SECOND NATURE

Economic Origins of Human Evolution

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2 Exchange in human and nonhuman societies

Upton Sinclair's novel, *The Jungle* (1906), is a brutally graphic account of the ruthless competition in the stockyards and slaughterhouses of Chicago at the turn of the nineteenth century. Literary observers like Sinclair, and social observers in general, have often appealed to an imaginary animal-like struggle for survival in search of analogies that describe human conduct in the marketplace. The analogy is unfair to humans as much as to animals. In reality, the essential pattern of market activities, perhaps more than any other pattern of human behavior, is marked by the *lack* of analogy with animals.

Exchange, or apparent exchange, among living organisms other than humans is largely confined to the realms of *symbiosis* and *nepotism* (i.e., transfers among members of separate species and transfers among *related* conspecifics, respectively). For human beings these two patterns of exchange are only part of a wider repertoire that includes a remarkable addition in the form of *mercantile exchange* (transfers among conspecifics at large). A preliminary survey of these three patterns of exchange will be given in this chapter.

Adam Smith's zoological digression

Adam Smith was a younger contemporary and, it is told, a great admirer of Linnaeus (Schabas, 1994:332). The Linnaean version of the "economy of nature" had already acquired some enthusiastic following among English-speaking readers like Erasmus Darwin, another contemporary of Linnaeus (and grandfather of Charles), who cast the Linnaean system into verse under the title *The Botanic Garden* (1789). Smith's main concern, however, was the man-made "political economy." It was natural for him to point out a fundamental distinction (one of many) between the two systems:

> Nobody ever saw a dog make a fair and deliberate exchange of one bone for another with another dog. Nobody ever saw one animal

> by its gestures and cries signify to another, this is mine, that yours; I am willing to give this for that. (1976:17)

This remark was meant to emphasize – by *lack* of analogy – the unique *manner* in which exchange operates in human affairs. It denies neither the existence nor the prevalence of exchange elsewhere in nature. "When an animal wants to obtain something either of a man or of another animal it has no other means of persuasion but to gain the favour of those whose service it requires," he states and adds the pivotal insight: "Man sometimes uses the same arts with his brethren" (1976:18). In other words, Adam Smith suggests two distinct mechanisms of exchange. First, a fairly formal mechanism exclusive to humans that operates "by treaty, by barter, and by purchase" (1976:19). The second is a universal mechanism common to humans and animals, relying – as Adam Smith saw things – on benevolence induced by begging, essentially, on emotional currency.

Adam Smith deserves some credit for noticing a pattern of begging in animal exchange. Manifestations of infantile and submissive modes of behavior (typical of mammals and birds) are prevalent between the young and their parents, between mating partners, and among members of packs, flocks, and other group formations in which members react to one another on the basis of individual recognition. The most obvious examples among mammals include some free-living relatives of the domesticated dog (wolves, foxes, bush dogs, and above all, African wild dogs) and to a lesser extent man's own relatives (the great apes and other primates). It does not take long to recognize the interplay of these preadaptations of begging and submissive behavior in the relationship between dogs and man, a relationship Adam Smith used as an illustration.

The main difficulty with Adam Smith's account of animal exchange, however, is that it relies on sentiments. Counter examples are easy to come by. Modern observers of animal behavior may call attention to instances in which exchange operates flawlessly by rigid stimulus-response mechanisms, or by outright reflex, rather than by cognition and sympathy. Little or no begging or benevolence is evident in the exchange between a bumblebee and the plant it pollinates or, for that matter, in exchanges among workers in a colony of social insects. Nestmates in a colony of ants, for instance, typically exchange liquid

food through regurgitation induced by a recipient touching her forelegs to the donor's head. A casual observer may view the event as an encounter between sisters that have the capacity to express and compassionately attend to each other's needs. However, as Hölldobler and Wilson report, the processes can be simulated mechanically by touching the same spot on the donor's head with a fine human hair. The ant will respond by regurgitating in front of its human handler (Hölldobler and Wilson, 1994:51). Evidently, a regurgitating ant scarcely exceeds the level of compassion expected of a vending machine. Exchange is effected, in this instance, by some sort of a vomit reflex rather than by emotional currency.

Adam Smith's skills as an observer of animal affairs apparently fell short of his skills as an observer of human affairs, but his mistakes should not be taken as an excuse to ignore his larger issue. In the end, his main assertions (starting with the one quoted above) echo fundamental evolutionary dilemmas that should challenge observers of humans and observers of animals alike. At issue are the peculiarities and origins of human exchange and, by implication, of division of labor and human diversity. To understand these peculiarities and fully appreciate his evolutionary dilemmas, one needs to refine and sharpen the borderline Smith himself sought to draw between animal exchange and human exchange.

Symbiotic exchange

Symbiosis is the phenomenon of reciprocal and mutually beneficial transfer – or "exchange" – of resources and services across species.[1] Some economists view it as the closest thing to formal trade that involves nonhuman players (e.g., Tullock, 1994:83). Agriculture and, in general, the relationship between humans and domesticated plants and animals is a primary example of *symbiosis*. Obviously, it is hardly an exclusive example.

The most commonly observed examples of symbiosis among nonhuman parties are animal–plant relationships (e.g., between the fig and the

[1] The term *symbiosis* is used here in a restrictive sense. It includes only interspecific relationships that benefit both sides. *Parasitism* and other forms of cohabitation that benefit only one partner are excluded.

fig wasp). Animals and plants best meet the two salient prerequisites of symbiosis: the parties do not compete for the same resources and they tend to make up for each other's shortcomings. Plants typically provide food and shelter in return for pollination, dispersal, fertilization, pest control, and so on. Symbiosis on a grander order of ecological organization takes place, of course, between all animals *as a group* and all (green) plants *as a group* through the exchange of oxygen for carbon dioxide in the atmosphere at large.

Symbiotic relationships between animals are less abundant. A conspicuous example in this category is cleaning symbiosis. Most prevalent among fish and other forms of marine life, cleaning is occasionally observed among land animals as well (e.g., between birds and ungulate animals).[2] Relationships between macro- and microorganisms (e.g., between termites and cellulose-digesting microbial symbionts that live in their guts) are probably more abundant, though obviously less conspicuous. But the most consequential of all the symbiotic relationships is reserved to exchange among microorganisms themselves. It may occur when one cell is engulfed by another, but instead of being digested by its host, the two initially establish a stable relationship of intracellular symbiosis and eventually become fused. In the end, this process of evolution (by infection) results in a new more complex cell. By establishing this process of symbiogenesis, Lynn Margulis (1981) managed almost singlehandedly to resolve one of the greatest mysteries in the history of organic evolution: the breakthrough emergence of cells equipped with organelles. On the whole, the list of ecological phenomena under the heading of symbiotic exchange is open ended, assuming one is willing to use the term *exchange* in a figurative sense.

Nobody can hold Adam Smith liable for all the figurative deflections of the word "exchange." Economists are reluctant to use the term in any but the strict sense (that is, when the transaction is made voluntarily and deliberately by the parties), and symbiotic relationships hardly apply. From an economic point of view symbiosis is little more than a procedure for acquiring resources from the environment, like grazing or, for that matter, mining. It is true that close proximity between "host"

[2] Not counting oxpeckers. Recent work suggests that oxpeckers get a large part of their daily food intake from blood, keeping old wounds in their hosts' skin open, or indeed inflicting new wounds (Weeks, 1999).

and "client" occasionally calls for refined skills of recognition and evasion in case one of the parties is a disguised predator or noxious creature – on this account, the analogy with human exchange is not so easily dismissed. Thus, individual recognition and even individualized pairing is occasionally evident (e.g., in cleaning interactions), apparently, in order to safeguard the approach and close contact between the parties. The essential point, however, is that symbiosis is a racial rather than individual experience. Though all transfers in typical symbiotic exchanges occur between individual organisms, the volume and attributes of resources exchanged are collectively regulated, in the evolutionary sense (and time scale) at the level of populations and species or even higher up in the ladder of organization, rather than at the level of individual organisms – let alone individual transactions. As such, symbiosis leaves room neither for competitive bargaining nor for free interplay of strategic behavior between traders. Exchange in the sense of physical transfer (delivery and collection, reciprocal or otherwise) is exposed to natural selection, but exchange in the strategic sense is largely shielded from it. Little selection pressure is consequently exerted at the level of intelligence of the parties beyond the call of one-sided smart procurement, as distinct from trade which is a two-sided activity. Symbiosis has apparently equipped its participants with the brains of resourceful harvesters rather than with the brains of shrewd traders. Above all, symbiosis is typically confined to the transfer of a particular resource or service in a well-defined environmental setting. In contrast, exchange (as economists make sense of the term) needs to entertain from time to time novel commodities in new settings.

Though symbiosis lacks a strategic dimension, it cannot be completely dismissed as an economically meaningless form of exchange. At least on the grounds of division of labor, a highly relevant facet of Adam Smith's analysis, symbiotic exchange has a fairly compelling economic meaning. The primary function of exchange, Adam Smith emphasized, is to promote the division of labor (mutually beneficial differentiation and specialization of function and form). Symbiotic exchange promotes division of labor between species. It does not promote, however, division of labor among individuals within a species. The task of promoting intraspecific division of labor is left to exchange among members of the same species.

division of labor, and cooperation. Such patterns are most apparent in the behavior of social insects among the invertebrates, and in the behavior of certain species of mammals (including humans) among the vertebrates.

Among nonhuman mammals, there are certain solitary species (notably, the naked mole-rat mentioned above) and at least one wider group of related species (in the *Canidae* family) that routinely rely on all three functions outlined above. The *Canidae* family includes the wild progenitor of the domesticated dog, presumably the gray wolf, and some of its close relatives (foxes, jackals, bush dogs, and the like). Patterns of exchange designed to take advantage of efficient redistribution, division of labor, transport, and cooperation are typical of many species in this

Figure 2.1 **Division of labor in mole-rat mining** A digging chain typical of the naked mole-rat (*Heterocephalus glaber*). A number of naked mole-rats cooperate in digging, performing different tasks. The animal in front is responsible for excavation using its protruding chisel-like incisors for digging. Once a pile of soil has accumulated, it brings both its hind feet forward, collects the soil, and kicks it backwards. The animal first in line behind the digger receives the soil and pulls it behind itself reversing along the burrow, the body close to the floor, until it can pass the soil to the animal responsible for soil dispersal at the tunnel's entrance. It then returns to the front, straddling the line of mole-rats pushing soil backwards, to start a new round. It should be noted that mole-rats easily and rapidly travel backwards in their compact burrows, where turning is often impossible (see also Box 6.1). From Macdonald 1984.

Box 2.2 The wild African dog

The wild African dog (*Lycaon pictus*) is probably the most highly social species within the *Canidae* family, and in many ways the very model of a sociable mammal. Members of this species live in tight packs of closely related males (and migrant females) headed by a single breeding pair. They rear their young and hunt cooperatively, and are generally engrossed in a lifestyle that entails intensive food-transport and food-sharing. A dog in dire need of a meal can acquire food from other members of the pack by means of infantile begging or display of active submission that seems to persuade fellow dogs to share kills or even disgorge recently eaten meat. The roles of donor and recipient alternate frequently among able adults. Such a pattern of food-sharing seems to suggest exchange of status (hierarchical rank in the pack along with prospects of breeding) for food.

Division of labor in energetically costly roles such as parenting, den guarding, and hunting, in combination with the ability to travel at high speeds for prolonged periods of time, enables the pack to operate over vastly extended food-sparse areas (typical home ranges are 450–2000 km^2). Special adaptations for food retrieval and transport further enable them to collect and return available food items to the lactating female and her altricial offspring which, at all times, are sequestered and guarded at fixed locations of maximum safety. Cooperative hunting, in turn, allows these lightweight carnivores (17–36 kg) to extend their sources of food to prey as heavy as zebra (200 kg). Food-sharing enables efficient utilization of large carcasses and the distribution among pack members is generally in tune with the rules of optimal investment. For instance, yearlings (that already represent a large investment of the pack) are given priority in feeding over pups (a smaller past investment). Similarly, the fact that pack members share food and provide care for sick adults represents an attempt to protect and, occasionally, recover even larger past investments (Wilson, 1975; Moehlman, 1989; and Sheldon, 1992).

family, but are probably most apparent in the behavior of the wild African dog (see Box 2.2). Food-sharing among pack members of these wild dogs bears a close resemblance to a form of exchange, not only because the roles of donors and recipients frequently alternate, but primarily because it facilitates an efficient system of transportation and redistribution of perishable resources.

For all their apparent versatility, the privilege of exchange among wild dogs is extended however only to fellow pack members: to close relatives and to breeding individuals who may produce or tend closely related pups. No strangers need apply. The same nepotistic pattern of exchange repeats itself (usually to a lesser degree) in other mammalian and avian species, and (to a much higher degree) in insects and other invertebrates.

While humans associate exchange with subsistence or accumulation of wealth, the key to animal exchange (among conspecifics) is procreation and kinship. Unlike human transactions that are often (but not always!) determined by the merits of the entities exchanged, transactions among animals are almost invariably determined by the identity of the trading parties or by the gregarious function of the interaction between them. Sometimes the entity exchanged completely loses its meaning. The transaction becomes a ritual. For instance, courtship feeding is a form of exchange widespread among mating birds and often no actual transfers of food take place (Immelmann and Beer, 1992:63).[3] As with wild dogs, intraspecific transfers in other nonhuman societies take place only among select members (closely related individuals or mating partners) or in the context of well-defined functions confined to the realms of procreation or kinship. Examples of voluntary transfers outside these realms are rare (see Box 2.3 for some exceptions that prove the rule). It is thus appropriate to qualify this pattern of transactions by the term *kin* or *nepotistic exchange*.

In one form or another, and to different degrees, nepotistic exchange (such as mutual aid among family members) is an integral part of the life strategy for many organisms. Humans are not exempt: In isolated tribal societies it is practically the only way by which exchanges are affected, simply because traders are recognized by kinship. The subtle pattern of

[3] The logic of this ritual is not confined to animal exchange. Reports of people exchanging like items (pigs for pigs) can be found in the anthropological literature, for instance, in reference to the ceremonial exchange system in Melanesia (Strathern, 1992:170).

Box 2.3 Business is business

Altruism in the realms of subsistence is exceedingly rare in nature. In every case known to me it seems possible to claim that voluntary transfers (to unrelated individuals) are associated with life-threatening contingencies, distinct from ordinary routines of subsistence. This includes the case of the vampire bat discussed above (Box 2.1) and most of the examples cited in the literature dealing with reciprocal altruism (e.g., Trivers, 1971, 1985). An instructive example is provided by species of penguins and other birds that practice communal defense of their breeding colonies. These birds may risk their lives fending off predators in an attempt to save temporarily abandoned or orphaned unrelated young, but will remain "indifferent" to the plight of the same chicks when they starve to death (Immelmann and Beer, 1992:64). As Darwin once relayed, a similar pattern can be seen amongst monkeys in captivity:

> Orphan monkeys were always adopted and carefully guarded by the other monkeys, both males and females. One female baboon had so capacious a heart that she not only adopted young monkeys of other species, but stole young dogs and cats, which she continually carried about. Her kindness, however, did not go so far as to share her food with her adopted offspring. (Darwin, 1874: 70-71)

gift-giving described by Marcel Mauss is a typical mechanism of exchange in such societies. According to Mauss (1967) the exchange of goods through gift-giving is not merely a mechanical institution but a moral transaction, bringing about and maintaining human relationships between individuals and groups (i.e., it has implications beyond the goods exchanged, as expected of all transactions in nepotistic settings). Obviously though, kin exchange (including gift-giving) is not confined to isolated societies but practiced side-by-side with formal trade in all market societies.

Traditionally, economists have been reluctant to deal with nepotistic exchange in a systematic way. Alfred Marshall, the most influential neo-

classical economist at the turn of the nineteenth century, was very explicit about this attitude. "Economics," he noted, "is a study of men as they live and move and think in the ordinary business of life. But it concerns itself chiefly with . . . man's conduct in the business part of his life" (Marshall, 1961:14). Yet even Marshall was willing to entertain a bit of nepotism (in what seems to be a moment of weakness) by approving as adequate for economic inquiry issues like "the distribution of the family income between its various members, the expenses of preparing children for their future career, and the accumulation of wealth to be enjoyed after the death of him by whom it has been earned" (Marshall, 1961:24). Ironically, in so doing, he managed to predict with remarkable accuracy the very topics through which the departure of economics from self-imposed compartmentalization was to take place half a century or so later, notably by economists like Gary S. Becker and Jacob Mincer.[4]

Nepotistic exchange is regulated in large part by universal and quite ancient evolutionary mechanisms: kin selection and sexual selection. It thus falls into an area where human behavior and animal behavior closely overlap. The fact that nepotism has not been as much perfected by humans as by certain species of social insects and colonial animals (given a head start of some 300 million years) should come as no surprise. What has been perfected and exclusively practiced by human beings at an altogether different level of social interaction, is not exchange among closely related conspecifics, but exchange among conspecifics at large: *mercantile exchange*.

Mercantile exchange

On the first day of March in 1834 the HMS *Beagle* was anchored off the coast of Tierra del Fuego, "moored by a beautiful little cove," in Darwin's words, "with her stern not 100 yards from the mountain side." The

[4] Rigorous economic inquiry by Becker, Mincer, and their colleagues, has been applied in recent decades to a wide array of "unconventional" topics: discrimination, fertility, parental investment, marriage, home production, crime, addiction, and so on (see, for instance, Becker [1976a,b], and his Nobel Lecture [1993]). Many of these new topics (especially the theory of the family, and to a lesser extent the theory of discrimination) actually deal with *nepotistic exchange*, though the term itself was not used as such.

ways of trade.[9] Human traders seem at times to overcome insurmountable obstacles, not the least of which is a lack of common language. Universal body language and gestures, and makeshift pidgin languages of all kinds, readily fill this gap. From Marco Polo to the crew of HMS *Beagle*, trade by gesture served the great explorers in their encounters with newly discovered civilizations (and it seems to serve well modern tourists in the same predicament). In light of all this relentless indulgence in trade, it is clear that at some point in its long natural history humankind acquired a curious disposition and made it its second nature.

Reasonable observers may disagree on the exact origin of this disposition. There should be little disagreement, however, about the role of trade in modern societies. Exchange (in labor and capital markets) is practically the only way the vast majority of modern humans earn a living and then (in consumer markets) spend it on the necessities of their life. What would it be like if the art of exchange had suddenly disappeared from the face of the earth? It is clear that civilization as we know it would cease to exist in a matter of weeks, if not days, and the bulk of the world's urban population would starve to death in short order.[10] Whether the final number of survivors would exceed or fall short of the number to survive a major nuclear confrontation is anybody's guess.

Contemporary human societies literally live by exchange and die by exchange. The toll claimed by the major famines of the twentieth century – a loss of 100 million lives or so – is almost equal in size to the toll claimed by the major wars of the century. In the public mind, famines are associated with droughts or other natural disasters, essentially, with "acts of God." Some social philosophers may attribute the phenomenon to Malthusian forces, again of no human fault.[11] However, when the data

[9] This is evident in formal provisoes of peace treaties, in the balance of trade between former enemy nations and, most vividly, in widespread and uninhibited exchange between individuals within hours of cessation of hostilities, if not before.

[10] Consider, for instance, the simple fact that less than 4% of the US labor force is employed in agriculture – the exclusive source of food for the entire population. This means that, at any time, more than 96% of the population relies on some form of exchange for subsistence.

[11] Famines (along with war and disease), according to Malthus (1976) are essentially checks on population growth. This Malthusian theory had great influence on scholars in the nineteenth century – Darwin and Wallace included. Its main tenets are fairly applicable to populations of nonhuman organisms. However, so far as human populations are concerned, the predictive power of this theory, at least in its original version, has been

are examined with some care, it soon becomes apparent that all too often famines are artifacts of human inexpediency: ill-advised or deliberate destruction of local exchange systems that in normal times coordinate the distribution of food and motivate its production (Sen, 1981; Devereux, 1993). In most cases of famine, an adequate supply of foodstuffs was piled up, or the capacity to produce it was in place, either in the midst of starving populations or in nearby regions.[12] In fact, export of food from famine-stricken regions has often continued unabated in spite of local starvation. The movement of food from Ireland to England throughout the Irish famine of the 1840s, and from Bangladesh to India in 1974, are two well-known examples (for other examples, see Sen, 1981).

Despite all these disturbances, at the fundamental level of bilateral transactions, mercantile exchange has proven time and again to be an indestructible ingredient of human behavior.[13] The fact that, in the end, the majority of the population in famine-stricken regions manages somehow to survive is the best indication to this effect. Evidently, some elements of the distribution system always remain intact. In this capacity, exchange seems to provide an invisible safety net to most people, most of the time, but does not necessarily guarantee the survival or well-being of any particular individual or group. In other words, it gives all the signs of a structure produced by natural selection.

Tentative conclusions

The following points should summarize the main conclusions from the discussion thus far. First, concerning basic patterns of either symbiotic exchange or nepotistic exchange, we find little difference *in kind* between human beings and animals. There are obvious differences in

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largely discredited by recent trends. Contrary to the Malthusian scenario, food supply has never fallen significantly behind the world population. For most areas of the world – with the exception of parts of Africa – the expansion in food supply has been comparable to, or faster than, population growth (Sen, 1981:7).

[12] This is true, for instance, for the famines in Russia (1934), Bangladesh (1943), China (1958–61), Ethiopia (in the 1980s), and more recently in Somalia and other African countries.

[13] Consider the lesson learned from the European experience with hyperinflation in the post World War I era. Networks of exchange remained largely intact and, against all odds, did not cease to function despite a catastrophic collapse of the entire monetary system.

form, style, and degree, but these differences do not exceed the variation one expects to find across different species. On the other hand, there is no instance in the animal kingdom that nearly resembles the basic pattern and function of mercantile exchange. No species other than humankind relies on free exchange among conspecifics-at-large for its subsistence, no other species is engaged in trade based purely on the merits of the commodities exchanged, and for that matter, no other species settles transactions – as Adam Smith used to say – "by treaty, by barter, and by purchase." With this understanding, his salient observation that "the propensity to truck, barter, and exchange one thing for another" is a human predisposition "to be found in no other race of animals," should be self-evident.

3 Classical economics and classical Darwinism

Darwin and the Scottish economists: The first point of junction

The fundamental economic problem of human evolution

In view of the discussion thus far, the issue is no longer the mere *existence* of a human predisposition to exchange, but its evolutionary *origin*.[1] Unsure of this origin, Adam Smith himself acknowledged (and deflected) in passing an intriguing question:

> Whether this propensity [i.e., to exchange] be one of those *original principles in human nature*, of which no further account can be given; or whether, as seems more probable, it be the necessary *consequence of the faculties of reason and speech*, it belongs not to our present subject to enquire. (1976:17, italics added)

The inception of modern economics was thus accompanied (in 1776) by an evolutionary question preceding by nearly a century the Darwinian notion of evolution itself. Adam Smith probably agonized over this question, though as it seems, had the good sense to abort it in due course. Neither he nor his pre-Darwinian readers could fully comprehend the question, let alone conceive a sensible answer to it. With the advantage of hindsight, however, the question seems to present a challenge of the highest order to the modern study of human evolution: Was exchange an early agent of human evolution, or was it merely a late by-product of previously evolved "faculties of reason and speech"?

With the publication of *The Descent of Man* a century or so later, Darwin had at his disposal a fairly mature notion of evolution applicable to human affairs. At long last a frame of reference for contemplating the dilemma posed by Adam Smith came into being (though a solution was

[1] When Adam Smith, like most economists, uses the term exchange (without a modifier!) he means, mercantile exchange. In the interest of brevity I will henceforth follow the same convention (except where the shorthand invites confusion).

not forthcoming). Darwin made a problematic distinction between the class of evolutionary phenomena associated with "the advancement of man from a semi-human condition to that of the modern savage" and the class of phenomena associated merely with "the action of natural selection on civilized nations" (1874:136). One can only wonder in which class he would place the phenomenon of human exchange. As far as I am aware, Darwin himself provided no clue to his position on the issue – except, perhaps, for one brief comment which I will discuss at a later point . However, the relevant tenets of his thinking and the principles he established shoulder to shoulder with Alfred Russel Wallace do, indeed, have some bearing on this particular issue.

Darwin's self-restraint

Exchange and other niceties of human subsistence play little or no role in *The Descent*, let alone in other written works by Darwin. For whatever it was worth, the influence of economics on Darwin was inspired by abstract ideas rather than by operational applications.

The core insight that links Charles Darwin to Adam Smith is a common recognition of the possibility of design-without-a-designer: the plausibility of spontaneous order. Of course, the clockworks differ and the watchmaker is not the same. There is no reason to turn a blind eye to crucial differences. For instance, to Darwin the individuals are evolving, but the niche that a population occupies in the environment is (more or less) fixed. To Adam Smith the individuals are fixed, but the niche (the economy) is evolving. Similarly, to Darwin the individuals are in a ceaseless state of competition *against* each other. To Smith, the individuals compete (most of the time) for trading partners; i.e., they are largely in a state of competition *for* rather than *against* each other (for other subtle distinctions between the two paradigms, see Gordon, 1989).

Yet, the two intellectual enterprises – "natural selection" and the "invisible hand" – are driven essentially by the same generic idea of competition and optimization (at the level of individuals) and equilibrium (at the level of populations). This metatheoretical connection, combined with the Malthusian theory of population, lends support to a general evaluation pointedly expressed by Stephen J. Gould:

> The sources [of ideas that most influenced Darwin] were many, various, and exceedingly complex. No two experts would present

associated with the human mind. As I have already indicated, the topic was undertaken with great reluctance. Some critics consider Darwin's overall treatment of this particular topic to be highly anecdotal, and he himself considered it (perhaps, intended it to be) incomplete (1874:129). The least impressed by Darwin's approach to the evolution of the human mind was none other than his loyal partner, the codiscoverer of natural selection, Alfred Russel Wallace himself. In a rare outburst of disapproval, he pointed out that

> . . . to prove continuity and the progressive development of the intellectual and moral faculties from animal to man, is not the same as proving that these faculties have been developed by natural selection; and this last is what Mr. Darwin has hardly attempted, although to support his theory it was absolutely essential to prove it. (1889:463)

Wallace was in a unique position to make this observation. Of all his contemporaries, within and without the Darwinian circle, Wallace was the one destined to sense and faithfully divulge the single most embarrassing difficulty confronting his own (and Darwin's) theory.

In coping with the question of the human mind, Wallace, for the most part, was far ahead of his own time. Though little in the way of paleontological findings was available, it was already clear to him and to most experts of his day that the expansion of the human brain represents an unprecedented example of plasticity in geological time. No single major organ has been observed to grow at nearly the same rapid rate (in proportion to the body size of its carrier). However, what was clear to Wallace, but not to most of his contemporaries, was that evolutionary dynamics on the scale of geological time do not carry over onto the scale of recent historical time. Variables in the long run are often short-run constants. If the human brain and its mental derivatives were produced by natural selection then they should be fixed on the average (and limited in variance) going back to prehistoric members of the species and, by implication, across existing human societies and races. With some important reservations, to be discussed later, Wallace accepted this state of affairs as an empirical reality and as a necessary condition for the action of natural selection. For him the faculties of the human mind (latent if not active), like any other species-specific characteristic, were

no subject for development ladders over recent historical events or across existing people. (Assignment of such ladders, it seems, was a popular preoccupation among nineteenth-century scholars.) He ascribed any deficiency in use or performance of mental faculties, if actually observed on the average in a (large) population, to insufficient "means" or "incitements" in the immediate society – that is, to instrumental latency rather than to evolutionary retardation. It comes as no surprise, as we will shortly see, that the existence of an agent unaccounted for by the prevailing description of human evolution did not escape Wallace's keen insight. It was probably the same insight which led the ninety-year-old Wallace, in the last year of his life, to take a solitary position in rejecting the significance of the newly found Piltdown man. It took his younger colleagues 37 more years to reach the same conclusion (when in the end the finding proved to be a hoax).

Darwin's principle of utility: The second point of junction

Any attempt to account for human exchange is absent from the writings of Wallace as much as from the writings of Darwin. But with Wallace the absence is more conspicuous simply because he was ready and willing to ponder the evolution of the human mind without the inhibitions typical of Darwin. There are other differences. Unlike Darwin who was first and foremost an advocate of descent and evolutionary continuity, Wallace was the guardian of natural selection. Certain conflicts between the partners, however rare, were inescapable.

In his autobiography, Wallace lists four areas of conflict between himself and Darwin (Wallace, 1908:236–37). Only one of these rare clashes is of direct relevance to the present discussion: the disagreement about the emergence of human intelligence. The legacy of Wallace was eventually badly marked by this very conflict.[5] At the bottom of this conflict lies a fundamental rule of natural selection: the *principle of utility*. In Wallace's own words,

[5] It is interesting to note that in two of the three remaining issues, the disagreements about sexual selection and about inheritance of acquired characteristics, Wallace was firmly on the defense of natural selection – strictly interpreted – whereas Darwin was in partial retreat. The fourth disagreement dealt with the mechanism of intercontinental seed dispersal as related to arctic and mountain flora.

> . . . none of my differences of opinion from Darwin imply any real divergence as to the overwhelming importance of the great principle of natural selection, while in several directions I believe that I have extended and strengthened it. The principle of "utility," which is one of its chief foundation-stones, I have always advocated unreservedly . . . [and] extended its range. Hence it is that some of my critics declare that I am more Darwinian than Darwin himself, and in this, I admit, they are not far wrong. (1908:237)

Natural selection, according to the principle of utility, can produce neither a structure harmful to an organism, nor a structure that is of greater perfection than necessary for an organism at a given stage in its evolutionary history. Neither overdesign nor foresight are admissible under natural selection. The term *Darwin's principle of utility* was probably coined by Wallace himself (economists who use "utility" in a slightly different sense would probably prefer here something like "parsimony" or "myopic efficiency"). Darwin implied that a single counter-example to this rule would be fatal to his theory (Darwin, 1964:200–2).[6]

Barely a decade had passed since the publication of *The Origin* when Wallace first sounded the alarm bells (1869, 1870). Equipped with the principle of utility, he called into question the applicability of natural selection to the evolution of the human intellect. The human brain, its higher mental faculties (the capacity for mathematics, music, poetry, etc.) and certain physical characteristics (the human hand) – all conveyed to Wallace attributes of greater perfection than was necessary for survival at the time in which they evolved. Wallace soon arrived (perhaps too soon) at the drastic conclusion that humankind's history cannot be reconstructed purely in terms of natural selection. In the end, he relegated the evolution of the human mind to "some agency other than natural selection, and analogous to that which first produced organic life." After some modifications, he confined his stipulation only to "moral and intellectual qualities" and not to "physical forms." Ironically, in his

[6] Perhaps too few authors in the Darwinian tradition, especially in the popular periphery of the literature, have paid heed to this rule by subjecting all their applications to its critical scrutiny. This should not be taken as an indication that the rule is no longer relevant. A vivid reminder can be found in a chapter from a recent work by one of Darwin's best known disciples (Dawkins [1995]). The chapter is entitled "God"s utility function."

attempt to shield natural selection he was willing partly to exempt human evolution from it.

Darwin's deep and understandable anxiety over his partner's unexpected willingness to throw away the baby (continuity) and keep the bathwater (natural selection) is implicit between the lines of the *Descent*. More explicit expressions to this effect are evident in private correspondences: "I hope," he wrote to Wallace when he first learned of his intention partly to exempt humans from the grip of natural selection "you have not murdered too completely your own and my child." Overwhelmed by the sound logic of Wallace's dilemma, or (more likely) bewildered by his solution at the borderline of "heresy," Darwin's most prominent backers (like T. H. Huxley and Asa Gray) were slow to respond in favor of Darwin on this issue. Some (like Charles Lyell) actually showed an inclination to side with Wallace (Bowlby, 1990:394). Attempts by less prominent supporters (e.g., Write, 1870), and by Darwin himself, to resolve the issue within the range of natural continuity produced some interesting specific explanations, but evidently failed to produce an overall plausible explanation capable of removing all doubts. "Any Darwinian has to admit," writes one of the most careful modern students of classical Darwinism in reference to the controversy surrounding Wallace's approach to human evolution, "that we humans present some awkward cases for natural selection" (Cronin, 1991:357). Sure enough, a prominent Darwinian like Edward O. Wilson is unafraid to acknowledge the difficulty in the open:

> Natural selection, in short, does not anticipate future needs. But this principle, while explaining so much so well, presents a difficulty. If the principle is universally true, how did natural selection prepare the mind for civilization before civilization existed! *That is the great mystery of human evolution*: how to account for calculus and Mozart. (1998:48, italics added)

Wallace's dilemma apparently still looms large in the minds of Darwinians and, next perhaps only to the missing gaps in the fossil record, it stands as one of the most important remaining enigmas in the modern study of human evolution.

Separate approaches to a common puzzle

In its most fundamental sense, the dilemma that Wallace failed to resolve neatly overlaps the very dilemma Adam Smith was unable to resolve a century earlier. Adam Smith, as we saw, was missing a clear concept of evolution. Alfred Wallace, on the other hand, was missing a clear concept of human exchange, or at least was unwilling to tackle its subtleties. In this respect the two are paradoxically connected by separate missing pieces to a common unresolved puzzle.

Adam Smith went to great lengths to emphasize the "utility" of exchange (the advantage it confers onto its participants through division of labor), but was ambivalent about whether exchange is a consequence of the faculties of reason (and speech), or whether it is an independent original cause. The ambiguity between these two alternatives is removed, however, when Wallace's argument is brought to bear on the issue. That exchange is a consequence of the human faculties of reason is clearly inadmissable under Darwin's principle of utility (as interpreted by Wallace). Thus, by elimination, the second alternative is more appealing from the standpoint of natural selection. The implication is that exchange was largely an independent agent of evolution and, as such, was more the cause of the faculties of reason and speech than their effect. I do not know if Wallace was altogether aware of the possibility that human exchange could have played an early and distinct evolutionary role in this capacity. An attempt to explore such a possibility might have saved him, however, an awkward detour in his long and unrewarding quest for the elusive origins of human intelligence.

Bootstrap encephalization

Whatever their source, the faculties of reason, speech, and intelligence in general, can scarcely reach levels of perfection deemed unnecessary under market exchange. The mental skills of traders that make strategic exchanges with genetically unrelated members of their own species are constantly challenged in an adaptive sense. The benefits from trade gained by exchanging parties depend not only on their *absolute* level of intelligence, but also on their *relative* level of intelligence with respect to each other. A trader endowed with a relatively inferior level of intelligence is in a position of *comparative* disadvantage. Natural selection,

> about one-fifth or one-sixth of the mean value – that is, if the mean value were taken at 100, the variation would reach from 80 to 120, or somewhat more, if very large numbers were compared. (1889:469)

Moreover, according to his observations and calculations, the proportion of specimens that reach extreme or nearly extreme performance (or size) in a given character is expected to be from 5% to 10% of the population examined (Wallace, 1889:81). Relevant characteristics of animals appear, at least in Wallace's estimations, to be in line with this law – as are probably many human characteristics. What he found to be in defiance of this law was, once again, the human intellect and its higher faculties. The proportion of individuals in any human population that possess the genius of composing a fine piece of music, or the genius of coming up with a deep and elegant theorem in mathematics, seems to fall far short of these expectations. Wallace actually surveyed music and mathematical masters (in one of the "great public schools") as to their students' prospects of reaching such levels of virtuosity. The response was quite dismal. Only 1 in 100 or so students was found to have "real or decided music talent," and, curiously enough, exactly the same small proportion (but not necessarily the same students) were found to possess "the natural faculty which renders it possible for them ever to rank high as mathematicians, to take any pleasure in it, or to do any original mathematical work" (1889:470–71). Such small proportions imply a sizable range and variance in human aptitudes which seemed, at least to Wallace, to exceed by far the regularities of natural selection. According to his interpretation, these observations provide an independent confirmation in support of his controversial stand on the human intellect; namely, that it could not have developed under the law of natural selection. He called it the "independent proof" (1889:469–72).

Any attempt to critically evaluate the "independent proof" should not rule out, I think, the possibility that variation itself is selected under phenotypic plasticity; that is, an adaptive characteristic may include variation (at the phenotypic level) as part of the adaptation itself. In all fairness to Wallace, such a critical evaluation should also recognize the fact that the distinction between phenotypic plasticity and genetic variation was not entirely clear in his time. Under phenotypic plasticity,

a genotype may develop different reversible states for a given character, or a population may develop different frequencies from within a given set of genotypes. In either case, a large degree of phenotypic plasticity entails no more genetic instability than, say, a large degree of sexual dimorphism. With this understanding, we may conclude that what the "independent proof" actually means is not a deviation from the regularities of natural selection, but the possibility that the human mind is subject to a remarkable level of phenotypic plasticity. Indeed, as we shall shortly see, the existence of plasticity over a wide range of human mental and vocational faculties is actually implied, rather than denied, by the very action of natural selection.

The blunder of Epimetheus

The heterogeneity (or inequality) in human native abilities was a source of curiosity and concern to insightful observers long before Wallace. It was certainly on the minds of some ancient Greek scholars as they reflected on nature and human nature. As it seems from the Great Speech of Protagoras, in the Platonic dialogue *Protagoras*, human diversity is part of an evolutionary fiasco (Plato 1978, 320c8–328d2).[7] The narrative is best understood when stripped of its mythical language (as the ancient author in his opening remarks implicitly urges the reader to do). In the idealized Protagorian "economy of nature" all animals were created morphologically and ecologically perfectly adapted "with the view of preventing any race from becoming extinct." The sole error of genesis and, so to speak, the only endangered species is the human being – a hairless, barefoot, helpless creature without means of protection from predators or means of subsistence. A belated compensating adaptation, the stolen *Promethean fire* (i.e., technology, along with the mental and vocational faculties that enable it, but as yet without political wisdom) turns out to be part of the problem as much as part of the solution. Unlike the homogeneous adaptations uniformly bestowed on members of other species, the *Promethean fire* apparently was unevenly and unequally distributed among members of the human species.

[7] The ancient Greeks had, of course, a number of free-spirited competing theories of evolution including, according to Osborn (1929), an embryonic theory of natural selection (advanced by Empedocles and rejected by Aristotle).

Consequently, left to their own devices, human beings could not survive in isolation, and human societies could not survive without institutions that coordinate the action of inherently dissimilar members. The capacity to form and maintain such man-made political and economic institutions was eventually delivered (by Hermes) in the form of morality, a sense of justice, and "the art of government." Unlike Prometheus, Hermes made sure – even double-checked with Zeus himself – that this redeeming adaptation would be fairly evenly distributed among all human beings. The *logos* behind this evolutionary *mythos* is, among other things, a psychological defense of democracy. In spite of all the natural inequality in their ability to master technical arts, all citizens can and should partake of the political art.

For all the difference in substance and style that set an ancient philosopher apart from a Victorian naturalist, there is a certain similarity between Protagoras (probably the man and certainly the dialogue) and Wallace's basic approach to human diversity.[8] Both use (intraspecific) variation in animals as a point of reference for human diversity. By this standard, both find excess diversity in certain human traits but not in others. Excess diversity in the "mechanical arts" is emphasized in the Protagorian dialogue. Wallace found it, close enough, in the "higher faculties of the human mind."

Moving from nature to politics, human diversity was still high on the mind of the ancient Greeks. Close attention to the problem of inequality in human native abilities is evident in the way they contemplated and practiced statecraft and public life. Thus, for instance, the ideal state in Plato's *Republic* – a segregated three-class structure ruled by a philosopher king – is a masterpiece of social engineering unmistakably designed to address this very problem. The Athenian model of democracy under the regime of Pericles (and the influence of his friend Protagoras) addresses the same problem but in quite a different, perhaps more appealing, way. In its ideal form it was conceived as a community of *citizens with dissimilar qualities and abilities*, but with equal duties, equal rights before the law, and equal opportunities (Loenen, 1941:13–14). On a more fundamental level their solution to the "problem" of human

[8] Though the dialogue itself was written by Plato, the most recent consensus among experts is that the Great Speech of Protagoras itself is, for the most part, an authentic reproduction of one of Protagoras' works (see, for instance, Schiappa, 1991:146–148).

diversity relied on two economic institutions: division of labor and exchange.

In practice, and purely as principles of action, division of labor and exchange were perfected in the ancient world before the Hellenic era. For a millennium or so the Phoenicians had dominated the Mediterranean precisely with the aid of these two principles. Their Greek neighbors did not trail far behind. The overall importance of division of labor and the degree of specialization in Greek societies is evident in historical accounts. The following by Xenophon (430–355 BC) refers to shoemaking in "large cities."

> one man makes shoes for men, another for women, there are places even where one man earns a living just by mending shoes, another by cutting them out, another just by sewing the uppers together, while there is another who performs none of these operations but assembles the parts. (*Cyropaedia* 8.2.5, reprinted in Finley, 1973:135)

A full appreciation of this phenomenon would have to wait for its interpretation by Adam Smith (or its implementation by Henry Ford) millennia later.

On their part, the Greek thinkers had largely associated division of labor and exchange with a solution to the problem of human native diversity. Exploring every avenue through which a society of dissimilar members can mitigate the ill effects of its own diversity, they came up with a practical arrangement: Each member needs simply to specialize in a narrowly defined activity, one in which his or her peculiar shortcomings are minimized. Thus, for instance, in Book II of *The Republic* (370a–370c), Plato reminds us that

> . . . there are diversities of natures among us which are adapted to different occupations. ... And if so, we must infer that all things are produced more plentifully and easily and of a better quality when one man does one thing which is natural to him and does it at the right time, and is free of other pursuits.

The fact remains, however, that narrowly specialized producers are never completely self-sufficient. They mostly work for the necessities of others, and they rely on others for most of their own necessities. Consequently, they cannot survive without exchange. "And they exchange goods with

one another, both giving and taking, under the idea that exchange is for their own good" (*ibid.*, 369c). Exchange, according to this ancient chain of reasoning, is a prerequisite of division of labor as much as division of labor is a prerequisite of sheer existence – assuming, to begin with, that human beings are created unequal.

Notably missing from this chain of reasoning is the silver lining: the recognition that division of labor is in itself a productive agent of great advantage, regardless of prior diversity in native abilities among the participants. Consequently, the main implication was kept at bay. So long as division of labor was viewed as a device largely intended to compensate for the ill effects of the diversity of human nature the advantage it affords was grossly underrated. This narrow view of division of labor fits neatly into the mindset of Hellenic philosophers and their need to explain the place of man in the cosmos (or the place of slaves in their own backyard), but had little to do with the real world as Adam Smith saw it.

The second fundamental problem

We have already had occasion to explore the first economic fundamental problem of human evolution raised (without being fully aware of it as such) by Adam Smith in reference to exchange and the emergence of the "faculties of reason." The second fundamental problem refers to human diversity. Obviously, Smith was no longer present when Wallace dealt with these two problems using his own devices (i.e., the principle of utility and the "independent proof"). However, he was surely familiar with the philosophical and practical thinking of the ancient Greeks as outlined above. In his own work, Smith adapted some of their more sensible economic tenets (such as the nexus between exchange and division of labor), but never really used them as touchstones for his own ideas. On the issue of human diversity his departure from the Greek position was clear:

> The difference of natural talents in different men is, in reality, much less than we are aware of; and the very different genius which appears to distinguish men of different professions, when grown up to maturity, is not upon many occasions so much the cause, as the effect of the division of labour. (1976:19)

In other words, he turned the Greek paradigm on its head. At the root of

4 Evolutionary implications of division of labor

Division of labor can evolve (i.e., be selected for) only if all its structures and partaking entities are properly exposed to natural selection. By implication, division of labor can be anticipated to readily evolve only if it occurs at a level of organization *strictly below* the unit of selection. For instance, the division of labor among cells and organs of a single healthy organism is possible largely because the unit of selection typically rests at the level of the organism, if not above it. By its very nature, division of labor is an interaction among two or more partly independent entities that have to share, somehow, the costs and benefits of their common endeavor. They need a system of redistribution. This is provided and best regulated by the designated unit of selection on behalf (and from above) all its constituents. For the same reason, division of labor can evolve only with great difficulty at or above the level of organization of the unit of selection. Ordinarily it does not successfully occur at such levels, and those rare instances where it does are invariably associated with evolutionary innovations of great interest. These innovations are the main subject to be discussed in the present chapter.

Some aspects of division of labor are transitory. They may rise in one generation only to fade away in another depending on the changing environment and, in human society, on the rise and fall of contemporaneous technologies (an example is provided by the ever-changing sexual division of labor in human society – to be discussed in a subsequent section). Notwithstanding such transient manifestations, the fundamental principles of division of labor are universal and timeless. The ultimate advantage afforded by division of labor – production of greater quantities at higher quality with less input over a shorter course of time – is generically applicable. This advantage was as germane to hunting-gathering and to early agriculture as it was to an eighteenth-century Scottish pin factory, or to an early twentieth-century assembly line, and is as germane today in the networks of modern industry as it is in a hive of bees. In all cases, however, the benefits of division of labor in society

depend in large measure on two conditions: on the capacity for specialization and differentiation in function and form, and on the capacity to mobilize large contingencies of constituents in conflict-free coordinated action (i.e., on the capacity for recombination). For the reasons just outlined, both capacities in their ideal form are readily observed in embryonic cells and tissues but are hard to come by in societies of free living organisms. Consider first the capacity for specialization.

The capacity for specialization and differentiation

The capacity for specialization can greatly enhance the advantage of division of labor. By its very nature, specialization displays endless peculiarities that differ from species to species (each according to the tasks important to its survival). All these peculiarities, however, are governed by a common principle: a high degree of task-oriented phenotypic plasticity either in morphology or in behavior, or in both. The degree of phenotypic plasticity is elevated precisely because diversity is selected for, and diversity is selected precisely because it maximizes the benefits of division of labor (through complementarity and synergy). The essential implication, other things being equal, is that the capacity for specialization on the part of individual members of a species is expected to be directly related to the extent of division of labor among them. Whether the necessary degree of specialization is achieved through the capacity for learning or through instinct, or simply through the capacity to produce a wide spectrum of (fixed) specialized offspring, is a question of secondary importance from a broader evolutionary point of view. These modes of specialization and differentiation are not mutually exclusive. All three are fairly enhanced in humans and, to different degrees, in other social species.

The action of natural selection with reference to division of labor provides therefore a plausible explanation, not only for the human propensity to exchange, but also for the exceedingly variant faculties of the human mind, the very question that for centuries troubled separate observers from the ancient Greeks to Smith and Wallace, and beyond. Still, one may actually wonder why the plasticity of the human mind does not carry over to the human body. Strictly speaking, the human body displays little out of the ordinary in morphological plasticity. A

Cover illustration: Lat. 209 *Merchants under the protection of Jupiter* (vellum) (detail) by Italian School (15th century) De Sphaera, Biblioteca Estense, Moderna, Italy/Roger-Viollet, Paris/Bridgeman Art Library

Was exchange an early agent of human evolution or is it merely an artifact of modern civilization? Spanning 2 million years of natural history, this book explores the impact of economics on human evolution. The theory of evolution by natural selection has always relied in part on progress in areas of science outside biology. By applying economic principles at the borderlines of biology, Haim Ofek shows how some of the outstanding issues in human evolution, such as the increase in human brain size and the expansion of the environmental niche humans occupied, can be answered. He identifies distinct economic forces at work, beginning with the transition from the feed-as-you-go strategy of primates through hunting-gathering and the domestication of fire to the development of agriculture. This highly readable book will inform and intrigue general readers and those in fields such as evolutionary biology and psychology, economics, and anthropology.

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