

Chapter 4

Born to Cooperate? Altruism as Exaptation and the Evolution of Human Sociality

Telmo Pievani

Introduction

In recent papers (e.g. Wilson and Wilson, 2007), it has been confirmed that the two standard solutions for the apparent paradox of the evolution of altruism and pro-social behaviours – ‘kin selection’, which leaves unsolved the question of population structure, and ‘group selection’ – can indeed be consistent with one other. The result is a possible explanation of the ambiguity between deeply entrenched attitudes to cooperation inside social groups and organized hostility among them (Bowles, 2008). Nevertheless, these models seem to undervalue the potential effects of ‘multilevel’ evolution and both notions remain strongly engaged with gene-centred interpretations of evolutionary dynamics – which lose their explanatory power when applied to group-living species that show unconditioned forms of altruism and pro-social feeling, especially when cultural evolution enters the process. In order to avoid ‘cultural discontinuity’ hypotheses at the other extreme, I emphasize the importance of ‘functional cooptation’, or ‘exaptation’ (Gould and Vrba, 1982; Gould, 2002) in arriving at a more satisfying explanation of the origins of free or reciprocal unselfishness, in group-living animals and in culture-bearing species.

Individuals or Tribes? A Pluralistic Darwinian Heritage

While the theory of evolution was developing in his private notes, between 1836 and 1842, Charles Darwin discovered the logic of the selective process and modified his perspective on the ‘transmutation’ of species, which he had previously viewed as an abrupt transition between discrete entities that were physically and geographically isolated. After incorporating ‘Malthusian’ ideas into his theory in September of 1838, he no longer saw change in species as ‘per saltum’ but as a gradual

T. Pievani (✉)

Department of Human Sciences, University of Milan II, Milan, Italy
e-mail: telmo.pievani@gmail.com

accumulation of ‘infinitesimal’ changes in populations of organisms exposed to selective environmental pressures:

Three principles will account for all:

- 1) Grandchildren like grandfathers;
- 2) Tendency to small change, especially with physical change
- 3) Great fertility in proportion to support of parents (Notebook E, p. 58 of the original; see Barrett et al., 1987, p. 412).

In order to implement this ‘tendency to small change’ in the struggle for existence, tiny infinitesimal advantages are enough:

Seeing the beautiful seed of a Bull Rush, I thought, surely no ‘fortuitous’ growth could have produced these innumerable seeds. Yet if a seed were produced with infinitesimal advantage it would have better chance of being propagated and so on (Notebook E, p. 137 of the original, see the edition quoted above p. 436).

Thus the language itself was changing in Darwin’s writings at that time, drifting towards a competitive and rigorous logic of selection in environments where there was limited supply (here a passage dated March 12th 1839):

It is difficult to believe in the dreadful but quiet war of organic beings, going on the peaceful woods and smiling fields (Notebook E, p. 114 of the original, see edition quoted above, p. 429).

It is still evident that the explanatory power of natural selection derives from the fact that it is a demographic, statistical, ecological mechanism involving individuals in populations. The process is without foresight, absolute perfection, and design. But in its explanatory power there also lies a weakness, because to be effective, natural selection has two significant requirements: a strict generational continuity in population lineages and an immediate individual advantage, however slight, that can slowly enhance the frequency of a variant in a population. No interaction between different species is possible:

Natural selection cannot possibly produce any modification in a species exclusively for the good of another species; though throughout nature one species incessantly takes advantage of, and profits by, the structures of others. . . . If it could be proved that any part of the structure of any one species had been formed for the exclusive good of another species, it would annihilate my theory, for such could not have been produced through natural selection. (*On the Origin of Species*, sixth edition 1872, Chap. 6, p. 162, www.darwinonline.edu)

Darwin’s risky prediction (‘if it could be proved that. . .’) is that natural selection promotes only individual advantage:

Natural selection will never produce in a being any structure more injurious than beneficial to that being, for natural selection acts solely by and for the good of each. . . . If a fair balance be struck between the good and evil caused by each part, each will be found on the whole advantageous. (ibid., pp. 162–163)

But it is equally evident that animal, and especially human, behaviours are frequently unselfish, occasionally threatening the life of the individual, and cooperation

is widely recognized as a powerful evolutionary strategy.¹ Following Darwin, when they are fixed in populations and well established, such behaviours can be easily understood in the light of natural selection, with concurrent individual and group advantages, as in cases of cooperation in hunting, mutualism, or defensive alliance. But it is more difficult, both theoretically and historically, to explain the origin of purely altruistic behaviours, because they simultaneously produce a disadvantage for the altruist and an indirect advantage for the selfish, who exploit the actions of the altruists without costs to themselves. So we must ask the following questions: what triggers unselfish behaviours? Why do egotists not prevail immediately, forestalling any ‘experiment’ of social cooperation and reciprocity? Let us listen to Darwin again, here discussing the case of the evolution of sterile castes in ants and bees:

Hence I can see no great difficulty in any character becoming correlated with the sterile condition of certain members of insect-communities: the difficulty lies in understanding how such correlated modifications of structure could have been slowly accumulated by natural selection. (ibid., Chap. 8, p. 230)

This paradox seems to need solution at several levels. A logic of individuals is no longer enough:

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, and may thus gain the desired end. (p. 230)

But how, precisely, can selection be applied to families or the group? Darwin’s central dependence here is upon the concept of ‘instinct’, developing through natural selection from the very simple to the highly complex. Darwin is saying that the foundation of moral qualities and sociality lies in social instincts, including the family ties, love, and emotions of sympathy. In his concluding remarks to *The Descent of Man*, Darwin writes that ‘Animals endowed with the social instincts take pleasure in one another’s company, warn one another of danger, defend and aid one another in many ways’. Nevertheless, ‘these instincts do not extend to all the individuals of the species, but only to those of the same community. As they are highly beneficial to the species, they have in all probability been acquired through natural selection’. (p. 610, on-line edition).

A benefit for the species is taken for granted, but nothing is said about how such behaviours originated in the first cooperators: ‘Social animals are impelled partly by a wish to aid the members of their community in a general manner but more commonly to perform certain definite actions’. Rapidly, Darwin’s discussion about sociality moves on to the human species, which has few or no special instincts about sociality (which is rooted anyway in the greatest-happiness principle and

¹In the XIX century debate about the priority of the common ancestorship and the degree of relatedness between man and gorillas and between man and chimpanzees, Darwin – in this case against the opinion of T.H. Huxley – argued that chimpanzees, rather than gorillas, would have probably been closer to humans because of their more developed feelings of sympathy and love, the instincts of cooperation at the base of human sociality as well. See *The Descent of Man*, first part.

in emotive sympathy, ‘strengthened by exercise or habit’), and which can express desires by words and reasoning power, no longer constrained by blind instinctive impulses but influenced by the praise or blame of one’s fellows: ‘and then the self-regarding virtues come within the scope of public opinion, and receive praise, and their opposites blame’. (p. 611)

Quite surprisingly, Darwin eventually finds adaptive power in sociality, not between individuals but between groups and human ‘tribes’:

It must not be forgotten that although a high standard of morality gives but a slight or no advantage to each individual man and his children over the other men of the same tribe, yet that an advancement in the standard of morality and an increase in the number of well-endowed men will certainly give an immense advantage to one tribe over another. (p. 166, on line edition)

Tribes of altruists are much stronger in the struggle for life, so this is natural selection after all:

There can be no doubt that a tribe including many members who, from possessing in a high degree the spirit of patriotism, fidelity, obedience, courage, and sympathy, were always ready to give aid to each other and to sacrifice themselves for the common good, would be victorious over most other tribes; and this would be natural selection. (ibid.)

In the end, when human instinctual sociality evolves in ‘the highest part of man’s nature’, the struggle for existence, and natural selection, lose their agency:

The moral qualities are advanced, either directly or indirectly, much more through the effects of habit, the reasoning powers, instruction, religion, &c., than through natural selection. (p. 618)

In sum, for the purposes of this chapter, we can represent Darwin’s legacy by citing the following three points:

- (1) He presents a conceptual frame for the evolutionary explanation of unselfish behaviours and sociality through a plurality of integrated factors and patterns, including standard natural selection among individuals, natural selection between families or ‘tribes’, and later habits of learning and culture.
- (2) Altruism is selective in origin; it is a good strategy for groups or tribes against others; In this way, Darwin attributes to altruism a substantially ‘defensive’ function; but, if this is true, altruism and cooperation *inside* the community would necessarily have their counterpart in hostility towards *outsiders*.
- (3) The evolution of the ‘highest part of man’s nature’ suggests that the reasoning power of humans can deny one side or the other of the paradoxical human ambiguity between high cooperation and of warfare, and it also suggests that in the human cultural and symbolic niches, previous adaptations can assume completely new functions.

Yet, the origin of unselfish behaviours in individual organisms, and the relationships between individual and group benefit, still needs clarification.

The Hardening of a Genetic Cost–Benefit Paradigm and the Unresolved Theme of Population Structure

With the ‘genetical theory of natural selection’ (Fisher, 1930) and the study of the genetic components of animal behaviour (Mayr, 1961; Tinbergen, 1963), the paradox of altruism assumed a new, more radical aspect, due to the fact that – in the mathematical and quantitative models of population genetics – the fitness of the individual precedes, and prevails over, any incidental advantages of species, families or tribes. If generous individuals neglect their direct interests, and thus have a lower reproductive fitness while the egoists on the contrary give up nothing, why are unselfish behaviours tolerated by natural selection?

Even if altruism is satisfying for the individual, it should be overwhelmed generation by generation, ultimately leaving no traces.² Altruism thus seems really improbable from a strongly selective and individual point of view, as well as from a gradualist and functionalist one. Nevertheless, we know that altruism, cooperation and sociality are widely diffused and successful evolutionary strategies’, and in many species, humans included, we see clear neurological and hormonal traits that reinforce pro-social behaviours.

But the mere presence today of physiological conditions enabling cooperation (‘proximate causes’) tells only half the story. We need also to understand the evolutionary ‘remote causes’ of the emergence of these behaviours (Mayr, 1961; Sterelny and Griffiths, 1999). In the history of biological and ethological thought of the twentieth Century, the following two main answers were provided:

- (a) The paradox does not actually exist because altruism is not an evolutionary reality: it is an indirect and sophisticated kind of selfishness, and there are in fact no pure acts of altruism in nature.
- (b) The paradox is a trade-off: altruism is an evolutionary reality, but it is also consistent, at a different level, with the basic selfish evolutionary logic of neo-Darwinism.

As we embark on the twenty-first century, a third solution is being crystallized, aiming not at the paradox itself, but at the background theoretical conditions that lie behind it.

The framework for the first solution recalls the work of J. B. S. Haldane, Ronald A. Fisher and Sewall Wright. In 1930, Fisher noted that a gene for a trait that is disadvantageous for the individual but useful for the group (such as a bad taste of an insect against its predators) could evolve only in populations where many others have the same gene for being disgusting. Otherwise, the sacrifice of the individual would be useless. This is possible in groups of organisms both closely related

²“If natural selection followed the classical models exclusively, species would not show any behaviour more positively social than the coming together of the sexes and the parental cares” (Hamilton, 1996, p. 31).

to each other and gregarious. The gene of the insect eaten will diffuse copies of itself through the survival of the others. But the problem of the ‘internal overthrow’ remains unsolved: a gene for the direct defence of the individual against predators would be much more effective, no matter what the fate of the others.

Haldane (1932) proposed a model of diffusion of unselfish genes where the lower reproductive fitness of the altruist is balanced by advantages given conferred by the presence of a high proportion of altruists in a small population. According to Haldane and Wright, the accumulation of a random mutation in a small number of individuals with a high level of inbreeding could allow the allele conferring altruism to spread rapidly, despite being detrimental to individual reproductive fitness. However, this advantage might still be subverted by a subgroup of aggressive egotists with a double advantage to their strategy. At that point, altruism and cooperation could survive only through a ‘trick’ whereby the population splits into different isolated groups, some composed by egoists and some not, with the second ones having a selective advantage over the first ones (Wright, 1945; see also Wilson and Sober, 1994).

In 1955, Haldane added another possible reason for the evolution of apparently unselfish genes: he calculated costs and benefits of altruistic acts in a population where all members are closely related. If selfishness acts in favour of relatives, then the genetic fitness (not the reproductive fitness) of the altruist could increase because the individual loses its genes but enhances the genes shared with relatives. A brilliant solution at a first glance: altruism is useful if the individual saves more than two sons, or four nephews, or eight cousins, and so on. However, since animals cannot measure their kinships, natural selection favours these behaviours only in small populations of individuals that are all closely related. Altruism is a kind of indirect genetic egotism (Haldane, 1955).

William D. Hamilton formalized this model of exclusive individual advantage in 1962 and 1964, including a possible solution for the initial diffusion of the ‘gene for altruism’ in populations of egotists, in order to explain eusociality in social hymenopterans. The central idea is that altruistic behaviour is a good strategy for the individual whenever group members around are closely genetically related, apart from their behaviours. If they are related sufficiently to altruistic me, then they will surely have alleles for altruism, so my altruism will have an ‘inclusive fitness effect’ on others in my social environment, and, as a result, the alleles for altruism will spread. The individual confers its fitness on relatives, producing a greater ‘inclusive fitness’ (that is, the contribution to the part of alleles shared with others, a measure of the fitness of relatives)³: but if the social environment is in fact predominantly composed by egotists, my altruistic genotype will be rapidly ‘diluted’. In Hamilton’s view, Haldane’s condition of small populations is no longer necessary.

If an individual gains an increment in individual fitness, and the sum of the effects on members of the social group is positive as well, we have mutualism. If the subject

³Inclusive fitness is not the sum of the direct individual fitness and the fitness of relatives (Grafen, 1982).

gains in fitness without affecting the fitness of others, we have selfishness between relatives or non-kin. Altruism is possible, on the other hand, only if the inclusive fitness is decisively higher than the contingent loss of individual fitness. Natural selection acts on animal behaviour accounting for the presence of relatives: they bear my genes, so it is a good strategy for me to be unselfish towards them ('kin selection' to use the terminology of John Maynard Smith in 1964). Altruism would be an unconscious calculation of individual genetic interests,⁴ but the possibility of explaining it without a consideration of the population structure of a species (e.g. in its division into many little isolated populations, as proposed by Wright) remains controversial.

It is possible to distinguish the following three clear methodological and epistemological assumptions of this approach:

- (1) Individual reproductive interest has priority with respect to ecological survival ('interactors' are just means for the maximization of the interests of 'replicators').
- (2) From the Darwinian organism, we move to the gene and genetic lineages as the central units of selection (relatives are bearers of percentages of shared alleles according to a correlation of kinship).
- (3) The logic of evolution follows a genetic instrumental and economical rationality based on cost/benefit.

Genes in Conflict or 'Parochial Altruism'?

When John Maynard Smith (1964, 1976) refuted the strong version of 'intergroup selection' in the evolution of social systems proposed in 1963 by Vero C. Wynne-Edwards, introducing the term 'kin selection' in the process, an interesting weak version of 'group selection' entered the debate and refreshed the old Darwinian intuition. According to the 'group selection' hypothesis, a gene advantageous for the group could succeed even if it were disadvantageous for the individual. A population of altruists has an independent higher fitness, and the internal growth of selfish subgroups is counterbalanced by the expansion of the group due to unselfishness. Let us see how.

Wynne-Edwards' ethological and biogeographical studies led him to believe that social animals are able to check both the dimensions and the ecological impact of their group. They manage the distribution of territories and control the density of population, maintaining its environmental sustainability like a homeostatic system. Since each group is a small society competing with others, organisms are not programmed for maximizing their individual interests but the interests of their society (Wynne-Edwards, 1986).

⁴Edward O. Wilson dates his "paradigm shift" towards Hamilton's approach at the spring of 1965 (Wilson, 1994, pp. 319–320).

This ‘strong’ version of group selection, based on spontaneous mechanisms of self-regulation that damages the interests of individuals, presented both theoretical and experimental problems, as Maynard Smith soon remarked. Study of the ‘regulation of numbers’ in biological populations had a long history, beginning with the Malthusian influence on Darwin’s idea of ‘struggle for existence’, and passing through Carr-Saunders’ ‘principle of optimal number’ (1922). And while in the Darwinian tradition the solution for the overgrowth of populations is natural selection between individuals, in Wynne-Edwards it is the sacrifice of individuals due to the capacity of self-control of the group.

However, Maynard Smith, and later Hamilton, easily showed how the behaviours advantageous for society cited by Wynne-Edwards could be traced back to the effects, in terms of costs–benefits, of standard natural selection between individuals – and even of balances between aggressive behaviours. No ‘laws of the group’, or sacrifices for the group, were needed. According to Maynard Smith, strategies of aggression/expansion vs. sociality/regulation are mixed up in any population (or even individual) at any one time, in an ongoing dynamic equilibrium depending on the frequency of one strategy with respect to the other. There is a plurality of ‘evolutionary stable strategies’, with a weaving of variables playing their role in animal behaviours; but in the end ‘genes are always in conflict’, through the different strategies of their bearers, even inside genomes and between parents and offspring.

Nevertheless, even if we do not need group selection to explain the natural management of resources and territories in biological populations, Maynard Smith noted that altruism remained the big issue to explain from the point of view of the maximization of individual performances. So, in his artificial ‘mouse of the haystacks’ model, he stressed a kind of kin selection where many competing groups of altruists and egotists (able to recognize themselves as separate) are involved in the evolution of apparent unselfishness, as in Sewall Wright’s idea of a species composed by many little isolated populations, and in George and Doris Williams’ model of altruism (1957) where a marginal consideration is given to competition between groups of donors and of non-donors.

Yet, as Elliott Sober and David Sloan Wilson noted in *Unto Others* (1998), it seems that some focus on ‘groups’ as independent entities are needed, even in models of social behaviour like those of Wright, Haldane, Williams and Maynard Smith.⁵ Competitions between groups of cooperators and of egotists produce a differential survival (of groups and therefore of individuals). Groups where unselfishness is dominant are more efficient, united and stronger against enemies. In Hamilton’s later models, when competition between groups is diminishing, the frequency of alleles disadvantageous for individuals tends to be reduced: altruism

⁵Most of them, and Hamilton specifically, were nevertheless suspicious about the possibility that such ecological systems could really exist, maintaining a high degree (but not too high) of isolation, a low degree of migrations and flows of individuals between groups, high variability between groups, therefore strong systems of recognition and separation between egoists and altruists: features not necessarily adaptive and eventually an handicap for the range of choice of partners, degree of inbreeding, etc. So, the role of group selection remains hypothetical (Hamilton, 1996).

needs a degree of competition between groups. We could name this kind of process a ‘weak version’ of group selection because it does not need a problematic self-discipline among animals as Wynne-Edwards’ model requires. With respect to the three methodological and epistemological assumptions proposed at the end of point 2, the weak version of group selection does not either refuse or confute any of them. In all cases, social qualities depend on the success of some genes that individuals or groups bear.

But what is interesting in this model from the point of view of the philosophy of biology is that altruism seems founded on conflict between groups, and the exclusion of outsiders. As in Darwin’ tribes, the ultimate selective criterion is efficiency in the struggle for existence among groups. Quite evidently, both kin selection and the soft version of group selection, attempting to explain sociality by natural selection (at different levels), assume that conflict and warfare among humans are the complementary expression of underlying behaviours toward strangers and non-relatives.

As Samuel Bowles (2008) pointed out in *Nature*, presenting the results of his simulations of game theory, conflict is ‘altruism’s midwife’: ‘Generosity and solidarity towards one’s own may have emerged only in combination with hostility towards outsiders’; in other words, this crucial ambiguity is historically rooted in human sociality, much more than happens in other primates. When they occur separately altruism and parochialism produce selective disadvantages; but they could have acted synergistically in human evolution, at the level of selection between groups competing for resources, to confer better reproductive fitness (especially in periods of intense environmental stress) upon groups with the most ‘parochial altruists’.

Toward Humans: Something Breaks the Logic

As a result of these considerations we might say that when we try to explain the biology of sociality we find an unexpected theoretical continuity between models based on inclusive fitness and on group selection. This was the later aim of Hamilton himself when, adopting the mathematical notation proposed by George Price in 1975, he advanced an allegedly integrated model for selection involving both selfish benefit and, given some special conditions in the structure of population, selection between groups. In the second case, the model showed how altruism might evolve. Similarly, Edward O. Wilson, father of sociobiology (Wilson, 1975), and his colleague David Sloan Wilson proposed a theory where selection acts at ‘multiple levels’ and upon different ‘units’ (Wilson and Wilson, 2007). Apart from the proclaimed ‘conversion’ of the influential E. O. Wilson to group selection, there are no new ideas here (Lewontin, 1970; Keller, 1999; Gould and Lloyd, 1999; Okasha, 2006) and the paper does not deliver quite what it promises. Instead, it is a manifesto for the diffuse role of group selection in evolution. It distinguishes between ‘intrademic selection’ (inside the same population) and ‘trait-group selection’ (the evolution of the traits in a group) but without distinguishing between

individual and social advantage or specifying how the two might interact. A simple individual–group dualism thus pervades the paper, despite the ‘multilevel’ theory promised in its title. Just as Hamilton considered inclusive fitness a more general model that includes group selection as a special case, Wilson and Wilson seem to incorporate kin selection as a special case of group selection. The difference lies in the explanatory ‘weight’ given to lower levels by Hamilton and to higher ones by Wilson and Wilson: it is not a matter of alternative and incompatible explanations. So leaving aside ‘strong’ versions of selection based purely on ‘selfish genes’, available hypotheses concerning the central role of cooperation and altruism in primate and human life are reduced to competition arguments, at different levels of selection.

Yet it would be much more interesting to understand the relationship between the ‘two selective forces’ of Hamilton. Are they coherent or antagonistic? Does group selection apply only to weak altruism (or cooperation, where the unselfish act has some social compensation via reciprocity) or also to strong and free altruism (when donor has no advantage at all, in a free and unconditioned act of generosity)? What degree of genetic correlation inside a group is needed for group selection? What about unselfishness in larger groups of non-relatives? What about free altruism without any reciprocity perceptible by the individual? What about acts of empathy and altruism between members of different species? What about altruism in species with social learning and cultural evolution? None of these questions is properly broached by the Wilson and Wilson approach.

At this point in many contemporary papers, even in strongly theoretical contributions such as Bowles (2008) and in those involving strongly biological hypotheses about social behaviours in animals, we typically read a ritual recitation about a theoretical ‘gap’. Usually the arguments are as follows: biology in humans is not fate; we are cultural animals; there is no linear genetic determination of complex social behaviours such as altruism; human plasticity has no equivalent; interactions between genes, individuals and cultures have completely different qualitative patterns; instincts are much less compulsory in human species; we are free to choose our social behaviours following a multiplicity of developmental, cultural and educational factors.

Of course, there is a lot of truth in these considerations, and this is the context in which an updated and non-simplistic evolutionary biology of sociality is desperately needed. Today’s primates are not our direct ancestors but cousins of different degrees, and millions of years of separate evolution in heterogeneous ecological niches make our natural histories divergent. Clearly we are special: we not only have ideas of altruism and justice and the rational dream of universal human rights but also the possibility of being freely evil without any advantage (the non-adaptive ‘spite’ strategy in Hamilton: damaging others without any advantage to the damager, something similar to stupidity for free). Nevertheless, a simple argument of ‘discontinuity’ does little to help us explain the unusual human condition. Human beings are both hugely different from other primates and show interesting behavioural analogies or even homologies with them (Cavalli-Sforza and Feldman, 1981; Boyd and Richerson, 2005), but continuities should be discernible even considering the uniqueness of our species.

So, beyond reductionist notions of ‘imperialist’ colonization by genetic benefits (Dupré, 2001), we need some bridges to approach our status as a cultural animal. It is one thing to say that our animal instincts, or emotional attitudes, or cognitive limits, are ‘vestigia’ of a deep and distant evolutionary past; it is entirely another to claim that natural ‘precursors’ were already present but were at different times co-opted for new uses in new ecological niches. In the first case, our evolutionary nature is seen as passive inertia; in the other it appears as a still-active constraint, one that we should be aware of even if it is now useless or has been co-opted for different functions. This, surely is where we will find those bridges.

Firstly, we can look for bridges in recent experimental approaches. The package of kin selection plus sexual selection plus ‘tit-for-tat’ cooperation plus punishment for free riders might be a good place to start explaining (with some case-by-case reservations) such things as eusociality in insects, opportunistic cooperation (for hunting), mutualism, parasitism, commensalism, reciprocal altruism between non-relatives and other classic convergences of reciprocal genetic ‘interest’. But what about the origins (not only the usefulness) of endosymbiosis, indirect reciprocity, sexual behaviours without reproductive interest, free altruism among unrelated strangers, cooperation without reciprocity, even between different species? Something here breaks the selective logic of the exchange, and it needs a satisfying evolutionary explanation because such cases are being documented in nature with increasing frequency.

The function of widespread cooperation as defence against predators, instead for the promotion of more coordinated and aggressive hunting, is one of the bridges between the social behaviours seen among living primates and the hypothetical social behaviours in groups of our hominid ancestors (Hart and Sussman, 2009). The range of behaviours that does not conform with models of mere kin selection is expanding (Clutton-Brock, 2002). While in some cases still debated, empirical clues are accumulating from behavioural comparisons that social animals empathetically react to the emotions of others (De Waal, 2006, 2008). We know cases of repulsion at the suffering of others, leading to self-sacrifice even where individual advantage in such suffering can be seen, and there are cases too of inter-specific empathy. Tomasello et al. have, for example, documented cases of spontaneous altruism and unconditioned assistance in chimps (Warneken et al., 2007). Since 1996 (de Waal, 2007), we have seen consolation of the defeated after conflict, and altruism toward strangers. Seyfarth and Cheney (1984) in vervets, and de Waal (1997) in chimps, have documented gratitude for grooming, implying reciprocal altruism and relational memory. Brosnan and de Waal (2003) have even hypothesized a sense of justice, or at least a reaction against inequity in exchanges without expectation of reward, in capuchin monkeys. According to Marc Bekoff and Jessica Pierce (2009), animals of a wide range of social-living species show clear signs of emotive and ‘moral’ intelligence in a set of behaviours including fairness, trust, reciprocity and a ‘wild justice’.

Such cases impressively remind us of Darwin’s anecdotes, in *The Descent of Man*, about acts of altruistic heroism in little monkeys and baboons, which he saw as deeply rooted evolutionary bases of our moral qualities and sociality. Nevertheless,

so far the argument still seems based on a shifting of explanatory weight: at one end of the spectrum envisaged by the ‘competitive paradigm’, cooperation and altruism are the widespread norm of behaviour in primate and human life, while at the other end, violence and aggressiveness are tolerated exceptions. But does this truly change our evolutionary hypotheses about the nature of social life? If it does not, then maybe we need something more than experimental bridges. We need new theoretical bridges, resting on an ‘extended theory of evolution’ in progress (Pigliucci and Kaplan, 2006; Pigliucci and Müller, 2010).

Indeed, it is fair to suppose in all these cases that the assumed immediate individual benefit of the cooperative behaviour (e.g. reducing stress, promoting social conformity) must coincide with an evolutionary benefit for the group. This also applies to the origin of the behaviour concerned, as it must to all coordinated behaviours and alliance formations for an immediate end: collective actions are a low-cost behavior, and this offers an evolutionary insight about the beginning of any behavioral trait.

Thus it is the logic itself of our evolutionary explanations that needs to be extended: this is not only a matter of ‘interactors’ belonging to genetic pools but also a matter of the economy of survival, immediate physical benefits, responses to contingent conditions in the surrounding ecological systems, the ability to learn new behaviours, phenotypic and behavioural plasticity and the flexibility of social patterns of interactions – all of them macro-evolutionary independent factors in a hierarchy of evolutionary levels (Eldredge, 1985, 1995, 1999; Gould, 2002).

Unselfish Behaviour as Exaptation in Group-Living Animals: Why Hypotheses Based on Cooperation and Altruism are Not Completely Reducible to Competition Arguments

So far we have developed mostly a theoretical bridge, dealing with the ‘adaptationist’ posture of many evolutionary explanations of human behaviours and sociality. One of the major difficulties in selectionist reasoning lies in the need to justify the adaptive value of intermediate structures: what can you do with half an eye or with incipient mimicry? Darwin had already sensed that there could not be a ‘teleological deployment’ of an organism towards perfection in the construction of its organs. In the chapter of sixth edition of the *Origin* dedicated to ‘difficulties’ with the theory of evolution, he advanced the hypothesis of the functional shift: a rough model of an eye is not used to see with but for a ‘pre-adaptive’ function that is later modified. An incipient wing, an early form of mimicry or parts of the organism selected for a certain ancestral function could then have been ‘re-adapted’ opportunistically for new functions. Something similar could happen in the evolution of animal behaviours, like in Darwin’s hypothesis of parental and filial affections ‘extended’ to pro-social general feelings.

The Darwinian intuition – which later faded into the background because of the strict adaptationist posture at the core of the ‘evolutionary synthesis’ – was that a

continuity of morphological transformation by natural selection did not necessarily correspond to a progressive continuity in function. Natural selection frequently results in ‘contrivances’, and sometimes in oddities because it uses the available material that carries historical and ‘architectural’ (structural) constraints. In a seminal essay of 1982, palaeontologists Stephen J. Gould and Elisabeth S. Vrba described the ensemble of currently useful characteristics as ‘aptations’, allowing for the identification of subsets of characteristics that were shaped for one specific reason yet available to selection for another function in different circumstances (Gould and Vrba, 1982; Gould, 1993). The hypothesis was that not all cases of similar structure should be considered as ‘adaptation for’ one specific function. Rather, we should speak of ‘exaptation’ (apted ‘from’ the structure) in all those cases where there is co-optation, for new functions, of structures employed in the past for something else.

Exaptation is thus the ‘effect’ (in the sense of Williams, 1966) of something evolved for other reasons and does not lead to the negation of adaptation as an evolutionary reality. Rather, it redefines and integrates the concept of adaptation. Feathers, used today (though not always) for flying, were initially selected for purposes of thermoregulation or sexual selection. Evolutionary outcomes appear in this perspective as the unforeseeable results of secondary and sub-optimal adaptations: the product of an opportunistic tinkering often due to trade-offs between genetic and ontogenetic constraints and environmental possibilities. The present perceived adaptive reason of a structure or behaviour does not imply that the structure concerned has been built selectively for that use: an organ’s *current usefulness* and its *historical origin* should be seen as possibly separate; to infer the second from the first could often be a mistake.

More importantly with exaptation we understand that natural selection is not a force freely acting on organisms but a force acting in a context of constraints. Furthermore, the available material used by natural selection might have had a functional origin (as in pre-adapted structures or vestigia, standard Darwinian processes) but not necessarily; it could also have had a structural, neutral, non-selective or non-adaptive origin (as in Gould’s metaphor of architectural ‘spandrels’; see Gould, 2002).⁶ The disjunctive rationality of some modern biology, habitually separating inside from outside, organism from environment, activity from passivity, replicators from interactors, seems to be checkmated by the development of a kind of evolutionary approach in which natural history appears like co-evolution amongst organisms and environments (Odling-Smee et al., 2003): a weaving of interactions among plastic systems, an opportunistic and creative tinkering reorganizing available materials.

⁶The explanatory role of the processes of exaptation is growing in recent literature of many evolutionary fields. Pre-adaptations and spandrels could be involved in the evolution of language according to Hauser, Chomsky and Fitch (2002), and more recently according to Lieberman (2006). Even some of the most important current faculties of the human brain, like reading, seem to be functional cooptations of evolutionarily older brain circuits, as in the interesting evolutionary reconstruction proposed by Stanislas Dehaene (2009).

Apart from other epistemological and experimental weaknesses (Buller, 2005; Richardson, 2007), this seems the major focus of dissatisfaction over the ‘just so stories’ of evolutionary psychology, the heir presumptive, with some non-crucial differences, of sociobiology. Criticism of the adaptationist programme, anticipated in an essay by Gould and Richard Lewontin more than 30 years ago (Gould and Lewontin, 1979), has focused on two epistemological proposals: (1) to demonstrate that a pan-adaptive problem-solving approach cannot be imputed to Darwin and (2) to outline an ‘extended taxonomy’ of adaptive phenomena, in which the general class of evolutionary innovations (*aptations*) includes neutral introductions (by genetic drift), *exaptations* and standard *adaptations*.

What is most interesting today is that, while adaptationist explanations are waning in general evolutionary biology because of their frustratingly limited explanatory power, they are still adopted, and publicized by the mass media, in a ubiquitous ‘pop evolutionary psychology’. The evolution of human sociality thus seems to be the last territory where a ‘stereotyped Darwinism’ reigns almost undisputed. This approach almost invariably involves the following: division of the object of study into discrete traits, the assumption of a linear association between each trait and one genetic codification, a speculative reconstruction of adaptive stories starting in mythical and stable ‘ancestral adaptive environments’ and the strong preference for a competitive paradigm of interpretation of any evolutionary phenomenon.

In 1986, in a second paper about exaptation, Gould and Vrba extended the idea of functional cooptation to ‘spandrels’ that pass through the different levels of an evolutionary ‘hierarchy’ composed of genes, organisms and groups: a trait recognized at one level could become an exaptation or indirect ‘effect’ at another level (cross-level spandrels; see Vrba and Gould, 1986). A random mutation at the level of the genes becomes an exaptation at the level of organism. Adaptations at the level of organisms could have consequences on the capability of a species to evolve or to resist extinction. This concept of exaptation is now crucial in Evolutionary Developmental Biology (Evo-Devo), for understanding the functional cooptation of regulatory genes, the role of epigenetic processes and the different utilization and regulation of the same structural information (Jacob, 1981), and is also extensively used in the field of human evolution as well (Tattersall, 1998, 2002; Pievani 2003a, b; Pievani and Serrelli, 2011).

Furthermore, with exaptation major transitions, for example in human behaviours, do not imply either discontinuities or hypotheses about cultural evolution as something completely new and disobedient of biological interests (as in the case of the ‘just so memetic stories’, where memes start an independent and divergent evolutionary path). What we call the Palaeolithic ‘Revolution’ might well have been a crucial event of exaptation of mental and linguistic faculties, potentially already present and triggered by an ecological opportunity or a cultural advancement (Tattersall, 1998, 2002). A new process of ‘niche construction’ began, ultimately leading toward our unusual symbolic and cognitive niche, and many abilities of our brain are clearly ‘exapted’. In this way, our current behaviours could have *originated* as collateral effects of ancestral adaptive constraints but then sporadically exapted for new functions – even in radically new frames of selective or cultural pressures.

We should, then, explore the possibility that human cooperation and free altruism could have had ancient natural precursors (not vestigia) in such characteristics as empathy, refusal of someone else's suffering, reciprocity. They could then have been retained by various hominid precursors as predator-protection mechanisms, in tribes of gatherers who were frequently victims of predators. Subsequently, this deeply rooted attitude was exapted in several different ways: firstly in the transition of later species of genus *Homo* to better articulated practices of organized hunting; then in the Palaeolithic transition to cognitively modern humans. Here we see the exaptation of altruism and human sociality from a defensive adaptation to a successful model of social organization with division of the work and new forms of exploitation of ecosystems (including big-game hunting). Though repeatedly exapted, these behaviours maintained their relationship with their natural precursors, which is why in various non-human animals we see echoes of them, and they appear to peep out as emotional and apparently instinctual attitudes in current cultural contexts that have nothing to do with its evolutionary history.

With exaptation, we also better understand a neglected claim by Darwin that could be crucial for the understanding of the evolution of altruism and cooperation. That is natural selection does not aim at perfection or optimization but at contingent survival. It tinkers with structural constraints of the moment, as a bricoleur more than an engineer. Even the optimal use of resources in an ecosystem and the best exploitation of evolutionary potential are not necessary results of natural selection: something that is also clearly true for our ambiguous and contradictory behaviours of former preyed-upon and predators at the same time. The exaptive idea is that the selective criterion of greater efficiency in the struggle for existence between groups was not the ultimate stimulus for the way we are but quite possibly the initial one. In the evolution of social animals, the effects of competition among individuals, constrained by an instinctive solidarity towards one's own, and suspicion towards strangers, have gradually receded in importance even as competition among groups has become more intense.

This provided evolutionary advantage for cooperators. Practices that suppressed the stress of direct conflicts inside the group (avoidance, toleration, negotiation, and so on) evolved, while individuals shared growing levels of reproductive (and cultural) success with other members of the same group. With social protections against exploitation by egotist free-riders, altruism became not only a possible social strategy but also an advantageous one, both inside the group and against other groups. Cultural evolution, language and learning radically renewed our social niches, and the legacy of this ambiguous disposition, both inside the group and among them, was 'exapted' for completely new functions.

There are, then, three interesting theoretical advantages⁷ to an 'exaptive' hypothesis about the evolution of cooperation in animals and humans and are as follows:

⁷Criticisms about the alleged irrelevant role of exaptation, or its reducibility to normal adaptation – advanced among others by Dawkins (1986) and Dennett (1995) – seem solved in Arnold (1994) and Gould (2002).

1. It does not see a conflict between selection for the individual survival or genetic benefit and the benefit of the group; this is consistent with both standard natural selection and the weak version of group selection: an adaptation, or a neutral non-adaptation, at the individual level could become an exaptation at the group level (Gould's 'cross-level spandrels', 2002).
2. It is consistent with a 'hierarchical' or 'multilevel' theory of evolution, where a plurality of factors, organized in two inclusive hierarchies, genetic and ecological, interact both inside each hierarchy and between hierarchies (as in Niles Eldredge's 'sloshing bucket model', Eldredge, 1999). Frequently, as in helping strategies among birds, cases of evident altruism do not match the calculations of kin selection because changing ecological constraints are the chief determinants: ecological survival and genealogical interests must interact and find trade-offs as two independent and inter-dependent logics (Vrba and Eldredge, 1984; Eldredge and Grene, 1992). According to the 'effect hypothesis' proposed by palaeontologist Elisabeth Vrba, an adaptive trait at a lower level could have an alternative 'effect' at a higher level (Vrba, 1983).
3. A series of multiple exaptations could explain the transition between a previously prevailing biological niche (now showing its weaker influences under the skin) and the currently prevailing cultural and symbolic niche in human evolution. This series would have involved trade-offs between opposite behaviours, leading to the current behavioural ambiguities so familiar in human beings. We no longer need a radical discontinuity between our biology and our culture.

This series of advantages has the potential to lead to a truly productive debate among the proponents of three methodological and epistemological assumptions at the end of point 2. This debate can take place in the context of an extended and pluralistic, although still Darwinian, theory of evolution. The multifactorial and integrated approach involved brings together, in a viable and testable way, genealogical, ecological and cultural logics that are not reducible to standard arguments based on competition. This allows us to approach the problem of human behavioural origins without having to adopt 'universal laws' for evolution (as in the universal strong Darwinian 'algorithm'), but instead by seeking at evolutionary law-like 'patterns', that are repeated schemes of regular events (Eldredge, 1999).

A Final Philosophical Caveat: Avoiding a 'Cooperative Evolutionary Psychology'

Altruism and selfishness both seem equally 'natural', intelligible, products of an evolutionary process. What is more, given the results of human evolution today, they seem both natural and cultural in the same way. They are cultural through nature (a series of exaptations) and natural through culture (in our symbolic niche). But it is clear that emotionally we react poorly to selfishness (at least in others) for

its ethical consequences.⁸ We do not like to consider that altruism is an advanced form of egotism and that there are no evolutionary foundations for solidarity and reciprocity. In twentieth-century debates about kin selection and group selection, this ethical side of the controversy could not remain hidden, implicit or otherwise. An excessively naturalistic and deterministic approach to human social behaviour seems to threaten the bases of personal responsibility, with the result that a possible ‘biology of generosity’ sounds very attractive.

But the eagerness to preserve a ‘natural’ foundation for the ethics of solidarity could be badly misleading. We saw that even group selection – and the idea that altruism is a real evolutionary possibility rather than an indirect form of selfishness – could have ethically unpleasant consequences: parochialism inside the group and aggressiveness against others in a competitive system. Though for impeccable ethical reasons we might wish to refute a selfishness-oriented paradigm for human behaviour, this would be mistaken – even if we kept firmly in mind that cooperation and altruism are at the core of primate and human life. The ‘exaptive’ interpretation adopted here could avoid this emotional dimension by emphasizing a very different point: the ultimate criterion should be explanatory power, not the possible ethical consequences. Let us look a bit more closely at this final caveat.

Thomas Henry Huxley, ‘Darwin’s bulldog’, was probably wrong to think entirely dualistically in his very effective metaphor for human emergence of the gardener taming the wilderness. He saw that there is a conflict between the gladiatorial biological aspects of the unheeding evolutionary process, ‘red in tooth and claw’, from which we derive and the recently acquired exquisite moral faculties of the educated man. But hewing more closely to Darwin himself, we know that there are strong natural precursors to the attributes of the modern human mind. Morality is an evolved trait, but we also have the power not only to understand biology but also to deny it. Biology is a way to illuminate both the past and the present of our condition within a ‘liberalized’ or ‘pluralistic’ interpretation of naturalism (De Caro and Macarthur, 2004). And understanding our evolutionary history might help us to improve our peaceful and social behaviours, based on our knowledge of the enabling conditions for human sociality.

If we discover that, for the greater part of our evolutionary history, the defence of ourselves and of our families from predators, and not the contrary, has been the main driver of our survival; that sociality and cooperation have had a function connected to avoid predators, and not to the glorious aim of hunting and dominating environments, we will have to change the major paradigm that has dominated our views of our essential selves from the earliest days of paleoanthropology. This paradigm concerns not only the origins of humans as physical beings but also the origins of human mind, most especially in terms of atavistic fears and remaining instincts (Hart and Sussman, 2009). This theoretical change has a *pars destruens*: It enables us to see

⁸Williams and Williams (1957), from the point of view of an evolutionary biology of social behaviour based on the exclusive interest of Darwinian selfish individuals, proposed for this reason to use more neutral categories like “donors” and “non donors”.

the fallacy embedded in many of the adaptationist, competitive and gene-centred stereotypes of evolutionary psychology. But it has a much more important *pars construens*: Through its lens, we better understand human evolution, in terms of a plurality of levels and units of selection and in terms of adaptations and exaptations.

Nevertheless, nature is not a norm, even if the norm is cooperation. If we state that we should cooperate because it is more natural to do so, then we are likely to undervalue the multilevel nature of the evolution of human behaviours. Searching in nature for what we ethically hope to find, and replacing a competitive-selfish model with its opposite one just because it is more edifying, is a recipe for misunderstanding the scientific data. In Europe, an influential movement of theologians and philosophers nowadays fashionably disputes the scientific solidity of the neo-Darwinian theory of evolution, asserting that we are moving towards a new, alternative theory based on cooperation, self-organization, complexity and symbiosis. Following this trend, one would be tempted to construct an opposite ‘cooperative evolutionary psychology’. But this would leave us vulnerable to the same epistemological fallacies I have already deplored in contemporary ‘pop evolutionary psychology’. Reversing competitive evolutionary psychology to its opposite is not enough: we need to oppose its seductive theoretical assumptions.

The ‘Man the Hunted’ paradigm is ‘positive’, with respect to the opposite ‘Man the Predator’ notion, because it offers much more effective and realistic evolutionary explanations (Hart and Sussman, 2009). Without denying that humans are extremely able in warfare, it removes the idea that egotism is natural and cooperation a cultural epiphenomenon. It also eliminates the concept that cooperation and sociality are marginal contingencies that may be explained merely as anomalies tolerated by an alleged ‘universal Darwinian algorithm’. And it does away with the idea of a supposed evolutionary determinism of selfishness, frequently used as a support for conservative and class-conscious ways of putting questions in sociological researches and biased questionnaires of evolutionary psychology (Dupré, 2001).

In sum, the approach based on the concept of ‘Man the Hunted’ opens the possibility that sociality is not only deeply rooted in our entire evolutionary history – genealogical and ecological, natural and cultural, multileveled and ‘exaptive’ – but has also been a crucial, independent factor for the definition of human species identity. We are born to cooperate as well as to be human.

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