REVIEW

On the current state of altruism: generosity in the eyes of natural selection from Darwin to today

Emanuele Coco

Abstract   The conference organized by the Lincei for the bicentenary of Darwin's birth offers the opportunity to investigate one of the key questions of evolutionism today: can *genuine evolution* keep itself stable in a population subject to natural selection? Four cycles of unpublished lessons edited by William Donald Hamilton during the period between 1965 and 1975 and recently found by Coco (Les leçons inédites de W. D. Hamilton, Du problème de l'altruisme à l'application des modèles mathématiques. Mémoire de DEA en "Histoire et Civilisation". Paris, 2003) at the British Library, London, offer the possibility to trace a framework of the theoretical positions of the founder of *inclusive fitness* and contest some interpretations of his thought that have been put forward in recent times by Sober and Wilson (Unto others: the evolution and psychology of unselfish behavior. Harvard University Press, Cambridge, MA, 1998b). An in-depth article regarding these matters is currently being written and will be published in this journal. In this study, I have proposed a critical framework of the problem of altruism from J. S. B. Haldane to our days, using Hamilton's unedited writings, edited literature and a certain heuristic use of Shakespearean characters, paradigmatic interpretations of the human condition, as already partially proposed in a book that came out this year in Italian (Coco in Egoisti, malvagi e generosi Storia naturale dell'altruismo. Bruno Mondadori, Milano, 2008).

Keywords   Altruism · Gene · Culture · William D. Hamilton · William Shakespeare

E. Coco (✉)
Università di Catania, Catania, Italy
e-mail: emanuele.coco@unict.it

E. Coco
Ecole des Hautes Etudes en Science Sociales, Paris, France

1 Altruism and nature: themes of Shakespearian drama

Listen to Macbeth: "Tears shall drown the wind. I have no spur/To prick the sides of my intent, but only/Vaulting ambition which o'erleaps itself/And falls on th'other" (Shakespeare 1947c, act I, scene VII).

In one of his *Lessons on Shakespeare*, the poet W. H. Auden said that tragic heroes like Macbeth and Iago suffer from "the Christian sting of pride: although they know they are not God, they try to become God—a temptation from which no-one is immune" (Auden 2000).

What can we say then about this presumed attempt to be God that seems to snatch us from every democratic principle and make us feel smug about presiding over others? The question could take on even more specific tones: what determines our social behavior? Is there such a thing as a natural foundation of moral attitudes? And if there is, what evolutionist laws determine them, change them and preserve them over time?

In the framework of biological theories that have tackled the problem of social behavior, both in man and in animals, two elements can offer today the opportunity for a new critical reflection on the heterogeneous positions that have emerged over time: the first is a return to the sources and in particular, to the unedited lessons of William Donald Hamilton, the young English man who took up the ideas of the founders of the *genetics of population of mathematical inspiration* and identified an interpretative key to resolve the paradoxical elements that altruistic traits of social behavior present in the light of Darwin's theory of natural selection (Hamilton 1963, 1964); the second element is offered by the contrast that some characters of Shakespeare's plays can provide to the complexity of the evolutionist theories: the fact that they do not fully respect Darwinian principles allows us to reveal the different capacity which living organisms have to "negotiate" with natural selection regarding their own relationship.

Let's open the discussion therefore returning to Macbeth. He is there on the scene. Invited to represent the human condition, he—thane of Cawdor and Glamis—is sincerely welcomed by the king, his cousin Duncan: "Oh worthiest cousin! The sin of my ingratitude even now/Was heavy on me: thou art so far before/That swiftest wing of recompense is slow/To overtake thee" (I, IV).

The king is optimistic. He knows he can count on Macbeth. He constantly pays him attention: he makes sure that he is among the guests at his table, that there are banquets in his honor and that he is given the title of noble thane. He goes to his house to spend the evening with friends. But, far from these thoughts of friendship, three witches have told Macbeth that one day he will be king. Ambition drives his desire. He speaks about it to his wife. For a few hours he is intoxicated by the idea: a crown on his head? Enthusiasm makes him impatient. Then he gets scared. It would be great to be king but what if things went wrong? And then his conscience bites: should he kill a friend? But his wife urges him: "Yet do I fear thy nature/It is too full o' the milk of human kindness/To catch the nearest way: thou wouldst be great/Art not without ambition, but without/The illness should attend it: what thou wouldst highly/That wouldst thou holily; wouldst not play false/That wouldst thou holily" (I, V).

It's Lady Macbeth speaking. Austere. Maternal. Someone has to look after the matter of fate, of the future. She invokes "you spirits, that tend on mortal thoughts" and tells them: "make thick my blood/Stop up the access and passage to remorse/That no compunctious visitings of nature/Shake my fell purpose, nor keep peace between/The effect and it! Come to my woman's breasts/And take my milk for gall, you murdering ministers/Wherever in your sightless substances/You wait on nature's mischief!" (I, V).

Duncan, Macbeth's guest, joins in the dinner given in his honor. Then he goes back to his room, as if he were just a normal young man, happy to be in his friend's house. He is serene and goes to sleep. A bell rings in the night: "Hear it not, Duncan; for it is a knell/ That summons thee to heaven or hell" (II, I). Macbeth drugs the servants, enters his guest's room, surprises him in his sleep and stains his hands with death.

It is not a woman that drives her husband to kill Duncan, it is not Lady Macbeth. If anything, it is one of the faces of *nature*. It is the *murdering ministers* that suck her woman's milk and instill bitterness in her: emptied of all possible mercy she must carry *nature's mischief* within her. This is an argument to which much could be added and on which pivots some of the affairs of Macbeth's family. But for the man of today, for the man who has already traversed the twentieth century, the word 'nature' has taken on a new meaning. It has been sectioned, taken to bits and ordered in the naturalistic compendiums of the data banks of genetics. The Macbeth of our days, in the presence of such heuristic news is astounded. Faced with the advance of the organic world, he has the feeling that everything—animals, plants, whole woods—try swallow him. He waits for the *becoming* to know his nature. The teeth of time are not chattering, the teeth of an unedited, unexpected, biological time: not that "emptied of all significance" (Auden 2000, p. 292) that on the death of his wife makes him say "she would have died hereafter" (V, V); and not even the time of Gassendi, Newton or Hume (Coco 2005). Rather it is the slow evolutionary process that knows the forms, urging them to a fitting adjustment to the environment: that *becoming* of evolution that drives organisms towards an atavistic propensity to the future (Coco 1994); a time loaded with meaning and effects. Modernity imposes on Macbeth a new concern: the tragedy (or the good fortune) of no longer being a spiritual essence, a platonic idea, divine breath, but flesh, enzymes, protein exchanges and evolution. From now on, he—or rather we—will want to show how nature to which he is inexorably linked is just and good and rewards the deserving. And so he will end up believing that the *baddies*, who have also made their mark on History, belong to a *corrupt* nature that is ill and mutated: a sign of biological decadence, of a genetic fall, evidence of which can be found in the hereditary heraldry of individuals, in that list of credentials that is rolled up in their DNA.

From theatre to natural history. Social attitudes have been one of the central themes of the debate on evolutionism. So much interest has been provoked not only by its extension to humans (trying to infer a natural government to the actions of man, getting its principles from the rest of the animal kingdom), but also the exquisite theoretical potential lying in one of the social aspects that is surely one of the most impassioned: generosity. In the wearying mishmash of ideas inspired by the *adaptionist* interpretation of behavior, generosity presents paradoxical aspects. As Hamilton wrote, "If natural selection followed classical models exclusively, species would not show any behavior more positively social than the coming together of the sexes and parental care" (1964).

The paradox in question appears evident when we try to reckon with subjects disposed to provide help. They cede part of their own resources operating in favor of those closest to them. For example, when an animal gives out a cry of alarm to warn the others of the arrival of a predator, it often risks becoming the first victim, which is certainly a great loss. Similarly, if an animal dedicates time to look for food for the young of another, it reduces the time it can dedicate to its own young. It could even happen that the efforts it makes tire it so much that it has a shorter life than those who are lazy. So, altruists miss opportunities that they could dedicate to themselves and especially to their reproduction: their generosity ends up with being paid for in terms of lack of children. Their fitness (their productive output that reaches a total in reference to the average output of the population) undergoes a decline. In certain cases the generous give up reproducing completely, responding to an instinct

determined by the genes. We can see examples of this radical vocation among Hymenoptera (bees, wasps and ants) or among Isoptera (termites); see among Alcock (1989), Coco and Cervo (2008), Krebs and Davies (1993), Wilson (1975b), Wilson and Hölldobler (1991). Their social organization provides for casts differentiated with working classes that help their mothers and sisters by giving up any possible reproductive inclination.

Darwin had already understood the paradoxical implications of this striking characteristic: how come we find numerous elements that never reproduce in colonies of bees or ants? If they do not reproduce, how can they leave heirs?

In this phenomenon, Darwin had seen one of the principles that could demolish his theory based on competition among individuals (Darwin 1872, p. 226, 230). According to the hypothesis of natural selection, the most celebrated of the five sub-theories that he included in his revolutionary vision of the organic world (Mayr 1982, 2000) individuals that possess the most fitting characteristics to a certain environment have an easier life and therefore leave more heirs; besides, as a consequence of the numerous heirs they produce, the characteristics present in these subjects become more frequent in the population: in fact, they are diffuse among sons who tend to look like their parents. On the contrary, the disadvantageous characteristics induce a less consistent descendent and in time can make it even disappear. So, the question is, how come individuals that are carriers of a decidedly inconvenient character (even not having sons) are numerous and in excellent health in a community? To tell the truth, Darwin does not give much space to the argument. In the sixth edition of *On the origin of species,* he explains that the difficulty of conciliating the existence of sterile casts with his theory disappear: "This difficulty, though appearing insuperable, is lessened, or, as I believe, disappears, when it is remembered that selection may be applied to the family, as well as to the individual" (Darwin 1872, p. 284). In this page he turns to the advantage of the *families* as evolutionistic justification of chastity: chastity penalizes the single worker but gives great benefit to the "family" (the *colony*?) and therefore is maintained in time.

The solution seemed plausible in the middle of the nineteenth century when they knew nothing of genes, allele frequencies and the genes of populations, etc. At the beginning of the twentieth century, however, to those who were more discerning, it seemed to be an inefficient justification, broken under the weight of genetic mathematics with which important scientists like Ronald Aylmer Fisher (1890–1962), John Burdon Sanderson Haldane (1892–1964) and Sewall Wright (1889–1988) had shown that a general advantage for the species does not impose on the reasons of the individual (Fisher 1930; Haldane 1990; Wright 1922, 1930, 1931, 1937). In fact, selection does not act on species but on individuals. It is the individuals who must face the test imposed by it. Only if a trait makes the subject able to maximize reproductive output can it find itself, thanks to its large offspring, in successive generations. Otherwise it will be cut down by the axe of selection together with the individual in which it finds itself. Therefore, if a trait offers the species privileges but leaves the individuals who present it to die, the species has no hope of seeing it become numerous among its line: it will disappear in a short while.

Those who invoked survival of the species were wrong. Under the sky, misdeeds and gestures of love happen only in the tumultuous lives of individuals.

2 The unedited lessons of William D. Hamilton and the family according to John Burdon Sanderson Haldane

How is it possible that altruists—those who give up every cautious and conscientious domestic economy of energies, abjurers in certain cases even of the right to reproduce—are

not yet extinct? In the early 1960s, the young William Donald Hamilton, just arrived in London looking for a scholarship, asked this question. However, at the British Library of London, we can seek in his unedited lessons a sort of Virgil, a guide who takes us along those years in which altruism could finally make use of a mathematical model able to resolve the evolutionistic rebus. It is not easy to describe. As Hamilton himself recounts, not having received a chair at the London School of Economics nor at the Imperial College (the two universities in which he finally managed to get accepted to do his doctorate) he often found himself in his bed surrounded by mathematical notes jotted down in the hope of finding the right solution. Attempts that did not succeed for a long time threw him into despair and defeatism (cf. Hamilton 1996).

The lessons that I have traced at the Department of manuscripts of British Library (London) number four cycles written between 1964 and 1975 (Coco 2003).

An article with an in-depth study illustrating the finding of these manuscripts, the dates, the methodological parabola contained within them and the theoretical positions with the group selection is being written and will be published in this journal. In this article, the specific considerations on the scientific sensitivity of Hamilton give way to a more general framework of the treatment of altruism. It's enough to say, therefore, that in the basic didactics of the course of *Population genetics* (1965–1970) held by Hamilton at the Imperial College of London, we can find once more the theoretical elements—that inspired the works of Fisher, Haldane, Wright, and also of Edmund B. Ford (mimicry), R. C. Punnett and Godfrey H. Hardy (populations in equilibrium and perturbing factors)—which Hamilton was to use to describe his mathematical solution to the problem of altruism. A solution that recuperated, though unwittingly as Hamilton claims (1996, p. 22), what Haldane had already hypothesized [Haldane 1955, 1990 (1a edn, 1932)].

As John Maynard Smith was to clarify, Hamilton's solution was based on a mechanism that we can call *kin selection* (Maynard Smith 1964). This principle applies to all organisms: *relatives share themselves their genetic material, though according to proportions that vary in relation to the degree of kinship.*

We can better understand the sense of this if we refer to what it was possible to see under the mathematical lens that the *genetics of population* had defined by then. Under that lens, the evolutionistic mechanism was read in genetic and quantitative keys. It rolled along a logical course of this kind: the gene is a feature of DNA, the minimum unit of heredity; each gene corresponds to a trait; every living organism is provided with genes (for example, 'the gene of eye color'); besides, each gene can exist in more specific, alternative forms called allele (for example, the hypothetical gene 'eye color' can exist in the form 'blue allele', 'green allele', 'black allele'); the mechanisms that preside over the reorganization of genetic material can give rise to causal mutations transmuting the allele into slightly different forms; the new allele forms can produce traits that make life easier for the subject that possesses them; this subject will therefore have more heirs and these will also tend to be in possession of convenient allele.

Therefore, the entire evolutionary mechanism reveals itself to be a statistical game: what probability does an allele have to find itself again in the future? If the probability is high, it means that it benefits the subject that possesses it. If not, there are disadvantages.

"I am a violent man by nature and education". In 1955, the English biologist John Burdon Sanderson Haldane had something new to propose to the scientific community. His view of generosity was based on the following supposition: if we look at evolution in genetic and statistical terms, it does not make much sense to speak about children produced. In order to understand if a certain trait such as altruism can evolve positively, what

Table 1 Coefficient of relationship (*r*)

parent - offspring	*r = 0,5*
grandparent - grandchild	*r = 0,25*
greatgrandparent - greatgrandchild	*r = 0,125*
identical twins	*r = 1*
full siblings	*r = 0,5*
half siblings	*r = 0,25*

is important is to understand how many copies of the allele will be found in future generations. Therefore, the dilemma of altruism becomes: how can the allele that makes the subject altruistic by driving it not to reproduce throw numerous copies of itself into the future?

His solution was based on a rather general principle that characterizes organisms which reproduce sexually: to each generation, the hereditary mechanism deals out chromosomes according to very precise rules; in this way, each parent hands to each of their children half of their chromosomes (the other half comes from the other parents) and therefore, the probability that a certain gene present in the parent will find itself in the child is equal to 0.5.

The consequence of such regularity in the handing out of genetic material is that, for every level of kinship, it is possible to calculate the probability that two subjects share the same genes. For example, for brothers (or sisters) the probability has the same value as the case of child–parent, that is 0.5; while in the case of uncle–nephew, the probability is reduced to 0.25. This means that if a parent possesses a hypothetical gene that leads to altruism, there is a probability equal to 0.5 that the gene is also present in each of his/her children, a probability of 0.5 that it is present in his siblings and a probability of 0.25 that it is found in the children of his siblings. This principle extends to all levels of kinship and can more or less be compared to what Wright defined the *coefficient of relationship* (*r*), or rather the average of genes with identical allele for those of the shared descent (Wright 1922).

If we look at evolution from this point of view, the statement 'what is convenient' takes on new characteristics: the loss of genetic material that a subject undergoes by not having children (equal to 0.5 for each 'lost' child) can easily be compensated for by the relatives that the subject gains thanks to his altruistic behavior (in the case of nephews and nieces equal to a 0.25 per heir gained). Haldane said 'I would be willing to give up a son in exchange for two nephews' (1955) (see also Table 1).

Developing Haldane's intuition, Hamilton constructed a model able to count the destinies of an allele that influences the productive output (*fitness*) of subjects that interact with the individual that possesses it, taking account of the possible diffusion of the allele in question among the subjects that surround the individual carrier. In other words, a model able to count the destinies of an allele that induces altruism in subjects who can be more or less genetically correlated with an altruistic subject. To do that, Hamilton also makes use of a new concept that he calls *inclusive fitness* and defined as "the personal fitness which an individual actually expresses in the production of offspring as it becomes after it has been first stripped and then augmented in a certain way." And in particular, it is:

stripped   of all components which can be considered as due to the individual's social environment, leaving the fitness which he would express if not exposed to any of the harms or benefits of that environment. And then

Table 2 Kin selection and coefficient of relationship

> Genetic output in the case of direct descendants (children)
>
> profit for 1 child   = 0,5x1 = 0,5
> profit for 2 children   = 0,5x2 = 1
> profit for 4 children   = 0,5x4 = 2
>
> Profit of nephews
>
> profit for 1 more nephew   = 0,25x1 = 0,25
> profit for 2 more nephews   = 0,25x2 = 0,5
> profit for 4 more nephews   = 0,25x4 = 1
> profit for 8 more nephews   = 0,25x8 = 2
>
> Total output
>
> if we consider that the behaviour of the altruist deprive him of the possibility to have children but allows him to have 8 more nephews than if he had behaved normally, it is possible to verify the genetic advantage obtained. In fact: lost children (– 0,5) + 8 nephews gained (+2) = + 1,5

augmented   by certain fractions[1] of the quantities of harm and benefit which the individual himself causes to the fitness of his neighbors.[2]

In Hamilton's definition, the *inclusive fitness* measure rather the contribution due only to the genome of the subject extends to the social environment (and therefore not the contribution that the subject is able to give thanks to the action of the genome plus possible help that he receives from the social environment).

Anyway, apart from formal specifications and Hamilton's mathematical formulae, the solution he proposed can be understood following a mere logical path. As he himself reassures, it should not surprise us if—omitting some precise aspects visible through numerical exactitude—it is possible to arrive at an approximation of principles expressed simply and with non-mathematical formulations (cf. Hamilton 1964, now in 1996, from which page 31 is here quoted).

And the intuitive formula of the solution to the problem of the altruist coincides with that put forward by Haldane years earlier: since relatives have a certain number of alleles identical to those of the altruist, from a genetic point of view, it is indifferent whether the altruist has children or prefers to raise the hopes of having new young relatives: the important thing is that the number of indirect heirs (nephews, great-nephews) earned for each lost child is proportionally adequate (Tables 1, 2).

---

[1] These 'fractions' are expressed by the coefficients of relationship (*r*) that express the genetic closeness between the subject and those near to him with whom he interacts.

[2] There has been some confusion regarding the definition of inclusive fitness. As the quoted passages makes clear (Hamilton, 1964a) and, as has been well shown by Alan Grafen, the "sum of individual fitness (reproductive success) should not be confused with the reproductive success of an individual's relatives, with each relative devalued in proportion to the kinship distance" as has sometimes been done erroneously (Grafen 1982, 1984). For a more extensive discussion on Hamilton's equation, on the definition of inclusive fitness and its theoretical and philosophical spin-offs, there will be an in-depth article in this journal in the coming months. See also Coco (2008; Coco and Cervo 2008).

3 Shylock and the reasons of the group

The *kin selection* explains how altruistic behavior determined in a purely genetic way can be maintained over time: guaranteeing its presence over successive generations will provide numerous nephews and nieces and great-nephews and nieces and other relatives that the altruist gains thanks to its solicitous behavior.

However, it is clear that altruism like this loses much of its romantic charm. It is not a genuine gesture. Rather, it is a form of profit 'I will help you because I can benefit through your heirs'.

Driven by the desire to subvert this sad prospective, a certain branch of scholars have tried to remodernise the old hypotheses of the reasons of collectivity. And it did so by defining a new subject in the context of survival: the group.

The theory that it is derived from, the theory of group selection, has had different formulations over the years (Borrello 2005; Grafen 1984; Maynard Smith 1964, 1976; Okasha 2005; Queller 1991; Wilson 1975a; Wynne-Edwards 1993). It comes from the idea that animals can sacrifice themselves exercising a kind of auto-limitation of exploitation of resources (so as not to leave future generations without any), to the idea that a group in which there is a high presence of altruists will benefit. The first hypothesis was well argued around 1963 by the Scottish naturalist Vero C. Wynne-Edwards (1967); the second by countless authors among whom Elliott Sober and David Sloan Wilson (Sober and Wilson 1998a, b; Sober 1984; Wilson 1975a, 1983, 1989; Wilson and Sober 1994; Wilson and Hölldobler 2005). Since the former turned out to be substantially unfounded (animals exploit to the limit the available resources, as show countless studies), we should dwell on the second formula (the only hope, for the moment, to find a natural principle of justice for our feeling of ethics).

The selection of the group maintains that since a group in which altruism reigns works better than one in which the subjects are prevalently egoistic; it increases more rapidly. The hypothesis is based on the following comparison: a *group A* in which the subjects are mainly altruistic is put in competition with a *group B* in which they are almost all egoists. What happens in these conditions is that, although the altruistic subjects within the group in which collaboration reigns decrease over time following the disadvantage they have compared to their egoist companions, group A however grows at a quicker rate than group B. Therefore, if after a generation one tries to mix the two groups, one discovers that the total number of altruists has risen. The game of prestige works. Mathematical simulations confirm it. In effect, it is possible that a hypothetical 'gene for altruism' has been evolved following the advantage of collectivity. However, the model does not hold up well to criticism: first of all, the possible existence in nature of the conditions necessary for it to work. Hamilton already underlined how unlikely it is for the conditions provided for in the model of group selection to be present in nature. In fact, he foresaw that the groups continually restock themselves: the egoists present in group A must transfer, at least most of them, to the group where they are almost all egoists; while the altruists present in group B have to transfer in large numbers to the group of collaborators. Only in this way can the two groups hold onto the difference necessary so that the group of collaborators reproduces itself better than the other. Evolution is based on a similar variability present between the groups called on to compare themselves. In the hypothesis of group selection, these subjects are the same groups that must show a variability sufficient for the trait in consideration. However, this variability tends to disappear because within the two groups the altruists are declining. For this, a mechanism is necessary by which the *baddies* are chased out of the *community of goodies* and the goodies decide to leave the community of the baddies (Hamilton 1975).

According to Hamilton, it is unlikely for a grouping like the one illustrated to operate in natural conditions. It only appears rarely. In any case, when it appears—insists Hamilton—it does make the model work but it deprives it of any presumed *democracy*. In fact, the group of goodies is forced to chase away the baddies. Only in this way does it manage to keep its genetic virtues intact. And this, obviously, is the forerunner of xenophobia (Hamilton 1996, p. 188).

Group selection does not release our idea of moral from the pessimism in which it has been confined by its naturalization. If altruism is moved by genetic reasons, it follows two mechanisms, neither of which are particularly appealing: either it leads to the profit-making of kinship or it creates groups that have to maintain themselves in some way 'pure' and so reserves scant mercy for those who are different.

On the Shakespearian stage in which I have invited evolutionism to talk about itself, Shylock would have something to say about it. We have to remember the occasion when the Venetian gentleman Bassanio wants to ask the rich heiress Portia to marry him, he finds himself lacking money for marriage. So he turns to Antonio, merchant and his dear friend for a loan: three thousand ducats. Antonio would give him it gladly but he does not have the cash: his ships are at sea and it would be a while before they come back with the merchandise. However, he offers himself to Shylock the Jew as guarantor.

Shylock, an elderly, clever businessman is scorned by Christians. There is no love lost between him and Antonio because Antonio does not miss an occasion to insult him. Despite this, he accepts to lend the money to Bassanio. However, when things go wrong, Shylock goes to court to get his due: after the way he has been treated he expects the contract to be respected. But the Venetians deem his determination to have his pound of flesh to be unjust. At the end he has to resign himself to giving it up. And that's not all. As the trial has already started, it must go on. Shylock's reasons will be turned against him by the jury (instigated by a fake lawyer, Portia, disguised to defend Antonio!). The court condemns Shylock. There will be no sympathy. His house and all his assets are confiscated. He will be poor and homeless. The famous words with which Shylock tried to explain himself when he did not know the destiny that awaited him, were of no use: "What judgment shall I dread, doing no wrong?/You have among you many a purchased slave/Which, like your asses and your dogs and mules/You use in abject and in slavish parts/Because you bought them: shall I say to you/Let them be free, marry them to your heirs?/Why sweat they under burthens? let their beds/Be made as soft as yours and let their palates/Be season'd with such viands? You will answer/'The slaves are ours" (Shakespeare 1947d; IV, I).

Antonio "hath disgraced me, and/hindered me half a million; laughed at my losses/mocked at my gains, scorned my nation, thwarted my/bargains, cooled my friends, heated mine/enemies; and what's his reason? I am a Jew. Hath/not a Jew eyes? hath not a Jew hands, organs,/dimensions, senses, affections, passions? fed with/the same food, hurt with the same weapons, subject/to the same diseases, healed by the same means,/warmed and cooled by the same winter and summer, as/a Christian is? If you prick us, do we not bleed?/ if you tickle us, do we not laugh? if you poison/us, do we not die? and if you wrong us, shall we not/revenge? If we are like you in the rest, we will/resemble you in that. If a Jew wrong a Christian,/what is his humility? Revenge. If a Christian/wrong a Jew, what should his sufferance be by/Christian example? Why, revenge" (III, I).

4 New horizons for altruism

Paradoxically, positive news for the human species comes from a character who is by no means a 'goodie'. It is Iago, he who filled Othello's ears with lies until he drove him mad:

driven to jealousy instilled by Iago, Othello ends up killing 'the beautiful and clever Venetian woman' who he would have given his eyes for: the sweet Desdemona.

But if Macbeth could leave us with the doubt that he operated from a hypothetical gene of egoism that commanded him to 'kill others to get a better position', Iago's situation is very different. As Hamilton (1970) noted, a hypothetical gene of spitefulness cannot hope to survive the effect of natural selection: it means costs (doing bad means a waste of energy) but it does not produce advantages (this is what is meant by spitefulness: to do evil gratuitously, without getting anything back). Therefore, the evil seems to be moved by different reasons than the mere presence of a gene (or a set of genes). But though it is not a gene that determines spitefulness, the exception can be extended to any other human social attitude.

Indeed, man is a product of a rather strange evolution. In the course of the second *world conference on the future of science* held in Venice in 2006 (an excellent synopsis of the papers is by Telmo Pievani with an introduction by Giulio Giorello) (Pievani 2008), scholars of great talent compared their views on the subject of human specificity. Man's diversity from animals (including primates) appears clear and today it has been better illustrated, under the functional profile, by the progress of neuroscience. However, it concerns a peculiarity on the grounds of biological evolution in that it owes nothing and has nothing to do with spiritualistic hypotheses or *intelligent design*. This is a clear fact that has already been written about (Pievani 2006, 2007) and we will not dwell on it here. The problem remains to establish to what idea of nature we refer to when we try to explain social behavior and man's moral attitudes. The real problem is this: the fact that our intellectual and emotional proprieties are located in organic structures that have been built through evolution by natural selection means that we they are predetermined in the subject?

Under this profile there are at least two possible classes of determinants that we should reflect on. Obviously the first class is formed by the genetic information present in the DNA of the subject; the second class depends on the cerebral structure that the subject obtains for its development.

The first class of determinants is substituted by the success of the gene-centric vision that characterized the twentieth century. The idea that the entire information required to construct an organism is contained in genes is weighty data for us. However, modern genetics shows us more and more that the gene–phenotype correspondence responds to an idealization of the process of construction of living organisms that is too simplistic and banal. A large amount of information belonging to the cytological environment in which DNA operates can modify the expression of traits and are handed down from one generation to another. The gene therefore does not know what will be done. Let's think how all the cells in a body contain the same DNA but different shape, structure, physiology. So, for example, although they all contain the same DNA, the epithelial cells give rise to epithelial cells and hepatic cells to hepatic cells. Epigenetic effects like this have been widely documented by Eva Jablonka (Jablonka and Lamb 2005). Other authors suggested that the functional impact of maternally acquired IgG in the newborn could be a good example of non-genetic inheritance (Lemke et al. 2004).

Environmental, epigenetic effects with an internal interaction are some of the new things that genetics and the biology of development are showing us better and which constitute a crucial node for a real understanding of how nature behaves (West-Eberhard 1989, 2007).

If we consider that DNA is constituted by less than 23,000 genes and that instead an organism contains more than 700,000 proteins, we have to admit a certain *ambiguity of*

genes (Buiatti 2004). The data appears more significant if we consider which kind of correspondence exits between genes and cerebral structure. Apart from the aforementioned gene–trait distance, we should add that the brain is a very particular organ: its functions are not rigidly determined by DNA but they spring from the personal history (ontogenesis) of the subject. When an embryo develops, it draws on information contained in the genes to know how to construct its own nervous system. However, a neuron does not follow millimetric indications such as 'go ahead for two millimetres, turn right for five' as if following the instructions of a satellite navigator (Richerson and Boyd 2005). Emerson Hibbard has shown that things operate in quite a different way. If small samples of tissue of the nervous system of salamanders are taken and then re-implanted in the opposite way, the axons that grow from the manipulated area are able to correct direction in order to reach the area to which they were originally heading. After being pointed in the wrong direction due to deceit (the tissue was inserted the wrong way round), they realize the mistake and invert direction, resolving the problem (Hibbard 1965). William Harris demonstrated a similar plasticity in the case of the optic nerve (Harris 1986; Harris et al. 1987). Therefore, *genetic information presides over the construction of the brain but it is used in a variable way.* DNA does not contain the exact design of how a person's brain will be made, but a generic draft of how a brain type will be made. This is a way to understand the relationship *DNA–brain–behavior* that is very different from what has been claimed in the past: it is the personal history of the individual, and not his genetic code, that determines how the brain will be made.

Once formed, the brain owes much of its capacities to the development (stimulated by the social environment) and its remarkable capacity of re-adaptation (vicarious effects) once more, its function is not rigid: every brain can delegate analogous tasks to different areas. In this sense we understand what Gazzaniga is referring to when he claims that "different people can do equal tasks with equal success, each one will use different areas of activation and diverse neurons" (Pievani 2008, p. 44).

Damasio claims: "the mind can be considered as the result of a phenotype which is without doubt determined by complex genetic networks (interactions of several genes) that cooperate to build the body and the brain, but at the same time cannot be considered without taking into account the socio-cultural context in which it is inserted that has played a fundamental role both in the development of the individual and in the evolution of the genome. Personally, I believe that it is useless to try to understand which part of the mind comes from the genome and which part derives from experiences of the individual or his ancestors" (Pievani 2008, p. 48).

All this leads us to believe that the element we call culture is neither physiologically nor genetically determined. To this we can add another consideration: *evolution follows at least two parallel paths (sometimes opposing) and the organisms can negotiate the terms of their relationship with natural selection in a different way.* This statement is full of implications and explains how biological evolution has led man, through natural selection, to have at his disposal traits that make him different from other organisms in the animal kingdom.

To clarify this better it is important to start from a central piece of data: every organism uses what is available to it—genes, physical form, behavior, companions of the group and culture—to be able to jump over the hole he risks ending up in. Life, in this sense, is a continual escape from death. Everyone equips himself as best he can for his appointment with natural selection. And because of this, everyone is able to negotiate in a different way with the selective effects. Organisms do not suffer passively the effect of selection, but they equip themselves with all means possible.

One can estimate this different capacity to respond to the selective effect considering how easy it is to poison fish in a pond and much more difficult to do the same to rats in the attic. Rats respond much better to the selective effect: while fish subject themselves to the possibility of poison and have to hope for a casual mutation of their chromosome makeup that enables them to survive, rats have evolved a much more versatile tool to face a similar situation: an agile behavior. The more one goes up the taxonomic scale, the more agile the behavior, able to modulate one's own responses on the base of previous experiences and even those experimented by others. Thus, one enters the great evolutionary flow that we call culture. Provided with a versatile tool that can introduce him into the flow of cultural evolution, man opens up his future to unexpected horizons. Not only through the powerful instrument of thought and the great tradition of culture is he able to negotiate a privileged relationship with natural selection (to such an extent that many selective effects that are lethal for other animals are almost imperceptible for him), but he is even able to contrast his own biological evolution and the dictates of genes. It is because of these abilities that man is the only animal able to contravene the most peremptory of the orders of the genetic code: 'reproduce!' Thanks to the invention of contraception, he can thwart as much as he likes the evolutionistic forces of DNA.

Cultural evolution forms the second kind of evolution with which organisms are called on to compare each other. A kind of evolution that is not genetically determined and that compared to genetic evolution is more rapid and more flexible. What's more, in some cases it is aimed in the opposite direction of the biological one: having the largest number of descendants is no longer a priority.

Someone in search of a Midsummer Night's Dream would say: "Dark night, that from the eye his function takes/The ear more quick of apprehension makes/Wherein it doth impair the seeing sense,/It pays the hearing double recompense" (Shakespeare 1947a, act III, scene II).

If one cannot count on a genetic grammar nor on an organic consistency that places itself as guarantor of our morals, what, therefore, is our moral based on? Since we are animals subject to selection, a selection that operates on different levels, we cannot exclude the persistence in our species of social behaviors of a type that leaves traces and is determining for genetic selection. An effect of kinship selection could have promised altruistic behaviors in the early hominids; so, the family selection there could have created the conditions for a certain group selection. We cannot exclude the fact that innate behavior modules may have operated among the early hominids. But this is a story lost in the past of our origins. Today, egoism, altruism, spitefulness and every other emotion move in a flow—that of culture and the psyche—able to overcome any genetic reasoning. Therefore, it is ridiculous to think that our feelings and our moral attitudes can be moved by a 'gene of'. The 'gene of altruism', the 'gene of jealousy', the 'gene of betrayal' and all the other scientific scoops which have turned out to be unfounded in the light of criticisms made by sharp, scrupulous scientists, can only make us laugh. Once more, man seeks in something absolute a reason that reassures him of the solidity of his choices. Whether it concerns a religious dogma or a scholarly precept, the impositions of a dictator or the presumed heraldic qualities of heraldry, the mistake is always the same: we seek a universal, unchangeable criteria with which to justify our position in the universe. Unfortunately, or fortunately, nature is the least universal and unchangeable possible. It changes all the time. In humans, evolution moves on cultural level. And this allows us to be disinterestedly generous or thoughtlessly spiteful: two attitudes that we cannot find anywhere else in the animal kingdom. It is our victory. Just as some animals see polarized light and others hear ultrasounds, we are able to move in the complex world of emotions and

Rend. Fis. Acc. Lincei (2009) 20:283–296

295

self-awareness. Darwinian evolutionism is a value to defend; a solid theory, well thought-out that has been able to benefit from the complexity with which time has enriched it. It is a conquest founded on human knowledge and has liberated man from superstitions. Man after Darwin is a better man: a man who knows his own nature. And it is just in virtue of this that we can say that there is no such thing as a natural principle to call upon to justify human action. In the theatre of nature, the misdeeds are the order of the day: profiteers, tricksters and charlatans are the rule among other animals. For us, the opportunity to get something back is to behave in an unnatural way: follow personal choices that we can construct thanks to our cultural distance. Ethics do not belong to nature anymore than they belong to religious dogma. The only moral that we can aspire to is that born from the democratic comparison between culture and personal sensitivity, which does not make things any easier. Once more, the voice of the playwright would have said "Sirs, do you know nothing of an imminent battle? (Shakespeare 1947b; IV, VI).

References

Alcock J (1989) Animal behavior, 4th edn. Sinauer, Sunderland, MA

Auden WH (2000) Lectures on Shakespeare. Princeton University Press, Princeton

Borrello ME (2005) The rise, fall and resurrection of group selection. Endeavour 1:43–47

Buiatti M (2004) Il benevolo disordine della vita. UTET, Torino

Coco E (1994) Cronosofie naturalistiche. Coscienza Storica, pp 10–12

Coco E (2003) Les leçons inédites de W. D. Hamilton, Du problème de l'altruisme à l'application des modèles mathématiques. Mémoire de DEA en "Histoire et Civilisation". Paris

Coco E (2005) Kant, Lorenz e l'a-priori naturalizzato. Spazio, Tempo e Conoscenza alla luce degli scritti di Konrad Lorenz e della moderna filosofia positiva. L'Acropoli Marzo, pp 217–229

Coco E (2008) Egoisti, malvagi e generosi Storia naturale dell'altruismo. Bruno Mondadori, Milano

Coco E, Cervo R (2008) Il comportamento degli animali. Giunti, Firenze

Darwin C (1872) On the origin of species by means and natural selection, 6th edn. John Murray, London

Fisher RA (1930) The genetical theory of natural selection. The Clarendon Press, Oxford

Grafen A (1982) How not to measure inclusive fitness. Nature 298:425–426

Grafen A (1984) Natural selection, kin selection and group selection. In: Krebs J, Davies NB (eds) Behavioural ecology. Blackwell Scientific, Oxford, pp 62–84

Haldane JBS (1955) Population genetics. New Biol 18:34–51

Haldane JBS (1990) The causes of evolution. Princeton University Press, Princeton, NJ

Hamilton WD (1963) The evolution of altruistic behavior. Am Nat 97:354–356

Hamilton WD (1964) The genetical evolution of social behavior. Part I & II. J Theor Biol 7:1–52

Hamilton WD (1970) Selfish and spiteful behaviour in an evolutionary model. Nature 228:1218–1220

Hamilton WD (1975) Innate social aptitudes of man: an approach from evolutionary genetics. In: Fox R (ed) Biosocial anthropology. John Wiley and Sons, New York, pp 133–157

Hamilton WD (1996) Narrow roads of gene land. Evolution of social behaviour. W. H. Freeman, New York

Harris WA (1986) Homing behaviour of axons in the embryonic vertebrate brain. Nature 320:266–269

Harris WA, Holt CE, Bonhoeffer F (1987) Retinal axons with and without their somata, growing to and arborizing in the tectum of *Xenopus* embryos: a time-lapse video study of single fibres in vivo. Development 1:123–133

Hibbard E (1965) Orientation and directed growth of Mauther's cell axons from duplicated vestibular nerve roots. Exp Neurol 13:289–301

Jablonka E, Lamb M (2005) Evolution in four dimensions. MIT Press, Cambridge, MA

Krebs JR, Davies NB (1993) An introduction to behavioural ecology, 3rd edn. Blackwell Science, Oxford

Lemke H, Coutinho A, Lange H (2004) Lamarckian inheritance by somatically acquired maternal IgG phenotypes. Trends Immunol 25:180–186

Maynard Smith J (1964) Group selection and kin selection. Nature 201:1145–1146

Maynard Smith J (1976) Group selection. Quart Rev Biol 51:277–283

Mayr E (1982) The grought of biological thought: diversity evolution and inheritance. The Belknap Press of Harvard University Press Cambridge, London

Mayr E (2000) Darwin's influence on modern thought. Sci Am July, pp 66–71

Okasha S (2005) Altruism, group selection and correlated interaction. Br J Philos Sci 4:703–725

Pievani T (2006) Creazione senza Dio. Einaudi, Torino

Pievani T (2007) In difesa di Darwin. Bompiani, Milano

Pievani T (ed) (2008) Book L'evoluzione della mente. Sperling and Kupfer, Milano

Queller DC (1991) Group selection and kin selection. Trends Ecol Evol 6:64

Richerson PJ, Boyd R (2005) Not by genes alone. How culture transformed human evolution. The University of Chicago Press, Chicago

Shakespeare W (1947a) A midsummer night's dream. In: Bullen AH (ed) The complete works of William Shakespeare. Odhams and Blackwell, London

Shakespeare W (1947b) King Lear. In: Bullen AH (ed) The complete works of William Shakespeare. Odhams and Blackwell, London

Shakespeare W (1947c) Macbeth. In: Bullen AH (ed) The complete works of William Shakespeare. Odhams and Blackwell, London

Shakespeare W (1947d) The merchant of Venice. In: Bullen AH (ed) The complete works of William Shakespeare. Odhams and Blackwell, London

Sober ER (1984) Holism, individualism, and units of selection. In: Sober ER (ed) Conceptual issues in evolutionary biology. MIT Press, Cambridge, MA

Sober E, Wilson DS (1998a) The golden rule of group selection. Reply to Trivers review. The Skeptic 4:83–86

Sober E, Wilson DS (1998b) Unto others: the evolution and psychology of unselfish behavior. Harvard University Press, Cambridge, MA

West-Eberhard MJ (1989) Phenotypic plasticity and the origins of diversity. Ann Rev Ecol Syst 20:249–278

West-Eberhard MJ (2007) Dancing with DNA and flirting with the ghost of Lamarck. Biol Philos 3:439–451

Wilson DS (1975a) A theory of group selection. Proc Natl Acad Sci 72:143–146

Wilson EO (1975b) Sociobiology: the new synthesis. Harvard University Press, Cambridge, MA

Wilson DS (1983) The group selection controversy: history and current status. Ann Rev Ecol Syst 14:159–187

Wilson DS (1989) Levels of selection: an alternative to individualism in biology and the human sciences. Soc Netw 11:257–272

Wilson EO, Hölldobler B (1991) The ants. Harvard University Press, Cambridge, MA

Wilson EO, Hölldobler B (2005) Eusociality: origin and consequences. Proc Natl Acad Sci USA 38:13367–13371

Wilson DS, Sober E (1994) Reintroducing group selection to the human behavioral sciences. Behav Brain Sci 4:585–654

Wright S (1922) Coefficients of inbreeding and relationship. Am Nat 56:330–338

Wright S (1930) Review of the genetical theory of natural selection. J Hered, pp 349–356

Wright S (1931) Statistical theory of evolution. Am Stat J March 26(Suppl):201–208

Wright S (1937) The distribution of gene frequencies in populations. Science 85:504

Wynne-Edwards VC (1967) Animal dispersion in relation to social behaviour. Oliver & Boyd, Edinburgh and London

Wynne-Edwards VC (1993) A rationale for group selection. J Theor Biol 162(11):1–22