Evolution and the Palaeolithic

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1. Introduction

Until quite recently, evolutionary approaches to hominin behaviour and culture in the Palaeolithic have been practically non-existent. While odd from an evolutionary frame of reference (evolutionary theory arguably being the most objective comparative framework one can think of), this may not be totally unexpectedWhile evolutionary theory is in principle non-teleological, and generally unconnected to complexity or progress, there is no way around the staggering diversity and complexity, and the occasional increases thereof, in the Palaeolithic archaeological record. While culture is more often than not inelegantly distinguished from behaviour (especially when the former is understood in non-material terms), many archaeologists have come to regard culture as an emergent property, which they feel escapes description and explanation in "biological terms"Still, evolutionary approaches have been deployed quite successfully by anthropologists as well as archaeologists, albeit mostly in Holocene American contexts (e.g. Smith, 1991; Simms, 1987), this being primarily due to top-down ways of thinking being more typical of the Anglo-Saxon take on anthropology. In the pages that follow, we will try to review the more common approaches to behaviour and culture build around a well-defined and coherent evolutionary core. To that end, we will discuss each approach's basic tenets and the possibility of using it in a human or hominin context.

The theory of evolution itself has been updated a number of times since its original publication by Darwin (1859), initially by himself in five subsequent editions of *On the Origin of Species* (the sixth and last seeing the light of day in February 1872) in order to accommodate for specific criticisms. Darwin's theory has been aptly summarised as follows: (1) individuals within a species differ in their morphology, physiology and behaviour (*variation*), (2) some of this variation is *heritable*; on average offspring tend to resemble their parents more than other individuals in the population, (3) organisms have a huge capacity for increase in numbers; they produce far more offspring than give rise to breeding individuals, (4) this capacity is not realized because the number of individuals within a population tends to remain more or less constant over time; therefore there must be *competition* between individuals for scarce resources such as food, mates and places to live, (5) as a result of this competition, some variants will leave more offspring than others; these will inherit the characteristics of their parents and so evolutionary change will take place by *natural selection*, and (6) as a consequence of natural selection organisms will come to be *adapted* to their environment. The individuals that are selected will be those best able to find food and mates, avoid predators, and so on (Krebs & Davies, 1993: 9 [*italics theirs*]; see also Mayr, 2001: 120).

Up until the first decades of the 20th century, alternatives to Darwin's evolution by natural selection were able to hold foot (Mayr, 2001: 80-90), but during the 1930's and 40's, his paradigm was confirmed, while the three others (orthogenesis, transmutationalism, and the inheritance of acquired characteristics) were rejected (Futuyma, 1998: 23-24;

Mayr, 2001: 305). Finally, Darwin's populational thinking was integrated with Mendelian genetics in a movement called the *Evolutionary Synthesis* (a.k.a. the *Modern Synthesis*, the *Synthetic Theory of Evolution*, or *Neo-Darwinism*), the foundation of modern evolutionary theory (Futuyma, 1998: 24-25; Ridley, 2004: 14-19; for an overview of the major tenets of the Synthesis, see Futuyma, 1998: 26-28). One of the most important subsequent discoveries included the DNA molecule, opening the way for molecular biology to contribute to the Synthesis. A merging with ecology and behavioural studies was another significant development, as this blend forms the basis of the hypotheses and models that follow below.

2. Niche Construction Theory

2.1 Key concepts

To its engineers (i.e. Odling-Smee *et al.*, 2003), this body of theory stands apart from the others as it is the most comprehensive in its rendering of the interplay between genes, cultural variants, and environment. As we will see, the theory applies to all life forms, to the point of suggesting a more complete account of the process of evolution than that captured by the Modern Synthesis, by drawing attention to the fact that evolution is dependent on two, rather than one selective process, i.e. natural selection as a phylogenetic process, *and* niche construction as an ontogenetic process. Moreover, and in contrast to adaptationist accounts, the authors argue that it has a greater potential of getting accepted by the human and social sciences, where it can be used

> "[...] as a hypothesis-generating framework around which human scientists can structure evolutionary approaches to their disciplines. While the processes involved in human evolution are very complex, this conceptual model reveals particular subprocesses, or suggests specific hypotheses, that are subject to empirical test and can be developed into formal models" (Odling-Smee *et al.*, 2003: 380).

In contrast to the adaptationist view the niche construction approach characterises phenotypes as interacting with their environments (by taking resources, emitting detritus, constructing artefacts, and ultimately, by dying) in such a way as to change some of the natural selection pressures in their own, and in other species' environments. In fact, and to some extent, the environment co-evolves with the organism (Odling-Smee *et al.*, 2003: 1-2). Obviously, in order to modify existing selection pressures, changes need to be persistent in some way (Odling-Smee *et al.*, 2003: 8-9), e.g. in the case when, for each generation, each individual changes its ontogenetic environment in the same way (i.e. repetitive niche construction). This is the case for spiders' webs for example: even after its destruction, spiders build a new one (as they are "programmed" by their genes to do so), resulting in the fact that in the local environment of the spider, a web is always present. As a result, and through natural selection (and evolutionary time), spiders adopt behaviours that are tailored to the presence of the web, e.g. by building dummy spiders to mislead avian predators. Alternatively, the results of the niche construction activities of individuals may (partially) persist in the selective environments of a next generation. An example of this can be found in the form of earthworms, which change the structure and chemistry of the soils they live in. As such, they stimulate plant growth, and subsequent litter formation, which they profit from. Consequently, most contemporary earthworms inhabit soils (their local selective environment) that have been altered by multiple generations of ancestors.

In such cases, a second inheritance system (i.e. on top of the genetic one) is at work, functioning through the environment. It must be stressed however, that this system is quite different from genetic inheritance as clearly, environmental inheritance does not depend on "environmental replicators" comparable to genes (Odling-Smee *et al.*, 2003: 13-16). Secondly, organisms do not inherit information at the molecular level, but rather modified environmental agents that select for their genes, and by doing so determine their phenotype (i.e. an ontogenetic influence). Thirdly, genes and selection pressures altered by biotic action are transmitted between generations by completely different processes, i.e. (sexual) reproduction (which entails a transmission to new organisms once during their life-time, and from parent to offspring) vs. ecological inheritance, which can happen between two unrelated organisms and even (very) different species, within and between generations, and at any moment during the organism's life. Finally, and already implicit in the above, the selective environment of one organism can be modified by any other organism, as long as the latter is ecologically related.

Evidently, according to this reasoning, the concept of adaptation has to be rethought, as according to the classic notion, selection pressures acting on an organism are independent of the adaptations of that organism (Odling-Smee *et al.*, 2003: 16-19), or as Lewontin (2000: 43) has put it,

> "The organism proposes and the environment disposes. The organism makes conjectures and the environment refutes them. [...] the environment poses problems and the organism throws up random solutions. [...] Adaptation is literally the process of fitting an object to a preexisting demand."

However, because of the existence of ecological inheritance, at least some selection pressures acting on organisms are linked to their (niche constructing) adaptations, or put differently, there is

> "feedback [...] between natural selection pressures in environments and adaptation of organisms" (Odling-Smee *et al.*, 2003: 16-19).

The NCT perspective has factual consequences as well as implications for the fields of evolutionary biology, ecology, and most importantly, the human and social sciences (Odling-Smee *et al.*, 2003: 19-28). Some of the impact on evolutionary biology has been mentioned above: apart from the possibility of "feedback", organisms inherit a modified environment associated with certain selection pressures (ecological inheritance). As such, the evolutionary dynamics are "tweaked" to the point that

> "[...] time lags (in the response to selection of the recipient trait), momentum effects (populations continuing to evolve in the same direction after selection has stopped or reversed), inertia effects (no noticeable evolutionary response to selection for a number of generations), opposite responses to selection, and sudden catastrophic responses to selection [...]" (Odling-Smee *et al.*, 2003: 20-21)

can occur. Thirdly, acquired characteristics can now play a (non-Lamarckian) role in evolution as they impact the selective environment through niche construction. These characteristics may result from learning (e.g. in the case of animals), or, in the case of humans, from cultural processes.

2.2. Human Niche Construction

While this "extended evolutionary theory" (Odling-Smee *et al.*, 2003: 35) is certainly important for evolutionary biologists, to the human sciences as well this body of theory is applicable in the form of what they call "triple inheritance theory". Firstly, niche construction constitutes a second role for phenotypes (on top of contributing to genetic evolution by differential survival and reproduction). As the authors argue, this must have been paramount to human evolution. Secondly, niche construction does not need to result directly from genetic variation before it can act on the selection of the latter. Applied to cultural processes in particular, these are not only a product of genetic evolution in the sense that their existence is made possible by the required mental make-up, but they can also *cause* genetic evolution. A well-known human example is the fact that during the neolithisation process, the selection pressure on the synthesis of lactase was changed, such that consequently, adults were able digest lactose. The authors differentiate between four kinds of niche construction, which can either be positive or negative, depending on the effect they have on the genetic fitness of the niche-constructing organism (see Odling-Smee *et al.*, 2003: 47).

Like the orthodox evolutionary view, *Niche Construction Theory* or *Extended Evolutionary Theory* (EET) has been introduced as being applicable to all life forms (including hominins), typically without elevating one species above the other, or conferring a status of uniqueness to humans. However, and in contrast to the Modern Synthesis, it additionally allows to accommodate the exceptional place hominins (and especially contemporary modern humans) occupy in nature, by recognising them as the ultimate niche constructors. In essence, the niche construction perspective entails important consequences for the relationship between genetic evolution and cultural processes (Odling-Smee *et al.*, 2003: chapter 6). For one, because of the feedback described before, humans are no longer mere vehicles for their genes, which at least 'feels' closer to the truth for researchers in the human and social sciences. Secondly, and more to the point, niche construction does not have to result from genetic variation to modify natural selection pressures: humans predominantly modify their environments through cultural processes, made possible by social learning. The environmental results of these processes, be it in the form of artefacts, institutions or infrastructure are very clear, and not only warrant, but as we will see force upon us, a model of triple inheritance.

The consequences on the human or hominin level of triple inheritance or extended gene-culture coevolution become more clear when NCT is compared to how other evolutionary approaches envision the relationship between biological evolution and cultural change (which will be discussed in more detail below; see also Odling-Smee *et al.*, 2003: 242-252). From the viewpoint of the average sociobiologist, evolutionary psychologist, or behavioural ecologist culture is considered either part of the phenotype as much as any morphological or behavioural trait (as such it is commonly regarded as an evolved behavioural trait evoked by environmental conditions), or as the main constituent of human behaviour in the form of cultural universals that are tied into our biological nature. Following standard evolutionary ideas, each generation, natural selection works on populations of phenotypes living in their environment, determining which genes are passed on to the next generation. These genes may be expressed throughout development, and may act on the culture of the population. Cultural inheritance is therefore irrelevant, as cultural diversity, while being based on genetically transmitted mental abilities, is commonly considered as a reflection of the variation found in human ontogenetic environments. The dual inheritance or gene-culture coevolutionary perspective builds on that view by posing that culture is comprised of a set of phenomena that includes ideas, beliefs and knowledge. These are transmitted between individuals through social learning, i.e. cultural inheritance. Importantly, this ideational legacy can influence some natural selection pressures in human environments, and thus the genes that are transmitted to the next generation, even to the extent that culture can be maladaptive in genetic terms (e.g. the concept of celibacy). Human NCT or *Triple Inheritance Theory* is yet a further expansion of that framework as genetic inheritance as the basis of the gene-culture coevolution mechanism is replaced by niche construction. As such, niche construction, resulting from ontogenetic as well as cultural processes, modifies human selective environments and thus acts as a generator of modified natural selection pressures that are passed on to the next generation. This idea differs from gene-culture coevolution to the extent that cultural inheritance can influence genetic inheritance in two ways rather than one, i.e. directly by impacting differential survival and reproduction, and indirectly by contributing to cultural niche construction (and ecological inheritance that includes culturally modified natural selection pressures) (Odling-Smee *et al.*, 2003: 251-252). Importantly, the authors also note that while gene-culture coevolutionary theory is species-specific, this is not the case with NCT: while humans are exceptional in the way they use culture to modify their environments, that (cultural) path merely represents one possible route to niche construction. In essence, humans use culture as the principal mechanism to do what other species accomplish in other ways.

Personally, we believe that the triple inheritance perspective may have a lot to offer to the human and social sciences, especially in such areas as palaeoanthropology *sensu lato*, and especially with reference to previous evolutionary accounts of human behaviour, as indeed, it is able to bring together in a very explicit way

> "culturally transmitted information (ideas), niche construction (behaviour), and ecological inheritance (artifacts)" (Odling-Smee *et al.,* 2003: 263).

There is also a growing recognition of the theory in (Late Pleistocene) archaeology, e.g. evident from the 2010 special issue of the Journal of Archaeological Method and Theory, "Archaeological Perspectives on Niche Construction Theory". However, while its authors suggest that EET should be regarded as a broad conceptual model that is to function as a hypothesis generator by using it to model and empirically test particular sub-processes that have occurred during human evolution (Odling-Smee *et al.*, 2003: 279-281), it may be difficult, in practice, to find a middle ground between using the theory as a general backdrop, and applying it in such a way that rigorous empirical testing of its predictions becomes possible. True, in contrast to other evolutionary approaches, EET deals with phenotypes (human beings) rather than genes, thus lending it a higher compatibility with the humanities and the social sciences than was the case with earlier (adaptationist) accounts for example. It is equally true that EET does not over-simplify human behaviour. Unfortunately, for the Middle to Upper Palaeolithic transition debate for example, there may simply be a lack of data with a high enough resolution and consistency to model the integration of all three inheritance systems. We agree that EET may be of qualitative rather than quantitative importance to studies of human evolution and behaviour of the deep past, but that still does not mean that a switch to EET is, in actual practice, the better move compared to the approaches based on orthodox Darwinism. There may in fact be topics with associated datasets for which the latter offers a good enough approximation so that EET offers little if anything in return for the greater complexity it espouses.

3. Sociobiology

3.1. Key concepts

Sociobiology can be viewed as having descended from ethology, which primarily targeted the causal processes involved in animal behaviour (linking particular stimuli to certain behaviours). Sociobiology shifted the focus to the functional significance of (social) behavioural patterns, asking why organisms had been selected to behave in the particular ways they did (Laland & Brown, 2002: 69). At the same time, the discipline has given rise to the other evolutionary approaches we will discuss. The key concepts of sociobiology emanate from several key figures that can be said to have shaped the field, such as G. Williams, E. O. Wilson, R. Dawkins, R. Trivers and J. Maynard Smith. It is clear from the summary of the process of evolution by Krebs and Davies mentioned earlier that the basic unit of selection, as envisioned by Darwin, was the individual organism. In the hierarchy of organisational levels (e.g. gene, cell, individual, kin group, population, species, ...), it is mainly at the organismic echelon that natural selection produces adaptations (being those features that increase the survival and more importantly, reproductive success of its bearer).

There is, according to sociobiology, another answer to the unit-of-selection issue (Williams, 1966; Lewontin, 1970; Dawkins, 1989; see Futuyma, 1998: 350-354 and Ridley, 2004: 292-312 for an overview): ultimately, the unit of selection may be that entity whose frequency is altered by natural selection. That entity is the gene, as defined by Williams (1966) and Dawkins (1989). Genes are crucial to natural selection and evolution, because they provide the raw material for inheritance between organisms; characteristics acquired by those organisms during their life, cannot be passed on by genetic inheritance. Therefore, it can be argued that the gene has priority over the organism as the fundamental or ultimate unit of selection. The fact that a change of gene frequencies within the gene pool (the collection of genes within the population) goes through the intermediary step of the elimination of inferior phenotypes is irrelevant according to the sociobiological view, as in the end, adaptations that benefit the organism usually benefit all genes inside (while the reverse is not always true, see e.g. kin-selected altruism below). That being said, these two senses in which the unit of selection problem can be formulated seem to be compatible however, as they centre on two different things: the first specifies the entity that generally shows phenotypic adaptations, while the latter represents the entity whose frequency is generally altered by natural selection.

From a point of view, this Selfish Gene model (Dawkins, 1989), gene's eye-view, or gene selectionism, does indeed appear to be more fundamental, and its importance as a heuristic device became more clear after the introduction of the notion of *Extended Phenotype* (Dawkins, 1999; see below). For some behavioural studies however, it can be convenient to treat the organism as the (according to sociobiology, proximate) unit of selection, whereby its behaviour tends to maximise its inclusive fitness (for the definition of the term, see Dawkins, 1999: 179-194; see also Smith & Winterhalder, 1992: 26-28). This equals considering the genes "for" that behaviour maximising their propagation, as envisioned in the gene-centred view. Both models can be applied with equal theoretical validity only in cases where all replicators (see below) within the body in question "cooperate" and where an organism's phenotype is always under the complete "control" of its own genes, uninfluenced by those of other organisms (Dawkins, 1999: 133-155, 248); in the other case, the Extended Phenotype perspective should be taken.

While we have remarked above that EET is able to capture "more" than the sociobiological stance, which only deals with genetic inheritance, the paradigm comprising the Selfish Gene and the Extended Phenotype viewpoints is imbued with a straightforward and parsimonious logic, certainly when advocated by somebody as eloquent as Dawkins. Additionally, Dawkins' account admittedly also has a subjective intuitive aesthetic, a combination Wilson (1998: 57) has called "elegance". The Selfish Gene model is again aptly summarised by Krebs and Davies (1993: 9; *italics theirs*):

1. All organisms have genes which code for protein synthesis. These proteins regulate the development of the nervous system, muscles and structure of the individual and so determine its behaviour;
2. Within a population many genes are present in two or more alternative forms, or alleles, which code for slightly different forms of the same protein. These will cause differences in development and so there will be variation within a population;
3. There will be competition between the alleles of a gene for a particular site (locus) on the chromosomes;
4. Any allele that can make more surviving copies of itself than its alternative will eventually replace the alternative form in the population. Natural selection is the differential survival of alternative alleles.

Taking the Selfish Gene model to its logical conclusion, Dawkins (1999) postulated the existence of an *extended* phenotype, which allows for a better understanding of manipulation (e.g. by chemical means), and evolutionary arms races. In this representation the phenotype is considered to extend into the world at large (which includes inanimate matter as well as other organisms), instead of being restricted to a body, or in other words,

> "An animal's behaviour tends to maximize the survival of the genes 'for' that behaviour, whether or not those genes happen to be in the body of the particular animal performing it" (Dawkins, 1999: 233).

This means that when a

> "[...] behaviour pattern is maladaptive [...] it is maladaptive for the *individual* [...] performing it. [...] the individual performing the behaviour is not the entity for whose benefit the behaviour is an adaptation. Adaptations benefit the genetic replicators responsible for them, and only incidentally the individual organisms involved" (Dawkins, 1999: 249).

Although the gene's-eye view can be of considerable importance on its own, i.e. as a conceptual framework (e.g. in the context of the Extended Phenotype), it gains its biggest momentum when used as a methodological device (together with evolutionary game theory, see Maynard Smith, 1982) to study the key research fields of sociobiology, i.e. kin selection, parent-offspring conflict, and reciprocal altruism (Hamilton, 1964a,b; Dawkins, 1989, 1999; Laland & Brown, 2002: 75-87; Trivers, 2002). The basic idea of kin selection is that close relatives share a large amount of copies of the same genes; consequently individuals that help close kin to reproduce help to increase the frequency of these common genes in the next generation. More technically, selection of this kind of behaviour will occur whenever the fitness cost (c) to the altruist is smaller than the benefit (b) to the relative multiplied by the probability that the latter shares the same gene (r, which is in fact the degree of relatedness), or when $c < br$. From this point of view, parental care (*a.k.a.* parental investment, see Trivers, 2002: 56-122) can be regarded as an example of kin selection. Building on this model, Trivers (2002: 123-153) deduced that as parents are related to each of their children to the same extent ($r = 1/2$), they will, all else being equal, divide their resources equally among them. The children themselves are obviously more related to themselves ($r = 1$) than to their siblings ($r = 1/2$), which entails that they will try to get more (as compared to their current or future siblings) than their parents are willing to provide, hence the potential for conflict. While first developed for and applied to social insects by Hamilton (1964a, b), it has also been used for human social relationships, by Wilson (2000) amongst others.

The concept of reciprocal altruism is another one of Trivers' contributions to sociobiology (2002: 3-55): unrelated individuals do act altruistically towards each other, provided that they can interact repeatedly throughout an extended period of time, and provided that the altruistic act (which is at first nothing but costly to the altruist and only beneficial to recipient) can be reciprocated.

Similar to the gene's eye-view, the importance of game theory is situated on the methodological as well as the conceptual level (Dawkins, 1989; Maynard Smith, 1982). On the one hand, it provides the means to investigate cheating strategies and counterplots deployed in kin selection mechanics (e.g. the differences in parental investment between male and female, see Dawkins, 1989: 140-165), parent-offspring conflicts and reciprocal altruism. In more general terms, it allows to think about evolution when the benefit of behaving in a certain way depends on what other individuals are doing (Laland & Brown, 2002: 85-87). On the other hand, it introduces a new idea of its own, the evolutionarily stable strategy (ESS). Such a strategy (which in principle does not need to be confined to behaviour; it can be extended to any phenotypic attribute) cannot be replaced by another when adopted by all members of the population.

3.2. Human Sociobiology

The adoption of a gene-centred view on phenotypic traits opens up a new way of looking at (social) behaviour. Although Dawkins never supported any direct application of sociobiological methods to humans as he believed culture constituted a realm that could not be described in terms of classic sociobiology (but rather as a consequence of a separate inheritance system driven by memes, Dawkins, 1989: 189-201), Wilson did so explicitly in the last chapter of *Sociobiology: The New Synthesis*, originally published in 1975. From biologists and social scientists alike, understandable criticism arose, including charges of genetic determinism, reductionism, and "story-telling". The latter is definitely a pertinent point, as "just-so" stories are easily come up with in the context of formulating evolutionary hypotheses (see also Weiss & Dunsworth, 2011). Paramount however, is that hypotheses be testable and actually tested; as such, it is a warning that must be heeded when applying any evolutionary approach to human and other animals' behaviour.

The first charge (see e.g. Ehrlich & Feldman, 2003) is actually unfounded as the presence of certain genes is not considered as inevitably leading to certain phenotypic traits. While such claims should be attributed to a flawed understanding of evolutionary theory itself, they undoubtedly find (misplaced) vindication in a convenient and colloquial short-hand that commonly appears in evolutionary studies. The expression "a gene for *X*", where *X* is a physiological or behavioural feature, is easily interpreted as "*X* is inevitable", which is perceived as nullifying our free will (Dawkins, 1982: 9-29). First of all, it is important to understand that "a gene for *X*" actually refers to the effect the gene has in comparison to its allele (see also Dawkins, 1982: 195). Additionally, it is very rare for a single gene to lead to a single phenotypic effect. Thirdly, a phenotype is the outcome of an interaction of genetic and environmental determinants during ontogeny. Therefore, there is no reason why either of both determinants should be considered more important than the other. Fourth, "*Y* has a causal influence on *Z*" in the present context means that, statistically, *Z* reliably follows *Y* in the presence of specific environmental conditions. This is not the same as claiming that *Y* is always followed by *Z*, nor that *Z* only occurs after *Y*: change the environment and the causal relationship may be weakened or overruled. Furthermore, the spectre of genetic determinism may well originate from confounding evolution with development. Genes basically have two characteristics: making copies of themselves and influencing phenotypes. Although the first is a rigid and inflexible process, apart from the occasional mutation; the second is very malleable. As such, gene selectionism by no means can be equalled to genetic determinism. Fifthly, it is of great importance to realise that genes function as blind programmers of phenotypic effects. They control the behaviour of their survival machine only by indirect means: they maintain and build the body, including the nervous system with some hardwired behavioural rules of thumb and a capacity for learning, in order to deal with the unpredictability of the environment and the contingencies in which the vehicle must live and reproduce.

The second criticism, basically the absence of culture in the model, was later addressed by Lumsden and Wilson (1981) by theorising that human behaviour is indeed influenced by culture, but that the probability that specific elements (so-called culturgens) which are transmitted between individuals are actually adopted, depends on the characteristics of the individual's brains. They believed that this occurred because of genetic biases which exert their influence through developmental mechanisms called *epigenetic rules*. The reasoning behind this view is that natural selection has favoured individuals holding epigenetic rules that bias them towards adaptive behaviour, so that some aspects of culture are more easily learned than others. In effect, culture is seen as constrained by the genetic system, while social scientists would rather argue that in the case of humans, genes are in practice inconsequential when studying social relationships. Laland and Brown

(2002: 88-94) place this work in the historical context of what is known as the *human sociobiology debate* to show why it was largely neglected. Nonetheless, it clearly reveals the germs of what was to become sociobiology's conceptual offspring, namely Human Behavioural Ecology (HBE), Evolutionary Psychology (EP), and Dual Inheritance Theory (DIT). The origins of another evolutionary approach, memetics, can also be linked to sociobiology, through Dawkins seminal volume on the *Selfish Gene* (1989, originally published in 1976).

As far as applications in Palaeolithic archaeology are concerned, it is difficult to see how this body of theory could be used. It has been developed to provide an (evolutionary) explanation for an observed social behaviour, so it loses a lot of its power when used in conjunction with a discipline in which social behaviour itself is derived from an incomplete material record, for which the social level is arguably the most challenging to reconstruct. The further into the past one ventures, the more pertinent this problem becomes, so it difficult to see how this body of theory could be used except as a generator of social hypotheses that may not always be testable.

4. Evolutionary Psychology

4.1. Key concepts

Evolutionary psychology (EP) is an approach to psychology that focuses on discovering and understanding the design of the human mind (Tooby & Cosmides, 1997). More in particular, its intention is to describe the psychological mechanisms that underlie human behaviour, and to find out how evolutionary processes have modelled them. This way, psychology was brought under the wings of biology, such that (some) models and concepts developed in the latter could be applied to the former. Tooby and Cosmides (1997) describe the theory as being built on four principles (what they regard as a fifth is not a basic principle as it can be deduced):

1. Our brain is a physical system, which functions as a computer. Its circuits are designed to generate movement (i.e. behaviour) that is appropriate to the environmental (*sensu lato*) conditions we are confronted with;
2. The neural circuitry constituting our brain was designed by natural selection to solve problems that our ancestors faced during our species' evolutionary history. Differently put, they were made to solve adaptive problems (i.e. problems that kept cropping up during our evolutionary history; the varying ways they were solved caused differential reproduction of individuals) in the ancestral environment. The latter is captured more accurately under the heading of *Environment of Evolutionary Adaptedness* (EEA). It is not a specific place or time, but rather the statistical composite of selection pressures for a given adaptation. Different mental adaptations typically have a different time-depth;
3. Our consciousness only represents a minute fraction of our mind; most of our mental processes are hidden from us. Therefore, the complexity of our neural circuitry is underestimated, especially when facing problems that we experience as easy to solve;
4. Different neural circuits are specialised for solving different adaptive problems. This functional specialisation came about because those different units or modules outperform a single, general purpose mechanism. This way, the brain is a collection of dedicated mini-computers, the operations of which are functionally integrated to produce behaviour. Tooby and Cosmides argue that "the only kind of problems that natural selection can design circuits for solving are adaptive problems". Necessarily, they are forced to assume that our ability to solve problems no ancient hunter-gatherer had ever been faced with (which are not all adaptive), such as driving a car, are a mere side-effect of circuits that do focus on adaptive problems.

These tenets have several consequences, as Smith (2000: 28) explains:

1. Valid adaptive (Darwinian) explanations of behaviour must refer to genetically evolved psychological mechanisms linked to specific features of the EEA;
2. "Culture", "learning", "rational choice" and "fitness maximising" are insufficiently modular to be realistic cognitive or behavioural mechanisms without further specification;
3. Contemporary human behaviour often involves responses to evolutionarily novel conditions using modular cognitive mechanisms adapted to the EEA, and hence some of these responses may be maladaptive. Or, as Tooby and Cosmides (1997) neatly put it, "Our modern skulls house a stone age mind";
4. Measuring fitness outcomes or correlates of contemporary behavioural patterns is irrelevant and misleading.

Despite its focus on the psychological mechanisms that produce behaviour rather than (social) behaviour itself, EP is clearly associated with sociobiology. Therefore, the discipline has been subject with the same charges, such as genetic determinism, see e.g. by Ehrlich and Feldman (2003). Basically, the latter comes down to one or another version of the nature-nurture debate, in which the question regarding the origin of our behaviour (genetic vs. cultural) is central. Being mostly a hurdle for non-Darwinian thinkers only, this debate was identified by Tooby and Cosmides (1992: 21) or Pinker (2002) for example as a non-issue: from the viewpoint of EP, the mind was rigged by natural evolution in a way that it becomes easier to learn some (i.e. adaptive) things rather than others (following Pinker, 1994 and 2002 we could call these propensities "instincts"), once the appropriate environmental triggers are provided.

While Ehrlich and Feldman (2003) may have been wrong to blame sociobiologists and evolutionary psychologists for being genetic determinists, they were right to point out the problematic nature of the concept of *environment of evolutionary adaptedness*, or EEA (2003: 88-89), and the associated *Adaptive Lag Hypothesis* (Laland & Brown, 2006). According to Jones (1999: 558-559), humans have both an ethology (a repertoire of species-typical behaviour), and a phylogeny. Combined with the Adaptive Lag Hypothesis, this leads to *adaptive mismatch*: changes of adaptive behavioural patterning are viewed as originating from an alteration of the underlying cognitive mechanisms, which in turn, is made possible by natural selection acting on the corresponding genes or gene complexes. Because natural selection is believed to be a relatively slow process, certainly as far as the alteration of complex adaptations (such as the domain-specific modules of our mind) based on co-adapted gene complexes are concerned, a sudden change of the EEA will introduce an adaptive lag causing the temporary occurrence of maladaptive behaviour before the genetic inheritance system is able to "catch up".

More specifically, the EP reasoning is as follows: while our genus is about 2 Ma old, our species originated about 150 Ka ago. As genetic evolution is believed to be a slow process, or in any case, too slow to inflict much change during the Holocene, the most determining period for our ethology must have been the preceding Pleistocene, which supposedly contained sufficiently long-lasting selective pressures (see also Laland & Brown, 2002: 178-179). Although the EEA does not actually represent a specific place or time (see above), any mental trait that matters (i.e. that is part of our ethology), must have developed (or perhaps more relevantly, come to maturity) during the Pleistocene, and more in particular, within the context of a hunter-gatherer lifestyle. Juxtaposed to the Holocene with its variety of often quickly changing subsistence activities, ranging from hunting and gathering to farming and working in a factory, this reasoning appears to be solid.

However, if the above is true and the orthodox EP view, we believe that this has a serious impact on the kind of modules or adaptive psychological mechanisms evolutionary psychologists can infer: i.e. they may not be species-specific or completely specialised. Our argument is this: the Pleistocene, considered by EPs as a relatively stable and long-lasting environment allowing for adaptive problems to arise and persist, was in reality far from stable: for one, as a very rough first order approximation, it can be regarded as a cyclical occurrence of glacial and interglacial periods. Closer inspection however learns that severe climatic fluctuations not only took place on timescales of several 10 000 years, but even on those of several centuries. Moreover, during the last 50 000 years or so (if one adheres to some form of the Out of Africa model), modern humans expanded across the globe, encountering environments very different from those of the African continent. So if (genetic) evolution is indeed very slow in building complex adaptations, inducing an adaptive lag, the only adaptive problems “typical” for the Pleistocene hunter-gatherer lifestyle must be, by inference, of a very general nature, transcending those major environmental fluctuations and their impact on subsistence. A related problem with the approach lies with the number and the specificity of instincts or modules we may expect to find in modern humans; too much modules that are very specific would lead to an unpractical hypermodularity, while a too limited number of modules with a more general field of application cannot be considered EP anymore. As Laland and Brown (2002: 182-184) point out, evolutionary theory does not particularly favour domain-specific, nor domain-general modules, only those that are good enough in getting the job done at a low cost.

Adaptations such as pregnancy sickness (Profet, 1992) or play fighting (Boulton & Smith, 1992), if they can indeed be considered adaptations, could indeed be understood in terms of general adaptive problems that were with us from the dawn of our species. In these cases, it is even debatable whether or not they are part of human ethology, i.e. that they are typical of our species typical. The EP explanation for the high occurrence of obesity in Western societies, i.e. a maladaptive reaction to a contemporary food surplus of especially energy-high foods in the form of a boundless fondness for sugar and fat rich foods (Ulijaszek & Lofink, 2006) suffers the same fate: ignoring the fact that extant dogs are domesticated animals with selection pressures that have been changed or were even created by human selective breeding, we can imagine that their generally low levels of physical activity combined with our high-energy foods will equally result in obesity. A possible exception to this might be the language instinct (Pinker, 1994), which can be imagined to have had clear adaptive benefits throughout the course of the Pleistocene, and which appears to be uniquely human, although not necessarily restricted to modern humans.

Until now, we assumed together with EPs that there is indeed a lag between a change of the EEA and the subsequent formation or alteration of an adaptation. The existence of such a lag has been questioned by Laland and Brown (2006: 101) on several grounds. Their first argument is that, save for some exceptions, the genetic base for the presumed evolved psychological mechanisms is unknown, which means that we can only guess if the adaptations are based on sturdy co-adapted gene complexes (instead of single or more modest aggregations of genes). While this is true, their guess is as good as the one made by evolutionary psychologists. Secondly, they doubt that human psychological mechanisms are indeed characterised by a considerable complexity. This argument takes a similar turn as their first, so again, nothing is conclusive, although as we will see later on, the fact that relatively simple models can (in some cases) describe average human behaviour quite accurately, may be suggestive of the fact that complex behaviour could be the consequence of rather simple rules of thumb. Furthermore, while the rate of evolutionary change of complex features is as yet undefined (in fact, evolutionary rates are the topic of intense debate, see Futuyma, 1998: 687-691; Strickberger, 2000: 597-600; Mayr, 2001: 214-219; Gould, 2002: 874-972; and Ridley, 2004: 590-611), they are able to refer to several studies according to which a quick response to selection pressure is at least possible. Finally, they point out that small genetic changes are known to potentially produce major changes in the way complex characters function. Notice that this may be because of NCT itself, as it allows for a positive feedback from the cultural and the environmental inheritance system to the genetic level, such that genetic evolution can proceed a lot faster than imagined by the orthodox Modern Synthesis view on which EP is based.

Another point of critique may be that, from a general viewpoint, human populations have expanded across the globe during the Holocene, perhaps marking their most successful presence ever. This may make it difficult to believe that we are currently maladapted (Richerson & Boyd, 2005: 146) because our genes could not keep up. As will be pointed out later, current maladaptations may equally well be explained as unavoidable consequences of cumulative cultural evolution: as adaptive information is costly to evaluate, selection cannot eliminate the spread of maladaptive variants (the so-called *Costly Information Hypothesis*). However, EPs can, in a way, still be right if we assume that the effects of cultural inheritance (see below) largely mask the maladaptiveness of our sluggish genes. This prevalence of cultural inheritance would be compatible with the NCT view, but EPs obviously cannot invoke it fully as they typically denounce the impact of cultural evolution by perceiving culture as a mere actualisation of the underlying instincts (e.g. Barkow, 1992; Jones, 1999).

4.2. A hominin evolutionary psychology

It seems to us that the logic behind EP as functionally explaining some cognitive features as adaptations that evolved in response to problems that arose and prevailed during our species' past, is impeccable. The actual challenge may be to ascertain the specific contexts in which the EP view offers a useful framework for Palaeolithic research, as the discipline is basically a branch of psychology. More in particular, as the discipline focuses on explaining *extant* modern human psychology underlying certain behavioural traits, we run into a circular argument when trying to use the EP reasoning on extinct hominins. Moreover, in the case of the latter, we are not able to use questionnaires and lab experiments to independently study and ascertain the psychological traits that, in the case of modern humans, had previously been inferred from current-day behavioural (mismatch) phenomena, phenomena which in the case of extinct hominins, must be inferred from a very sketchy archaeological and palaeontological record.

Despite this rather prohibitive remark, EP has been used in palaeoanthropology, albeit as a conceptual basis. Although Mithen (1996) started out by denouncing the modular view of the mind, he only tweaked the EP's point of view in a minor way (although there is no denying that this led to a fundamentally different perspective on the mind) to explain the Human Revolution: he saw the evolution of our mind as beginning with a general (non-modular) intelligence, after which four different faculties (i.e. functional groups of modules) appeared and developed: a natural history, a language, a social, and a technical intelligence. All four were considered as separated from one-another and from the general intelligence. Made possible through minor genetic changes, the walls between the five intelligences were broken down, after which the general intelligence became a meta-representational module, in essence a hub that facilitated an interchange of information between the other four modules. Mithen called this state cognitive fluidity, and perceived it as a requirement for symbolic or abstract thought (i.e. cognitive and behavioural modernity). Although perhaps plausible at first sight, the theory rather resembles a patchwork of barrowed partial ideas and models. This eclecticism itself does not have to be a problem, but it does rob the idea of cognitive fluidity from a robust theoretical foundation while being implausible from an evolutionary standpoint (e.g. the separation of the faculties for more than six million years, while connecting them – with major fitness benefits – supposedly requires only minor genetic changes). Furthermore, just like the Human Revolution model it is supposed to back up, it cannot handle what we previously called "modernity singularities" (Jehs, 2011), the attestations of which have only increased in number since 1996. Mithen (1996: 183) either has to assume that Early Modern Humans (after 100 Ka BP) drifted in and out cognitive fluidity, or he needs to invoke a state of partial cognitive fluidity. It makes no sense however for any number of genes to display such repeated switching behaviour, as he himself states on the following page that

> "[...] there was an evolutionary momentum to cognitive fluidity; once the process had begun it could not be stopped."

If the latter is indeed correct, Mithen has neglected the possibility (within his own framework) that fluidity was fully established before the MUPT, while the bulk of the associated phenotypic capacity (e.g. the capacity for cumulative culture) was left untapped until the transition, e.g. because of low population densities (Shennan, 2001) or more generally, because expressions of cognitive fluidity that leave archaeological traces (e.g. symbol use) simply were not worth the investment (why make and use symbols when this has no fitness-enhancing effects ?).

5. Gene-culture Coevolutionary Theory

5.1. Key concepts

Considered by Durham (1990) to be arguably the most important evolutionary approach to culture, gene-culture coevolutionary theory has its roots in one of the final chapters of Dawkins' *The Selfish Gene* (1989: 189-201). There he argued that culture, as an analogue of the gene pool of a population, may consist of discrete packages of information. These units, a.k.a. memes, jump from brain to brain to propagate themselves in the meme pool by means of, broadly speaking, imitation. Thus conceived off, memes (whereby a particular meme would consist of all individual copies within the meme pool) can be regarded as selfish parasites of the brain, competing for neural (or by extension, billboard or library shelf-) space.

From this idea, two distinct bodies of theory have originated, i.e. memetics and gene-culture coevolutionary theory, the latter also known as dual inheritance theory (DIT). As we are focusing on the three most important approaches that came out of the sociobiology debate (following Smith, 2000), we will not dwell on memetics here. For an introduction and evaluation of the field, we direct the reader to Laland and Brown (2002: 197-239) and Aunger (2000). We do want to add however, that memetics remained closer to the characterisation by Dawkins of cultural units of selection (memes) as being parasites (e.g. Blackmoore, 1999) than DIT, such that, in contrast to the latter, the genetics of the organism are of lesser (or, once memes came into being, no) importance. More specifically, memes can promote the genetic fitness of the organism (humans), but this may be exceptional as genetic fitness may only be one way in which memes can be replicated. For example, music may be there solely for the benefit of music memes (Laland & Brown, 2002: 206). This meme's eye view did in fact influence archaeology in the form of "evolutionary archaeology" *sensu stricto*. As Shennan (2011: 1071) argues,

> "It is [...] important to look at the processes from the meme's eye-view [...], the perspective of the cultural attributes themselves. This perspective matters because these culturally transmitted features are the only data accessible to archaeologists [...]. In fact, they are the only direct data about past cultural traditions and the forces affecting them that we have available."

Since 1976, DIT has made significant progress both conceptually and mathematically, although it may still lack rigorous empirical testing (Smith, 2000: 32), notwithstanding the increasing attention it is receiving (see Philosophical Transactions of the Royal Society B, vol. 366). In contrast to memetics, the theory puts that

> "the ultimate explanation for cultural phenomena lies in understanding the genetic *and* cultural evolutionary processes that generate them (Richerson & Boyd, 2005: 238)."

While it is acknowledged that the genetic factors influencing human phenotypes are governed by the same processes that affect changes in other species (as described by neo-Darwinian synthetic theory), evolutionary theory is furthermore used as a source of analogy and as a mathematical toolbox in tackling the evolution of culture. Boyd and Richerson (1985: 33) define the latter as

> "[...] information capable of affecting individuals' phenotypes which they acquire from other conspecifics by teaching or imitation.",

i.e. by social learning *sensu stricto* (for a concise overview of the different kinds of social learning, see Boyd & Richerson, 1985: 34-36). In spite of significant differences between both inheritance systems, the parallels are judged profound enough to tinker with one's descriptive apparatus in order to apply it to the other, as opposed to coming up with an entirely different approach. Most importantly, like genes, culture has population-level consequences. Treating it as an element of mere phenotypic flexibility to environmental variation, where the latter is more specifically understood as the behaviour of con-specifics is typically regarded by DIT's practitioners as unsatisfying (*vs.* behavioural ecology below), because according to such a view cultural elements acquired by individual learning (or any form of phenotypic flexibility) die with the individual that holds them, leaving only the genes underlying the capacity to learn to reach the next generation. In other words, acquired variation is not heritable by genetic means. DIT stresses that culturally acquired variations (called *cultural variants*) really are transmitted down through the generations (and just like genetic evolution, this proceeds in a cumulative way), so the concept of environment should be reserved to processes that affect the population without actually being part of it (Boyd & Richerson 1985: 4-7; note how this contrasts with the NCT view).

In order to fully grasp the interplay between both inheritance systems, is it important to know exactly at what points they differ. According to Boyd and Richerson, a first important difference is the nature of cultural variants: unlike genes, they are not replicators in the same strict sense (*vs.* memetics): they not only lack a discrete nature, but apart from the fact that two individuals may deduce different cultural variants from the same phenotypic behaviour (because of culturally induced propensities held by both beholders), it is also likely that the same variant is stored in a different way in a different brain. Regarding the brain as a black box as far as cultural inheritance is concerned does not affect the evolutionary study of culture because the essential Darwinian processes appear to be quite sturdy in the face of different modes of maintaining heritable variation (Richerson & Boyd, 2005: 80-94): basically, they are general mechanisms describing the transmission of information, leading to the production of heritable variation and modification through time (Shennan, 2002: 264). The genetic and cultural systems of inheritance merely represent two particular forms. As Shennan (2002: 48) points out, the pre-Mendelian understanding of the genetic inheritance system proved to be a viable construct for evolutionary studies too.

Boyd and Richerson (1985: 7-8) point at four other significant points of divergence: a first concerns the "mating system", by which they mean the individuals from which the information is inherited, or the cultural parents. While this is quite rigid in the biological case, cultural parents can be quite numerous and diverse, including the genetic parents, teachers, highly regarded individuals (such as idols), and even peers. Even the respective contribution of either one of them (including the biological parents) can be and usually is disproportionate in comparison to the other(s) (see also Shennan, 2002: 50, fig. 4). Secondly, and because of the existence of intra-generational (i.e. horizontal) transmission, the cultural generation length is variable, either shorter or longer than in the genetic case (e.g. fashion or technological innovations). Furthermore, cultural transmission occurs after birth in a sequential way, instead of all at once. This means that genetic mechanisms can affect the probability of acquiring differing cultural variants (or else that cultural evolution is still embedded and constrained by genetically evolved psychological mechanisms), and at the same time cultural traits can affect the cultural acquisition of traits later in life, while different cultural parents can come into play at different ages. Finally, culture is obtained by directly copying the phenotype: an individual may be affected by events in his or her life, after which the changes are transmitted to his/her cultural offspring (so-called *naive individuals*) so culturally acquired variation is passed on, in contrast to genetic information which is unaffected by events in life (and evolves or changes by means of differential reproduction of variant individuals in the population).

These differences generate a dynamic interaction between both inheritance systems, and give rise to several forces of cultural evolution (Boyd & Richerson, 1985: 8-11, 283-284; Richerson & Boyd, 1992: 64-69). *Random variation* can be considered as the cultural analogue of mutation. Errors in storage or transmission of cultural information are likely to be more extensive than in the genetic case, however. Populations in which the number of cultural parents is small, may be subjected to an analogue of genetic *drift*: chance may dictate which cultural variants are observed and remembered, creating significant changes in their frequencies over time. Rare (or rarely performed) cultural variants may thus disappear entirely. A third evolutionary force is *guided variation*: information that is culturally acquired by a naive individual is consequently affected through individual learning during the individual's life, because of the latter's own experience, effectively altering the cultural variant in question. Consequently, the next generation learns the modified version of the initial variant, which is then again subjected to further tweaking. As such, learning can lead to cumulative change, which will often be adaptive (on the level of the population); this way a changing environment can be tracked quite effectively. Now individual learning is not random, but governed by rules that dictate which traits are rejected and which are retained. Some of these rules may be cultural, but in a causal chain in which one is determined by the other, in the end they must all go back to genetically determined propensities or learning rules. The direction (the kinds of traits that are retained) of guided variation depends on the nature of the evolutionary forces that have formed those learning rules, and its strength on the ease with which individuals can evaluate alternative behaviours. *Biased transmission*, a forth evolutionary force, exists because cultural transmission as a process can favour some cultural variants above others. Three kinds of biased transmission can be discerned: *direct bias* gives rise to the differential adoption of different cultural variants on the basis of the way the properties of these variants are judged. It closely resembles guided variation, because it draws on the same learning and decision-making capabilities, but the difference between both lies with the fact that in the case of guided variation self-generated behaviours are judged against those that were inherited, while with direct bias the presumably best suited behaviour is chosen out of the extant collection of alternatives held by the population. The more complex a variant is, the easier it will be to evaluate the alternatives at hand relative to inventing a new one. Direct bias is fed by and consumes existing cultural variation, while guided variation does not. The propensity of an individual to acquire a given cultural variant can be influenced by the commonness or rarity of the variant among its cultural parents, even when that variant runs counter to the individual's own experience, which is called *frequency-dependent bias* (respectively *conformist* and *non-conformist bias*). *Indirect bias* on the other hand, involves the acquisition of cultural traits, solely because these happen to be found together in individuals that are considered to be particularly attractive cultural parents (e.g. because they are wealthy or prestigious). This can cause the cultural counterpart of the genetic runaway process referred to as the *Handicap Principle*, by which for example some male characters (such as a pea-cock's tail) get exaggerated until, from a genetic point of view, they become maladaptive. The last force operating on cultural variation is *natural selection*. While natural selection on genetic variation can function as the external process establishing the criteria used by both guided variation and biased transmission to either differentially transmit or retain variants, natural selection on cultural variation can produce quite different behaviours from the ones expected as a result of selection acting on genetic variation, as there are significant structural differences between genetic and cultural transmission. In other words, the behaviour that maximises an individual's chance to produce cultural offspring, may not be the one that maximises the transmission of his genes to the next generation. Only when both inheritance systems are symmetric, i.e. when they have similar life-cycles, it's likely for natural selection to favour the same phenotypic variants.

Given the danger for genetically maladaptive outcomes, one should wonder how the capacity for culture, in the form of a high level of observational learning (*true imitation*, see Richerson & Boyd, 2005: 108-111) could evolve. Clearly, the cultural inheritance system must provide us with a considerable adaptive advantage, that on average, outweighs any maladaptive feature imbedded within it (vs. the meme's eye-view). Most likely, this advantage is the shortcut culture provides to individual learning, or put differently

> "[...] culture is adaptive because populations can quickly evolve adaptations to environments for which individuals have no special-purpose, domain-specific, evolved psychological machinery to guide them" (Richerson & Boyd, 2005: 166).

In variable environments, like other organisms humans try to attain a locally adaptive phenotype. In order to determine what that is like, organisms possess genetically inherited criteria by which to judge outcomes of behavioural strategies (pain, hunger, fear, satiation), as well as general behavioural patterns and ways of learning. Alternative behaviours have to be tried out, after which those that are accompanied by "good" sensations are retained; this allows for the construction of complex behaviours suited to local conditions. This kind of individual trial-and-error learning can be costly (in terms of time and health) and it can lead to errors (because the adaptive strategy was not found, or because chance reinforcement retained a maladaptive one). A way to acquire phenotypic flexibility and more particularly phenotypic tracking of the environment while diminishing the costs of learning, e.g. by means of culture, will thus be favoured by natural selection. In a population living in an environment that is not excessively variable, and in which modest amounts of individual learning can be combined with imitation of the more common adaptive behavioural traits, cultural transmission will lead to guided variation and bias that will generally produce adaptive abilities far more quickly than would be the case with genetic evolution alone. As long as the net effect of social learning is positive, natural selection will favour it (Boyd & Richerson, 1985: 14-16; Richerson & Boyd, 2005: 111-131; see also Alvard, 2003; Henrich & McElreath, 2003; Kameda & Nakanishi, 2003).

Assuming that social learning really is adaptive invites an obvious question: why did it allow our species to evolve culture in the way it did, or better, why did it not do so in other species? Possible reasons for the lack or extreme rareness of culture in other species could be attributed to the lack of an unusual preadaptation (Lumsden & Wilson, 1981: 325-331; Alvard, 2003), or to supplementary costs associated with this kind of transmission (Boyd & Richerson, 1985: 130-131). Whatever the position of researchers in this regard may be however, they seem to agree on the fact that something sets apart human cultural dynamics, i.e. the cumulative nature of our culture, or the so-called *ratchet-effect* (Boesch & Tomasello, 1998: 602-603; Tomasello, 1999; Alvard, 2003; Laland & Hoppitt, 2003: 156-158; *contra* Whiten *et al.*, 2003), although the search for the underlying psychological mechanisms is still on-going (see Boesch & Tomasello, 1998: 603 and comments). This effect is clearly visible in the present, as well as in the overall succession of lithic industries during the Pleistocene. Although the distinctiveness of our cultural abilities appear to be linked to our understanding of the making and use of stone tools (Wynn, 1979, 1981, 1985; Wynn & McGrew, 1989; Foley & Mirazón Lahr, 2003; Davidson & McGrew, 2005), marking them as important objects for hominin culture studies (for a link with language, see also the contributions in Gibson & Ingold, 1993), it should be (and has been, see Laland & Hoppitt, 2003: 157) remarked that the eye-catching cumulative nature of culture as we know it is perhaps misleading, considering the relative stasis during the Oldowan and

Acheulean. In other words, even if e.g. chimpanzee culture would be cumulative (today), we might not notice because of the limited amount of time we have been observing them. The paper by Shennan (2001), linking the spread of innovations through a population with the size of that population hints at the complexity of the matter.

In any case, some conditions need to be fulfilled in order for social learning to evolve into a system of cultural inheritance: social learning must be more accurate and less costly than individual learning, and environmental variability has to be predictable, in a sense that it cannot change too fast (which would make imitation less accurate than individual learning) or too slow (allowing for the genetic system to track the changes on itself, making cultural inheritance superfluous and very likely too costly) (Boyd & Richerson, 1985: 130). Richerson and Boyd (2005: 131-147) believe this to be the case for the latter part of the Pleistocene (see the debate mentioned in the EP section), which is, all things considered, fairly recent. This would begin to explain why we are the first lineage to discover the benefits of cultural inheritance: the costs involved in setting up and supporting the necessary phenotypic modifications must have been lower than the benefits. The way they put it "all animals are under stringent selection pressure to be as stupid as they can get away with", which is logical given the large metabolic requirements (see e.g. Aiello & Wheeler, 1995) and other costs of having big brains, such as an increased chance of debilitating head trauma or complications during birth, or a longer juvenile period. Since a considerable number of individuals within a population are required to have a mind capable of imitative behaviour before cumulative culture (complex cultural artefacts and behaviour) can be sustained and profited from (in other words, a single individual with the mutation would not lead to a spread of the trait, because the individual in question will bear all the costs without reaping the benefits), it is likely that such an evolved cognitive state, including for example a theory of mind, was a consequence of the increasing social complexity within the primate order (Aiello & Dunbar, 1993; Dunbar & 1995). If so, this theory of mind incidentally could have made cheap and accurate imitation possible, setting off a rudimentary form of complex cultural traditions. Once this existed, a barrier was crossed: increasing cultural complexity drives the evolution of superior imitative and information storing abilities.

5.2. Dual inheritance theory and hominins

We definitely agree that the study of culture, and more importantly cultural inheritance is imperative to the understanding of the way our species (and other cultural beings such as Neanderthals) behaved and evolved; criticisms on the approach in general are therefore easily put aside (see also Laland *et al.*, 1995). Nevertheless, despite its potential in offering explanations that can incorporate and go beyond the genetic psychological mechanisms inferred by EP, the use of DIT to examine hominin variability during the MUPT for example is rather problematic. First of all, we are dealing with two populations, the social systems of which, and kinds of social learning (and therefore the way transmission of cultural variants occurs) are as yet unknown. This is true for the Neanderthals, as well as (A)MHs, and the problematic nature of the issue becomes even more pertinent when we realise that the transition itself may have been caused by distinct social changes (Kuhn & Stiner, 2006; see also Shennan, 2001). Moreover, when using DIT in any other capacity than a hypothesis generator, lots of specific data are required, which are generally unavailable for the Palaeolithic. At least until well into the UP, lithic remains are the only guides to culture that are sufficiently abundant and distributed to use as potential indicators of cultural variants. While it is true that the period under consideration is characterised by an increasing rate of cultural change and a distinct regionalisation of material (lithic) culture, it remains unclear how the differences between traditions should be interpreted, which is especially pertinent for the MP (the so-called Mousterian debate, see Mellars, 1996: 315-355 for an overview). While perhaps not immediately deployable to study specific attestations of cultural or coevolutionary variability between Neanderthals and modern humans, DIT may help provide answers as to the possible origins of certain phenomena, e.g. a sudden increase of cultural diversity (Shennan, 2001), and consequently, the creation and persistence of symbolic markers of group identity (Richerson & Boyd, 2005: 211-213), which are believed to have been attested within the timeframe of the MUPT (e.g. Kuhn *et al.*, 2001). Therefore, we feel there is much potential to DIT, as it is able to model both genetic and cultural processes, and as it may be used as a simplification of NCT in cases where the impact of the third (environmental) inheritance system is negligible. However, unless used in a general way, e.g. to explain general cultural tendencies (e.g. the spread of agriculture, see Richerson *et al.*, 2001), we may simply lack the necessary fine-grained data to apply the theory in a MUPT context.

6. Behavioural Ecology

6.1. Key Concepts

Behavioural Ecology or BE, as a subdiscipline of evolutionary ecology (i.e. the application of natural selection theory to the study of adaptation and biological design in an ecological setting [Winterhalder & Smith, 1992: 5]) is as the name implies directed towards behaviour, focusing on the interplay between environmental stimuli, behavioural responses, and the ensuing fitness effects (Smith, 2000: 35). It is a meeting point for behaviour, ecology, and evolution, in such a way that ecology acts as a stage on which organisms display their behaviour, with evolutionary processes “rewarding” those individuals who perform best by increasing the frequency of their genes in the gene pool (Krebs & Davies, 1993: 21-22). As such, BE studies the phenotypic consequences of the basic evolutionary principles as captured by the Modern Synthesis, while its ultimate goal is to try and determine why both different species and representatives from a single species may behave differently (Winterhalder & Smith, 1992: 8). This “why” should be understood in terms of the extent to which these differences can be interpreted as differing adaptive responses to the environment (Laland & Brown, 2002: 22).

BE’s action radius covers a diverse range of topics which can be subsumed under the heading of “lifetimes as effort”. This includes both somatic effort (with topics such as resource acquisition and resource distribution, i.e. sharing, reciprocity and trade) and reproductive effort, itself split into mating effort (mating systems, mate choice, marriage transactions, mating strategies, and socio-cultural change) and parental effort (sex-biased parental investment, inheritance patterns, paternal behaviour, parent-offspring conflict, and indirect reproduction). Life history theory tries to bind all of these together by studying the strategies individuals use to achieve multiple (and often conflicting) goals at once, and how they allocate effort to do so (for an overview of these themes, with references, see Cronk, 1991).

For several reasons that will become clear, BE may currently be the most usable of the evolutionary approaches to gain insight into the hominin behaviour. As such, we will treat the theory in greater depth than the ones above, by means a sectional approach that highlights its general research strategies and assumptions (some of which being shared with the approaches discussed previously).

6.1.1. Hypothetico-deductive method

Behavioural ecologists, and evolutionary ecologists in general typically follow the hypothetico-deductive (HD) method, involving a cyclical or dialectical movement between theory and the real world, whereby a logico-mathematical model is set up, out of which a formal hypothesis is deduced. The latter is consequently interpreted in an operational form allowing for empirical testing by means of experiment or observation. The test results are finally fed back into the model inductively. After testing the hypothesis, and in the case of disparities, it is subjected to adjustment (marking the beginning of a new cycle) rather than full rejection. As such, a HD process closely resembles the way science is actually done in the mind of the researcher (Smith, 1991: 8-10; Winterhalder & Smith, 1992: 11-12).

6.1.2.The use of simple models

Employing simple models to grasp the overwhelming complexity of reality may at first appear illogical and deeply unsatisfying: intuitively, we may require our models to be realistic in order to be useful. However, it has been argued that realism is only one aspect of a model, and that no model can at the same time maximise generality, precision *and* realism (Smith, 1983: 637). The preferred pay-off between these three must be dictated by the empirical data and research question at hand, and as Smith points out, BE tend to sacrifice realism in favour of generality and precision, such that empirical validation or refutation is facilitated. Moreover, as Winterhalder and Smith (1992: 13-14) indicate, simple models are not merely a temporary or primitive stage in the scientific process, although more advanced approaches can grow out of them once the formers' dynamics are completely understood. There are several reasons why (relatively) simple models, which also dominate dual inheritance research, are preferred to complex ones (Boyd & Richerson, 1985: 25-26; Laland, *et al.,* 1995: 145). For one, detailed models are not useful for representing generic processes. Unlike the natural sciences, social and biological phenomena cannot be expressed through universal laws, from which exact predictions can be deduced. Rather, only generic theoretical constructs (e.g. natural selection) that represent the general properties of a class of processes can be set up. Therefore details concerning particular cases, e.g. of natural selection, must be sacrificed; failure to do so will result in a model without much relevance beyond the case under consideration. Consequently, the hypotheses produced by BE favour generality when searching for form, direction, and degree of relationship between variables (Winterhalder & Smith 1992: 17). Secondly, complex and detailed models are often difficult to understand, in the sense that when more realism is added in the form of mutually interacting processes, they become as clouded as the real world we wish to understand. In the words of Boyd and Richerson (1985: 25),

> "[...] to substitute an ill-understood model of the world for the ill-understood world is not progress".

Furthermore, the analysis of complex models is both time-consuming and expensive: adding more variables to a model seriously increases the number of possible interactions. Fourth, detailed models are often less productive than simpler ones. The former are usually more data-consuming while the necessary data often have a limited availability, which is especially true in archaeology. On top of that, small errors in the formulation of the model can often produce radically different predictions; adding complexity allows for them to sneak in more easily, while filtering them out becomes increasingly difficult because a complex model is more unwieldy. Finally, easily-understood simple models are usually combined into families to increase their explanatory power (Winterhalder & Smith, 1992: 14), which has been called the "piecemeal" approach (Smith, 1991: 10, 2000: 29). When set up properly, such a suite of complementary models becomes an analytical tool (a theory). Naturally, for that to happen, each of their limitations, applicability and representativeness have to be known.

6.1.3. Reductionism

When BE is charged with being reductionist, this is in part true (Winterhalder & Smith, 1992: 14-16). These authors present an overview of the different kinds of reductionism, and conclude that evolutionary ecology presumes *constitutive reductionism* (and to some extent *explanatory reductionism*), which means that phenomena are dissected into their lower-level constitutive elements (events and processes), which preserve their integrity in whatever context they appear. Therefore, they argue that understanding the higher level phenomena does not change anything about our comprehension of the constitutive elements. The emergent properties at higher levels however, can only to some degree be explained by lower level processes (culture obviously cannot be described in terms of molecules). As such, Winterhalder and Smith conclude that BE is not any more reductionist than many other social sciences, nor does it invoke the indeed more problematic *theory reduction*, which states that higher level theories are merely special cases of lower level ones, and hence can be reduced to them (e.g. Mendelian inheritance vs. chemistry).

6.1.4. Methodological individualism

The principle of methodological individualism (MI) states that the properties of groups are a result of, and are best explained by, the actions of individual actors (Smith, 1983: 637-638, 1991: 11; Smith & Winterhalder, 1992: 39). In anthropology however, the reverse is often believed to be true: social processes and needs are thought of as overriding or determining those of the individual. The assumption of methodological individualism effectively denotes any group-level functionalism, reaping supra-individual processes (e.g. population pressure, classes, cultural systems of meaning, social equilibrium, see Smith & Winterhalder, 1992: 40) from the self-determining and autonomous thrust and rationale they have often been imbued with.

Closely associated with methodological individualism are the notions of individual benefit and rational choice. However, these are not necessary outcomes of MI (Smith, 1991: 12-13): the first is nothing more than a convenient methodological assumption with a rough empirical validity, and only so if it is defined in terms of some specific currency or goal. While we must add that the notion of individual benefit is of theoretical importance as BE is rooted in evolutionary biology (by means of the concept of inclusive fitness), Smith is right to note that a proximate currency is commonly used as a proxy for fitness, the link of which to inclusive fitness remains, although highly plausible (as it has been chosen as such), an assumption. Rational choice on the other hand definitely is a factor of individual decision-making, but it is essential to point out that it is far from the only one: non-rational decisions (genetically or culturally inherited; people do not act independently of their culture [Kelly, 1995: 53; Boyd & Richerson, 1985; Richerson and Boyd, 2005]) are equally important in understanding individual behaviour. As such, EB does not try to discriminate between substrates underlying the behavioural strategies it studies (i.e. the so-called *Phenotypic Gambit*).

6.1.5. The Phenotypic Gambit

Behaviour, while rooted in genetic or culturally inherited instructions, is considered highly flexible by BE practitioners. Conveniently, it is modelled in the form of different, highly plastic conditional strategies, decision rules, and rules of thumb, which may or may not be conscious to the individual. Again for the sake of theoretical convenience, these are believed to be subjected to selection for maximum fitness (representation in future generations) or evolutionary stability (competitive superiority when fitness is frequency-dependent) (Smith, 1991: 10-11). So basically, selection is assumed to work directly upon phenotypic, and more in particular, behavioural traits, bypassing the often difficult to disentangle genetic (vs. EP which assumes that the genetic mechanisms are under selection, and not the behaviour that results from them) and cultural mechanisms that lie at their bases. In theory, a trait is analysed as if the very simplest genetic system controlled it: as if it there were a haploid locus at which each distinct strategy was represented by a distinct allele, as if the payoff rule gave the number of offspring for each allele, and as if enough mutation occurred to allow each strategy the chance to invade (Grafen, 1984: 63-64, cited by Smith & Winterhalder, 1992: 33).

In practice it is believed that selection will favour traits with high fitness or evolutionary stability, irrespective of the specifics of the inheritance system (and the underlying cognitive mechanisms) involved. This point of view has clear ramifications for BE's view on culture as an inheritance system, i.e. culture is believed to lead to adaptive change. This shortcut, which takes away the need to identify the link between heritability and the phenotype, is called the *Phenotypic Gambit*. In addition to extreme phenotypic flexibility, it requires the existence of a wide set of strategies, and the ability of the individual to determine payoffs and choose or learn the best alternative under any given set of circumstances (Smith & Winterhalder, 1992: 33).

6.1.6. The role and characterisation of the environment

In BE, the environment is defined as everything that is external to the organism in question, and that influences the organism's probability of survival and reproduction. It affects development, physiology and behaviour by physical, biological or social means. The nature of the environment dictates the theoretical machinery that is to be deployed: in a *strategic* context, the consequences of a particular strategy depend on its frequency within the population, as well as that of other strategies (typical for social environments). This effectively means that truly independent variables are non-existent, while the results of strategies pursued in *parametric* contexts are independent of their own, as well as other strategies' frequencies. In this case, the independent variable may be deterministic or probabilistic, such as in physical environments. The latter is studied by means of optimisation models, while the former by using game theory and the concept of evolutionarily stable strategies (ESS) (Winterhalder & Smith, 1992: 8-9). Although the environment is an essential part of any explanation in BE, or evolutionary ecology in general, BEs do not subscribe to environmental determinism in the strong sense: the environment (*sensu lato*) is merely part of the factors that influence short-term behavioural responses (Winterhalder & Smith, 1992: 20-21; Smith & Winterhalder, 1992: 26).

6.1.7. Optimality

Optimality is not a basic principle in nature, nor do optimisation models provide a realistic description of the behaviour of individual actors or the process of adaptation. It does allow to apply a general methodological framework to any particular behavioural aspect, when certain basic assumptions connected to that framework are met. In any given specific case, a tight fit between these assumptions, and the predictions that result from applying the framework may not be possible, but this does not appear to impair capturing the basic elements well enough to result in empirical support (a review of such support for non-humans is provided in Stephens & Krebs, 1986: 183-205). Furthermore, changing the model's currency or constraints can increase realism in the case under investigation (consistent with a HD approach), and the consequent empirical validation implies that the model has correctly identified the adaptive goals involved. Therefore, it is important to stress that optimisation is not a real theory (in the sense of providing an explanatory framework consisting of propositions about the real world) but a method that offers a systematic means of generating hypotheses about the structure and function of living things. Although optimisation lies at the basis of ESS analyses of selection in strategic contexts, it is more commonly associated with studies in parametric environments (Smith & Winterhalder, 1992: 50-52).

The assumption of optimality in BE originates out of the latter's selectionist logic. In short, behaviour can be looked upon as having both costs and benefits. It is reasonable to assume that natural selection favoured individuals able to maximise the net benefit, which, ultimately, should be measured in terms of genetic contribution to the following generations (Krebs & Davies, 1993: 46-47). Broughton and O'Connell (1999: 154) clarify that an optimising approach does not imply for natural selection to produce the best imaginable design or behaviour; selection will only tend to favour

> "[...] the best strategy among *a defined set of alternatives possible in the context of interest*. It makes no claims about optimization in any absolute sense" [italics theirs].

Bamford argues that the assumption of a fairly direct link between natural selection and optimality, and optimal foraging in particular, must be approached with vigilance. While foraging as good as possible for example, certainly contributes to an organism's somatic effort, it is not a sufficient prerequisite for its reproductive success:

> "[...] survival and reproduction are [...] linked, but it is important to recognize that they are not the same thing" (Bamford, 2002: 437).

So to put it more correctly, not the association between food and reproduction, but that between food and reproductive *capacity* is quite strong.

Smith (1983: 262) and Smith and Winterhalder (1992: 51-53) explicitly characterised optimisation as a mere convenient heuristic tool or a simplification for analysing evolutionary outcomes: even if natural selection was an optimising force, other processes or constraints may lead to sub-optimal effects. An example of such a constraint would the time lag between an initial selection pressure and the subsequent adaptive response, e.g. the inefficacy of the hedgehog "anti-predator" response against a car, or the tendency for moths to fly into a compact source of light, such as a candle flame (Dawkins, 1999: 35-38) mentions. As we argued above when evaluating the EP approach, the importance of such a lag effect may be minor in the case of humans even when the lag is a result of predator-prey coevolution (*contra* Winterhalder, 2001: 32), because of our ability to develop cultural adaptive responses quite rapidly. Still, depending on the case at hand, and on the moment of observation, the lag effect *may* be relevant. Another, second source of suboptimal effects stems from the way natural selection works: it favours only existing variants with higher fitness, without any foresight. This can easily produce historical contingencies that inhibit the best possible variant to be selected for (Dawkins, 1999: 38-41, see also the concept of adaptive landscapes). A third factor, which is especially relevant for humans, and despite of its ability to speed up the process of adaptive match between organism and environment when compared to the genetic inheritance system, may be the cultural inheritance system, as it is able to produce genetically maladaptive variants. A further cause for suboptimal behaviour may also be a lack of genetic (Dawkins, 1999: 42-46) or cultural variation. Constraints on costs and materials (Dawkins, 1999: 46-50) can figure as a fifth, e.g. the extent to which bodily structures can respond to forces of selection given the resistance of other components (Mayr, 2001: 158-159). As an example of the latter, the limitations on brain size (in terms of energy expenditure) in human evolution may have been released by a reduction in gut size once more nutritional foods, such as meat, were incorporated into the diet (Aiello & Wheeler, 1995). Yet another factor that may produce non-optimal phenotypic traits may be "mistakes" made by an organism because of the unpredictability of the environment, as natural selection can only respond to the latter as a statistical average, unable to cater for every possible contingency (Dawkins, 1999: 53-54). To our benefit, studies in which the observed behaviour is time-averaged, i.e. that incorporate behaviour spread over substantial time-frames such as archaeological applications of optimal foraging models, may be expected to obscure the lag effect to a (large) extent. Finally, BE mostly focuses on one behavioural strategy set (e.g. foraging) at a time, as if it were independent of other, potentially interacting problems such as predation. Considering all but the one concerned as part of the static environment of the latter may severely impact the model's realism, as theoretically, investigating only one strategy set at the expense of the others would require an understanding of the inner workings of and the interplay with all the others. As a result, finding the optimal trade-off between dependent strategy sets becomes impossible, which leads Smith and Winterhalder (1992: 53) to wonder how optimality can be applied to a single set, especially when failures of such single-trait analyses can be easily explained away as caused by competing adaptive goals. This is indeed a very pertinent point of criticism, to which both authors respond by highlighting that a piecemeal approach (of each set) may still be the best way to subsequently ascertain to what extent compromises between various traits of an organism really exist.

6.1.8. The role and characterisation of culture

A major difference between DIT and BE concerns their view on culture. By holding two of the three factors determining the phenotype (genes, culture and environment) constant, behavioural ecologists can assign a causal role to the environment, albeit a partial one (Smith, 1991: 20). Smith further argues that although in order to attain full understanding all three should be known, much insight can be gained from a unifactorial analysis, especially when there are considerable difficulties in separating the effects of cultural and genetic inheritance. However, if BE is to have any connection with the real world, there should be some justification why culture can indeed be held constant, at least in the specific circumstances of the case that is being studied. Practically, behavioural ecologists believe they can predict the kinds of behaviour in a certain environment, by determining the behaviour that maximises individual fitness, which means that behaviour as studied by BEs will generally be adaptive. Therefore, BEs have to assume that cultural inheritance will, on average, be adaptive (in the genetic sense) as well. Depending on the case at hand, this may not be a bad approximation (see e.g. Jehs & De Smet, 2011), but on both sides of the divide, it is believed that the matter is at least partially empirical and as yet undecided: while there is no proof that cultural inheritance is not fitness-maximising in certain areas of application (Smith, 1991: 22, 24), there also is no proof that it is (Boyd & Richerson, 1985: 12-14; Richerson & Boyd, 1992: 92).

6.2. BE and anthropology

Given the diverse array of research subjects subsumed under the BE approach, and given their usability for addressing issues highly relevant to anthropologists, it is no wonder that ethnographers began to set up both modest and large scale empirical tests of BE (in this case often referred to as Human Behavioural Ecology), and optimal foraging in particular. These include Baily (1991), who focused primarily on hunting in a forest setting (and the role it plays in marriage opportunities), Smith (1991), directing his attention towards both prey and patch choice models in the Arctic, as well as the social setting in which foraging takes place, Hill and Hurtado (1996) applying life history theory to the Paraguayan Ache hunter-gatherers, and Hawks and co-workers (2001) dealing with the dynamics of meat sharing among the Hadza. Several conference bundles, in which typically the advances on the theoretical level addressed in the first part, are followed by chapters containing the (at the time most recent and arguably the most telling) empirical applications of BE, should certainly be noted as well, as these had a seminal influence on the development of the discipline. They include Winterhalder & Smith (1981), Smith & Winterhalder (1992) and Cronk *et al.* (2000). A wide range of societies, with diverse topics such as foraging, mating, parenting, sociality, and, perhaps typically for such recent compilations as the last bundle, the challenging case of the demographic revolution have been investigated (see also Winterhalder & Smith, 2000: 54-59 for an overview of HBE research up until 2000). Archaeologists have embraced (H)BE as well, although they have traditionally been a minority among behavioural ecology minded anthropologists. With few exceptions (e.g. Dusseldorp, 2009, 2010; Jehs 2011), the models have been implemented by New World archaeologists, and most of the time, case studies centre on sites on the American continent. Simms (1987), Broughton & Grayson (1993), Madsen (1993), Hildebrandt & McGuire (2002), and some contributions in the above-mentioned conference bundles are witnesses to that observation. Hominins however have been the subject of BE research too, e.g. by Foley (1992), Stiner (1994), Hawkes and co-workers (2000), Grayson and co-workers (2001), Grayson & Delpech (1998, 2002, 2006), Dusseldorp (2009, 2010), and Jehs (2011).

We have already argued that BE, and optimal foraging theory in particular may currently be the most likely choice of the evolutionary approaches to gain more insight into hominin behavioural variation in the Palaeolithic. There are several arguments to support that claim. First of all, BE allows for a study of behavioural strategies indiscriminate of species boundaries, and without getting lost in risky assumptions about the cognitive mechanisms underlying those strategies (*contra* EP). This may be especially pertinent for the Neanderthals, but, by going back far enough in time, also for (anatomically) modern humans. Secondly subsistence, and foraging in particular, is one of the oldest and most vindicated topics in BE, for animals and (modern) humans alike. Existing models, and the basic prey model in particular, have proven their empirical worth in ethnographical, as well as archaeological (i.e. mostly Holocene) contexts, so applying them to the Palaeolithic is a logical step. Thirdly, despite the considerable weight we attribute to cultural inheritance, through BE behaviour can be investigated without worrying too much about its intricate particulars (including potentially maladaptive outcomes), by assuming as a first order approximation that culture will tend to be fitness-maximising. However, considering DITs (and NCTs) take on human behaviour *sensu lato*, the reasons why we believe that BE is likely to be adequate in the case at hand, requires some elaboration.

As we mentioned before, lithic artefacts are the only direct guide to cultural variation until the latter part of the Middle Palaeolithic or Middle Stone Age, for the entire Old World, because of their abundance and the virtual absence of artefacts made from other materials. Despite this abundance, lithic traditions are considered as having been very stable for a long time, during the Oldowan, the Acheulian, and the Mousterian. Especially during MIS3 however, a regionalisation and a more fast-paced cultural evolution can be witnessed, the causes of which still being difficult to ascertain. More or less in tandem, a more generalised storage of symbolic information outside the body begins to appear, as well as hints at cumulative cultural evolution. This means that until well into MIS3, or even MIS2, there is little cultural data of a sufficiently small grain to work with, a problem aggravated further by the inability to securely link hominin populations (Neanderthals and modern humans) to lithic traditions, and by the limitations of carbon dating. Interpretations can range from the idea that the cultural side of life was either relatively limited, to the option that the majority of culture was not preserved archaeologically. In any case, even if the cultural repertoire was more extensive than we are led to believe based on archaeological remains, there may simply be a lack of data to fit fine-grained DIT models that could study hominin variation, such that we are forced to accept the BE approach as the best we can do (at the moment). This is not necessarily a bad thing: when the question whether culture is fitness-maximising or not remains undecided in cases where cultural processes cannot be discerned, the most economic approach (BE) may be warranted until proven otherwise. In fact, BE is found to be useful even in some contemporary studies of human behaviour (e.g. contributions in Winterhalder & Smith, 1981; Smith, 1991), so the matter really *is* empirical.

This obviously does not entail in any way that culture will have been predominantly adaptive and therefore, BE an adequate approach. However, as culturally acquired variation is heritable, culture will tend to be cumulative, once certain conditions are fulfilled (e.g. Shennan, 2001). Therefore, by going back in time, the cultural repertoire will tend to shrink, and at the very least in absolute terms, but probably also in relative terms, less of it will be maladaptive. More in particular, maladaptive cultural variants will be limited when the forces of guided variation and direct bias (the sociobiological forces, which enhance the adaptiveness of the genetically inherited mechanisms) are strong, and when cultural transmission is mostly vertical (as opposed to horizontal or oblique). The latter is likely given the low population densities typical until the end of the Middle Palaeolithic (Stiner *et al.*, 1999, 2000), which entail that most of the time, group sizes will be small, and opportunities for non-vertical transmission limited. Moreover, assuming that life-expectancy before the Upper Palaeolithic was indeed quite short (Caspari & Lee, 2006), a major influence of elders (i.e. an increased chance of non-vertical transmission) would have been limited as well. Thirdly, as the changes during MIS3 are likely to have had a strong social component, they may have sown the seeds for subsequent social stratification (see e.g. Vanhaeren & d'Errico, 2005). In absence of the latter during MIS3 proper, forces such as indirect bias, whereby prestigious members of society are copied, may be expected to have been small. This is especially relevant when these members have had a genetically sub-optimal fitness (e.g. in the case of celibacy).

The direction of guided variation and direct bias are another matter: as we saw in the DIT section, the kinds of traits enhanced by guided variation depend on the evolutionary forces that shaped the underlying learning rules. As Richerson & Boyd (1992: 64-65) note, the case in which the latter are genetically transmitted and shaped by natural selection, is of particular importance, not only because that is the primitive state (potentially increasing our knowledge of the origins of guided variation), or because it is still relevant for modern humans (the EP standpoint), but because it is highly pertinent for the study of foraging activities, as in this domain, the goals of the learning rules are closely correlated with genetic fitness. The authors explain that when foraging practices are judged according to their energy payoff per unit of time (which is the case in optimal foraging theory), they will adapt to a changing environment as if they were subjected to natural selection. On the other hand, if they are judged by their impact on other matters, such as prestige, they could evolve in another direction (which can be studied by BE as well, albeit with models other than the diet model). In the case of prestige in particular, it may not be possible to reject that possibility outright. A similar argument goes for direct bias (Richerson & Boyd, 1992: 65,67): if the underlying guiding rules for individual choices are the result of selection on genes, direct bias will favour adaptive cultural variants.

Although Shennan (2002: 288-289) wisely urges us to evaluate every case separately, from an empirical point of view Smith (1991: 22-24) presents a strong case for maladaptive traits to be limited in the case of subsistence and more in particular, foraging: selection pressures on variation in foraging practices will potentially be high for people who depend heavily on this way of making a living, including both present-day and ancient hunter-gatherers, as the impact foraging has on survival and by inference, successful reproduction, is high. His second argument is that foraging has a very long evolutionary history, not only within our species, but extending into the primate and even the mammalian line. This will result in strong genetically programmed propensities ("modules" in EP terms) to forage in an adaptive way (he mentions the example of the capability to judge the caloric value of alternative prey through proxies such as taste, fat content, size, ability to satiate, etc.), and it is only logical to assume that these will indeed have persisted up until now. By extension, they will have been present in the Palaeolithic, and given the smaller cultural repertoire, perhaps even in a less diluted way. Thirdly, he believes that foraging practices will primarily be learned from parents or other close relatives (the kin group), resulting in less systematic conflict between the genetic and the cultural inheritance system. Although he admits that this is only approximately true now, it may actually be correct for a general (i.e. beyond mere subsistence) Palaeolithic setting, which we also argued for above. Finally, he calls in the fact that reliance on social learning, and therefore culture will only occur if decision-making based on genetic inheritance plus individual (trial and error) learning are on average less efficient, i.e. more costly in terms of fitness (see also Boyd & Richerson, 1985). When these are more efficient on the other hand, culture (and the associated danger for maladaptation) will be of lesser importance. Because foraging is a highly repetitive activity, in which payoffs are allocated very rapidly, this might arguably be the case. Alternatively payoffs associated with foraging practices which were actually adopted culturally, will perhaps be easier to evaluate than those resulting from conscious individual trial and error. So foraging, in contrast to domains such as religion or kin systems, is an area where we might expect that individual experience plays a large role in shaping behaviour, whether that behaviour was initially acquired by social learning or not.

7. Conclusion

As far as ethnographical applications of the evolutionary approaches to behaviour and culture are concerned, we tend to agree with Smith (2000), who stated that the three “styles” in the evolutionary analysis of human behaviour that he discerned and discussed (EP, Human Behavioural Ecology, and Dual Inheritance Theory) target different levels of enquiry (e.g. they consider adaptive change over different timescales), usually focus on different research questions, and use different methods to collect data and verify results. Therefore they should either be considered complementary if a more complete picture of behaviour is required or attainable (at least for cases in which NCT has not been chosen), or they should be carefully selected depending on the dataset and research question at hand.

For archaeologists however, the matter is not that simple. From a theoretical point of view, it is difficult to see how evolutionary psychology could be used in research matters where hominins other than modern humans are involved. It is also unclear how far back in time one can go and apply the EP assumptions to modern humans themselves. Due to its focus on social behaviour, sociobiology is difficult to put into archaeological practice as well, as its input, social information, is usually an error-prone end-product of archaeological enquiry, rather than primary data. As this is definitely the case in the Palaeolithic, sociobiology may be of limited importance for archaeologists of the Palaeolithic. Dual inheritance theory on the other hand is quite comprehensive conceptually, but at the moment it may lack the associated analytical tools to move beyond the role of a hypothesis generator. While the latter may not be necessary, to be used at its fullest, the approach nevertheless requires quite fine-grained cultural data, which are arguably unavailable in research matters pre-dating the Neolithic. Niche construction theory, being even more encompassing than DIT, is subject to the same critical remarks. The current attention this rather young theory is receiving, also from within archaeological circles, may mend that situation to an extent, but for studies involving different hominin groups, the significance of NCT may primarily be found in guiding and fine-tuning our research questions rather than coming up with new analytical ways of answering them. Still, depending on the research question at hand, like DIT, the refreshing perspective Niche Construction has to offer may prove to be invaluable at exploring established topics in new ways.

The most useful to archaeology may currently be behavioural ecology, for several reasons. The approach has matured under the wings of anthropology, such that it covers a wide range of topics, while being applied to a wide range of places, times and ecological contexts. Not unlike other bodies of theory, HBE is a pay-off: while it may only be deployed when studying (genetically) adaptive phenomena, it allows us to remain ignorant as to the behavioural (genetic) or cultural origin of the phenomenon in question, as well as the specifics of their interactions, which is especially useful in the case of Palaeolithic archaeology. As actual applications show, it is vital to be aware the theoretical and empirical assumptions, as well as the nature of the predictions of HBE models, but this is not different from other models. In the end, HBE, like NCT and DIT functions as a framework that generates hypotheses. As such, it does not only produce falsifiable hypotheses, but additionally allows for their empirical testing and tweaking in a dialectic way within the conceptual framework of HBE, by making use of a range of extant analytical tools associated with HBE, and BE at large.

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Abstract

Evolutionary theory, which has been designed with the sole purpose of describing and explaining phenotypic variability within and between species, is considered to be the base paradigm for the study of all living organisms. Basically, evolution as a process is nothing more than a continuous alteration through time of elements that are already there, without foresight or predetermined goal and therefore not necessarily leading to increasing complexity. The latter puts (palaeo)anthropologists, and archaeologists in particular, in a difficult position, as humans seem to have developed behavioural characteristics and cultural achievements that clearly point to the opposite. As such, and until very recently, they (and scholars of the human and social sciences in general) have largely shunned evolutionary approaches to behaviour and culture. By reviewing the most important of these approaches, and evaluating them in terms of their utility for hominin studies, we will show that an evolutionary take on behaviour and culture does harbour a significant potential for scholars of this period in prehistory.

Keywords: hominin studies, Palaeolithic, evolution, behaviour, culture.

Samenvatting

De evolutietheorie, ontwikkeld met de bedoeling phenotypische variabiliteit binnen en tussen soorten te beschrijven en te verklaren, wordt algemeen als het basisparadigma beschouwd voor de studie van alle levende wezens. Als proces houdt evolutie echter niets meer in dan een voortdurende wijziging doorheen de tijd van reeds aanwezige kenmerken, zonder vooropgesteld doel, zodat dit niet noodzakelijkerwijze leidt naar een steeds groeiende complexiteit. Dit laatste plaatst (paleo)antropologen, en archeologen in het bijzonder, enigszins in een moeilijke positie, gezien de mens gedragsmatige eigenschappen en culturele verworvenheden ontwikkeld heeft die dit duidelijk tegenspreken. Dit ligt grotendeels aan de basis van het feit dat ze (en onderzoekers binnen de humane en sociale wetenschappen in het algemeen) grotendeels evolutionaire benaderingen van gedrag en cultuur geweerd hebben. Door de belangrijkste benaderingen te bespreken en ze te evalueren in termen van hun bruikbaarheid voor Paleolithisch onderzoek, willen we aantonen dat een evolutionaire kijk op gedrag en cultuur wel degelijk een aanzienlijk potentieel herbergt voor vorsers binnen het prehistorisch onderzoek.

Trefwoorden: hominine studies, Paleolithicum, evolutie, bedrag, cultuur.

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