent. The corresponding situations vary from species to species, but the dynamic interrelationships between fear and aggression are basically identical in all vertebrates, and particularly all mammals (Leyhausen, 1967).

Rasa's Model
Rasa (1981) distinguishes ‘property defence’ (more or less ritualized competition for resources) versus fear-motivated damage-inflicting self-defensive behavior (the ‘cornered cat phenomenon’). Ethological analyses of fighting behavior in a number of species have shown that a fear component is almost always present under normal conditions. Scott & Fredericson (1951) recognized this fact early on in the study of aggressive behavior and proposed the term ‘agonistic behavior’ for all elements of the fight situation including both attack and flight tendencies. The causal analyses of fighting in fish, which are probably the best investigated animals from this point of view, have proved that most threat postures, which make up a large proportion of the fighting repertoire, are a balance between tendencies to attack and flee (Baerends & Baerends-van Roon, 1950; Brawn, 1961; Sevenster, 1961; Wiepkema, 1961; Rasa, 1969; Frank & Wilhelmi, 1973).

In Rasa's model, a conspecific may be either ‘friend', ‘rival' or ‘enemy'. An 'enemy' is responded to with self-defensive behavior, a 'rival' with property-protective behavior, these differing both in the motor patterns involved and in their motivational bases. Enemies evoke fear, rivals evoke aggression. The fear-induced self-defensive fighting may inflict severe damage and may even be lethal. In the case of species with individual recognition, the concept ‘enemy’ may become fixed between two individuals with previous experience of escalated fighting with one another, and subsequent fights may even start with damaging behavioral components.

In Rasa's (1982) model, an individual is conceptualized in the agonistic situation as consisting of concentric circles, the outer one being termed its 'ego', the inner one its 'soma'. The ‘ego’ can be regarded as the animal's 'concept' of its potential at any one time: how high its rank could be, how large a territory it could hold, how many mates it could have, etc. This ‘concept' of potential may not calibrate with physical potential but depend heavily on experience (Rasa, 1981).

The individual's ‘soma' is conceptualized as a second circle within 'ego', this consisting of the animal's body, the gene carrier, and a small space around this (e.g. nest) and may also be expanded to include the individual's offspring and even close relatives in highly social species. The size of the circles delineating ‘ego' and ‘soma' are extremely variable and can fluctuate depending on a number of factors.

An intruder approaching an individual is first considered ‘neutral' or ‘friend' (for social animals) when outside the animal's 'ego'. As soon as the boundary of 'ego' is penetrated, however, its classification changes to that of ‘rival' and, should the intruder reach the level of ‘soma', its connotation changes to that of ‘enemy'. For conspecifics, there is a sliding scale between these three concepts depending on the degree of penetration. For predators, the concept ‘enemy' is immediately activated and the animal responds accordingly.

Concomitant with the change in conceptualization of the intruder goes a change in motivation within the individual. Outside ‘ego', the intruder activates no motivational system unless, in social species, a system of ‘social attraction' or ‘friendliness' can be postulated. As soon as ‘ego' is breached, however, the intruder is responded to with aggression.

Aggression continues to dominate the motivational construct until the level of the ‘soma' is reached. It is at this point that it gives way to ‘fear', and the borderline between ‘ego' and ‘soma' is the point at which escalated fights, which are an expression of fluctuation between
the two motivational systems, take place. Energy output along this gradient increases steadily the nearer ‘soma’ is approached.

The animal can be considered as having a hierarchical series of behavior patterns and their alternatives that bar an intruder's path to the gene carrier - its own body. An intruder approaching ‘ego’ first encounters low-energy barriers such as olfactory marks, visual displays, bird song, vocalizations, etc.

If an intruder progresses beyond this point, the second barrier is then activated, this being vocal and/or visual bluff or threat. Further penetration results in property protective fighting that is highly ritualized. Should the intruder continue its pressure on the individual, even more violent fighting is the outcome which, should it be unsuccessful, can end in flight. When the level of the ‘soma’ is reached, however, this fighting changes in nature and becomes damaging and no longer ritualized. The behavior patterns used in such an escalated fighting sequence change and the animal is no longer motivated by aggression but by fear. ‘Ego’ has become equated with ‘soma’.

The change from aggression to fear motivated behavior is associated with ‘cornering’, either physical or motivational. In the latter case, the animal is ‘held’ near the intruder by some motivation stronger than and in conflict with flight (e.g. territoriality, brood care, etc.).

Once the level of ‘soma’ is reached, and despite the damaging attack designed to drive off the intruder by all means possible, the animal has failed to do so, it is left with two choices. It must either flee the situation temporarily or subordinate itself, depending on whether it is a social species or not. In both cases, however, it must relinquish its previous ‘ego’ concept. Should the pressure on ‘soma’ still continue, then only total abandonment of the situation is possible or an abject submission, whose physiological correlates differ from those of subordination (Fuchs & von Holst, 1980) and whose ultimate expression is stress death. The boundaries of ‘ego’ and ‘soma’ are not fixed entities but fluctuate under the influence of many variables, only one of which is the intruder itself. The animal cornered is also influenced by internal variables, such as genetically determined predispositions (e.g. body size, strength, sex, learning ability, agility, etc.), some of which, in turn, may be influenced by its experiences in ontogeny (e.g. if it has had sufficient food during development, this regulating in part body size and strength, its previous successes and failures in the fighting situation, etc.).

All such factors ‘mould' the animal into an ‘ego' situation that optimizes its personal ability to survive at any point in time, this being expressed in its ‘ego' which mirrors its genetic fitness, innate or acquired.

**Criticism**

Rasa's assumption of ‘minimal energy expenditure' is probably not warranted. See Van der Molen & Van der Dennen (1981), in which it is pointed out that organisms periodically launch themselves willy-nilly into ‘trouble', i.e., into potentially dangerous, potentially exciting situations (Cf. also Apter, 1982), which may be considered to be high energy expenditure situations.
Secondly, Rasa does not elucidate the possible motivations of the ‘intruder’, in contrast with those of the ‘defender’.

**Archer's Model**

A highly interesting and fruitful approach to a novel theoretical framework for the evolution of aggression - based on the ‘attack-fear system’ - is provided by Archer (1976). After reviewing a substantial portion of the, mostly experimental, literature, he reasoned as follows:

The common factor involved in situations evoking attack is that they provide a discrepancy of some magnitude from the animal's expectation model, or models of its environment. This process is regarded as essentially the same as that suggested by Sokolov (1960) in relation to the orienting response: he proposed that when the sensory input did not coincide with the animal's previously established ‘neuronal model’, certain vegetative changes, comprising the orienting response, occurred. Such changes have the effect of maintaining the sense organs in contact with the particular sensory input and preparing the animal for further more specific responses. Thus, it is suggested, first, that any perceived discrepancy activates the orienting response, which has the effect of increasing the input in relation to the relevant stimulus source; and second, that if the discrepancy is sufficiently large, a system capable of producing fear behavior or attack also becomes activated.

Archer's hypothesis postulates a common type of mechanism for situations which can evoke either attack or fear behavior. It does not, however, necessarily suggest that the same neurophysiological structures or the same types of neuronal models are involved in all the different types of attack-evoking and fear-evoking situations. The sharing of common properties between the various situations lies in the way the different processes can be represented at the behavioral level by a single model.

It would appear that there are three basic variations on this model, representing pain, novelty, and frustration. These involve, respectively, a form of aggression involving a very simple comparison process, a comparison with the animal's representation of its environment in spatial terms, and a comparison with the animal's representation of its environment in temporal terms (i.e., its expectations).

It may be helpful to amplify this type of reasoning by placing it into a possible evolutionary perspective. It is envisaged that the first stage in the evolution of attack and fear-avoidance systems occurred because animals had to counteract stimuli in their environments that were capable of producing physical damage. Thus, most animals from the Protozoa onwards show some form of escape or avoidance responses, and the selective advantages of these are obvious. An alternative to avoiding or escaping from a noxious stimulus would be for the animal to remain where it is and to remove the noxious stimulus from its vicinity. Such aggressive responses (found mainly in arthropods and vertebrates: Scott, 1971) would have clear advantages over escape where the noxious stimulus could readily be removed, and where escape would have placed the animal in a suboptimal environment.

As animals evolved more sophisticated sensory equipment, the problem of deciding which stimuli were potentially noxious became important, because it would be advantageous for the animal to react to such stimuli in advance rather than waiting for actual damage to occur before taking action.
It is therefore possible that pain-induced attack represents the simplest form of attack; i.e., any damage to the animal's body is counteracted by attack or escape responses, and pain receptors provide a way of monitoring such changes. To fit such a mechanism into the discrepancy model would entail a central monitoring process which matches incoming stimuli (pain signals) with a neuronal model (representing no signal), so that in this case the resulting discrepancy would represent the extent of the pain stimulus. A more sophisticated mechanism would entail changes in the neuronal model as a result of chronic pain. Thus habituation could occur in response to prolonged painful stimuli. Where the animal possessed the neurosensory equipment to react to potential rather than to real noxious events, the comparison process would become more important. Here the animal's 'defended area' would no longer cease at the border of its body and the environment, and therefore it could not rely on responding merely to tactile stimuli of sufficient intensity to activate pain receptors. The simplest way of assessing potential danger would appear to be for the animal to respond to any major change in its immediate environment. Thus the animal builds up a neuronal representation of the stable properties of its surrounding area defined either in terms of its own body (‘individual distance’) or in relation to a fixed area of the environment (‘a territory’) and the input is repeatedly compared with this representation. Again, any large discrepancy evokes attack or fear behavior.

A more subtle form of assessing environmental change occurs in animals capable of building up temporal as well as spatial expectations of what will occur in their environment. Thus, the animal builds up a representation of what is expected on the basis of past reinforcement. Again, the input is matched with this neuronal representation as the animal performs the learned response sequence, and the discrepancy between the input and the neuronal model may occur in one of several ways; e.g. by the absence or delay of the expected reward, or by the animal's being physically prevented from completing the response. Other forms of mismatch are also possible.

In this way, Archer suggests that the situations evoking attack or fear form a graded sequence, involving increasing reliance both on cognitive interpretation and on matching an external event to a central representation of the environment. These different forms of aggression and fear evoking situations involve a similar type of comparison process, but it is not suggested that the same type of neural structures are involved.

As factors affecting the process of decision between fear or aggression, Archer mentions:

- degree of discrepancy between observed and expected events
- strength of ongoing motivation
- hormonal factors (sex hormones, hormones of the pituitary-adrenocortical system, catecholamines)
- experiential factors (early social experience, social isolation, reinforcement of attack and fear behavior)

Once this decision process has occurred (the animal has 'decided' to attack), the final behavioral outcome is then determined by a number of other variables, most notably the following target properties: spatial proximity, degree of similarity to the source of the discrepancy, target size, target movement, among others.
Fear-Aggression as Blocked Escape Behavior

According to Archer (1976), the general term ‘fear behavior’ includes two contrasting types of responses: ‘freezing’ (tonic immobility, lethosis) and fleeing. Freezing presumably evolved as an anti-predator device, since many animals perceive only moving prey (von Uexküll, 1934).

Recent studies have separated some of the factors that determine which of the two types of fear behavior will occur in a given situation (Ratner, 1967; Fentress, 1968; Blanchard & Blanchard, 1968; 1970; Barcik & Collins, 1972; Archer, unpubl.).

As a tentative conclusion from these few studies, it can be suggested that low-intensity diffuse stimulation is more likely to produce immobility, whereas high-intensity localized stimulation is more likely to evoke active flight.

When escape is physically blocked attack is likely to occur, even though the animal still shows general indications of fear behavior (e.g. distress vocalizations, autonomic responses). In this case, it is suggested that in the absence of a space in which to escape, the motor command for escape is changed to attack, even though no general tendency to attack exists. It is presumed that if attack is successful in removing the blocking stimulus, escape can then occur unimpeded. In connection with this point, Hediger (1950) showed that animals respond by flight when a potential predator comes closer than a certain distance (the ‘flight distance’); however, if escape is not possible, and the potential predator ventures even closer (exceeding the ‘critical distance’) attack is likely to occur.

A third possible type of fear behavior, not mentioned by Archer, might be submissiveness (timidity, docility) which is clearly advantageous in social animals, allowing the subordinate individual to remain a group member, even at the bottom of the hierarchy.

Criticism

Even a superficial analysis would reveal, according to Toates (1980), that the model proposed by Archer is vulnerable to instability and dithering unless additional features are proposed. Consider an animal at the point of transition between avoidance and attack. One might imagine that disparity would fluctuate with the moves of an opponent. The animal might therefore dither between attack and avoidance, hardly a profitable strategy. This problem was taken up by Toates & Archer (1978), who argued that in the case of fear the system must involve a mechanism that gives momentum. In other words an initial fear-eliciting stimulus goads the appropriate escape/freezing response for a period of time which extends well beyond the time at which detectable disparity is present.

For example, to end freezing and move off immediately a predator passes would invite detection. In the case of active escape the animal does not switch to attack when disparity falls to a value which would otherwise be associated with attack. There appears perhaps less need to provide momentum to attack than to fear. If the opponent flees or withdraws, the reduction in magnitude of disparity could perhaps profitably be associated with an immediate reduction in attack behavior. It might be maladaptive if this were not the case, since the object of attack is to restore the status quo, not to get locked in a deadly struggle. It probably would not be wise to pursue a retreating intruder. However the results suggest that sometimes the attack tendency slightly outlives the stimulus.
Toates (1980) notes that the catastrophe model of Zeeman (1976; Vide infra) very clearly accounts for the problem of persistence. If we start from causal factors of unambiguous fear then escape persists even though the causal factors for escape are reduced to a minimum and causal factors for attack have arisen. Conversely, if we start with causal factors unambiguously associated with attack then a considerable fear component can enter the causal factors but still attack persists. Of course a point may be reached where if fear is very great the animal reaches an escape catastrophe. In other words this describes a very stable behavioral system, not prone to dithering.

The theoretical position represented by Archer dovetails neatly with that of Bolles (1970). Bolles notes that much of the theory of avoidance learning (reacting so as to avoid a noxious stimulus) which has developed in the laboratory tacitly assumes that avoidance in the wild is largely due to classical conditioning. We can put it slightly facetiously as follows. An owl hoots just before pouncing. The mouse feels the pain of the talons but escapes. Next time the mouse hears the hoot it escapes before the owl has time to pounce, and hence lives to pass on its genes to another generation. But Bolles argues that the chances for learning in such situations are absolutely minimal, and that animals such as mice are equipped with innate species-specific defense reactions (SSDR). Rather than avoidance being the result of conditioning, the SSDR occur when animals ‘encounter any new or sudden stimulus'.

The congruence of Archer's and Bolles' arguments may be appreciated by the following quotation from Bolles (1970): "These defensive reactions vary somewhat from species to species, but they generally take one of three forms: animals generally run or fly away, freeze or adopt some type of threat, that is, pseudo-aggressive behavior. These defensive reactions are elicited by the appearance of the predator and by the sudden appearance of innocuous objects. These responses are always near threshold so that the animal will take flight, freeze or threaten whenever any novel stimulus event occurs. It is not necessary that the stimulus event be paired with shock, or pain, or some other unconditioned stimulus. The mouse does not scamper away from the owl because it has learned to escape the painful claws of the enemy; it scampers away from anything happening in its environment, and it does so merely because it is a mouse. The gazelle does not flee from an approaching lion because it has been bitten by lions; it runs away from any large object that approaches it, and does so because this is one of its species-specific defence reactions. Neither the mouse nor the gazelle can afford to learn to avoid; survival is too urgent, the opportunity to learn is too limited, and the parameters of the situation make the necessary learning impossible. The animal which survives is one which comes into its environment with defensive reactions already a prominent part of its repertoire".

Leshner (1975 et seq.) also proposed a model of agonistic behavior, i.e., attack and fear. In this model, based on rats and mice, the organism's baseline hormonal state gives it a predisposition to be more or less aggressive and more or less submissive. Increasing androgen level up to a point increases tendency to attack. Hormones of the pituitary-adrenocortical axis are also implicated, according to this model. Increase in ACTH levels increases the tendency to show fear (Toates, 1980).

Is it possible to extend Archer's model to more types of aggression, even to those forms of aggression peculiar to humans? It is possible, granted some additional assumptions:
(1) It is assumed that the number and kinds of ‘expectation copies’, ‘cognitive maps’, or ‘templates’ as we shall call them, are species-specific, to account for the fact that different types of aggression figure in the behavioral repertoires of different species.

(2) Furthermore, during ontogeny the number as well as the quality of the templates may change. We assume that a continuous process of calibration is operative, adjusting the template to the immediate circumstances as well as to the particular needs of the organism during different stages of its development.

(3) We assume, furthermore, that in humans we may expect a dramatic increase in templates, as well as profound qualitative modifications, reflecting man's extended repertoire of aggressive and/or violent behaviors, as well as his superior cognitive status. In humans it is the ego-system and its vulnerable sense of self-esteem and the peculiarly human capacity for group identification which generate peculiarly human forms of aggression ranging from narcissistic aggression to moralistic and ethnocentric-xenophobic aggression.

Self-esteem is a ‘mental reality’. Animals cannot be humiliated by denouncing their self-concept or group affiliation. Humans can be, and they may retaliate with paroxysmal violence or more enduring feelings or attitudes of hatred, spite, indignation, hostility, animosity, vindictiveness, etc. Not only self-esteem and a strong sense of group-belongingness are ‘mental realities', but so are social cosmologies and ‘definitions of reality', giving rise to particularly malevolent conflicts between individuals and groups. ‘The appearance of an alternative symbolic universe poses a threat because its very existence demonstrates empirically that one's own universe is less than inevitable' (Berger & Luckmann, 1966). This points to the fact that human ‘reality' is a collective delusional system, a vulnerable social construction. It also points to the fact that human beings may fight as much over values, norms, and meanings as over material resources and commodities.

With these additional assumptions it is possible to extend Archer's model to human aggression: for instance, moralistic aggression implies the perception of a discrepancy between abstract group norms, standards and rules (the template), and the actual deviation from these standards by some member of the group, thus jeopardizing group cohesion (or even threatening the 'natural order of things'), triggering punitive sanctions against the transgressor in order to enforce conformity.

Scott's Model

According to Scott (1976), the most probable general theory of the evolutionary origin of social fighting is that it began with defensive fighting. Defensive reactions to pain or the threat of injury are found almost universally in any species that is capable of inflicting damage on another. Anyone who has attempted to hunt or capture animals is familiar with the reactions of the cornered animal. The behavior is adaptive both against attacks by predators and accidental injury by species mates. Given such a beginning, various secondary social functions of fighting could have been evolved in different species. The principal general theory underlying various attempts to explain the evolution of agonistic behavior is similar to that underlying ritualization. Originally proposed by Huxley (1923) in connection with his studies of mating behavior in grebes, this theory avoids the difficult problem of the origin of behavior patterns. Rather, it suggests that the function of a behavior
pattern may be transformed; in Huxley's case from a directly adaptive pattern into a signalling function in mating behavior.

Two basic concepts are involved in this theory: (1) that behavioral function may be transformed, and (2) that the ultimate transformation is into a signal. Thus in agonistic behavior, fighting may be transformed into harmless behavior patterns, often called displays, that signal threat, avoidance and submission.

Scott (1972) has pointed out that this process can also occur within the lifetime of an animal as well as on an evolutionary basis. In many species, when two individuals fight, one wins and the other loses, and a combination of adaptation and learning eventually reduces fighting and escape to patterns of threat and avoidance. In such a case, the function of injury is transformed, but the general adaptive function of the agonistic behavior is retained.

Assuming that transformation of function of agonistic behavior does occur, the question then arises: what function or functions were transformed in the past, and into what new functions? Here Scott (1981) makes a further assumption, that the most probable transformation is from one closely related function to another. On this basis he constructed a diagram of transformation of function of agonistic behavior. In this diagram Scott suggests a common origin of agonistic behavior arising from the function of defense, either against predatory attacks by other species, or against accidental injury by conspecifics.

Since some form of defensive behavior, adaptive against potential predators as well as against accidental injuries or attacks by species mates, is very widespread in the animal kingdom, Scott suggests that agonistic behavior is likely to have evolved from defensive behavior into functions closely related to defense. This does not exclude the possibility that agonistic behavior may have arisen de novo in some species, or that it may in some species have evolved from a different function. The most common alternative hypothesis is that agonistic behavior arose from predatory behavior, and we do have examples in certain predatory fishes of predatory attack behavior extended against members of the same species, resulting in cannibalism. However, as indicated in the figure, predatory behavior itself arises from quite different functions than are usually involved in agonistic behavior.

The predation hypothesis is often expressed as the idea that human agonistic behavior arose because man was a blood-thirsty hunter. Such a hypothesis does not fit the known facts about agonistic behavior and predation in mammals. Aside from the fact that the skeletons of our remote ancestors (Johanson & White, 1979) indicate that early man without tools would have been a very inefficient hunter, this hypothesis will not explain the existence of agonistic behavior in totally herbivorous animals such as sheep. Also, as Eibl-Eibesfeldt (1961) and Lorenz (1966) have pointed out, agonistic behavior in carnivores such as wolves takes very different forms from predation. Wolves rarely, if ever, attack a fellow wolf as if it were a prey animal.

As the diagram shows, there are at least three different functions of defensive behavior that could evolve into agonistic behavior. The most general and basic of these is that of attacking and driving away the apparent cause of any sensation of discomfort or pain. This has been classified by Moyer (1968 et seq.) as irritable aggression. On the left hand side of the diagram is the function of defense against conspecifics. This function can be elaborated in several different directions. One of these is the defense of living space around the animal and this could evolve into the defense of a particular area of ground, or defense of territory.
Defense against injury from conspecifics could evolve in at least three other directions: fighting over food, fighting for the exclusive possession of females and, finally, and perhaps most importantly from the human viewpoint, fighting used as a tool, or instrumental aggression in Moyer's terminology.

On the right hand side of the diagram is indicated the function of defense against predators. This can evolve into the defense of young or of other conspecifics and has been labelled parental or maternal aggression. As indicated in the diagram, the defense of young, while it has a definite social function, falls outside the limits of agonistic behavior. However, young can also be defended against conspecifics, and this is definitely agonistic behavior. The diagram provides a family tree of the ways in which the functions of agonistic behavior could have evolved from basic behavior patterns of defense. Applied to any given species, an animal may have evolved in several of these ways, or only one, or perhaps two or three. The function of agonistic behavior in a species can only be determined by observation and experiment on that particular species. From the viewpoint of evolutionary theory, the best we can do is to provide a hypothetical picture of how the existing agonistic behavior may have evolved. Such data as we have with respect to human agonistic behavior indicate that such behavior may have all the functions that are listed in the diagram, with particular emphasis on fighting as a tool, and irritable aggression. It does not follow that these functions have a purely biological basis in evolution, as culture and cultural evolution have major effects on human behavior, and much of what we see in humans may be simply a cultural elaboration of a basic capacity, which Scott suggests is the general capacity for defense against injury.

The Origin of Agonistic Behavior: Evidence

Our best evidence on this point comes from the distribution of agonistic behavior within the animal kingdom. If we look at its reported occurrence among the different phyla, it occurs commonly among vertebrate species, more sporadically among arthropods, and rarely among the annelids and cephalopod mollusks. There is little evidence that it occurs in other invertebrates. This may be explained by the fact that agonistic behavior, which has the potentiality of damaging other individuals, is adaptive only where other conspecifics can be recognized in some way, either as a class or as individuals. Thus, ants will not attack other ants that have the same colony odor, but will attack those from a different colony; and hens will respond differentially to each member of a flock. Most of the lower invertebrates either lack the sensory capacities to differentiate between other individuals or have a very low degree of social organization.

If we now consider the different classes of vertebrates, agonistic behavior occurs commonly in the fishes, reptiles, birds and mammals. It is less common in amphibia, which have neither teeth nor claws, and it has not yet been reported in the cyclostomes, which are a group of semi-parasitic fishes that show little if any social organization.

Among mammals agonistic behavior has been reported in both marsupials and placental mammals. Among the latter, it has been reported in all of the major orders. Its wide distribution suggests that agonistic behavior is a primitive ancestral characteristic among vertebrates and probably has been secondarily lost in those few species which do not show it.
Thus there is no need to hypothesize a unique origin for human agonistic behavior. Since it is generally found both in other mammals and other primates, we can assume that its origin was the same as that hypothesized for other animals; namely, that it was evolved from patterns of defensive behavior (Scott, 1981).

The Polysystemic Theory of Agonistic Behavior

The polysystemic theory of agonistic behavior (Scott, 1981) has its origin in multi-factorial theory which states that causal factors affecting agonistic behavior could be demonstrated on every level of organization from the genetic, physiological, organismic, societal, to the ecological. Abundant evidence has been accumulated to support this assumption. The multi-factorial theory, however, is deficient in that it does not provide for interaction between factors at different levels. Polysystemic theory, on the other hand, assumes that living phenomena are organized in nested systems and subsystems, each corresponding to a level of organization, all related to each other and showing interaction between systems at different levels. Such interactions are in many cases reciprocal (Scott, 1975; 1981).

According to Scott, evidence has been gradually accumulating that destructively violent agonistic behavior is largely the result of disaggregation of systems at any level of organization. Thus he considers destructively violent agonistic behavior to be a more or less pathological phenomenon.

There is a hierarchy of stability in systems, with genetic and physiological systems being the most stable, and social and ecological systems being less so. Consequently, disaggregation is most probable, and hence most important, in social and ecological systems.

According to Scott, differential reproduction (usually called selection) can be produced by factors originating from any level of organization, including the genetic level itself and extending up to ecosystems and the physical environment. Conversely, it is theoretically possible for selection to act on any level of organization, even that of ecosystems (Lewontin, 1970). The relative importance of selection at these different levels is an arguable point, depending on the particular kind of character that is affected, but there is no logical reason why such multi-level effects cannot occur.

Of particular importance to the evolution of agonistic behavior, Scott insists, is selection at the social level. Campbell (1975) has suggested that this is true of culturally based systems as well as biological ones; that selective survival of varying human cultural systems takes place. One obvious variable in such systems is the uses of and emphasis on agonistic behavior. Correlated with this, each social system exerts pressures on its component individuals that we may call social selection (Cf. the concept of ‘social spoliation or spoiling’: Van der Dennen, 1980). Systems theory thus implies that selection pressures are very complex, not only because of their numerous sources, but because the sources themselves interact. Further, complexity arises because cultural evolution and ecosystem change occur independently of genetic change. Consequently, selection pressures originating from these system levels are constantly being altered.

In conclusion, the effect of polysystemic theory is to render the genetic theory of evolution much more complex as it transforms an essentially reductionistic theory that implies one-way
causation from lower to higher levels into an interactive theory that assumes two-way causation between all levels.

Scott derives some important inferences from this polysystemic theory of evolution.

First, there are no ‘genes for’ particular characteristics. There is no gene for aggression. Instead, a gene can modify the expression of behavior in various ways, including its frequency, intensity, and so on. Second, gene action is always expressed as part of a genetic system, and the action of a particular gene varies with the system involved.

Furthermore, Scott asserts, the polysystemic theory rules out any hypothesis that assumes individual selection only.

Finally, agonistic behavior is primarily functional with respect to social systems and hence it should be most strongly affected by social selection pressures. For example, at the time when small, isolated human cultural groups were rapidly diverging from one another, different cultures should have selected different aspects of agonistic behavior, but today such differential selection is decreasing rather than increasing. In any case, effective selection always emphasizes survival and reproduction. There should always be, in either individuals or groups, selection against reckless bravery and death and in favor of cautious survival.

Contrast Scott's (somewhat eclectic) view with the contemporary perspective of evolutionary (or Darwinian) psychology (e.g., Wilson & Daly, 1985; Daly & Wilson, 1988; A.Campbell, 1995; Buss & Shackelford, 1997). "From the perspective of evolutionary psychology, human aggression is not a singular or unitary phenomenon. Rather, it represents a collection of strategies that are manifest under highly specific contextual conditions. The mechanisms underlying aggression have emerged, on this account, as solutions, albeit repugnant ones, to a host of distinct adaptive problems" (Buss & Shackelford, 1997) experienced during hominid/human evolution. As adaptive problems, for which aggression might have evolved as a solution, are identified: co-opting the resources of others (bullying, mugging, raiding); defending against attack (defensive aggression); inflicting costs on same-sex rivals (male-male and female-female aggression); negotiating status and power hierarchies (dominance-submission aggression); deterring rivals from future aggression; deterring mates from sexual infidelity (sexual jealousy); and reducing resources expended on genetically unrelated children.

The evolutionary psychology model suggests that aggression is highly context-specific, triggered only in contexts in which the specific adaptive problems are confronted and the adaptive benefits are likely to be reaped.

Adaptive problems must also be evaluated within the context of costs. Aggression, by definition, inflicts costs on others (humiliation, pain, injury or even death), and those others
cannot be expected to absorb the costs passively or with indifference: "Lethal retribution is an ancient and cross-culturally universal recourse for those subjected to abuse" (Daly & Wilson, 1988). Thus, one dimension of costs pertains to the ability and willingness of the victim to retaliate. Another context for costs pertains to the reputational consequences of aggression. Cultures and subcultures differ tremendously in whether aggression enhances or depresses status. In academic circles, physical aggression is shunned. Among male adolescent gangs and other 'cultures of honor', on the other hand, failure to aggress when insulted can lead to serious status loss. "The point is that an evolutionary psychological perspective predicts modularity and context-sensitivity, not the rigid invariant expression of aggression depicted in earlier instinct theories... From this perspective, variability in aggression - between the sexes, across individuals, over the lifespan, and across cultures - is predicted theoretically" (Buss & Shackelford, 1997).

**Escape vs. Submission**

Aggression does not, except at high intensities, disperse animals of the same species, but rather brings them together. This *prima facie* paradoxical proposition has been highlighted by Chance (1966).

In a variety of ways aggression is held in balance with flight tendencies and this balance is manifested during combat by ambivalent postures. The mating drive also brings animals together, and so, probably, does a tendency towards social investigation. These 3 drives modulate the approach tendencies (though they may themselves be in conflict with each other for control of the final common pathway), but above all, sociability depends on a sufficient availability of social submission. The complex of Submission, Investigation, Aggression and Mating can, for short, be called the SIAM-structure (Chance, 1966; Grant, 1963; Cf. the FAM-system: Morris, 1956; the 4-F's: MacLean, 1958).

If the term 'drive' is used to describe the internal state of the brain, uniquely responsible for the coordination and expression of behavior, let us use the term 'motivation' to designate the contribution each of the internal states of the brain makes towards channelling the responses into the known sequences. We can then see that some ambivalent postures can be the result of the interaction of 2 or more drives.

The built-in way of terminating combat by social submission enables the rat to set up a stable relationship with other male rats in a colony, without actually terminating its agonistic relationships. It is, in effect, always testing the suitability of their relationship to its own state and to that of others in the colony. The mating drive has long been recognized as holding individuals together, but we now see that aggression can do the same.

The act of submission allows a flight-motivated rat to remain close to its companion in an agonistic encounter. If the rat differs from the mouse in having a built-in submission posture, there is in addition to this a new twist to the escape pathway of baboons and macaques which turns them back towards a more dominant monkey and also makes them move towards it. Kummer (1957) has found this, especially in the female hamadryas baboon, and it is equally, if not more, characteristic of the males in the rank order of breeding male macaques. "It seeks out the highest ranking of the animals present, though this individual has himself been the cause of its fear". Kummer (1968) has worked out in detail how this escape behavior is
transferred. In addition, Harlow's evidence shows that young macaques regard their mother rather more as a refuge than as a source of food.

As the need for more persistent sociability increases, it is fulfilled not by increasing the strength of the approach drives but, in the first stage, by blocking escape by means of submission built into an agonistic social repertoire. Later, this is supplemented by turning back the residual escape towards the aggressor, and so converting a withdrawal tendency into an approach drive. This latter change, however, could not have been achieved without a submission posture first being provided for agonistic situations, since the reflected escape drive increases the frequency of agonistic situations (Chance, 1966). Despite the fact that the ultimate orientation of the subordinate animal is towards a more dominant male, the behavior of a subordinate animal which comes close to a more dominant one, under these orientating influences, shows evidence of conflict, such as displacement activities, ambivalent movements, and sometimes screeching behavior.

Even when a threat is directed at a subordinate animal by a more dominant one, the subordinate is under a compulsion to move towards the source of this threat. Little wonder, therefore, that in this situation of conflict, many stereotyped forms of behavior appear which have, in part at least, the function of temporarily preventing the animal from precipitating an open attack upon itself. In captive colonies where this relationship is intensified, and presumably, in any comparable situation in the wild, a large amount of time is occupied in such stereotyped activity, especially so-called ‘cut-off’ acts and postures (Chance, 1966).

The Phylogenetic and Ontogenetic Development of Fear Susceptibilities

If emotion is in some sense a breakdown of the thought process, Hebb & Thompson (1968) point out, it seemed that emotionality would become more marked when thought is more complex. The more elaborate the machinery the more ways its operation can be disturbed. It seemed therefore that development of a higher level of intelligence would mean an increased vulnerability to emotional disturbance. There were hints of an ontogenetic correlation of increased emotionality with intellectual development from infancy to maturity.

"Now we come to our problem: adult man should be still more emotional than the very emotional chimp and more emotional than the 3-year old child, and he does not seem to be. But certain aspects of man's social behavior were very suggestive when they were examined from this point of view, and led us to the conclusion that the predicted susceptibility exists, that it is a major influence on social evolution, and that it tends to produce societies such as ours in which it can hardly be detected. This view depends in part on the phylogenetic correlation" (Hebb & Thompson, 1968).

The are certain primitive causes of avoidance and aggression that seem to work equally well at all levels of mammalian development: pain stimuli, sudden loud noise, sudden loss of support, restriction of movement.

But as we go from rat to man there is a progressive increase in the range of effective stimuli to avoidance and aggression, and in the duration and complexity of the response. The period of emotional disturbance following a brief stimulation also increases from rat to dog to chimpanzee.
The phylogenetic development of fear susceptibilities is even clearer. As for man's nearest relatives, the apes, it would take a page or more to list the specific objects and situations that are known to have caused persistent fear in the chimp, as reported in the Yerkes Laboratories Diaries and in systematic experiments (Koehler, 1927; Yerkes & Yerkes, 1936; McCulloch & Haslerud, 1939; Hebb, 1946).

To this phylogenetic correlation may be added an ontogenetic one. In the observations with anesthetized animals as test objects, the frequency and degree of excitation aroused in the half-grown chimps was markedly less than in the full-grown. The clay model of a head hardly got a second glance from the one- and two-years olds; it absorbed the attention of the 5- and 6-years old but produced no avoidance; in most of the adults it produced strong fear, with some avoidance in all of them.

Jacobsen, Jacobsen & Yoshioka (1932) and McCulloch & Haslerud (1939) have described the increasing emotional responses of the chimp in the first years of life. Jersild & Holmes (1935) have shown a similar increase in children up to the age of five; they conclude that the trend is thereafter reversed, but Hebb & Thompson (1968) try to show that this may indicate, not a reduction of emotional susceptibility after five years, but the success of our society in protecting us from most of the situations that would produce fear in older children and adults. The capacity for emotional breakdown may, in fact be self-concealing, leading the animal to find or create an environment in which the stimuli to excessive emotions are at a minimum. So effective is our society in this respect that its members - especially the well-to-do and educated ones - may not even guess at some of their own potentialities.

There must be doubt concerning any treatment of emotion as a state or process independent of intellectual processes, and having a separate seat in the nervous system. Brainstem theories of emotion, as developed originally by Hebb and by Cannon & Bard or more recently by Lindsey do not seem to give enough weight to the evident cortical elements in the fears and angers of the higher animals, as well as in the correlation with intellectual level that has just been discussed (Hebb & Thompson, 1968).

Timidity and Aggression

There is evidence that timidity, as such, may incite aggression. Hebb & Thompson (1968) report the results of their 'Bold and Timid Man' experiment performed with chimpanzees. Both roles were played by the same person. A significant result was the high frequency of aggression and quasi-aggression (a combined category of intimidating and nuisance behavior) to the timid man, and especially the frequency of behavior which enticed an innocent close just to scare the hell out of him. Many animals found the temptation irresistible, only 9 out of 30 failed to show such behavior. To my knowledge, there are no equivalent experiments performed with humans, but I would suspect that the proposition that timidity may incite aggression is also valid for humans, especially children. The observations by Olweus (1978) on the victims of bullying in Swedish schools may be pertinent in this respect.

The Conflict- or Ambivalence Hypothesis

The conflict- or ambivalence hypothesis states - somewhat oversimplified - that agonistic and related behaviors are the product of activation of, and interactions between, two major
antagonistic ‘drives’ or ‘tendencies’: the attack- or approach-tendency and escape- or withdrawal-tendency. Many courting behaviors may similarly be considered as the product of activation and interactions of 3 tendencies, viz. the attack-, escape-, and sex-tendency (See e.g. Tinbergen, 1952; Baerends, Brouwer & Waterbolk, 1955; Kruijt, 1964; Hinde, 1966; Baerends, 1975).

‘Approach’ and ‘withdrawal’ behaviors may shade off into one another through intermediate -compromise - types of response, depending upon the balance between the attack- and escape-tendency. Such compromise movements or postures are often postulated to be the evolutionary origin of a communicative signal or display.

If the basic tendencies are highly activated, the antagonist behavior types tend to change in a more sudden and dramatic way than if they are moderately activated. In the former case attack may suddenly change into escape and escape may suddenly (catastrophically) change into attack.

This state of affairs may graphically be represented and mathematically be described with the aid of the bi-stable models from the mathematical branch of catastrophe theory as presented by e.g. Thom & Zeeman (1974) and Zeeman (1976) (Vide infra). This model of agonistic behavior, however, accounts only for short-term changes in mood and behavior. No predictions are implied that reach beyond the particular agonistic setting under scope. The catharsis hypothesis, on the other hand, is primarily concerned with long-term prediction.

The Psychohydraulic Model: The Catharsis Hypothesis

The catharsis hypothesis, when applied to aggression (Lorenz, 1950; 1963; Leyhausen, 1967; Eibl-Eibesfeldt, 1975), states that the longer an individual has not shown aggressive behavior, the easier aggressive behavior is evoked by external stimuli. Eventually the aggression-deprived individual will even start to seek opportunities to direct his aggressive behavior towards something or other and thus release his internally stored reservoir of ‘aggressive energy', ultimately to the point of releasing it in vacuo. This process can be visualized through what has been called the ‘psychohydraulic model’, or, less respectfully, the toilet flush model.

Whereas this model may be quite adequate for describing some other functions like, for example, male sexual tendencies or feeding behavior, its use for describing aggressive behavior has become somewhat obsolete (Hinde, 1960; 1966; Manning, 1969; van Dijk, 1977; Zillmann, 1979; Van der Dennen, 1980; van der Molen, 1981), mainly because little evidence has been found in support of the hypothesis that long-term deprivation of an opportunity to fight causes an increase in the readiness with which fighting can specifically be elicited. Yet appetitive behavior for agonistic interaction can nonetheless be demonstrated in a wide range of species, from fish to monkeys.

But in every case investigated, such alleged appetite for aggressive behavior could equally well be labelled as appetite for certain other functional patterns such as e.g. territorial behavior and/or as attempts of the individual to maintain an optimum level of arousal.

"Excitement and kinetic activity are shown to be dependent on the external stimulus state of the animal, decreasing under conditions of low mean environmental stimulation. These
findings indicate that an animal attempts to regulate its internal stimulus state by behavioural means when the component variables of this state have been disturbed by environmental conditions" (Rasa, 1971).

Sevenster (pers. comm. in Van der Molen & Van der Dennen, 1981) arrived at similar conclusions in his experiments with sticklebacks, when evaluating his results on the rewarding effect of opportunities to interact aggressively. He investigated the rewarding properties of each component of the situation of agonistic interaction separately, and concluded that it is, in particular, the element of environmental change which works rewarding for the (somewhat arousal-deprived) male stickleback, but only so, if the environmental change induces no flight behavior. Parallel to these findings are experimental results such as those of Kavenau (1967), who showed poignantly how mice, being forced to respond in stereotyped experimental situations, will give 'incorrect' responses as a means of introducing variability. From all these considerations we may conclude that for understanding function and (long-term) causation of aggressive behavior, it is apparently of great importance to include phenomena such as ‘boredom’, ‘excitement-seeking’, and ‘anxiety' in our models.

Specific appetite for aggressive behavior may in fact not exist at all in ordinary natural settings in which plenty of opportunity is available for attaining proper arousal levels. This is also suggested by, for instance, Goodall's (1971) descriptions of the occurrence of aggressive episodes in the daily life of free-living chimpanzees. The frequency of intraspecific aggressive behavior varies strongly for every individual and for the whole group in question, and is highest whenever hierarchical relations have become unclear. The readiness to show intraspecific aggressive behavior does not seem to depend at all on the period of time that has elapsed since the last agonistic confrontation, but rather on circumstances which make it difficult to avoid the application of coercive means.

It would appear that the regularity with which the males of certain species carry out charging displays can be more adequately explained by the ‘hierarchico-cybernetic' model with the aggression-system as a low-level subroutine, than by an energy model of aggressive motivation.

The existence of a drive for aggression, irrespective of a functional context, would, in fact, be highly improbable from an evolutionary point of view, the rationale of which has been analyzed in game-theoretical and Evolutionary Stable Strategy terms. An individual runs heavy risks every time he engages in aggressive encounters. Therefore it seems good strategy to reserve aggressive behavior for situations in which the risk of damage is sufficiently counterbalanced by a possible raise in the chances of survival and/or propagation of the specific genetic information in question, after successful agonistic action.