20

Implications of Sexual Selection for Variation in Human Personality and Behavior

John S. Price

Darwin made it clear that natural selection is based on differential ability to deal with the physical environment, including predator and prey relations with other species, but at the same time he recognized that selection occurs as a result of interactions with members of the same species. In *On the Origin of Species* he wrote, ''This form is selection depends not on a struggle for existence in relation to other organic beings or the external conditions, but on the struggle between individuals of one sex, generally the males, for the possession of the other sex'' (Darwin 1859, p. 69).

In 1871 Darwin published *The Descent of Man, and Selection in Relation to Sex*, which was devoted to a meticulous analysis of sexual selection. In this book he introduced the term ''sexual selection'' for the first time, and he pointed out that it has two components:

> Sexual selection depends on the success of certain individuals over others of the same sex, in relation to the propagation of the species; whilst natural selection depends on the success of both sexes, at all ages, in relation to the general conditions of life. The sexual struggle is of two kinds; in the one it is between individuals of one sex, generally the male, in order to drive away or kill their rivals, the female remaining passive; whilst in the other, the struggle is likewise between the individuals of the same sex, in order to excite or charm those of the opposite sex, generally the females, which no longer remain passive but select more agreeable partners. This latter kind of selection is closely analogous to that which man unintentionally, yet effectually, brings to bear on his domesticated productions, when he preserves during a long period the most pleasing or useful individuals, without any wish to modify the breed. (1871, p. 916)

Darwin used the theory of sexual selection to explain the evolution of bizarre male adornments such as the tail of the peacock and the antlers of the stag. He pointed out that sexual selection and natural selection tend to operate in different directions, so that the characters that make for success in sexual selection may make it more difficult for a bird, say, to fly in search of food, and they may also make it more conspicuous to predators. On the other hand, the two types of selection may work in the same direction, as when an individual who is good at getting food and therefore is well nourished may be more able to compete with members of the same sex and be more attractive to members of the opposite sex. Those animals who are successful in social competition may obtain large territories and therefore be less susceptible to starvation, predation, and disease; in such cases a positive feedback cycle operates between natural selection and sexual selection.

These observations of Darwin raise some important questions about human social life, for instance:

1. How much of human differential reproduction can be accounted for by sexual selection?
2. What are the criteria for selection? In other words, what is the human equivalent of the stag's antlers and the peacock's tail?
3. How can we classify the criteria for sexual selection into physical and psychological?
4. What is the nature of the social process by which the selection is made?
5. What is the fate (or social role) of those who are not selected?

It is the last question in which I as a psychiatrist am most interested, but since the answer depends to some extent on the previous question about the nature of the selection process, I should devote some time to that issue.

PROCESSES OF SEXUAL SELECTION

Darwin recognized two types of sexual selection, which came to be known as *intrasexual selection*, in which the members of the same sex compete together for access to the other sex, and *intersexual selection*, in which members of one sex choose members of the opposite sex as partners in mating (Ryan, 1985; Bradbury & Davies, 1987; Andersson, 1994). In some species these processes are not entirely separate, as when a female sheep encourages two rams to fight and then mates with the winner (Geist, 1971). Those structures that are attractive to members of the opposite sex are sometimes intimidating to members of the same sex. The term "intersexual selection" has been criticized with some justification by Cronin (1991), who prefers "epigamic selection" or "mate choice."

INTRASEXUAL SELECTION

The evolution of human social life can be seen as the evolution of ever more sophisticated and effective methods of sexual selection, and it might be helpful to enumerate some of the possible stages, concentrating mainly on the intrasexual component of sexual selection.

Unritualized Social Competition

Many insects kill members of the same sex, some worms plug each other's sexual orifices, some beetles spray each other with antiaphrodisiac gas, and various forms of sperm competition are practiced by different species; this category includes any action to reduce the other's viability or fertility over which the victim has no role in "consenting." Possibly the suppression of sexual development by pheromones in some rodents and New World monkeys comes into this category. Otherwise, it does not occur in vertebrates.

Ritual Agonistic Behavior

In ritual agonistic behavior the loser, being unharmed, must consent to lose. He has the option (at an unconscious level) of not consenting and can be said to choose between a consenting strategy (in which he submits or flees) and a nonconsenting strategy (in which he retaliates).

In evolutionary terms, ritual agonistic behavior seems to be performing two rather separate functions. To the extent that it takes the form of intergenerational conflict, it serves to delay reproduction until later in the life span. To the extent that it is intergenerational conflict, it serves to create lifelong variation in social status and hence in fertility within a socially interacting cohort of conspecifics. It is this second function that subserves intrasexual selection and that concerns us here.

According to the simplest view, each individual has to choose between two strategies, a dominant strategy in which he reproduces more and a subordinate strategy in which he reproduces less. The dominant strategy is designed to maximize his own reproduction; the subordinate strategy is designed to "make the best of a bad job" in terms of his own reproduction, to avoid the mortality that dominant strategists inflict on each other, and to maximize the reproduction of his close kin (and raise the kin-selection component of inclusive fitness). For individuals in this system, the overall strategy is similar to Maynard Smith's (1982) "assessor" strategy; on at least one occasion in their ontogeny they have to assess their chances and choose between the dominant or "hawk" substrategy, on the one hand, and the subordinate or "dove" substrategy, on the other.

How do they make this choice? There are a number of possibilities that have not in fact evolved. They could leave it entirely to the opposite sex and adopt the strategy "If chosen as a mate, adopt dominant strategy; if not cho-

sen, adopt subordinate strategy,'' thus relying entirely on the intersexual component of sexual selection and eliminating the intrasexual component. Or they could do it by counting heads, such as, ''If the home/nest contains more than *x* individuals when you reach age *y*, adopt subordinate strategy; otherwise, adopt dominant strategy.'' What has in fact evolved is a form of social comparison that bears a certain resemblance to coconsultation. We can imagine a primitive vertebrate scratching its head and wondering whether to adopt a dominant or subordinate strategy, so it chooses a consultant and says, please help me make up my mind. The consultant says, use me as a yardstick. If you find yourself superior to me, your chances are good and you should adopt the dominant strategy; otherwise, you should play safe and adopt the subordinate strategy. The consultation takes the form of a fight in which our indecisive individual uses the strength of the consultant as a yardstick to estimate his own strength, and after the consultation he either says to himself, ''I am a strong person,'' and adopts a dominant strategy, or ''I am a weak person,'' and adopts a subordinate strategy. Of course, the interaction is symmetrical and the ''consultant'' is making a similar decision (it is a coconsultation). This could be called *dyadic comparison* because, in each comparative episode, each individual compares himself with one other. It is the main form of vertebrate social comparison and is called ritual agonistic behavior.

Group living provides the opportunity for more sophisticated social comparison, and probably the selection mediated by ritual agonistic behavior in groups is more effective than that in territorial species. The opportunities for effective comparison in a single fight are limited, but if animals live in groups, they have extended time in which to evaluate each other's strengths. Fights can follow a long period of mutual assessment, can be protracted, and can be divided into bouts. As a result, the rank order in a group should reflect small differences in strength, skill, intelligence, and courage. Ritual agonistic behavior amplifies these small differences into gross social disparity.

External Mediation of Intrasexual Selection

In human evolution there has been a major change in ranking behavior. Instead of two rivals A and B fighting it out between themselves, the choice between A and B is made by C, D, E, and others. This is the change that Gilbert, Price, and Allan (1995) drew attention to as important in evolution. In order to achieve greater social success than B, A has to make himself attractive to C, D, and E rather than make himself intimidating to B. Selection is now by external judges rather than by interaction between the rivals themselves. The scope for greater efficiency of selection and for cultural variation in the criteria of selection opens up an entirely new ''ball game'' of the sexual selection process. In fact, this development must have been about as important as the development of sexual selection itself. To distinguish it from the dyadic comparison that occurs in ritual agonistic behavior, the evaluation of A and B by C, D, E, and others

could be called *polyadic comparison*. Of course, it is seldom as simple as that, and in most cases everyone is evaluating everyone else. In the same way that a person "cannot not communicate," he or she cannot not evaluate or be evaluated.

Does this kind of sexual selection occur in animals as well as man? In macaques, baboons, and chimpanzees the outcome of ritual agonistic behavior is affected by alliances with same-sex conspecifics, so that the capacity for alliance formation is being selected as well as fighting ability. The choice between two potential allies offers a primordium of polyadic comparison, in that the criterion of choice is not so much "Does he intimidate me?" as "Is he likely to intimidate the other fellow (and, if so, is he likely to favor me)?"; this is still some way from "Which of the two is more attractive?" but it is a major advance from the evaluation of others entirely in terms of dyadic comparison. In chimpanzees, in addition, the influence of female group members affects the rank order in males, and this is a further step toward intrasexual polyadic comparison; in fact, it is similar to the situation reported to occur in at least one tribe of American Indians in which only males are allowed to run for office and only females are allowed to vote.

In human society polyadic comparison has been enormously increased in importance, particularly due to language and the opportunity this gives for the comparers to discuss those being compared and to make a careful allocation of prestige; it also gives the group members the opportunity to discuss the criteria for the allocation of prestige. But it has not replaced the other forms of social competition, and so we see them operating side by side.

THE FATE OF SEXUAL SELECTION'S UNSELECTED AND DESELECTED: MILTON FILLS IN FOR DARWIN

Darwin wrote little about the fate of those unselected by sexual selection or about those who became deselected after once being selected. He spoke of them being killed or driven away, but he does not appear to have speculated on the behavior of those who were driven away. He did not recognize the need for a behavioral strategy to deal with this group, or any psychological or emotional state that might pertain to them. In particular, he did not consider them as a special case in his book on the expression of the emotions (1872).

It is ironic to note, therefore, that his favorite poet, John Milton, who had been at the same Cambridge college 200 years previously, and a copy of whose *Paradise Lost* Darwin took with him on his voyage in the *Beagle*, was at least interested in and one might almost say obsessed by the fate of those who were "driven away." In two of his major poems, *Paradise Lost* and *Samson Agonistes*, he examines the situation of someone who is defeated by overwhelming force.

In *Paradise Lost* the rebel angel Satan, together with Beelzebub and his other followers, has been cast out of heaven because he challenged God, who

> Hurled [them] headlong flaming from the'ethereal sky,
> With hideous ruin and combustion, down
> To bottomless perdition, there to dwell
> In adamantine chains and penal fire.
>
> (Gilfillan, 1853, vol. 1, p. 5, ll. 6–9)

The action of the poem opens as they regroup themselves in Hell and consider their options. There is no hint of remorse or submission in the mind of Satan, who mixes his ''deep despair'' with ''obdurate pride and steadfast hate.'' Reconciliation with his victor is rejected:

> What though the field be lost?
> All is not lost; th'unconquerable will,
> And study of revenge, immortal hate
> And courage never to submit or yield
> And, what is else, not to be overcome;
> That glory never shall his wrath or might
> Extort from me: to bow and sue for grace
> With suppliant knee, and deify his power.
>
> (Gilfillan, 1853, vol. 1, p. 6, l. 32, p. 7, l. 6)

Tauntingly, he asks his followers if they have ''sworn to adore the conqueror.'' Even though his first lieutenant, Beelzebub, points out tactfully on two occasions that God must be omnipotent to have defeated the rebel army, Satan determines to fight on with ''force and guile,'' determined that it is ''better to reign in hell, than serve in heav'n'' (Gilfillan, 1853, vol. 1, p. 11, l. 25).

In *Samson Agonistes*, Samson, betrayed by Dalilah, blinded and imprisoned by the followers of the god Dagon, is visited by his father, who is planning to arrange a ransom and who tells him to keep on fighting. But Samson rejects this advice and expresses his depressive position:

> So much I feel my genial spirits droop,
> My hopes all flat, nature within me seems
> In all her functions weary of herself,
> My race of glory run, and race of shame,
> And I shall shortly be with them that rest.
>
> (Gilfillan, 1853, vol. 2, p. 91, ll. 27–31)

Samson's father then tells him to be calm and to accept healing words from his friends, but Samson does not follow this advice; he expresses the idea that his mental torment is even worse than his physical torment, and he contemplates the idea of suicide:

> Sleep hath forsook and given me o'er
> To death's benumbing opium as my only cure:

> Thence faintings, swoonings of despair,
> And sense of heav'n's desertion.
>
> (Gilfillan, 1853, vol. 2, p. 92, ll. 28–31)

Then Samson's father leaves, and he is visited by Harapha, a champion of the Philistines who was not involved in the previous battles with Samson. Here Samson is roused out of his depression and challenges Harapha, finally dismissing him with the words

> Go, baffled coward, lest I run upon thee,
> Though in these chains, bulk without spirit vast,
> And with one buffet lay thy structure low,
> Or swing thee in the air, then dash thee down
> To the hazard of thy brains and shatter'd sides.
>
> (Gilfillan, 1853, vol. 2, p. 111, ll. 2–6)

The chorus then counsels Samson to patience. But patience, acceptance, and reconciliation are not a part of Samson's reaction to defeat, and the poem concludes with his splendid act of vengeance in which he destroys both himself and his conquerors.

In both these poems Milton is exercised about the reaction of the man who is defeated and cast down. Does he fight back in spite of his depression and his chains? Or does he accept his lot, in the one case to accept the advice of Beelzebub that his opponent is omnipotent, and in the other to accept the advice of the chorus to be patient? In both poems Milton portrays a fallen hero who is chained and in deep despair, but in both cases the despair does not inhibit pride or the determination to retaliate. He is portraying a society that does not admit voluntary submission and reconciliation.

The message seems to be that the ancient way of man, illustrated in the tales of gods and heroes, is one of unmitigated fighting and retaliation—the only way to keep a defeated enemy down is to bind him in adamantine chains, and if, as in the case of Satan, this is not enough, to "transfix him with linked thunderbolts to the bottom of the gulf." The new way, characterized by Christianity, is one of forgiveness, repentance, voluntary submission, and reconciliation. Only briefly, in the case of Samson, does Milton consider that the aggression of a defeated champion may be inhibited by a depressed mood.

SEXUAL SELECTION AND PERSONALITY VARIATION

Intrasexual selection is mediated by agonistic behavior in most vertebrates, and the result of agonistic behavior is social asymmetry, which takes the form of owner/nonowner in territorial species and high/low social rank in group-living species. These asymmetries are associated with conditional behavioral strategies that we have called the high– and low–self-esteem strategies, because at the

intrapsychic level the role of owner or high-ranking person is associated with high self-esteem, whereas the role of nonowner or low-ranking person is associated with low self-esteem (Price, Sloman, Gardner, Gilbert, & Rohde, 1994). This variation probably accounts for much of the variation in what has been called upperness/lowerness, or the vertical dimension of two-dimensional personality space (the other dimension being closeness/distance) (Birtchnell, 1993).

SEXUAL SELECTION AND MENTAL ILLNESS

When someone has been selected and has enjoyed the privileges of ownership and high rank, the change to the role of being deselected is likely to be a drastic one and to result in a major change in behavior. This, we think, is what we observe in depressive illness (Price et al., 1994).

Biologists, on the whole, do not share Milton's preoccupation with the underdog. One might almost suspect that researchers are obeying an innate human instruction to "attend to the winner." An exception is a comment by Welch (1967) that may be the earliest suggestion that human depression might be related to social subordination. It occurs in the discussion following a paper on dolphins by Bartholomew. Welch says: "Some animals are pushed aside, prohibited from participation. . . . Because social hierarchies exist, this happens to some extent in all societies. Some animals, usually the dominants, do very well both behaviorally and physiologically, while some, usually the subordinates, do very poorly. Whether the differences are maintained by physical contact and actual expressions of physical aggression, or whether they are maintained and reinforced simply by ritualised behavioral signals, the subordinate animals do, in fact, appear to recognise when they have been reaffirmed in their status. . . . This emphasises in a very real way the dictation, by social pressure, of different states of being: the state of being in a position of subordination, or in a position of dominance, and the various gradations in between." He then discusses the physiological abnormalities that occur in subordinates, including the fact that they are "psychologically sterilised, although not physically abused," and adds, "Might not the depressive psychotics in our human population—particularly abundant at very high population densities and characterised by high activation of sympathetico-pituitary-adrenocortical activities—produced by extreme social environments and reinforced in social subordination, be analogous to them?" (pp. 239–240).

In fact, the Norwegian zoologist who first discovered animal social hierarchies commented on the "depressed" behavior of low-ranking birds, particularly those who had lost former high rank (Schjelderup-Ebbe, 1935); the fact that Schjelderup-Ebbe made this discovery while still a schoolboy may reflect the fact that hierarchies are much more visible to low-ranking than to high-ranking people. Abraham Maslow, one of the earliest scientists to work with monkey hierarchies, reported that a subordinate rhesus monkey was more like another subordinate monkey than like himself when dominant, and it is probably no

coincidence that Maslow went on to study the self-esteem of American women and discovered the enormous variation in self-esteem that occurs from one woman to another (Maslow, 1937). Depressive behavior has been reported not only in low-ranking birds and monkeys, but also in low-ranking reptiles and in birds of territorial species who have failed to obtain territories (references are given in Price et al., 1994). In the laboratory, social defeat produces depressive behavior and lasting physiological changes such as increased secretion of corticosteroids, which is also seen in depressed patients (Price, 1995).

SOME CONSEQUENCES OF POLYADIC COMPARISON

I think that it would be difficult to overestimate the importance of the switch from dyadic to polyadic sexual selection. For the first time in evolution, selection can be determined by cultural factors, which can themselves be the subject of selection. The criteria of selection, being determined by culture, can allow for the selection of characters that were previously unselectable. The switch to polyadic selection alters the mathematics that have been applied to the evolution of altruism, the detection of free riders, and the possibility of selection at the between-group level. We should note that the switch to polyadic selection applies also to epigamic selection in that in most human societies mates are chosen at least partly by the parental generation rather than by the mating dyad, and many parents know to their cost that the criteria used by the two generations are not the same. The evolution of polyadic comparison and its coexistence in human societies with dyadic comparison have other consequences, some of which I will now discuss.

Proscription of Agonistic Behavior by Society

Groups practicing polyadic comparison would have an enormous advantage over groups still limited to dyadic comparison (agonistic behavior). Culturally they would be at an advantage because their leaders would have those characteristics that are the criteria for the allocation of prestige, and in most human groups these appear to be a combination of competence and dedication to the interests of the group. Groups with such leaders should outperform groups whose leaders were selected for power to intimidate. Genetically, the polyadic groups would tend to have more members with qualities of competence and unselfishness because there is a correlation in most human groups between prestige and reproduction (Perusse, 1993); therefore we have probably experienced a gene/culture coevolution for competence and group loyalty.

Among those groups practicing polyadic comparison, there would be an advantage to those groups in whom selection was entirely by polyadic comparison, and therefore there would be an advantage in preventing agonistic behavior as much as possible. Thus we can expect ritual agonistic behavior to be proscribed by groups, both in their childrearing practices and in their code of behavior for

adults. In childhood there is an enormous parental influence toward nonintimidating behavior; see, for instance, the life histories described by Vaillant in his *Adaptation to Life* (1977), in which a cohort of American college men report severe sanctions on aggressive behavior during their childhoods. The proximate reason for parents stopping their children from quarrelling may well be that they find the noise irksome, or that they consider it bad manners, or that they think that the children should spend the time improving themselves in some way; but the ultimate, evolutionary reason may be that they want to decide the children's rank order themselves by the giving and withholding of praise and criticism, and so they do not want the rank order decided by the children themselves in the course of quarrelling (ritual agonistic behavior). Also, they want to develop in their children the mentality that looks for self-esteem in the form of praise rather than in the form of the submission of others, so that when they leave home they will still be oriented toward polyadic comparison. The widespread existence of bullying in school playgrounds (Rivers & Smith, 1994) might seem to gainsay this thesis, but it is probably due to the fact that there were no schools in our "environment of evolutionary adaptedness." Glantz and Pearce (1989) have pointed out that in hunter-gatherer societies children are always with adults who prevent bullying.

In adult life, fighting between same-sex adults is also proscribed. Duelling was forbidden by monarchs, not because of the fear of loss of life (which was slight), but because the king wanted prestige to go to people he approved of rather than to those who were skilled with the sword or pistol. What dyadic competition is allowed between adults is governed by society's rules rather than by nature's. Fine differences in ability can be assessed by pitting individuals against each other in sport and in intellectual tests, but these are polyadically controlled dyadic comparisons. Prestige is allocated not only for performance but also for sportsmanship, and bad marks are allocated to those who are seen to cheat or who do not accept the decision of the referee.

Because of this proscription, ritual agonistic behavior is only seen in situations over which society has little control: in prisons, on street corners, in the school playground, in the family, and in situations in which master and servant are alone together. Also, society does not proscribe ritual agonistic behavior in marriage; in fact, sayings abound to the effect of "Never interfere between husband and wife." This may well be because the rank order within marriage does not affect the rank order in the group as a whole, and therefore it affects neither the choice of leaders nor the correlation between prestige and reproduction. This leaves us with the paradoxical situation that agonistic behavior, which evolved to subserve competition between males, is now mainly seen to occur between male and female in their roles as husband and wife.

Societal prohibition of agonistic behavior complicates the study of human aggression and anger. He (or she) who fights has two adversaries, one being the opponent, the other being society as a whole. It is often difficult to tell whether the expression of anger has been inhibited because of intimidation by the op-

ponent or because of obedience to an internalized social norm forbidding angry expression.

Development of a Latency Period

Students of baboon social life have pointed out that the brief period of immaturity before the adolescents join the adult dominance hierarchy is a time in which they evaluate each other, and each group of peers has worked out its rank order by the time the canine teeth have developed. The human latency period allows a much-extended time of mutual evaluation by the peer group. It also allows the previous generation to play an important part in the evaluation, and of course in human life we see a whole professional class of evaluators ranking our adolescents according to adult standards. Therefore, whereas the accepted function of the latency period is to allow more learning, we can add the additional function of allowing ranking according to ability to learn and according to other prosocial attributes manifested during development.

Religion and War as Projective Tests

Society wants individuals who are assertive and capable and yet have the capacity for submission of their individual goals to those of the group. The induction of children into religious practices allows an evaluation of this capacity for submission and also provides a test of memorizing capacity by requiring the child to learn scripture and ritual.

The wars of primitive man are ritualized, and the death rate is low. There is much observation of individual fighting attributes. In this way society can allocate prestige to those who will risk their lives for the sake of the group. This is a possible explanation for the universality of religion and war in human groups: those groups that lacked these aids to polyadic comparison did not survive.

Why People Are Nice

On the whole, society allocates prestige to people who are nice. ''Nice'' means that they are decent, honest, reasonable, cooperative people who put the good of the group before their own selfish interests; they are also likeable and interested in their fellow human beings. Thanks to polyadic comparison, human groups have been selecting for niceness for millions of years, and we have become very good at it. Therefore, we have to some extent overcome the legacy of dyadic comparison, which is to select for intimidating, selfish bullies. The genes may be selfish, but the people are unselfish, and it is the people we have to interact with, not the genes. I think that in this sense the message of evolutionary biology is an encouraging one. We are nice because, for a very long time, we have selected each other to be nice.

ALTERNATIVE SUBORDINATE STRATEGIES

The subordinate strategy has two components. The first is the decision to be subordinate, and this decision is taken in negotiation with one or more fellow group members, as described earlier. The second component is the decision as to how to conduct oneself as a subordinate. There are a number of choices, depending on the ecology of the species. A major issue is whether to remain close to, or avoid, the dominants, and there is variation here both between and within species (Price, 1995). Some animals make a virtue of the fact that they do not have the responsibility of defending a territory through what may be a hard and even lethal winter, so the low–self-esteem individuals who have lost out in the battle for territories do something entirely different, such as migrating to a warmer climate or going into a state of hibernation, and often when they come back, they find the territory owners dead. The variation between strategies in these partially migrating and partially hibernating species is maintained by negative frequency-dependent selection.

The human problem of how to conduct oneself as a subordinate is the subject matter of much of philosophy and religion. These disciplines usually counsel patience and self-abnegation, as did the chorus to Samson. But there is another way, which was taken by both Satan and Samson and appears also to have been taken by Milton and Darwin.

MILTON AND DARWIN AS NONYIELDING REBELS

In order to understand human subordination, it is necessary to appreciate that a decision between the dominant and subordinate strategies is taken relatively independently at two levels of the human brain (Stevens & Price, 1996). There is a lower, reptilian level (MacLean, 1990) at which there is a decision to provide or withdraw the basic materials needed for fighting; here, the dominant strategy takes the form of an elevation of mood, giving energy, optimism, and sense of ownership, while the subordinate strategy of depression takes away these armaments, leaving the individual tired, pessimistic, and with no sense of entitlement. At a higher level, in the neomammalian brain, another type of decision is made, and this is conscious, rational, voluntary, and deliberative and takes the form of deciding whether to give in or fight on. Even the individual who suffers the incapacity and torment of depression (metaphorically expressed by Milton as ''adamantine chains and penal fire'') can fight on by an act of will, even though willpower itself is sapped by the depression.

Milton rebelled against the state (he was the principal Roundhead pamphleteer, attacking the monarchists) and lost; Darwin rebelled against the church (the doctrine of the Creation), and although he did not actually lose, his diaries and letters reveal his constant anticipation of losing, as a result of which he withdrew from the London arena and delayed publication of his theory for twenty years, suffering almost constant nervous symptoms. In spite of their real and imagined

defeats, they both fought on, Milton writing pamphlets and poetry, Darwin elaborating his theory of natural selection. Their heads were "bloody but unbowed." Acts of submission at the higher, neomammalian level would have preempted or relieved their suffering, but their resources of ambition, pride, and courage enabled them both to bend their adamantine chains and to make their unique contributions to the human record. It is this triumph of the will over the flesh that Milton celebrates in the first books of *Paradise Lost*.

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