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Primates' fertilization systems and the evolution of the human brain

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Abstract Since the time of Darwin and Wallace, the origin of the human brain has been a controversial issue in evolutionary biology. The development of the human brain has been a matter of dispute between those who attribute it to the forces of natural selection and those who emphasize the role of sexual selection. Building on Darwin's original insights, in this paper we argue that the uniquely human cognitive capabilities are likely to have been initially spurred by sexual selection. We consider the incentive properties of fertilization systems and, pursuing this 'economic' perspective, we compare human gender relations with those of other primates. We argue that, because of its potential egalitarian nature and its consequent quasi-monogamic gender relationships, the human fertilization system is much more likely to have given selective advantages to investments in emotional and rational intelligence, thus favoring the development of many fundamental human capabilities. Even if our brain was initially spurred by sexual selection, after some time, unlike the famous case of the peacock's tail, it proved extremely useful also in the domain of natural selection. Thus, differently from explanations based on the effects of either natural or sexual selection alone, we show that favorable selection complementarities may have had a crucial role in the evolution of the human brain.

Keywords Gender relations · Sexual selection ·
Emotional and rational intelligence

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1 Introduction

Ever since Darwin's and Wallace's contrasting views, the origins of the human brain and of human (rational and emotional) intelligence have been controversial issues in evolutionary theory.

Extant theories relate human intelligence to: (i) the complexity of group life and the consequent advantages of deception and exploitation (the 'Machiavellianism' hypothesis, or the more recent social brain hypothesis: see Whiten and Byrne (1988), and Dumbar (1998); (ii) the increase in life expectancy that enabled the initial investment in the human brain fully to repay its cost (Robson and Kaplan 2003; see also Kaplan and Lancaster 2003); (iii) an innate predisposition to trade, and the subsequent development of the division of labor and tool-making (Ofek 2001); (iv) the role of sexual selection in favoring the evolution of maladaptive traits that, like the celebrated peacock's tail, function as 'fitness indicators' (Miller 1999).

Given the nature of the subject, all these theories seem to have certain merits.[1] However, in this paper we shall argue for another possibility: starting from Darwin's original insight that sexual selection is of fundamental importance in the explanation of the development of emotional and intellectual faculties, we shall seek to support his thesis by comparing the human fertilization system to that of the other primates who share a common ancestor with ourselves.

If we take an economist's point of view, different fertilization systems may favor the development of different kinds of gender relationship. In particular, the human species' unique fertilization system may have created a system of rewards in the domain of sexual selection that led to the formation of quasi-monogamic relations, and as a consequence, gave an initial impetus to the development of our emotional and intellectual faculties, as opposed to the investments in body size or reproductive capabilities made by our closest biological relatives. We shall argue that, after this initial impetus, the relations of complementarity between sexual selection and natural selection may have helped make the process self-reinforcing and irreversible by modifying the marginal costs and benefits of these alternative strategies.[2]

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[1] Even though Miller does not consider the specific characteristics of the human fertilization system and focuses on the most creative features of the human mind, his emphasis on the role of sexual selection is very close to our approach.

Dumbar (1992, 1998) argues that the main selective force behind increased intelligence arises from the complexity of social interactions. Dumbar identifies the complexity of social life only with the size of group but his view is not incompatible with the approach taken by our paper (if we include the human fertilization system among the factors that 'complicate' our social interactions). Our paper is concerned only with the origin of the human brain (or its 'bioeconomics'), but interest in this field has also been spurred by the recent neuroeconomics literature, which studies how neuroscience can inform economics (Camerer et al. 2005).

[2] In game theory, strategic complements are defined in terms of the (positive) sign of the cross-partial derivative, and are illustrated by a standard reference to Bertrand competition (see Vives 1999). The related notion of institutional complementarity (Pagano 2007) and its co-evolutionary interpretation is used to analyze selection complementarities in the last section.

The paper is structured as follows.

In the following section we consider the role that sexual selection may perform in the process of speciation. We argue that, in cases where epistatic relations[3] inhibit speciation, and where natural selection has a stabilizing role, sexual selection may favor the selection of populations better able to cope with the environment. In this sense, contrary to the (perhaps overvalued) case of the peacock's tail, sexual selection may yield positive effects in terms of natural selection as well. If, because of epistatic interactions, natural selection inhibits evolutionary change, sexual selection may produce conditions analogous to those that economists have argued to be useful for 'infant industries', where it is claimed that some sort of subsidy is necessary for their initial take-off.

In the third section we focus on the fertilization systems of humans, gorillas and chimpanzees, showing that each fertilization system entails a different marginal opportunity cost for males seeking to get exclusive access to females. The gorilla and chimpanzee fertilization systems lie at opposite extremes (the harem and the promiscuous solution, respectively), while concealed ovulation and other characteristics of the human system may favor an egalitarian distribution of exclusive access to females.[4]

Unlike the third section, which takes a single male perspective (or from the other point of view regards female choice as the first, standard ingredient of sexual selection), the fourth section explicitly considers the role of male competition. By referring to the well-known hawk-and-dove game, we show how, in each fertilization system, males have different incentives to display a hawkish or dovish attitude towards their competitors in trying to acquire exclusive access to females. Again, while the gorilla and chimpanzee fertilization systems make these two species polar opposites, the

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[3] The term 'Epistasis' is often used synonymously with the phrase 'gene interaction' and it is analogous to the strategic complementarities, which, in economics, characterize the interactions among different domains of choices, making the relative value of one strategy dependent on the strategy chosen in another domain. These gene interactions take however two different meanings in genetics. In molecular and biochemical genetics, one gene is 'epistatic' to another if the function of its gene product in a biochemical pathway is conditional upon the success or failure of the other gene operating at an earlier step in the same pathway. In statistical and quantitative genetics epistasis is not a property of a biochemical pathway but rather a population concept describing the relationship between the phenotypic variations among individuals and the genotypic variations among them. 'Epistasis is the between-locus "on-additive" variance for a trait.' (Wade 1992, p. 86). If these interactions are important, 'significant evolutionary advance can take place only after a breaking up of previously existing epistatic balances' (Mayr 1988, p. 471).

[4] Throughout the paper, concealed ovulation is taken to mean the broad set of circumstances related to females' extended and selective receptivity (Diamond 1998). Thus interpreted, the contrary claims that concealed ovulation is not a rare trait in the animal kingdom (Pawlowski 1999), or that ovulation is not actually concealed in human females (Roberts et al. 2004), seem to miss the point. Species where females are receptive only during fertility cannot be said to have concealed ovulation, and David (2001) shows how human females were consistently mistaken about their fertility periods until these were recently clarified by modern science. Rather, our interpretation is in line with the established anthropological literature on the subject, where the selective advantages of concealed ovulation range among increased male cooperation (Etkin 1963), increased parental care (Alexander and Noonan 1979), and decreased infanticide risk (Hrdy 1979). According to Sillén-Tullberg and Moller (1993), concealed ovulation evolved first to reduce infanticide, and then facilitated the evolution of monogamy. However, to be noted is that the gorilla and chimpanzee fertilization systems can be seen as different solutions to the same adaptive problem of males' violence on infants, either by completely clarifying paternity issues (the case of gorillas) or by completely confusing them (the case of chimpanzees).

human fertilization system may entail quasi-monogamic arrangements that are much more demanding in terms of emotional and rational intelligence.

The fifth section introduces the concept of selection complementarity. We show how complementarities between natural and sexual selection may give rise to multiple equilibria where the marginal advantage of one trait over another in one selection domain depends on the characteristics of the selection process in the other domain. We thus point out that, while in principle the complementarity of the two domains implies that causation can operate in both directions, sexual selection had a decisive role in the development of the human brain. A focus on the co-evolution between natural and sexual selection seems to offer the most promising approach to these complex problems.

2 The 'sexual selection subsidy' and the development of the human brain

Sexual selection involves striking runaway effects, such as the growth of the peacock's tail, which have no direct (even negative) value for the species in terms of its successful adaptation to the natural environment, and which are instead related to a costly signaling of fitness, which helps keeping out fakers (Zahavi 1975; see also Hamilton and Zuk 1989).[5]

While the literature has stressed the possible contrast between sexual and natural fitness, we would like to point out that, in very relevant cases, sexual selection may also be useful in obtaining adaptive advantages in terms of natural selection which would not occur if only the latter were at work. In other words, in this paper we consider a case opposite to the runaway effect associated with the peacock's tail. In the peacock's tail case, the advantages in sexual selection are a substitute for forgone advantages in natural selection. By contrast, the focus of our paper is on the complementarity between sexual and natural selection.

In the case of complex organisms, fitness-improving speciation can be easily inhibited by the epistatic relations existing in their genotypes. These epistatic relations—which are in some way equivalent to strategic complementarities—entail that complex organisms may be trapped in some of the many possible, and often inefficient, multiple 'Nash equilibria'. While each characteristic of the species is optimally adjusted, given the other characteristics, a change in two or more complementary characteristics may, in fact, lead to the formation of a new species better adapted to the environment. In this situation, the pressure of natural selection may have an inefficient stabilizing role for the incumbent species because it may eliminate the individuals of a population that, because they have changed only one characteristic, fall into a 'fitness valley'. The latter is the valley separating the present local peak from the new higher peak, and

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[5] 'Peacock's tail competition' helps indirectly the species to cope with the environment by selecting efficiently the males with the fittest genes. The overall effect is doubtful. The same long peacock's tail, which may make it more difficult escaping from predators, has enhanced the overall fitness of the species by helping to select the best genes.

it may be a prohibitive obstacle when adaptation to the environment involves change in the complementary characteristics among which these epistatic interactions occur.[6]

Owing to the characteristics considered above, speciation in sympatry[7] is considered to be rather difficult. Allopatric and peripatric speciation may be required to render the continuity of the evolution associated with the Darwinian theory consistent with the long period of stasis[8] and the sudden changes that have characterized the evolution of many species.[9] There is another possibility, however: that the runaway effects associated with sexual selection bring about a major change in the situation of stasis that characterizes the notion of punctuated equilibria (Eldredge and Gould 1972). In this case, a change in one characteristic would not be eliminated by the forces of natural selection because it increases the fitness of the individual in terms of sexual selection.[10] By contrast, owing to natural selection, other complementary characteristics may later adjust to this change (made irreversible by the 'sexual selection subsidy') and make it more useful to cope also with the natural environment.

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[6] The point is clearly very close to the problems raised by the shifting balance theory (Wright 1931) and amounts to a further illustration of the fruitfulness of a bioeconomic perspective. Also, according to Wright, natural selection could give rise to multiple local peaks where each adaptation was optimally adapted to the other, blocking the change to higher peaks. In Wright's framework, genetic random drift performed a role analogous to the 'trembling hand' of the players which, many years later, was used to justify the elimination of inferior Nash Equilibria (Selten 1975).

[7] Speciation (i.e. the set mutations leading to the formation of a new species) occurs in sympatry when the new species emerges in a location where the old species shows a very high population density. Peripatric speciation and allopatric speciation refer to cases where the new species emerges in locations characterized by a low population density of the old species and, sometimes, isolated by geographical barriers.

[8] Darwin (1859) was well aware of the problem but attributed the discontinuity to the incompleteness of the fossil record. This explanation became increasingly unconvincing with the progress of field research. The fossil record seemed to show long periods with no major evolutionary change (i.e. periods of stasis) 'punctuated' by relatively short periods of fast and relevant evolutionary change. The theories of allopatric speciation have had the merit to conciliate the continuity following from the Darwinian theory with the jumps found in the fossil record. If complex organisms are characterized by numerous epistatic relations, single mutations may decrease their fitness even in the cases in which, when coupled with other mutations, they may eventually lead to a superior rearrangement of a genotype. One-by-one mutations can only occur in relatively isolated locations (allopatry). If the new species moves back to the centre of the old species and replaces it, the fossil record is well likely to show an evident discontinuity.

[9] The case of allopatric speciation (i.e. the emergence of new species in isolated locations) is similar to an infant industry theory of the firm where new organizations can be established only if, at an early stage, some protective barriers exist. On the fruitfulness of the analogy between species and firms see chapter 9 of Ghiselin (1997). Pagano (2001) considers a similar analogy and observes that, in economic history as well, the 'speciation' of new organizations if often of an allopatric nature. We shall see that sexual selection may provide an alternative way to subsidize 'infant industries'.

[10] What matters is the overall reproductive advantage due to the different types of selection. The latter cannot be distinguished according to their effects, which may be same and/or go in opposite directions; rather, they should be related to the characteristics of the selective agent (the one which makes the selection). For instance, in most species the dimorphic nature of horns (i.e. their different sizes and characteristics in males and females within the same species) shows that their development has been mainly due to sexual selection and, in particular, to male combats. However, they also have also a positive fitness value in terms of natural selection in fighting predators, although they may have the disadvantage of restricting their possessors' mobility (Ghiselin 1974, p. 135). Whilst the effect may be the same (the development of the size of the horns) the different forms of selection can still be distinguished in terms of the different selective agents, these being the forces active in the environment in the case of *natural selection*, a mate or a rival in case of *sexual selection*, and humans in the case of *artificial selection* (Ghiselin 1974, p. 130).

In this paper, we consider the possibility that we differ from other species because our peculiar rules of sexual selection have helped us to 'unfreeze' our genotype and break the many complementary characteristics that inhibited the development of a large brain. The 'sexual selection subsidy' is likely to have been necessary for the early evolutionary stage of the human brain until other complementary characteristics adjusted and made convenient its large size. These new specific human characteristics, complementary to our large brain, are likely to have included: (i) the menopause (Williams 1957; Diamond 1998), which establishes an optimal cut-off time for women, given their high risk of death during delivery and the dependency of the existing children (both phenomena due to large brain size), (ii) increased length of human life, so that the huge initial cost of investment in the brain is repaid (Robson and Kaplan 2003), (iii) cultural selection and the accumulation of culture (Boyd and Richerson 1985); and (iv) the acquisition of the technical and scientific knowledge that evinces the enormous advantages of our brain.

Thus, in the case of the human brain, the runaway effect that often characterizes sexual selection later proved useful in terms of natural selection, increasing even further the advantages of evolving in that direction. Just as male peacocks kept increasing their tails because this attracted more females at the same time keeping out fakers, so humans kept increasing their brains because sexual selection implied that individuals with more developed brains could attract more partners and defeat their social competitors.

However, here the similarity stops. The human fertilization system is based on female concealed ovulation and implies that the ability to make commitments (and all the related social and communication skills normally regarded as implying a sophisticated view of other people's minds) is crucial in finding good mating partners and cooperating with them in exclusive relations. Unlike the peacock's tail, these brain-intensive capacities cannot be a cause of sexual dimorphism (i.e. distinct traits for males and females within a species). They are intellectual skills stemming from the practice of sophisticated emotional relations which involve both women and men with equal intensity.[11]

Moreover, the peacock's tail only proved useful in attracting partners; it was a disadvantage in dealing with nature and, in particular, in escaping from predators.

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[11] However, this outcome is not simply due to concealed ovulation; it results from other characteristics of the human fertilization system as well, such as an active female choice among the potential male partners. Female orangutans 'have no external sign of ovulation but they develop pale labial swellings during pregnancy' (Rodman and Mitani 1987, p. 146). However, in this case, concealed ovulation may have produced a rather tragic result: since non-pregnant females can always be fertile and concealed ovulation makes exclusive access very costly, males constantly seek to force mating. In spite of these very promiscuous arrangements, both males and females lead solitary lives, and males, because they have no control over the transmission of their genes, furnish no form of individual or collective parental care. Females resist most attempts at mating but are (rarely) successful in doing so only with the smallest sub-adult males. This may (ironically) suggest that female 'may exercise choice in mating'—a doubtful hypothesis that is 'currently debated' (Rodman and Mitani 1987, p. 150). The orangutan fertilization system has encouraged high sexual dimorphism (because male size may favor reproductive success) and limited investment in the development of emotional and rational intelligence. The orangutan case shows that concealed ovulation had such an important effect on the development of human faculties only because it was coupled with other traits, including a sophisticated form of female receptivity, or in other words, a highly developed form of female choice (see footnote 3).

By contrast, when our brain was complemented by other characteristics and empowered with the cumulative accumulation of knowledge, it gave us an immense advantage even over our closest relatives like chimps and gorillas.

3 The costs and benefits of exclusive sexual access

Our closest relatives happen to have fertilization systems that lie at opposite extremes.

Gorillas are characterized by a mild advertising of fertility, which occurs over a relatively short period. This prompts control over females,[12] the development of harems, and investment in body size in order to win females. Mildly advertised ovulation favors the monitoring of harems, because it furnishes quasi-private information to the dominant male controlling a given territory. The dominant male can easily know which females should be inseminated and controlled without attracting too much attention from the other males. The competition with the latter is mainly in physical strength, and this has given rise to an enormous difference in body size between males and females (typically, the weight of a male is about twice that of a female). A visible and paradoxical (though perfectly consistent with economists' concerns about the inefficiency of monopoly) result of gorilla male dominance is the very small size of their penises and, especially, of their testes.

That chimpanzees lie at the opposite extreme is immediately testified by the remarkable investment that has gone into their male testes, which are about three times the size of a gorilla's,[13] and also by the small difference between male and female body size (which is even smaller than in humans). Female chimpanzees engage in very long and evident advertising of fertility, which makes the costs of monitoring a harem very high. Moreover, because of the public and stimulating nature of the female fertility signal, exclusive access to a single female is prohibitively costly. Chimp society is sexually highly promiscuous. Fighting, or seeking to develop relationships, have high opportunity costs in terms of the only activity that really determines the males' reproductive fitness. Investing in testis size is more advantageous than investing in body size (or in brain size).[14]

In some respects, the human fertilization system occupies an intermediate position. But this is not because human females emit fertility signals of intermediate intensity: indeed, intermediate signals may be unstable because they neither ensure an

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[12] However, females also seem to exercise choice (even if the bases on which they choose males are still poorly understood). In any case, 'once a female finds a suitable male, she may remain with him for many years' (Stewart and Harcourt 1987, p. 163).

[13] The average size of testes is 120 g against the 35 g of the gorilla. Note that when they are compared to the weight of the body they are ten times bigger (0.3% in the case of the chimpanzee and 00.3% in the case of the gorilla). See Gribbin and Cherfas (2001, p. 170).

[14] Observe that the information structures, which are available to identify fertility, can explain the different gender and social relations which characterize chimps and gorillas. From this point of view, our approach is very close to the spirit of Landa and Tullock (2003) who relate the different social organizations of ants and honeybees to the different information structures which are available to identify group membership.

abundant supply of males nor grant exclusive access and incentives for parental care. By contrast, concealed ovulation implies a cost of exclusive access to females that places it in-between a strong and a weak signal.

Unlike female gorillas' weak fertility signals, concealed ovulation makes exclusive access very costly, because it makes unclear to the male which female is worth his attentions and his monitoring effort. Thus, concealed ovulation hampers the formation of gorilla-type harems and decreases the evolutionary fitness of the related hawkish investment in body-size. Unlike the strong and public chimp fertility signal, concealed ovulation makes exclusive access to females possible (although at a cost well above that sustained by the gorillas). By contrast, concealed ovulation can favor the creation of long-term quasi-monogamic bonds between a male and a female. Since every female (including the present partner) can in principle be fertile, additional exclusive access is costly. Each male has little information about the fertility state of the new partner and of the present partner, both of whom are equally likely to be fertile. Under the human fertilization system, exclusive access can be only gained by reciprocal commitments requiring huge investments in rational and emotional intelligence. It involves the development of many of the skills that make us human: our capacity for and the interest in communication, ability to make (and break) deals, willingness to share, and propensity for joint parental care.[15]

In a single-male perspective, the fertility signals of these three primates imply different marginal costs (MC) and marginal benefits (MB) in gaining exclusive access to females, and hence different optimizing choices.[16] A mating system can be considered an equilibrium in which the 'quantity' variable is a single male's exclusive access to his fellow females, and the 'currency' of its costs and benefits is 'fitness', that is, the total offspring. While the marginal benefit of exclusive access can be assumed to be always positive but decreasing in the number of females, and roughly equal for all the three species considered,[17] the 'technology' of fertility signals determines radically different cost functions. This is shown in Fig. 1, where CMC, HMC and GMC stand respectively for the marginal costs of Chimps, Humans and Gorillas in gaining exclusive access to females (EA).

Consider in particular the opportunity cost of the 'quantity' variable: that is, the fitness value of the number of forgone alternative mates that a male 'pays' in securing

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[15] We have developed an argument that explains certain social and gender arrangements of a species on the basis of their fertilization system. We find that this argument is more plausible than the ones that moving in the opposite direction by explaining fertilization systems on the basis of the social and gender relationships prevailing in a certain species. However, an interesting topic for future research would be the hypotheses that both directions of causation may have had a role in the evolution of each species, and that fertilization systems have co-evolved with social and gender relations.

[16] Note, however, that different fertility signals can be taken to mean that females choose differently in the first place (Hrdy 1979). Therefore the present analysis introduces the typical ingredients of sexual selection—female choice and male competition—step by step. See the discussion at the end of the section.

[17] We are therefore assuming that there are no differences in reproductive rates (offspring number per birth, births intervals, and so on). Since a species-specific 'revenue' function would make the results more robust, the assumption is simplifying and does not imply loss of generality.

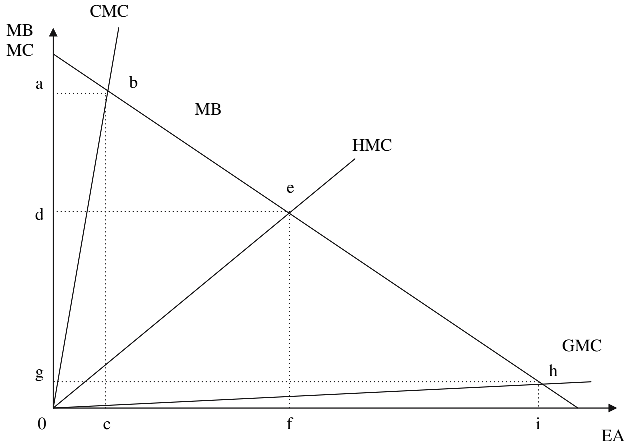

Fig. 1 MB: Marginal benefit of exclusive access, CMC: Chimp marginal cost of exclusive access, HMC: Human marginal cost of exclusive access, GMC: Gorilla marginal costs of exclusive access

exclusive access to a particular female.[18] When the fertility signal is short and weak, as in the case of gorillas, the marginal cost (GMC) increases slowly in the number of exclusive accesses. In other words, when the signal is both time- and space-concentrated, the securing effort does not imply significant losses in terms of alternative mates, and the gorilla male 'maximizes' fitness by choosing a large number of exclusive accesses (the harem solution). Indeed, in the limiting case of perfectly sequential ovulation periods, this marginal cost function actually coincides with the X-axis, obviously implying a zero marginal opportunity cost of exclusive access.

The chimpanzee solution is at the opposite extreme. A chimp male has to forgo a large number of alternative mates in securing exclusive access to a chimp female performing her typically strong and prolonged advertisement of current receptivity. Note again that in the limiting case of a perfect synchronization of ovulation periods, the chimps' marginal opportunity cost (CMC) schedule coincides with the Y-axis, since the resources consumed in trying to secure access to only one female could have been employed in 'producing' offspring with all the other females of the group. Hence the 'promiscuous' solution of zero exclusive access seems to equalize marginal costs and benefits in the normal case.

Independently of sequential or synchronized fertility periods, concealed ovulation in human females implies that the signal is absent: that is, it is time and space indefinite. Assuming that the only female characteristic relevant to the male's interests is fertility, the 45° line represents his marginal opportunity cost schedule (HMC), which reflects the one-to-one nature of the human male choice, and quite clearly the potential egalitarian nature of this pattern of fertility resources distribution. Should one male try to secure exclusive access to one particular female, he will lose the opportunity

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[18] Other specifications of the relevant costs, such as the number of expected fights or the length of expected contestation, could have been fruitfully employed and will be considered in the next section. The opportunity cost specification, however, most conveniently illustrates the 'egalitarian' nature of the concealing of ovulation in human females.

to reproduce with another equally attractive (in fitness terms) female, and so on. The sequential monogamic mating system typically attributed to hunter-gatherer societies (Miller 1999; Hrdy 1999) could easily be an equilibrium under this fertilization system.

As mentioned, implicit in this formulation of the costs and benefits of exclusive access is a trade-off between offspring quantity and quality, which in turn derives from the more general trade-off between mating and parenting effort (Trivers 1972). In this respect, it is also important to note that different fertility signals may be taken to mean different types of female choice in the first place (Hrdy 1979). In particular, assuming that females are generally interested in two males' characteristics—'good genes' and parental care (or defense against predation and strange co-specifics)—and also assuming that there is a trade-off between the two characteristics analogous to that between mating and parenting just mentioned, the above point can be restated in the following way. While chimps females' fertility signals imply a choice only of the former characteristic, and gorilla females' fertility signals imply a choice only of the latter, human females' concealed ovulation and selective receptivity allow for a choice to be made of a combination of the two characteristics. An exogenous shift to what economic textbooks call 'well-behaved' preferences may thus provide another route for an economic interpretation of the first typical element in the standard treatments of sexual selection—female choice. Indeed a 'female choice' interpretation of Fig. 1 may also be supported by observing that the total expenditure that human males pay for exclusive access is the highest one. Gorilla males invest a certain amount in exclusive access, but its cheap price sets reasonable limits on total expenditure (the area 0ghi, in Fig. 1). Chimp males would pay a high price to secure exclusive access but, for exactly this reason, low investment in exclusive access limits their total expenditure (the area 0abc). The 'intermediate' price paid by for exclusive access has maximized our expenditure in the related investment activities (the area 0def).

4 Fertility signaling and sexual competition

If, from the single-male point of view, different fertility signals imply different opportunity costs and choices of the scarce resource, it is by no means surprising to find that they also imply different types of competition.

Indeed, when the signal is mild and short-lived, as in the case of gorillas, not only will competitors be few and concentrated but also fights will be correspondingly short, implying a relatively low opportunity cost in terms of forgone activities. In this situation, an aggressive behavior and the associated investment in physical strength may be the best strategy. By contrast, when the signal is strong and prolonged, as in the chimps' case, expected competitors are so numerous and time-distributed, and expected fights are so long-lasting, that a non-possessive and promiscuous attitude, coupled with an investment in testis size, may prove to be the most attractive strategy.

These two kinds of behavioral response—the 'fight' or 'flight' options[19]—find a natural representation in the well-known hawk-and-dove game originally proposed by

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[19] Pedersen (2004) conducts a very interesting analysis of the proximate causes that may have led humans, and particularly human females, to develop emotional control over rage and fear, and to choose between such options in an appropriate way.

	H	D
H	**(V-C)/2**	**V**
D	**O**	**V/2**

Fig. 2 H: hawk strategy, D: dove strategy, V: value of the resource, C: cost of fighting

Maynard-Smith and Price (1973) to study the behavior of a population of randomly paired animals contesting for a resource of value V and which can behave in an aggressive 'hawkish' way or in a 'dovish' peace-loving manner. Hence, when there are two hawks, each of them has an equal chance of winning the prize, or of losing the cost of fighting, C. However, when a hawk meets a dove, the latter retreats and the former takes the prize for free. Finally, when two doves meet they share the prize (Fig. 2).

In this game, when $V > C$, the only evolutionary stable strategy is the Hawk strategy and the population will end up being entirely composed of hawks. By contrast, when $V < C$ the only ESS strategy is a mixed one with a corresponding hawks' equilibrium fraction of V/C, of course increasing in V and decreasing in C.

The link with the previous argument is evident. Recall the opportunity cost considerations above: A weak and short signal corresponds to a relatively weak competitive pressure and to a correspondingly low opportunity cost of fighting. Hence the harem solution of the gorilla-case can be represented by the hawk-hawk equilibrium (low C, $V > C$). On the other hand, the strong and prolonged advertisement of chimp females implies an extremely high cost of fighting, and the equilibrium population state will be composed almost entirely of doves ($C \to \infty$, $V/C \to 0$).[20]

Even if our account of gorillas and chimps has perhaps been taken to two idealized opposite extremes, it is clear that the obvious superiority of one strategy (dove-type in the case of chimps and hawk-type in the case of gorillas) makes social life relatively simple. Indeed, this simplicity of social life is embodied in the physical competition over testis size (in the case of chimps) and over physical strength (in the case

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[20] The dovish attitude of chimps is only related to sexual relationships. In the case of chimps sexual relations occur in three patterns. 'Possessive mating' involves some hawkish behavior: A male (typically the alpha) uses threats or aggression to prevent other males from mating. 'Consortships' occur when a male (not the alpha) and a female move away from other members of the community and maintain an exclusive mating relationship for a few days. However, in large communities, 70–90% of the matings are 'opportunistic': A male copulates freely in the presence of other males 'with no indication of male-male competition' (Nishida and Hiraiwa-Hasegawa 1987, p. 170). In any case, this dovish attitude is limited to the members of the community. Encounters between different communities carry a risk of severe aggression and they may involve killings, infanticides and subsequent cannibalism. Bonobos (which we group here as doves together with their sister species chimps) provide an even better example of a dovish and particularly promiscuous attitude. For a comparison of chimp and bonobo sexual relationships see Furuichi and Hashimoto (2002, p. 165) who observe that female bonobos copulate less frequently than chimps during the swelling phase, they 'show oestrus for much longer periods' and use 'non-copulatory sexual behaviours to regulate tension or enhance social bonds'. Among bonobos the dovish promiscuous attitude implies that sex, far from creating tensions and combats, is often used to make peace and reinforce social ties (de Waal 1995, pp. 82–88).

of gorillas).[21] One would expect the complexity of social life to increase greatly for fertilization systems characterized by the fitness of both hawk and dove behavior.

We have seen that intentional receptivity signals of females, their consequent bargaining power, and their request for parental care and cooperation, the long term commitments of males and females as well the ability to break them (often concealing the fact from the partner) are all consequences of the human fertility that makes our social life so brain-demanding. We may add in this section that this increased complexity of social life can also be understood in some depth within the framework of the hawks and doves game itself.

The gorilla fertilization system implies a simple rule: behave like a hawk and demand as much exclusive access as you can.

The chimpanzee rule is also simple: behave like a dove and share females, because fighting for exclusive access is pointless.

The human rule is much more complicated: it is certainly worth fighting like a hawk to acquire and defend exclusive access to one female, but a certain amount of dovish behavior may be very advisable beyond that point. Indeed, the human mating system seems to fit the well-known ‘bourgeois’ strategy: behave like a hawk if an owner, and like a dove if an intruder (Maynard-Smith and Parker 1976; see also Maynard-Smith 1982).

While the ‘bourgeois’ strategy is the first and main attempt to explain the rule of respect for property in terms of individual selection, it may suffer from two basic problems that are of particular relevance here.

The first, pointed out by Grafen (1987), is that in cases where some individuals are in a persistent position of non-owners, a sort of ‘desperado effect’ may make the ‘bourgeois’ strategy unstable, pushing the equilibrium towards the hawk-hawk corner. When the cost of fighting is calculated in terms of the expected future reproductive success (EFRS) (associated with fighting and losing, relatively to the EFRS of retreating), it may become so low that the necessary condition for the evolutionary stability of the ‘bourgeois’ solution ($V < C$) ceases to hold. The conclusions of the argument are particularly significant in our context, where the possibility of the above egalitarian distribution of females depends on complicated rules of exogamy and relations between groups: in a wide variety of situations the entire endeavor to explain respect for property in terms of individual selection may be flawed, and closer attention to the role of group selection and of complementary institutions may be required.

The second problem concerns the necessary cognitive prerequisites of the solution itself. According to Hirshleifer (1982), the individuals in the game must know how to play both strategies, and this requires consideration of an additional cognitive cost when determining the viability of the solution. Of course, the same is true, and *a fortiori*, of the specular problem of assessing which strategy the opponent is going

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[21] Typically, the weight of a gorilla male is about twice that of a female, whereas the difference between male and female chimpanzee body sizes is even smaller than in the case of humans. As for testis size, the chimpanzee average is 120 g against the 35 g of gorillas. Note that when they are compared to the weight of the body they are ten times bigger (0.3% in the case of chimpanzees and 0.03% in the case of gorillas). See Gribbin and Cherfas (2001, p. 170).

to play.[22] Moreover, according to Hammerstein and Parker (1982), the ‘bourgeois’ solution may be prone to errors due to imperfect information about possession. As emphasized by Bowles and Choi (2003) with explicit reference to human societies, its successful spread may have required as a prerequisite the co-evolution of institutional elements (like individual property rights) with technological change (the shift from hunting and gathering to agriculture). Such caveats are especially relevant because it is likely that the institutions needed to clarify possession (like ceremonies, rituals, and ‘marriages’), as well as those needed to collectively enforce the above egalitarian rule (gossip, ostracism and even execution), were not fully available until complementary institutions (like food sharing, variance reduction practices, and political egalitarianism) were in place in other related domains of social life (see Boehm 1999; Knauft 1991). Framing these problems can clearly benefit from an analysis of the complementarities between sexual and natural selection.

5 Selection complementarity and the development of the human brain

Since the time of Darwin and Wallace the development of the human brain has been a divisive issue between those who considered only the forces of natural selection (like Wallace) and those who (like Darwin) tried to explain it with the forces of sexual selection.[23] However, the relation between the two mechanisms should be seen more in terms of selection complementarity[24] than as a case of selection substitution. If in some cases, like the peacock’s tail, one may substitute environment-related fitness

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[22] Based on physical attributes, an Assessor strategy dictates behaving like a Hawk if you are bigger than your opponent and like a Dove if you are smaller. This was first introduced by Parker (1974), and further elaborated by Maynard-Smith and Parker (1976). In a manner more similar to our perspective, Panchanathan and Boyd (2003), analyze a ‘Discriminator’ strategy, which enables the players in a public game to assess whether a non-cooperative action derives from a selfish or a punisher strategy. Their aim is to emphasize the adaptations—such as language—that are pre-conditions for the evolution of moral systems based on the notion of indirect reciprocity (see also Alexander 1987; Wilson 1999).

[23] According to Darwin (1879, [2004 edition, p. 687]): ‘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.’ Wallace rejected the role of sexual selection and relied only on natural selection. However, he failed to explain the existence of human intellectual faculties and ended up claiming that, for these faculties, ‘we can only find an adequate cause in the unseen universe of spirit’ (1889, p. 478). On these contrasting views between Darwin and Wallace (see Gould 1980, p. 49).

[24] Selection complementarities are analogous to ‘institutional complementarities’—the interdependencies among the performances of the arrangements existing in different domains, which may make many institutional reforms such a challenging task. In the case of institutional complementarities, individuals choose in each domain the best institutional arrangements, taking as parameters the choices of other individuals. This implies that multiple equilibria may exist and that, in spite of their stability, existing institutional arrangements may be inefficient. Similarly, in the case of selection complementarities, the fitness of each trait in a particular domain depends on the traits that have been selected in the other domains. Economic treatments of institutional complementarities can be found in Landa (1981); Pagano (1992); Pagano and Rowthorn (1994); Aoki (2001); Greif (2006) and Pagano (2007).

for mating success, in other cases, like horns, there is some degree of complementarity between them. Within certain limits, in so far as they do not impair motility (i.e. the ability to move), horns also have a positive fitness in terms of natural selection (Ghiselin 1974, p. 135).

In the sexual and the natural selection domains, individuals are selected according to two different rules corresponding to two different types of selective agents (a mate or a rival in the case of *sexual selection* and forces active in the environment in the case of *natural selection).*[25] Even if the two domains are clearly distinguishable on the basis of the different agents making the selection, the individuals subject to the phenotypic changes associated with a certain type of 'investment' in one domain may sometimes coincide with the individuals investing in the other domain. What matters is that, because of the different nature of the selective agents, the rules by which they are selected in one domain act as parameters in the other.[26]

Assume also that all the individuals acting in each domain derive equal fitness from having a certain trait and consider two domains of 'choices' X and Y, defining respectively the *natural selection* and the *sexual selection* domains. X is defined by two traits $\{X_1, X_2\}$, which influence the natural fitness u of the individuals i 'choosing' their traits in the natural domain X. Similarly, Y is defined by two traits $\{Y_1, Y_2\}$, which influence the sexual fitness v of the individuals choosing their traits in the sexual domain Y. The advantage (disadvantage) of the trait X_1 over the trait X_2 increases (decreases) when the trait Y_1 instead of the trait Y_2 is chosen in the sexual selection domain and, similarly, the advantage (disadvantage) of the trait Y_2 over the trait Y_1 increases (decreases) when the trait X_2 instead of the trait X_1 is chosen in the natural selection domain. We therefore have that the two standard 'supermodularity conditions' (Aoki 2001, p. 226) are satisfied:

$$\text{for agent i}: u(X_1, Y_1) - u(X_2, Y_1) \geq u(X_1, Y_2) - u(X_2, Y_2)$$
$$\text{for agent j}: v(Y_2, X_2) - v(Y_1, X_2) \geq v(Y_2, X_1) - v(Y_1, X_1)$$

Suppose now that the species is able to evolve different characteristics concerning horns and motility traits. Big horns are useful in sexual combat and in defense against predators, but they may be demanding in terms of reduced motility. High motility traits can greatly help successful mating and the escape from predators, but they may be demanding in terms of body size and, in particular, horn ramifications. While both motility and horns can be useful in both domains, assume that the motility traits are 'chosen' in the natural selection domain and horns are 'chosen' in the sexual selection domain.

The first inequality can now be interpreted as follows. The selection of big horns Y_1 in the sexual selection domain makes it more convenient in the natural selection domain to choose traits X_1 involving low motility and high defense capabilities relatively to X_2 (traits associated with high motility and modest defense capability). Horns can easily develop other traits that make them more efficient against predators; and

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[25] On the distinction among sexual, natural and artificial selections see Ghiselin (1974, p. 130).

[26] This parametric behavior also arises in the case of institutional complementarities. See Aoki (2001, p. 225).

other characteristics such as large body size can be helpful in pursuit of the same strategy of enhanced defense capability and reduced motility. The big horns Y_1 (instead of small horns Y_2), chosen by the 'sexual selection agents', are taken as parameters by the selection agents acting in the environment, and they yield an increased advantage (or, a decreased disadvantage) of low motility traits X_1 (relatively to high motility traits X_2).

The second inequality can be interpreted similarly. The selection of high motility X_2 by the natural selection agents makes small horns Y_2 more convenient in the sexual selection domain relatively to big horns Y_1. High motility may enable males to out-compete other males by dispersing more efficiently on the territory, rather than relying on costly sexual combats. Sexual competition may involve further investment in motility traits. Because small horns are consistent with high motility, they are more likely to be selected.

The effect of one trait chosen in one selection domain may not be powerful enough to make another trait preferable in the other selection domain. However, when these effects across domains are sufficiently strong, multiple equilibria may arise, and the species may either evolve low motility and big horns traits (X_1, Y_1) or high motility and low horns traits (Y_2, X_2).[27] When multiple equilibria exist, we can say that X_1 and Y_1, as well as Y_2 and X_2, are *selection complements*.

Consider now that the human brain, too, involves the development of many complementary traits. For instance, it is much more demanding on downsized motility than are horns. Because of their large brains, young babies cannot move autonomously for a long time; nor are they able to cling to the bodies of their parents like other primates. Moreover, large brains impair the motility of mothers during the last period of the pregnancy and during the difficult delivery.

However, if the large brain Y_1 is selected in the sexual selection domain, many traits involving low motility X_1 (such an intensive use of intellectual capabilities) may then be, conveniently, selected in the natural selection domain. The brain itself may be further developed, reducing motility but allowing a cheap reshaping of its capabilities to deal with the natural environment as well. Language skills used in sexual communication can be enhanced to coordinate hunting and defense against predators, while other traits, such as bipedalism, may evolve to transfer and re-adapt organs from motility to brain-intensive activities such as tool making.

Again conversely, if the selective agents in the natural selection domain choose high motility traits X_2, in the sexual selection domain the features which rely on a large brain Y_1 will diminish appeal compared to the traits Y_2 compatible with a small brain.

Also in the case of the brain, therefore, we have two selection equilibria: one equilibrium (X_1, Y_1), characterized by low motility traits and a large brain, and another equilibrium (Y_2, X_2), characterized by high motility and a small brain. And when both equilibria are possible, we can again say that X_1 and Y_1, as well as Y_2 and X_2, are *selection complements*.

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[27] Complex species, characterized by numerous complementarities among the effects of their genes and by the pressure of different selective agents, may remain in one of these equilibria for long periods of evolutionary stasis, which are rarely punctuated by major evolutionary changes (Eldredge and Gould 1972).

In the two cases considered, our argument includes the fact that the same organ (the horns and the brain) can be adapted to work in both the sexual and the natural selection domains. This circumstance is not necessary for the existence of selection complementarities. Many organs may become relatively more valuable in terms of final reproductive fitness when *some other organ* is developed, generating selection complementarities between the two domains. However, the most important complementarities are likely to arise when the same organ selected in one domain can be adapted to perform functions useful in the other domain. The division of labor among different organs is only useful when the same organ cannot efficiently perform more than one function. Otherwise, when an organ can be easily adapted to perform an additional function without interfering with the original functions, the per-function fixed costs of that particular organ are reduced and economies of scope are consequently realized.[28] Consequently, numerous complementarities may arise among different domains, and the 'work' of the selective agent in one domain may have 'unintended consequences' for the agent selecting in the other domain.[29]

When an organ has a positive fitness value in two domains, it becomes difficult to know in which domain it was originally selected. Whilst brains and horns are useful in both domains, we have assumed that they have been selected in the sexual selection domain. Is this assumption justified?

In the case of horns, sexual dimorphism can be taken as evidence for the fact that sexual selection domain has had the prominent role in the development of that trait.

Other cases are much more doubtful, and the human brain must be included among them. In the case of the human brain much cross-subsidization is likely to have taken place between the two domains. However, we have already argued in the second section that a 'sexual selection subsidy' was initially needed because, at an early stage, a large brain may not have been advantageous in terms of natural selection alone. The natural environment is unlikely to be the selective agent able to explain such a major differentiation between humans and the other species.

The emergence of the savanna environment (see, for instance Rapoport 1999; Kaplan and Lancaster 2003) due to climate change may well have created a situation of cognitive stress and thus favored the selection of a large brain. However, the opportunities and difficulties of the new savanna conditions affected many other species as well, which also shifted to forms of co-operative hunting and to a diet similar

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[28] Ghiselin (1978, p. 235) points out that 'where functions do not interfere with one another there is no advantage in the division of labor and its combination is more economical.' As a consequence 'the division of labor is not, as early economists believed, a unidirectional trend, nor an advanced condition' (p. 236). A related observation is made by Pagano (1991), who argues that, unlike the 'minimization of learning' principle formulated by Gioia (1815) and Babbage (1832), the classic Smithian 'learning by doing' principles of the division of labor do not necessarily imply extreme specialization.

[29] According to Hayek (1949), in the realm of social sciences, these unintended consequences or invisible hand explanations distinguish true from false individualism. Here, the Hayekian 'true individualistic' approach holds for the two agents selecting in the two different domains. In particular, for humans, the 'decisions' made by the sexual selective agent have had positive unintended consequences for the natural selection domain. Of course, the 'unintended consequences' of the decisions taken in one domain are not always beneficial for the other domains. Much ecological literature concerns the negative unintended consequences that the humans, the selective agents, acting in the artificial selection domain, have on the other selection domains.

to that of humans. While the environmental stress due to climatic change may have been a major factor in the development of human capabilities, it cannot be the specific element that explains the 'unique major transition in evolution' (Maynard-Smith and Szathmary 1995) whereby humans alone have evolved a language and a culture.[30] After all, humans were not the only species that had to adapt to savanna conditions.[31]

We have already argued that concealed ovulation implies a more stressful and brain-demanding social environment which may help select brainy individuals in spite of their initial disadvantages in the domain of natural selection. Here, we would add that *the way in which the transition to a regime of concealed ovulation is likely to have happened* must have given rise to a dramatic discontinuity which caused endogenous social stress. Unlike the new savanna environment, this stress was specific to the human species and may be a better explanation for the development of the large human brain.

It is indeed highly likely that the concealment of ovulation was preceded by a weakening of the signal of fertility periods. This gradual fading of the evidence of female fertility probably made exclusive access to females initially easier. Humans may have gone through a 'gorilla-type' fertilization system where it was relatively cheap to have stable harems. It is likely that the initial weakening of the signal made it more private for a dominant male and enhanced his ability to control his harem. However, a dramatic discontinuity must have occurred when the signal weakened to the extent that it could not be easily detected even by individuals nearby (and, in most cases, by the fertile female herself). Suddenly, controlling his 'fertility resources' became terribly difficult for the dominant male, who was now unable to know which female was currently fertile. While the initial weakening of the fertility signal probably decreased the cost of exclusive access, after a certain point a further fading of the signal must have

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[30] Commenting on the love songs of gibbons, Darwin explained how sexual selection could explain the evolution of human language. Darwin (1879, [2004 edition, p. 109]) observed how '... some early progenitor of man, probably first used his voice in producing true musical cadences, that is singing, as do some of the gibbon-apes at the present day; and we may conclude from a widely-spread analogy, that this power would have been especially exerted during the courtship of the sexes—would have expressed various emotions, such as love, jealousy, triumph—and would have served as a challenge to rivals. It is, therefore, probable that the imitation of musical cries by articulate sounds may have given rise to words expressive of various complex emotions.' On modern research on the monogamist relations of gibbons see Leighton (1987).

[31] According to Strum and Fedigan (2000) exaggerated stress on the importance of the transition to savanna conditions led in the early stages of primate ecology to an excessive concentration of studies on baboons 'because they were one of the few primates (besides humans) to adapt successfully to the life of savannah' (p. 44). Besides its specific limitations, the emphasis on the common savannah conditions could never explain the dramatic differentiation between human and baboons and, in particular, the dramatic development of human intellectual abilities. The savannah baboon fertilization system fits rather nicely with our analysis. The female 'exhibits a dramatic visual indicator of sexual receptivity many days before ovulation occurs' (Hrdy and Whitten 1987). This visual sign (evident only to surrounding males) allows some access for some younger members of the group before fertility period, while during ovulation the female is monopolized by older and higher ranking members of the group. The fertilization system allows some sharing of females and cohesion of the group. However, exclusive access is easier than in the chimps' case. As expected, while high male–female differential body-size expresses that it is worth fighting for exclusive access, the large testis size is consistent with the fact that society is very promiscuous. Different species of baboons are, however, characterized by different gender relations (Stammbach 1987) related to male or female migration in the formation of new groups—the relation between migration and relative weakness of intra-gender relations is a general pattern of primate societies (Smuts 1987).

dramatically increased this cost. The new situation is likely to have stimulated brain size, linguistic communication and intellectual faculties, not only because (as we have already seen) the new fertility regime demanded these qualities with much greater intensity but also because the abrupt nature of the transition implied a sudden and dramatic social stress. This endogenous social stress presumably generated the specific human selection environment that spurred the development of the human brain. In the domain of sexual selection, intelligence suddenly increased its importance relatively to the other characteristics of the body. As a consequence, in the domain of natural selection, the benefit of investing in brain-size is likely to have increased relatively to other characteristics, such as motility traits, body-size and testis size.

Under the new fertilization system, a new equilibrium, characterized by new selection complements, could come about and be characterized by an intensive use of the brain in dealing with both gender relations and the environment. This new equilibrium may have favored individuals endowed with the capacity to put themselves in the situation of others and with the ability to think ethically along 'Kantian lines'. Human intelligence may have originated together with moral sentiments and, in particular, with sympathy.[32] Being successful required seeing and feeling oneself a member of society. In this way, human intelligence may have co-evolved along with another important characteristic of humans: their consciousness. According to Antonio Damasio (1999, p. 127) 'the essence of core consciousness is the very thought of you—the very feeling of you—as an individual being involved in the process of knowing of your own existence and of existence of others.' This 'very thought of us' may have co-evolved with our ability to see ourselves as members of society and, ultimately, with our inclination to feel sympathy, and sometimes love, for other individuals.

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[32] In *The Theory of Moral Sentiments*, Adam Smith was already well aware of the neurological basis of the feeling of sympathy towards other human beings and clearly grasped the adaptive significance of moral sentiments (Ghiselin 1974, p. 257). For instance, he observed how 'Men of the most robust make, observe that in looking upon sore eyes they often feel a very sensible soreness in their own. . .' (Smith 1759, [1790 edition, p. 5]). His insights have been confirmed by recent neuropsychological research (Decety and Chaminade 2003) conducted with positron emission tomography (PET). In particular, they are consistent with a model of sympathy-feeling that relies on both the shared representation and the affective networks, and that (as Adam Smith had anticipated) is not activated when individuals watch distress associated with inappropriate social behavior.

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