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## Altruism and fairness: Unnatural selection?

*Altruisme et impartialité : sélection non-naturelle ?*Camilo J. Cela-Conde <sup>a,b,\*</sup>, Lucrecia Burges <sup>a,b</sup>, Marcos Nadal <sup>a,c</sup>, Antonio Olivera <sup>a</sup><sup>a</sup> Laboratory of Human Systematics, University of the Balearic Islands, 07122 Palma de Mallorca, Spain<sup>b</sup> Department of Philosophy, University of the Balearic Islands Edifici Ramon Llull, carretera Valldemossa s/n, km 7,5, 07122 Palma de Mallorca, Spain<sup>c</sup> Department of Psychology, University of the Balearic Islands, 07122 Palma de Mallorca, Spain

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## ABSTRACT

Darwin admitted that the evolution of moral phenomena such as altruism and fairness, which are usually in opposition to the maximization of individual reproductive success, was not easily accounted for by natural selection. Later, authors have proposed additional mechanisms, including kin selection, inclusive fitness, and reciprocal altruism. In the present work, we explore the extent to which sexual selection has played a role in the appearance of human moral traits. It has been suggested that because certain moral virtues, including altruism and kindness, are sexually attractive, their evolution could have been shaped by the process of sexual selection. Our review suggests that although it is possible that sexual selection played such a role, it is difficult to determine the extent of its relevance, the specific form of this influence, and its interplay with other evolutionary mechanisms.

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## R É S U M É

Darwin a reconnu que la sélection naturelle ne peut pleinement expliquer l'évolution de phénomènes moraux comme l'altruisme et l'équité. Le comportement moral semble conduire loin de la maximisation du succès de la reproduction. Plus tard, divers auteurs ont proposé des mécanismes supplémentaires, comme la sélection de parentèle, la *fitness* inclusive et l'altruisme réciproque. Dans le présent travail, nous nous demandons dans quelle mesure la sélection sexuelle a joué un rôle dans l'apparition des traits moraux. Certains auteurs ont suggéré que certaines vertus morales, y compris l'altruisme, sont sexuellement attrayantes, et que leur évolution pourrait avoir été modelée par le processus de sélection sexuelle. Notre étude suggère que, même s'il est possible que la sélection sexuelle ait joué un tel rôle, il est difficile de déterminer la portée de sa pertinence et la forme spécifique qu'elle revêt, et son interaction avec d'autres mécanismes évolutifs.

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## 1. Introduction: explaining the evolution of moral behaviour

In a well-known section of his *Descent of Man*, Charles Darwin grounded the capacity to behave in a moral manner on a uniquely human feature: the *moral sense*

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(Darwin, 1871, Chapter IV) [1]. He believed that this trait distinguished human beings from other living animals, though some, such as other primates, would exhibit it if their capacities were developed enough.

In the ethical naturalism inaugurated by Darwin, this notion of a moral sense linked morality to human nature. However, the specific mechanisms underlying the alleged moral sense were unclear. Darwin suggested that it resulted from the addition of sympathetic – i.e., emotive – impulses and the specifically human ability to reflect upon the consequences of our acts. Nevertheless, neither can the actual combination of these components be easily demonstrated, nor does the result seem compatible with the laws of natural selection. Even in Darwin's own writing, it was clear that altruistic behaviour (leading an individual to invest his or her own resources to maximize the adaptive fitness of another), as well other moral phenomena, was in opposition to natural selection. How could a mechanism that maximizes individual fitness favour altruistic strategies? Natural selection would probably eliminate any individual who tended to decrease his or her own fitness in favour of another's. In spite of this fact, some animals (among which we find ants, rodents, and humans) carry out certain forms of altruistic acts.

## 2. Attempts to fit altruism with natural selection

The modern study of the biological foundations of social behaviour can be traced back to the flowering of a new approach to animal behaviour that grew from ethology during the 1960s and consolidated in the mid 1970s. This field came to be known as sociobiology. Wilson [2] described sociobiology as the systematic study of the biological basis of any social behaviour, exhibited both by animals and humans. The most remarkable feature that sets sociobiology apart from ethology is the adoption of the gene's point of view and the development of a conceptual apparatus from this perspective. Prior to the consolidation of the actual field of sociobiology, many ethologists assumed that natural selection had favoured the appearance of certain behaviour patterns that were costly for the individual but favourable for the group. Hence, some aspects of animal social behaviour could be explained as individual sacrifices for a collective good. Wynne-Edwards [3] made some of the most significant contributions to this way of thinking. For instance, he argued that the altruistic renunciation of reproduction by number of individuals is responsible for the fact that groups of individuals or species that limit their growth as a function of environmental resources have higher survival rates than those that overexploit their habitats.

The criticism of group selection models elaborated by Williams [4], as well as his convincing arguments in favour of more parsimonious explanations, paved the way for the work of Edward Wilson [2] and Richard Dawkins [5], who championed the gene's point of view for the adequate comprehension of social behaviour. From this perspective, animal behaviour, especially social behaviour, was viewed as a means developed by genes to ensure their own transmission to offspring. As expressed by Laland and Brown [6], the body and its functions became mere

vehicles for gene transportation and transmission. However, this perspective did not make the explanation for altruist behaviour appreciably easier. If the objective of genes, and the social behaviours related to them, is to maximize their own possibilities of transmission to future generations, how can we explain the behaviour of individuals who reduce their own chances of survival and reproduction to increase others'?

In an attempt to explain these seemingly paradoxical acts, sociobiologists began using the concept of "inclusive fitness" [7], and developed a non-individualistic model of evolution by natural selection: "kin selection". This notion was based on the fact that closely related individuals share copies of many genes. Hence, animals can increase the presence of those common genes in subsequent generations by favouring the reproduction of close relatives. Although altruistic acts of self-sacrifice to benefit another involve losing the opportunity to transmit one's own genes, they also increase the chances of transmitting other copies of those genes if the beneficiary is a close relative. In fact, Hamilton [7] predicted that this behaviour would be selected if the cost to the altruistic individual is less than the benefit to the recipient or recipients multiplied by the probability that the recipient possesses the same gene. Thus, the closer the relative, the greater the sacrifice we are willing to make.

Robert Trivers [8] introduced the notion of reciprocal altruism as an answer to the question that arises immediately from Hamilton's [7] arguments: how can we explain altruistic behaviour among non-related organisms? Trivers suggested that altruistic behaviour – which would initially be costly for the actor but beneficial for the recipient – could appear between non-related individuals that interact for extended periods of time. They would be especially likely to appear if there were a high probability of the altruistic act being returned by the other individual on a future occasion. Under these circumstances, over time, both individuals will have benefited more from their altruistic interaction than if they had not collaborated. In this case, the difficulty is to overcome the tendency of individuals to behave non-reciprocally, that is to say, to cheat. Reciprocal altruism is frequently observed in human beings, who have developed special procedures, such as altruistic aggression [9,10], devised precisely to avoid the appearance of cheaters and to deter them from reiterating their behaviour.

## 3. Human altruism

The implications of group selection, kin selection, and reciprocal altruism have been of enormous interest for the comprehension of animal altruistic behaviour. Granting that these models can successfully explain the altruistic behaviour of ants and rats, are they also useful to explain human altruism? To put it in other words: are we referring to the same phenomenon when we speak of altruism in both ants and human beings? The relation between moral altruism (exhibited by humans) and biological altruism (exhibited by other animals) is too complex to answer those questions with a simple yes or no. Several authors [11–14] have underscored the numerous difficulties that

arise when models and theories developed for the interpretation of the behaviour of hymenoptera are transferred to the study of human behaviour. However, even accepting that such difficulties exist, we cannot agree with those who believe that there is no relation between biological and moral altruism [12,14]. Human behaviour is also the result of natural selection, so it falls under the definition of biological altruism that we noted above. By means of moral behaviour, humans reduce their own resources in favour of other individuals. Hence, “moral altruism” is a special kind of “biological altruism”. The same could be said of “social altruism”, referring to altruistic behaviours exhibited by insects belonging to the order *Hymenoptera*. Natural selection has fixed extreme altruistic behaviour in at least four instances: hymenoptera (ants, wasps, bees, termites); parasitic prawns of coral sea anemones (*Synalpheus regalis*) [15]; naked mole-rats (*Heterocephalus glaber*) [16]; and primates (with humans as the best example). Thus, the true question is whether explanations for altruism in one of these special cases can be extrapolated to the altruistic behaviour exhibited by the others.

Clearly, altruistic behaviour has appeared four separate times during the phylogenesis of pluricellular animals. It would seem unreasonable to believe that extreme altruistic behaviour in those four sets of species was inherited from their most recent common ancestor. The trait is thus a homoplasy, meaning that its similarity among species is due only to convergence during separate adaptation processes. It has no significance regarding evolutionary relatedness. The evidence we obtain of the behaviour of any of those eusocial lineages cannot, therefore, be straightforwardly extrapolated to that of any other. The scientific success of the explanation of the evolution of the social behaviour of bees and ants does not afford many conclusions about humans. A different issue is that kin selection and other approaches constitute elegant mathematical models, capable of explaining the way in which a gene that promotes altruistic behaviours could be inherited. The speculations as to whether an allele, capable of promoting cooperative behaviour, is “altruistic” or not, clearly reveal the risks of confusing a purely biological concept with a common sense one. An “altruistic gene” or a “selfish gene”, as conceived by Richard Dawkins [5], should not be understood as possessing the same features that altruistic people do. But it is difficult to avoid the semantic load of language.

There is no doubt whatsoever that humans exhibit both selfish and altruistic behaviours. But is our altruistic behaviour accurately described as the biological altruism conceived by kin selection and other models? It seems that parents actually sacrifice much for their children, for instance. But cultural deviations from this simple behaviour can introduce significant complexity. We mean to say that reducing human altruism to a simple behaviour, under the control of a few genes, is of little help to understanding the evolution of human moral cognition and behaviour.

Elliot Sober and Robert S. Wilson [17] convincingly showed that the universe of human ethics is explained better by the model of “group selection” than by models of individual selection. This notion was already introduced by

Darwin himself when, incapable of explaining the ultra-social behaviour of hymenoptera, he spoke of the adaptive advantages that a group of cooperators would have over a group of selfish individuals. However, this common sense idea again seems to violate the principles underlying the mechanism of natural selection.

In the original Darwinian conception, natural selection refers to the individual adaptation of each organism. Let us grant for a moment that a group of altruists could actually adapt collectively, outcompeting other groups because its members engage in behaviours such as helping the sick and protecting each other against predators. Applying schemes from mathematical game theory, John Maynard Smith [18] demonstrated that the adaptive strategy of such a group would not be evolutionarily stable. If because of genetic mutations, recombination or immigration a selfish individual were to appear in this group, that individual would have a great selective advantage over the rest. Assuming simply that altruistic and selfish behaviours are determined by a single allele, the “selfish genes” would eventually spread within the group, ending its cooperative nature. Maynard-Smith [18] notes that a group of altruists can avoid the inconveniences caused by the presence of a non-cooperative individual if they are endowed with mechanisms capable of detecting and isolating any selfish individual that appears. However, this requires the members of the group to have sophisticated cognitive mechanisms. Sober and Wilson [17] showed that, unless the scope and content of such cognitive mechanisms are known, the explanatory power of group selection models cannot be properly assessed.

Thus, one century and a half after Darwin’s proposal of the mechanism of natural selection, we are faced with the same vagueness regarding the constituent processes involved in the human moral sense that Darwin himself expressed in the Chapter IV of the *Descent of Man* [1]. How can the combination of emotive and rational mental mechanisms that produce altruistic behaviour be understood?

The moral act is still described by authors like Hauser [19] as a combination of rational and emotive components, which are hypothetically linked in the way that competence and performance are in a Chomskyan understanding of human language. Hence, it could be possible to conceive something like a cerebral “moral grammar” that guides “our intuitive judgments of right and wrong” [19]. This is just a conjecture at present, and does not explain how this grammar could have evolved by natural selection. Perhaps it actually did not, which would mean that it is not necessary to search for an explanation of how a trait such as altruist behaviour, which cannot be the result of the maximization of individuals’ fitness, was selected.

Some authors have suggested that human traits like language and moral sense could perfectly be regarded as by-products of other adaptive episodes that caused certain neural modifications [20]. As we have already mentioned, Darwin [1] stated that any animal with enough social instincts “would inevitably acquire a moral sense or conscience, as soon as its intellectual powers had become as well developed, or nearly as well developed, as in man.” [1, pp. 68–69].

Ayala [20] believes that in the Darwinian conception, the moral sense is a necessary consequence of high intellectual powers. “Therefore, if our intelligence is an outcome of natural selection, so it would be the moral sense. Darwin’s statement further implies that the moral sense is not by itself directly conscripted by natural selection, but only indirectly as a consequence of high intellectual powers.” [20].

If the moral sense is not a direct result of natural selection, what mechanism could explain its appearance as a consequence of high intellectual powers, or of any other cause, for that matter? Taking these hypothetical thoughts further, could the moral sense be a result of sexual selection?

#### 4. Sexual selection of moral behaviour

Darwin considered that it was difficult to explain the evolution of embellished, ornamental, colourful, and flashy traits that appear to lack a clear utility, such as the male peacock’s tail, by means of natural selection. His observation that many of these traits were related to mating processes led him to elaborate his theory of sexual selection, which he defined in the *Descent of Man* as “the success of certain individuals over other of the same sex, in relation to the propagation of the species” [1, p. 638]. As noted by Paul [21], Darwin believed that such an advantage was the result of two possible types of competition: “In the one it is between individuals of the same sex, generally the males, in order to drive away or kill their rivals, the females remaining passive; whilst in the other, the struggle is likewise between the individuals of the same sex, in order to excite or charm those of the opposite sex, generally the females, which no longer remain passive, but select the more agreeable partners” [1, p. 638]. It must be noted that sexual selection cannot be considered as distinct from natural selection. Ethology and sociobiology provided evidence that such conspicuous traits as the male peacock’s tail have an adaptive meaning. However, sexual selection is regarded as a special kind of mechanism involved in certain selective episodes that drive newly evolved traits.

Darwin believed that sexual selection had profoundly marked the evolution of humans, and he stated that this process not only shaped physical traits, but also cognitive processes and behaviour patterns:

“He who admits the principle of sexual selection will be led to the remarkable conclusion that the nervous system not only regulates most of the existing functions of the body, but has indirectly influenced the progressive development of various bodily structures and of certain mental qualities. Courage, pugnacity, perseverance, strength and size of body, weapons of all kinds, musical organs, both vocal and instrumental, bright colours and ornamental appendages, have all been indirectly gained by the one sex or the other, through the exertion of choice, the influence of love and jealousy, and the appreciation of the beautiful in sound, colour or form; and these powers of the mind manifestly depend on the development of the brain”. [1, p. 641]

During Darwin’s time, the theory of sexual selection did not receive the same amount of attention as the notion of natural selection. Nevertheless, as Paul [21] noted, research on the mechanisms underlying sexual selection and mate choice thrived during the last quarter of the twentieth century, leading to interesting theoretical and empirical developments. The main shift was related to the role of males and females during mate choice: the notion of aggressive males competing to access passive females was gradually abandoned in favour of a view in which both sexes actively prefer and choose potential mates.

As we have seen, several different models have been put forward to explain altruistic and other moral behaviour in humans and other social species. These models are not necessarily incompatible. In fact, claiming that one can explain human moral behaviours with reference to a single evolutionary mechanism would constitute a great oversimplification. In this spirit of arriving at a comprehensive and integrative view of the evolution of altruism, fairness, and other moral behaviour, some authors, like Tessman [22] and Miller [23], have contended that there is evidence that some human moral behaviour evolved through sexual selection to serve display functions, just as sexually attractive physical traits and ornaments serve as signals of health, fertility and longevity. These authors have not stated that sexual selection created moral behaviour. Rather, they claim that sexual selection transformed a set of primate cognitive mechanisms into our uniquely human moral virtues. Also, they have not claimed that sexual selection was the only force involved in this transformation. Its effects must have intertwined with those caused by the other mechanisms we mentioned above.

Miller [23] has presented his arguments with the greatest detail. He begins by reviewing evidence suggesting that many moral traits are sexually attractive. While some moral virtues may be attractive in themselves, the attractiveness of others resides in their function as signals for other desired traits. They may serve as indicators that their possessors are capable of having lasting cooperative relations and of investing in offspring.

From this point of view [22,23], moral virtues and behaviours constitute costly signals. Costly signals are indicators, resulting from natural selection, that usually advertise good genes, good parenting abilities, good long-term relation abilities, or a combination of these. Moral behaviour is a trait exhibited prominently during courtship. During this process, the potential partner evaluates such moral behaviour as generosity, sincerity, empathy, or self-control. Evidence for moral flaws, such as greed, envy, cheating, or lying, is also carefully sought.

It is argued that certain personality traits, mental health traits, and intelligence have a moral or almost moral rank. For instance, given that conscientiousness and agreeableness, two personality traits, are highly valued in long-term mates and are highly associated with partner and parenting traits, Miller [23] concludes that they “are most likely to have been shaped as moral virtues by sexual selection”. Also, it is posited that sexual selection acted upon the evolution of intelligence and mental health, given the fact that statistical tests have shown that they predict a broad range of righteous behaviour. Models of the

evolution of morality based on sexual selection need not posit the presence of moral traits only in one sex, because both male and female humans actively choose their partners.

Miller [23] argues that sexually selected moral traits should exhibit most of a set of 12 features. Their simultaneous appearance in relation to a moral trait would be a clear suggestion of the role of sexual selection in moulding such a trait. There are three groups of such features: genetic; phenotypic; and those related to the sexual selection of moral traits.

#### *Genetic features*

- 1) Moral virtues should be genetically heritable and expressed mostly in adults.
- 2) Interbreeding and increased paternal age should have negative effects on moral behaviour due to harmful homozygous mutations and increased mutation load in sperm, respectively.
- 3) It is expected that alleles that reduce moral behaviour appeared fairly recently, and have not yet been eliminated by the effects of sexual selection.

#### *Phenotypic features*

- 4) Moral behaviour should be conspicuously displayed during courtship.
- 5) Moral behaviour should represent a significant cost to the producer and they should correlate with other fitness indicators, such as mental and physical health, intelligence, body size and symmetry, and so on.
- 6) The absence of moral behaviour should correlate highly with neurodevelopmental disorders.
- 7) Males should exhibit greater variance in their moral behaviour than females, given the level of polygyny observed in our species.
- 8) Conspicuous moral behaviour should peak during young adulthood, when the effort invested in mating is at its peak.
- 9) It is expected that those individuals exhibiting low levels of sexually attractive moral behaviour should attempt alternative mating strategies, including short-term opportunistic mating, deception, harassment or coercion.

#### *Features associated with sexual selection*

- 10) Individuals expressing moral traits should be highly regarded by potential mates, who are expected to actively test whether potential mates exhibit such traits.
- 11) It is expected that individuals who frequently exhibit moral behaviour should mate with each other, and that individuals showing fewer moral behaviour traits have no other choice than to mate among themselves.
- 12) Rivals of the same sex are expected to criticize each other based on moral flaws, such as lying or cheating, whereas gossiping about potential mates with friends should revolve around the mates' moral character.

Although Miller's [23] approach is currently the most comprehensive effort to explore the influence of sexual selection on the evolution of moral behaviour, it still faces some important challenges. The challenges are to: (i) the way Miller and Tessman, among others, have conceived the mechanism of sexual selection; (ii) the breadth of moral virtues they consider; (iii) the relation between the phenotype and genotype of morality; and (iv) the unclear nature of the mechanisms that evolved along the human lineage.

- (i) Although Miller and Tessman speak of the relation between moral behaviour and sexual selection, as Paul [21] has so clearly shown in his review, there are a number of diverse sexual selection mechanisms. First, there are various mechanisms related to mate competition, such as endurance rivalry (extending periods of reproductive activity), scramble competition (locating potential mates before possible rivals), contest competition (using display or combat to eliminate rivals), reproductive suppression (inhibition of rivals' reproductive functions through endocrine mechanisms), sperm competition, or alternative mating tactics. Second, sexual selection encompasses mate choice mechanisms, which can be classified in three groups: precopulatory choice (behaviour that reduces copulation with certain potential mates); postcopulatory choice (female selection of different males' sperm after copulation); and postfertilization choice (using selective abortion or investment in zygotes, embryos or young). Third, Paul [21] notes male sexual coercion as a different mechanism of sexual selection.

Attempts to explain the evolution of moral behaviour by means of sexual selection have not been explicit as to which of the mechanisms, or combination of mechanisms, they actually refer. Nevertheless, from these authors' work, it can be deduced that they specifically regard mate choice as the preferred mechanism related to moral virtues. Kokko [24] defined mate choice as "the outcome of the inherent propensity of an individual to mate more readily with certain phenotypes of the opposite sex (i.e., mating preference or bias) and the extent to which an individual engages in mate sampling before deciding to mate (i.e., choosiness)". In this sense, both male and female humans are expected to prefer mates who exhibit moral behaviour as part of their phenotype, and to spend time assessing such traits in potential mates. It remains to be shown whether sexual selection mechanisms other than mate choice are relevant to the evolution of moral behaviour and how these diverse mechanisms interact among each other.

In addition to there being several mechanisms of sexual selection, there are different models that attempt to explain mate choice [20,23]. The direct benefit model assumes that the choosy individual obtains resources such as food, protection or parental investment. However, some authors have posited that the true benefits are actually indirect, and that the choosy individual gains only good genes for their

offspring. Finally, there are authors who have proposed nonadaptive models of sexual selection, arguing that traits could be favoured merely as byproducts of other processes. Miller [23] and Tessman [22] seem to favour indirect benefits models. Among these, they prefer the handicap view that moral behaviour is costly and, hence must be honest signals of high heritable quality.

Again, it remains to be explored whether moral behaviour susceptible to sexual selection could be explained by either direct benefits models or nonadaptive models. In fact, there is no general agreement as to the superiority of any of these conceptions of mate choice. Kokko [24] noted that the importance of indirect benefits has been questioned in many instances. Given that a relatively long series of processes is required to achieve the genetic benefits, profit can be minimal if one of the events turns out wrong, making choosiness a strategy that could reduce benefits in the long run. Paul [21] noted that mate preference seems neither to be species-specific nor uniform across the individuals of the same species, given that there is a fair amount of variation among individuals' choosiness and preferences. Additionally, it is not clear that what is best for one individual is also best for another one. An individual's choice could be based on the search for potential mates whose genes constitute good complements for their own, and on the avoidance of homozygosity. This would lead to preference for mates carrying different alleles to one's own.

- (ii) The second general issue we noted concerned the range of moral virtues considered by Miller [23] when he argued for the quasi-moral status of certain personality traits, mental health traits, and intelligence. However, the conclusion that agreeableness and conscientiousness were moulded into moral virtues by sexual selection because they are highly regarded in potential long-term partners and associated with positive and partner traits should be taken with caution given the conceptual nature of these personality dimensions. It has been pointed out in several occasions that the big five dimensions (openness, extroversion, conscientiousness, agreeableness and neuroticism) portray personality at the highest level of abstraction. Each of them, including agreeableness and conscientiousness, encompasses a fairly large amount of specific personality traits ([25], for instance). Hence, the big five should probably not be seen as personality traits, but as the names representing sets of concrete personality traits. It thus seems that research into the relation between moral behaviour and personality would profit more from a lower, more specific, level of analysis.

Miller [23] noted that potential mates value agreeableness and conscientiousness positively because they predict good partner and parenting behaviour. However, agreeableness is defined as a prosocial and communal orientation towards other individuals, the presence of altruistic behaviour, tenderness, trust and modesty [25]. Conscientiousness, in turn, “describes socially prescribed impulse control that facilitates task- and goal-directed behav-

our, such as thinking before acting, delaying gratification, following norms and rules, and planning, organizing, and prioritizing tasks” [25]. Thus, rather than both personality dimensions being preferred in mates because they predict attractive behaviour, it seems that they actually summarize a broad variety of behaviour that is attractive to potential mates, rendering the level of personality dimension superfluous. Probably the same can be said about intelligence and mental health.

- (iii) We turn now to the third challenge we noted above, the relation between the phenotype and genotype of morality. Miller's [23] proposal rests on the assumption that there are certain “genes underlying virtues”. However, recent research concerning the genetic bases of language raises serious questions as to whether we can ever expect to find such clear-cut association between moral behaviours and specific genes. The gene *FOXP2*, the mutation of which is known to cause a severe speech and language impairment [26], seems to be involved in the development of corticostriatal and olivocerebellar circuits, including the caudate nucleus and putamen, crucial to sequencing orofacial motor activity. However, there are serious doubts as to the language specificity of these neural circuits. They actually seem to be involved in a number of motor tasks.

Additionally, *FOXP2* is not only expressed in the brain. It also seems to play a crucial role in guiding the development of other tissues – including lungs, some organs in the digestive apparatus and the heart, as in various tissues of the adult organism [27]. Back to the evolution of morality, the expectation of identifying genes which are exclusively related to the organization of neural structures underlying moral behaviour is probably unreasonable. We must expect the genetic underpinnings of complex cognitive processes to be an intricate pattern of relations among various non-specific genes.

With regards to the heritability of the two personality dimensions discussed by Miller, agreeableness and conscientiousness, results from twin studies [28] show that these traits are actually among those influenced most highly by a person's environment. Furthermore, in line with the notion that the level of abstraction at which the big-five personality dimensions are defined make them too general to relate to a genetic basis susceptible to sexual selection, Lang and colleagues concluded: “Our results suggest that genetic and environmental effects are not uniform across all facets of a dimension. For example, our data suggest that not all facets of Conscientiousness are influenced to the same degree by genetic factors. Individual differences in Order, Self-Discipline, and Deliberation appear to be largely determined by environmental influences. The implication is that some of the broad dimensions may not be etiologically homogeneous” [28]. Hence, the pattern of heritability of behaviours related to morality also seems to be a complex issue that requires further detailed research.

(iv) The fourth challenge facing any model dealing with the evolution of moral behaviour is the fact that other primate species share with us certain behaviour that has been considered the building blocks of human morality. There is a wealth of data indicating that our close primate relatives are endowed with complex social cognition, engage in reciprocal exchanges, have a sense of equality, have conflict resolution mechanisms, are capable of consolation, show sympathy to others, and express other traits that are related to moral behaviour [29]. Hence, not all forms of human moral behaviour appeared solely at some point during human evolution. Our morality did not appear in a vacuum, it is the result of modifications and additions to an initial state of moral behaviour, that which we share with other primates. Thus, approaches to the evolution of human moral behaviour, whether they are based on natural or sexual selection, should take this fact into account.

## 5. Conclusions

In this article, we have shown why the evolution of altruism and other forms of moral behaviour is not satisfactorily accounted for by means of natural selection alone. In a nutshell, Darwin's main evolutionary mechanism is better suited to explain the phylogenetic history of traits that maximize individual fitness than those that increase others'. Models and approaches such as kin selection, reciprocal altruism, and group selection, that aim to provide the theoretical underpinnings of the evolution of moral behaviour, assume that such behaviour does in fact afford benefits, albeit indirect ones, to the individual, its descendants, or the genes it carries. We have briefly sketched these alternative views, underlining their explanatory power and noting each of their weaknesses.

Sexual selection has recently emerged as a strong complementary explanation for certain moral phenomena and their evolution. Sexual selection operates at diverse biological levels, though in relation to morality, the most relevant of these seems to be precopulatory mate choice, or the restriction of all possible mates to a small set exhibiting certain features or behaviour. Theorists have favoured the perspective that choosy individuals receive indirect benefits, in that the preferred traits are highly costly and, hence, honest indicators of great heritable quality. In essence, it is argued that humans' moral behaviours were shaped by both sexes' preference for mates that exhibited them because they signalled good genes, or good mate or parenting abilities. We believe that this constitutes an appealing and original approach, which has proven to have a great heuristic value, suggesting novel and interesting questions. However, systematic research on the role of sexual selection on the evolution of moral behaviour is fairly recent. This is why there are still many issues to be resolved and limitations to overcome. These have to do mainly with the definition of moral traits, the way they are related to human genetic constitution, the interaction between sexual selection and other mechanisms, and the way the models regard the initial state of the evolution of moral traits. We have suggested some research avenues

that might be helpful in the clarification of such issues and that could stimulate further work in this area.

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