The Evolution of Exaptation, and How Exaptation Survived Dennett's Criticism

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1 Introduction

In one of the concluding chapters of his last monumental work, the late palaeontologist Stephen J. Gould quoted Thomas H. Huxley in affirming that he was "prepared to go to the stake for exaptation", for this term, he continued, "stands in important contrast to adaptation, defining a distinction at the heart of evolutionary theory" (Gould 2002b: 1234).

Making things clearer about this distinction has been one of the main aims of Gould's overall reflection on the theory of evolution and its extension and revision, and this is why under the term 'exaptation' lies a whole set of interrelated concepts and theoretical perspectives. It should not surprise, then, that the debate concerning the concept of exaptation has historically been very harsh and can be seen, among the many within contemporary philosophy of biology, as one of the most famous and long-lasting: the reader can see its development throughout the years and the pages of various journals and books. In his reconstruction of the debate, Kim Sterelny (2001) speaks of two different views on evolution, embodied by Richard Dawkins and Gould, colliding on almost every relevant aspect of the evolutionary theory. Andrew Brown has even termed such disputes the *Darwin Wars* (Brown 2002).

The aim of this work is to offer a new perspective on this complex matter. In order to do so, we will proceed in three main steps. Firstly, we will provide a brief exposition of the theoretical background that accompanied the birth of the concept of exaptation. Then, we will take into consideration the strong critiques of the Gouldian position that philosopher Daniel Dennett developed in his *Darwin's Dangerous Idea* (Dennett 1995),[1] and the philosophical framework behind them. Taking them as a guideline, we will finally try to critically approach his position in two ways: from an

[1] Henceforth: DDI.

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C. AM. La Porta et al. (eds.), *Understanding Innovation Through Exaptation*,
The Frontiers Collection, https://doi.org/10.1007/978-3-030-45784-6_1

empirical point of view, we will show how the concept of exaptation can be a viable hypothesis whose implications have been seriously addressed in recent research; from a conceptual perspective, we will focus on Dennett's last work, *From Bacteria to Bach and Back* (Dennett 2017)[2] in order to show how, quite ironically, he has come to accept a few insights that were typical of the Gouldian position.

2 Exaptation: A Brief Archaeology

One of the chief problems of neo-Darwinian evolutionary theory is how to account for the apparent and often astonishing complexity of biological organisms and structures in a way that is consistent with our scientific knowledge of the world. In this regard, the process of natural selection (in its many forms) has been, and still is, one of the main instruments capable of explaining the coming into being of said complexity. In their famous *spandrels* paper, however, Gould and Richard Lewontin denounced what they believed to be the explanatory trend prevalent at their time.

They argued that biologists tended to embrace a strong version of natural selection as an optimizing agent, conceiving it either as the *sole* agent responsible for the modification of organisms or, at least, as *the* most important one, to which all the others could be reduced. It is beyond dispute that, in a certain sense, "eyes are for seeing and feet are for walking" (Gould 1997a); however, Gould thought that many were too hasty in assuming that organic traits were forged by natural selection to carry a specific function (that would have remained the same since the very beginning of the evolution of the trait), thus becoming too easily convinced of having found it. Gould argued that this had been a drawback of the success of the Modern Synthesis, which had resulted in an excessive focus on the role of natural selection as the main cause of evolution and on adaptation as the explanandum *par excellence* of evolutionary biology.

This way of thinking, that according to the authors "dominated evolutionary thought in England and the United States" (Gould and Lewontin 1979: 581) was criticized for two main reasons: firstly, it analysed the structure of an organism by 'atomizing' it into a bundle of traits defined by their function and then it proceeded to give an account of how said functions could have been favoured by natural selection from the beginning. This resulted in an underestimation of the causal power of organisms, which came to be conceived as passive entities in front of environments and their selective pressures; furthermore, in many cases this atomization at the organismal level was pushed even further by considering organisms and traits as 'vehicles' for genes, the only truly 'replicating' entities (Dawkins 1976).

Secondly, when and if the atomizing and functionalist strategy failed, the result was just to try out another 'adaptive story', always focusing on present utility and excluding other attributes of form. The authors suggested that, even if allowed in principle, other forces except natural selection where never taken seriously as explanatory

[2]Henceforth: BB.

hypotheses, even in cases of evident sub-optimality of parts. Instead of focusing on the production of 'adaptive stories', or adaptive 'just-so stories', Gould was much more interested in questioning how *limited* was the power of selection to change organisms, wondering if it was possible to find "alternatives to immediate adaptation for the explanation of form, function and behaviour" (Gould and Lewontin 1979: 590).

Even after this brief presentation, we can appreciate how behind the critique of the 'Panglossian' paradigm there was more at stake than the colour patterns in snail shells. As Gould once wrote, his critique can be traced back to three main theoretical roots:

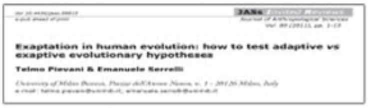
> The first arose from seven years' composition of *Ontogeny and Phylogeny* (1977), and my growing respect for the great European structuralist literature on laws of form (dating to such seminal thinkers as Goethe and Geoffroy). The second developed from a series of technical articles, written [...] between 1973 and 1977, on ordered patterns in phylogeny that arise within purely random systems (but were previously attributed without question to Darwinian adaptation). Sociobiology did provide the third – as I struggled to understand what seemed so wrong about a speculative literature that reached conclusions about people so out of whack with my concepts of reality (Gould 1987a: 41)

We can thus individuate a philosophical root, coming from Gould's respect for the structuralist tradition in biology, which he read in an anti-functionalist fashion; an experimental root, that focused on structural homologies coming from purely casual systems and the internal constraints; and a political root, that is, his opposition to many socio-biological theories popular at his time, that offered a hyper-reductionist treatment of complex human behaviours. We believe that by disentangling these topics we can come to appreciate how much the difference between adaptation and exaptation—here not intended as mutually exclusive phenomena—touches the 'heart' of evolutionary theory.

2.1 A Dialectic Between Functions and Forms

Gould's interest in the structuralist tradition was motivated by his conviction that a purely functionalist approach to evolution was insufficient to explain the complex and, in a sense, dialectical relationship between function and form (Gould 2002b). This aspect of his thought can be seen clearly in the essay written in 1982 with palaeontologist Elisabeth Vrba (Gould and Vrba 1982). The authors proposed the general term *aptations* to indicate those biological traits that are somehow useful (*aptus*) for the fitness of organisms, and then identified two meanings and subsets of the concept: (1) the set of traits forged directly by natural selection for the same function they maintain in the present (*adaptations*); (2) then, the set of characters that, born for a certain reason or for no functional reason at all, where co-opted for a different or a new function.

They proposed to consider as *ad-aptations* those cases where the relation between structure and function was provable with evidence, and to use instead the term


Exaptation in human evolution: how to test adaptive vs exaptive evolutionary hypotheses
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Taxonomy of evolutionary innovations

Process	*Character*	*Usage*
Natural Selection shapes the character for a current use.	Adaptation	Function
A character, previously shaped by natural selection for a particular function (an adaptation), is coopted for a new use.	Exaptation 1 (by cooptation)	Effect
A character whose origin cannot be ascribed to the direct action of Natural Selection (a non-aptation), is coopted for a current use.	Exaptation 2 (by non-aptation) or "spandrels"	Effect

Fig. 1 (A schematic representation of the differences between standard adaptations, exaptations and spandrels, with the proposal to distinguish two types of exaptation, frequently confused even in evolutionary literature)

ex-aptation to refer to a *functional shift* of preexisting structures that had a different function. While in the first case the function could be seen as the *raison d'etre* of the form, in the second the usefulness of the trait (*aptation*) did not precede but followed the organic structure or form (*ex*). Nevertheless, we should define such a taxonomy further (cfr. Fig. 1). We can distinguish two main processes of exaptation (Pievani and Serrelli 2011).

The first one comes from the need to separate the origin of a trait from its present fitness. Feathers could have been used to protect the bearer from cold temperatures (hence with a thermo-regulatory function) and only later be used to aid flight or for sexual selection, as it can be conjectured from traces of feathered and coloured dinosaurs unable to fly. The second meaning of exaptation covers instead the case of architectural *spandrels*, made famous by the now homonymous essay. The first meaning of exaptation, while important and very frequent, still assumes that the trait had *a* function, even if it changed during evolution and following the phylogeny of the species considered. The second one, instead, wants us to allow for the possibility of traits not developing for *any* function, in other words not being selected for a specific function.

Although less frequent, this second meaning of exaptation is very important, since it carries with it Gould's own study of the European tradition of the 'biology of form' (from Goethe to Haeckel) that had been neglected in the Anglo-American world due to a preference for a strict functionalism. In their article, Gould and Lewontin proposed to rethink the concept of *Bauplan*, that is, to see organisms as integrated wholes whose organic structure is not just a passive and plastic material upon which selection can act, but is a level of organization with proper constraints, past history and causal force. The term *spandrels*, taken from architecture, refers in fact to what the authors called a 'by-product' of a certain structure, that is, an element that does not come from a specific project (following the metaphor of architecture), but is bound to be present once a certain set of constructive rules has been fixed.

The authors wanted to give much more credit to those traits that did not arise for evident adaptive reasons at the beginning but as by-products of what Charles Darwin called 'laws of growth', and that we can now study in evolutionary developmental biology (evo-devo). We can recall one example given by Darwin himself: the sutures on the skull of many mammals seem perfectly 'adapted' to make the birth process easier, making it tempting to assume that they 'evolved for' this very reason. However, as Darwin noted (1859: 197) and ingeniously argued from a comparative analysis (the tree of life is the second pillar of any evolutionary explanation), skull sutures are present in reptiles and birds too, i.e. in animals that hatch from eggs. Most likely, these sutures came from a common ancestor of different taxonomic groups, due to ontogenesis (laws of growth), and were later opportunistically co-opted by mammals to make birth easier.

In this regard, the term 'function' should be reserved for the proper outcomes of adaptation, while for exaptation it is better to speak of 'effects'. It must be said that the reference to Darwin is not irrelevant, because the distinction of adaptations *strictu sensu*, exaptations by co-optation of already existing functional traits and *spandrels*, corresponds exactly to the three hypotheses that Darwin proposed in the final edition of *The Origin of Species* (1872) in order to explain how natural selection can produce very complex traits. Changes of function and tinkering with already existing material were the original Darwinian theoretical strategies for saving the idea that natural selection can make even very complex structures in a continuous and gradual way (Pievani 2013). Other scientists like François Jacob (1977) have then recovered this seminal idea.

2.2 *Contingency and Exaptation in a Hierarchical Perspective*

From these remarks it should be clear that, since the beginning, the notion of exaptation was not meant to replace the standard notion of adaptation, but to complement it by stressing the role of *functional redundancy* and *functional shifts* in evolution (cfr. Fig. 2). The relationship between adaptation and exaptation is in fact a complex one, that admits of interrelations and degrees: a certain trait can undergo an exaptation and then an adaptation 'founded' on the former, or vice versa (Gould and

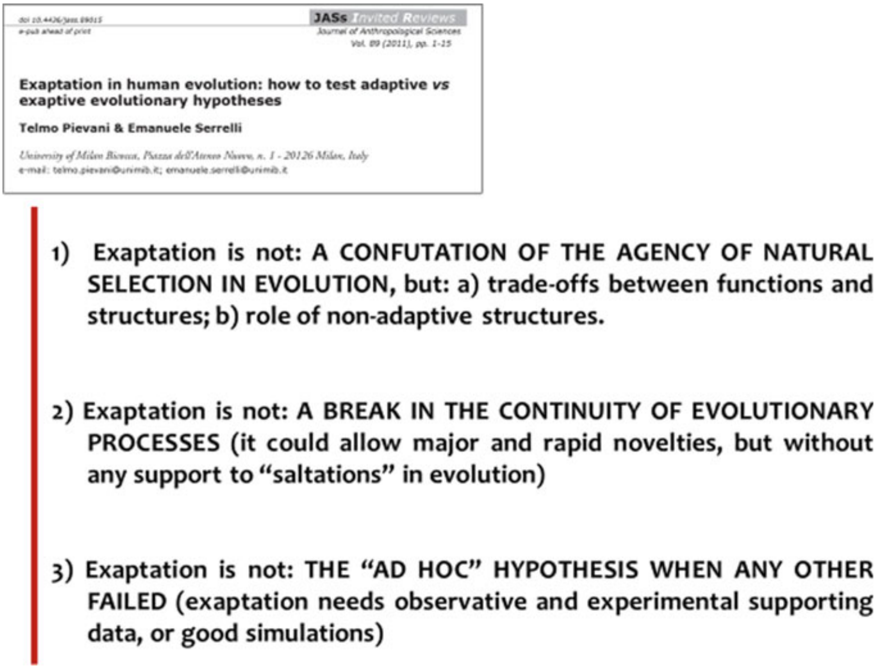

Fig. 2 (Exaptation is neither an anti-Darwinian nor a post-Darwinian concept; here depicted the relationships between exaptation, natural selection and gradualism, that is, the theoretical core of the current neo-Darwinian research programme in evolutionary biology)

Vrba 1982: 12). Once the feathers have been 'exapted' for flight (being evolved to satisfy completely different previous functions, such as thermoregulation and sexual choice), they have probably undergone an autonomous adaptive process that has made them better suited for that function. The same seems to be true for the evolution of limbs from fins, another very important evolutionary transition: as noted by biologist Michael Coates, the picture of the transition towards limbs that emerges from a detailed study of fossils and phylogenesis is increasingly complex and, while functional explanation may indeed be proposed for these changes, it does not allow for simple and unidirectional interpretations (Coates et al. 2002: 398–399). Many changes in the anatomy of tetrapods that were crucial for the fins-limbs transition have been found in animals that were still mostly aquatic, challenging the established notions that limbs evolved for terrestrial locomotion; furthermore, bony fishes as a whole share most of the same genes and developmental regulatory systems, and the same materials are deployed and used similarly in paired fin buds and limb buds. For this reason, the authors see digits as a new arrangement of fin radials, whose development co-opted more general patterns of gene regulatory activity (Coates et al. 2008: 577–583). We can say then that it is from the interplay between adaptations and functional co-optations that the amount of evolutionary possibilities always finds new strategies.

These examples allow us to appreciate the precise sense in which the process of natural selection was put into question by Gould: his approach aimed at conceiving the force of natural selection as a major factor among others, that can change the organism but is also *constrained* by structural limits and developmental rules as well. Instead of seeing organisms as 'free' to roam within an adaptive space, constrained only by the competition with others and by environmental limits, he argued that there are certain routes that natural selection cannot, or can with high improbability, act upon.

Gould suggested that organisms should be seen as biological 'polyhedra' capable of moving only by proceeding side by side, unlike billiard balls than can go in any direction according to the selective environmental accidents (Gould 1993: 422). However, the term *constraint* also has a positive meaning in this view: the organic exaptations and *spandrels* do not only limit the power of selection. Instead, precisely due to their lack of immediate function or due to their functional plasticity, they can constitute a 'reserve for potential exaptations' that can be exploited when environmental conditions change, allowing for transitions that could not have happened by simply improving already existing adaptations (Gould and Vrba 1982: 8). The fecundity of this view keeps showing itself even in recent studies: a review published this October in *Nature* (Levy 2019) analysed a series of studies showing that many important genes essential to survival did not evolve from preexisting, functional genes but from the combination of nonfunctional genetic sequences that lay in that portion of the genome that was once improperly called 'junk DNA'. A recent example of these newly termed 'de novo genes' is the antifreeze gene present in the Atlantic cod (*Gadus morhua*)—essential to its survival—that was shown, after an analysis of the fish genome, to have been built 'from scratch'. The cod, however, seems to be in good company: researchers have found many similar genes in the lineages they surveyed. The ability of organisms to acquire genes this way is certainly a sign of the role played by plasticity in evolution and its power to produce novelty against improbability.

This implication of the concept can be seen as seminal, since it allows us to appreciate one of Gould's most cherished topics: the role of *contingency* in evolution. As noted by Brandon and Misher (1987) and Alhouse (1998), the *spandrels* paper was not refuting the role of selection but arguing for a multiplicity of causal agents (both functional and structural), allowing arguments about which agents(s) should be seen as more explicative in a particular case. This is what we call *evolutionary pluralism*.

Evolution is hereby seen as the interplay between many different causal pathways that forge the contingent story of populations of individuals, full of suboptimal traits and unforeseeable tinkering or *bricolages*. If organisms are integrated entities, not separable into 'single traits', the frequency of correlations capable of producing non-adaptive traits, as Darwin already noted, can be very high: not only the white colour of bones, the redness of blood and male nipples (Gould 2002b: 1572), but also the form of the shell of many snails, among many others traits (Gould 1980). The more complex the organization of an organ is, the more likely it is to generate non-adaptive traits that can form the basis for future exaptations.

As Gould and Vrba mentioned in an article published a few years later (Gould and Vrba 1986), the concept of exaptation can receive new light if interpreted alongside a hierarchical perspective on evolution. The hierarchical theory, developed with palaeontologist Niles Eldredge in the 80s, has been developed over the course of the years even after Gould's death, proving to be a viable framework that can offer an updated perspective on many different fields of the life sciences, from both a theoretical and empirical point of view (Eldredge et al. 2016). Limiting ourselves to what concerns the present topic, we can stress that if the units of selection are not just single organisms bearing genes, but also multiple forms of 'unities' arranged in a hierarchical structure (groups, species, ecosystems, etc.), then we can allow for characters that were adaptive at the original level but can be interpreted as exaptive if considered from the point of view of other levels. These interactions between different levels have been termed *cross-level spandrels* and constitute one of the most promising applications of the concept, insofar as it admits a peculiar form of circular or 'downward' causation between evolutionary levels of change (Gould and Vrba 1986: 225).

Hierarchical theory gives proper attention to the causal power of the basic 'organismal-level', since it stresses the importance of behavioural tendencies that influence the heritability of traits by modifying key aspects of the life of organisms, like diet: a case that is particularly interesting in human evolution. Adaptation is then a phenomenon that happens at multiple causal levels (genetic, cultural and phenotypic) at the same time, generating possible cascades of exaptations at different levels (Pievani and Parravicini 2016).

2.3 Niche Construction as a Critique of the Adaptationist Programme

Another aspect of the critique of the strong adaptationist programme was put forward by Richard Lewontin in a series of essays published around the same years as the *spandrels* paper. In *The Organism as Subject and Object of Evolution* (Lewontin 1983a)[3] Lewontin argued that Darwinism had been successful in showing how organisms should be seen as 'objects' of evolution and its 'forces', like genetic mutation, genetic drift and natural selection, that are "autonomous and alienated from the organism as a whole" (Lewontin 1983a: 87). Lewontin proposed, however, that we now need to see organisms also as *subjects* as well as objects of evolution, with respect to both the production of individual phenotypes and their relations to the environment, because organisms actively participate in their own development and build the environments they encounter.

In a sense he was anticipating the concept of *niche construction* (Odling-Smee et al. 2003) that has become much more popular in recent years. By defending the

[3] For a more recent take on the matter, cfr. Godfrey-Smith (2017): *The Subject as Cause and Effect of Evolution*.

active role of organisms in mediating the selective pressures of their own environment, Lewontin wanted to criticize an excessive 'gene-centric' approach and also to question two strong principles of the adaptationist thinking. The first is the framework according to which the environment poses certain 'problems' that organisms have to 'solve' and that natural selection is the mechanism that allows them to do so, in a quite passive way. This approach implies that researchers ought to start from the 'problem' and then study the organism as a machine that is being built to solve it.

The second principle is the postulation of an environment per se, conceived *before* the presence of any organism actively living into it. Lewontin argued that the concept of *niche construction* puts radically in question both of them, insofar as it does not make sense to speak of the niche of a potential organism before the organism exists: niches are *defined* in practice by the organism's metabolism, anatomy and behaviour and for this reason it is incorrect to conceive an 'empty niche' that awaits the organism to evolve 'into' it (Lewontin 1983a: 98).

This contradiction, he argues, cannot be solved by admitting that the 'problem' preexists the solution. It is also impossible to conceive physical 'constants' of the environment as 'problems' that concern each organism: even gravitation, for example, is not applicable in practice to bacteria since they are very small in size and live in a liquid medium, while they are instead subject to the Brownian motion of molecules, that we human beings can safely ignore (Lewontin 1983a: 104).

3 Dennett's Defence of the *Panglossian Paradigm*

A few years after the publication of the aforementioned essays, the position advanced by Gould was harshly criticized by philosopher Daniel Dennett in an essay with the programmatic title *The Panglossian Paradigm Defended* (Dennett 1983). This started a heated debate that went on for many years[4]: Dennett moved his critiques to Gould in many books of his, especially in his *Darwin Dangerous Idea* (Dennett 1995), where he devoted almost two whole chapters to a refutation of Gould's positions, presenting himself as a proud adaptationist. Since his critiques can be seen as paradigmatic in many senses, we will now examine them and try to give a proper answer updated to the current scientific literature, 25 years later.

As a way to begin this analysis, it could be useful to apply a bit of 'reverse engineering' to Dennett's philosophical position, in order to better understand his own project against Gould and exaptation. Much of the prominent work done by Dennett in his field, the philosophy of mind, can be traced back to his critique of the common knowledge we have of ourselves—our 'folk psychology', as he calls it—and to a background assumption that often accompanies it, the myth of the *Cartesian*

[4] Cfr., for example, Lewontin (1983b), Eldredge (1983) (in response to the target article by Dennett), Gould (1992), Dennett (1992), Gould (1997a, b), Dennett (1997); then the reader can find an explicit rejection of Gould's position in most of Dennett's books, notably, Dennett (1987), Dennett (1995), Dennett (2017).

Theatre. This kind of reasoning, which Dennett criticizes effectively in many books (notably Dennett 1991a) can be summed up in the conception according to which the human mind is a *representational centre* that governs thought and actions due to its intentionality, the capacity to refer to things and states of the world.

This kind of theory of mind is often at the centre of the *manifest image* (Sellars 1965) of the world that we, as persons, inhabit and share with others. To be precise, Dennett has never been an 'eliminativist' towards the manifest image[5]: his position requires him to show how to retain many of the philosophical attributes of the manifest image (such as the freedom of the agent, one of Dennett's main goals) without committing himself to a Cartesian ontology of the subject. The solution to this problem has been a commitment to a particular form of *functionalism*, that sees meaning and intentionality as defined by their function and not by ontological considerations. His theory of the *intentional stance* can be seen on this regard as a way of preserving our 'mentalistic' talk without endorsing the ontological assumption according to which when we say that 'Smith *believes* something' there is a Cartesian subject that represents and endorses this belief. The same is true even with respect to animals, which can be treated as *intentional systems* (Dennett 1971).

The intentional stance is then a sort of theory of the mind that we have come to endorse and that must be explained in functionalist terms: we *assume* a certain degree of rationality in other beings as a strategy "to organize data, explain interrelations and generate questions to ask Nature" (Dennett 1983: 353). This methodological treatment of intentionality, however, was not enough to complete Dennett's project: he needed also a way to explain away ontological implications about 'minds' and to show that a functional classification of 'mental' states was enough. This led him to develop his interest in Artificial Intelligence, as a way of showing how complex tasks whose completion was normally attributed to a form of 'original intentionality' in human mind could be done by 'sharing' this higher-level intentionality of the 'man in the brain' with many unintentional 'homunculi'. In this regard even artefacts can be studied intentionally (methodologically speaking), while admitting that you can reach a level where

> the homunculi are no more than adders and subtracters; […] by the time they need only the intelligence to pick the larger of two numbers when directed to, they have been reduced to functionaries who can be replaced by a machine (Dennett 1978a: 80)

As this passage clearly shows, this approach sees the intentional stance as a way of describing the behaviour of an entity without any form of ontological mind, describable in purely functional terms. It is by recognizing this feature of his thought that we can understand Dennett's enthusiastic endorsement of Richard Dawkins' metaphor of the *selfish gene*: his refutation of the Cartesian conception was completed by recognizing that even our intentionality was phylogenetically 'derived', since we humans were *like* machines designed by nature to transmit and perpetuate our genes (Dennett 1987: 298). This ultra-Darwinian and gene-centric perspective on

[5]Cfr., for example, his reply to P. Churchland (Dennett 1991b), and his critique of Harris' position (Dennett 2017: 394, fn. 368).

evolution was in fact approached by Dennett as a way to show how the 'original' intentionality of mind, instead of being an 'all-or-nothing' phenomenon that stood in the way of a proper naturalization, could be traced back to the anonymous work of a myriad of non-intentional processes, in the same way that the apparent 'intelligent' design of organism could be created by "cascades of selective processes lacking any intelligence" (BB: 68).

Dennett's defence of strong adaptationism was thus philosophically motivated: from this point of view, the cognitive psychologists who, as 'intentionalists', assume that other living beings have intentional states (that is, possess a degree of *rationality*), are ideologically in the same boat as evolutionary biologists who, as 'adaptationists', assume that everything they find in nature is adaptive (that is, has a *reason* to function the way it does). In other words, there is the strictest connection between the intentional stance, the optimality stance and adaptationist thinking (Dennett 1987: 277): in this way instead of crediting the subject (man or other animal) with the rationale of their own actions we can translate the view of it *"from the individual to the evolving genotype"* (Dennett 1983: 351). In this way Dennett could employ the intentional stance without admitting the Cartesian theatre: the subject represents reasons that he was not the source of, while 'Mother Nature' could be seen as the source of them, but without being capable of representing anything.

3.1 The Critiques of the Concept of Exaptation in DDI

These considerations can shed light on how evolution was depicted in *Darwin's Dangerous Idea*[6]. There Dennett affirmed that Darwin's merit was not to have simply described the evolution of organisms through the tree of life model (descent with modifications), but to have argued that all happened *through natural selection*, the only unintentional and blind agent that can explain the coming into being of complex structures. In fact, what is 'dangerous' about the Darwinian idea of selection is that, like a universal acid, it is applicable not only to biology, but to our whole vision of the world (DDI: 77), serving the purpose of Dennett's own critique of the *Cartesian Theatre*.

Evolution by natural selection is then described through three main metaphors: first, it is for him an *algorithmic process*, that is, "a certain sort of formal process that can be counted on—logically—to yield a certain sort of result whenever it is 'run' or instantiated" (DDI: 50). Given a certain frequency of variations, a population with enough members and a lot of time, the Darwinian algorithm must produce complex structures out of simpler materials in a purely automatic way. Nature works, in this respect, *as if* it were an *engineer*, to the point where Dennett dedicated an entire chapter to defending the second metaphor, according to which *Biology means*

[6]The theorical position presented in the book received a few critiques not only from Gould (Gould 1997a, b): cfr., for example, the review by Orr and Dennett's reply: Orr (1996b, c); Dennett (1996); Orr (1996a) and also Alhouse (1998). For a defence of Dennett's position see Carroll (2004).

Engineering (chapter VIII). Given his commitment to optimality assumptions, he affirmed that the correct way to reconstruct the evolutionary history of organisms is through the 'reverse engineering' approach. By this he meant that we should first individuate the function of a certain trait and then reconstruct the environmental problem whose 'solution' was provided by that adaptive function, treating organisms as machines subject to a never-ending 'research and development' process.

Finally, evolution by natural selection, in this sense, is essentially a gradual process of functional refinement that proceeds by serial accumulations: it works as a *crane* (third metaphor), capable of lifting organisms through the 'design space', a (likely) Platonic space of ideal forms (the 'library of Mendel') that selection can reach by improving organic designs (DDI: 80). Anything that is not a *crane* working with bottom-up causation is for him a *skyhook*, a term used to indicate mystical appeals to unnatural forces. The radical opposition between *skyhooks* and *cranes* is stressed over and over throughout the book: it seems that the fear of falling back into a 'Cartesian' conception of mind lead Dennett to accept a strong dichotomy between a purely mechanical account of evolution, on one side, and a mystical faith in a prime mover on the other, without a middle way in between. In this *aut-aut* sense, one is either a 'Darwinian fundamentalist' (Gould 1997a) or a creationist, and this is the 'fundamental truth' of Darwinism (Dennett 2006: 2).

If this analysis is correct, it can safely be said that Dennett's disagreement with Gould had deeper roots than just the role of natural selection in contemporary evolutionary theory. Dennett's own research in the philosophy of mind led him to a form of strong *functionalism* that was in sharp contrast with Gould's reflection on the 'philosophy of form' and structuralism. Furthermore, Dennett's interest towards Artificial Intelligence supported the 'reverse engineering' hypothesis, that could be seen as the very target Lewontin was attacking with his defence of the concept of *niche construction*.

It is then quite natural and consequent that Dennett criticized every aspect of the Gouldian position that we have previously presented: he depicted Gould as a 'failed revolutionary', thus proclaiming the death of the Modern Synthesis without being able to offer any alternative to it, since removing adaptationism from its place is tantamount to 'refuting Darwinism' itself (DDI: 249). Put briefly, Dennett defended all those aspects of the Modern Synthesis that Gould was criticizing at the time (gene-centrism, exclusive focus on selection, adaptationism, gradualism and the reverse engineering approach) since he could not allow the undermining of the notion of nature as an optimizing agent.

For our purposes here, we can restrict his critiques to three main points related to exaptation:

(1) He maintains that it is impossible to distinguish an adaptation from an exaptation correctly, since every exaptation presupposes a previous adaptation.
(2) He allows for an evolutionary role played by constraints and spandrels, but he marginalizes it, saying that the only way to discover them is through reverse engineering. Following this perspective, we can show the correctness of non-adaptive hypotheses only after having all the possible adaptive alternatives tested. Saying

that a trait did not arise for any apparent function is absurd for Dennett, since it would be like calling for nothing less than a skyhook, a metaphysical hole in the mechanical process of evolution.

(3) Finally, he is entirely critical of Gould's defence of the concept of evolutionary *contingency*: putting contingency at the centre of evolutionary explanations is for Dennett tantamount to leaving it to mere chance. He even implies that Gould's hidden aim is to oppose the Darwinian perspective in order to give the "*mind* some elbow room, so it can *act,* and be *responsible* for its own destiny instead of being the mere effect of a mindless cascade of mechanical processes" (DDI: 300). So, the Cartesian conception of the mind remains the overarching polemical target for Dennett, even though Gould never thought in Cartesian terms.

We can take these objections to exaptation as a guideline and divide them into *experimental* and *conceptual* ones. The experimental ones will be answered through a confrontation with recent experimental evidence and empirical studies, 25 years after this philosophical debate. As regards the conceptual issue, we will look at BB and decide whether or not Dennett himself has changed his position during the years and after Gould's death.

4 Exaptation as an Operational Concept

The first critique we can examine concerns the alleged indistinguishable nature of exaptations and adaptations, and the indispensable character of optimality assumptions. One of the authors of this paper (Pievani) and Emanuele Serrelli (2011) call this the *non-operationality objection* and show how to reply to it in detail through a pluralistic approach. Even those scholars who accept the conceptual utility of the exaptation hypothesis are in need of differentiating it from adaptations. By examining some empirical studies, we suggest a few ways to differentiate the two concepts with more clarity, showing how exaptation can be an 'operational' and not only a 'theoretical' concept (Pievani and Serrelli 2011: 16–17).

(1) Instead of taking adaptation as a null hypothesis that does not need independent testing, researchers could *devise detailed mathematical and biomechanical models to test the real relationships between a function and a structure*. For example, in a very interesting study published in *Nature* (Barve and Wagner 2013) the authors analysed the ability of a metabolic reaction network to synthesize biomass from a single source of carbon and energy. They applied complex computational models to sample many metabolic networks randomly, that could sustain life on any given carbon source but contain an otherwise random set of known biochemical reactions. The authors verified that once a certain system is set to synthetize a certain source of carbon, it becomes capable of acting on other sources that were not the direct 'target' of selection. For this

reason, they have shown how "any adaptation in these metabolic systems typically entails multiple potential exaptations. Metabolic systems thus contain a latent potential for evolutionary innovations with non-adaptive origins" (Barve and Wagner 2013: 205).

(2) *Testing for effective correspondence between structure and function in living and fossil species*. Adopting the 'tree thinking' perspective, to employ both a synchronic and diachronic perspective at the same time can reinforce the adaptive or exaptive hypothesis with more accuracy. If the distribution of a trait was random regarding behaviour and lifestyle, an adaptive hypothesis would be undoubtedly weakened. On the contrary, the 'convergence approach' (Kivell and Begun, 2007) can potentially give strong support to an adaptive hypothesis.

(3) *Exploring multiple functions of a structure* and *structural alternatives for the considered function.* Exaptations refer to a functional redundancy that allows for gradual shifts between functions. For example, Shimizu and Macho (2007) state that researchers have considered scallops primarily as a crack-stopping mechanism. Now experimental studies reveal that the latter function has been overestimated: scallops prevent delamination of enamel, as their primary function, with crack-stopping as an indirect effect. On the other hand, the existence of actual structural alternatives for the same function can weaken the structure-function correspondence necessary for a strictly adaptive hypothesis.

(4) *Enlarging phylogenetic context to improve knowledge*. From this point of view, even the most famous 'adaptive story' can be questioned: as noted by Tecumseh Fitch, the adaptive basis for the form of the giraffes' neck is questioned when noticing that almost every mammal has seven neck vertebrae, even the apparently 'neckless' narwhal (Fitch 2012: 618). It would have been a 'simpler' strategy to add new vertebrae with the augmentation of the length of the neck, but that did not happen. Since that trait is not present in birds or reptiles, it is likely that it is a constraint fixed in early mammals, and that it would have been too costly for natural selection to act upon it. For this reason, it should be said that the *length* of the neck is an adaptation, while "other correlated traits such as the number of the vertebrae and the form of the larynx nerve were due to developmental constraints and were not optimized during the evolution of the long neck" (Fitch 2012: 619).

(5) *Improving knowledge concerning ontogenetic and developmental processes underlying organic structure:* adaptationist views often rely on the assumption of direct genetic control upon structures. However, this assumption became less central in recent years because of new advancements in developmental biology: the increasing attention to the role of epigenetics in acting as a mediator between genotypes and phenotypes, for example, is putting in question the assumption that selection can act directly on genes. As an illuminating example, a study that appeared a few years ago in *Nature* (Ataman et al. 2016) has shown a gene (OSTN) expressed in the bones and muscles of mice and other mammals that, over the course of evolution, was re-functionalized to act in the neurons of primates. OSTN encodes a secreted protein that is involved in

glucose metabolism in the muscles and bones of mice; then the authors over-expressed or repressed OSTN in human neuronal cultures, and discovered that the expression of the gene regulates the shape of dendrites—the branched parts of neurons that receive and integrate synaptic information from other neurons. Then the authors supposed that the same gene had been 'co-opted' in primates for a different function: this result suggests that, in primates but not in other mammals, OSTN might regulate structural changes that neurons undergo during learning. Given the fundamental importance of neural plasticity in primates and *Homo sapiens*, such an approach could be seminal for our comprehension of the evolution of genetic regulation (Burns and Boeke 2008).

These considerations ask researchers to adopt a different set of guiding questions, as philosopher of biology Elizabeth Lloyd notes. An adaptationist approach takes as a guiding question: "what is the function of this trait?" (Lloyd and Gould 2017: 54), whose consequence is that cases of exaptations can have the role of 'null hypotheses' at most. In a pluralist approach, instead, there should be more questions from the start. Lloyd proposes the following: "What evolutionary factors account for the form and distribution of this trait? How did this trait come to be present in this population? And does this trait have a function?". These guiding questions (that call for the joint approach of different evolutionary disciplines) maintain a key aspect of the concept of exaptation.

In fact, even if the effects of exaptations and spandrels can contribute to the total fitness of the organism, it should be highlighted that they are not simply the *solution of an adaptive problem*, but are maintained "mostly through other mechanisms, such as developmental constraints or [...] other structural mediums as by-products or genetic correlations" (Lloyd and Gould 2017: 51). In this regard Fitch notes that disciplines such as Evo-Devo put into question the Dennettian metaphor of nature as a chess player that 'hides' moves from us (DDI: 252), since they allow us to 'read the rules' by studying developmental processes. Furthermore, other inferences can be made after a detailed study of phylogenesis and ontogenesis together (Fitch 2012). For this reason, he believes that the 'adaptation hypothesis' should not be the default assumption but "an onerous concept to be invoked only after a pluralistic set of plausible non-adaptive hypotheses (chance, constraints, spandrels, exaptation, phenotypic plasticity) have failed" (Fitch 2012: 616).

Finally, it is interesting to note that those aspects of evolutionary theory that were put forward by Gould as 'correctives' with respect to the strong 'adaptationist' core of the Modern Synthesis have become much more central recently. Many scholars have become critical towards that perspective and advanced the need for an 'Extended Evolutionary Synthesis' (EES) (Pigliucci and Müller 2010). As Müller notes (2013), many of the key concepts employed in this approach where anticipated in Gould's thought and owe to him a strong debt, since he was one of the first theorists to criticize the Modern Synthesis as the standard view. He wished for its development and reformation when it was certainly uncommon in the field: he anticipated models and concepts like niche construction, soft-inheritance (Avital and Jablonka 2000), phenotypic plasticity (Jablonka and Lamb 2005) and mostly the role of constraints in evolution.

These recent lines of research (still Neo-Darwinian, but in an extended sense) have put in question the assumption that natural selection "is a sufficient descriptor for all directionalities in phenotypic change and that most characters are independently adaptive" (Müller 2013: 10–11), calling instead for a pluralistic and less gene-centred approach to evolution. While it is indeed a debated topic still today, with distinguished scholars on both sides (for a confrontation between 'reformists' and 'conservatives' about the legacy of the Modern Synthesis, see Laland et al. 2014), we can safely say that the Gouldian 'revolutions' were not just a baseless approach (as Dennett maintained), but theorical insights that could open different research pathways. We can say that exaptation has had its empirical revenge 25 years later.

5 From Bacteria to Bach and the Conceptual Objections

As a second part of our strategy, it is now our purpose to make a confrontation between DDI and BB in order to see how Dennett's view changed regarding some of the conceptual problems we have mentioned here. To do so, we will have to read between the lines of the text. Actually, Dennett explicitly reiterates his sharp critiques of Gould (who unfortunately cannot reply) in his recent book. He affirms that the *spandrels* paper was an "unfair caricature of the use of optimality assumptions in biology" (BB: 41). He defends reverse engineering (BB: 42) and invites the reader to abandon Gould's 'ecumenical' view of the evolution of culture, adopting instead that of Richard Dawkins (BB: 210). However, we will argue that this critique remains quite superficial, by examining three conceptual features that are important to Dennett's arguments throughout the book: his use of the concept of *Umwelt*; the analysis of the phenomenon of 'de-Darwinization'; and the development of his thought concerning the metaphor of organisms as machines.

5.1 The Concept of Umwelt and Its Relationship to Natural Selection

One of the key concepts that are found in his latest book and that were completely absent in DDI is that of *Umwelt*. He also heavily applies the concept of *niche*, which in DDI appeared only marginally. Dennett describes the *Umwelt* of an organism as "the behavioural environment that consists of all the things that matter to its well-being" (BB: 86). These objects make up the 'ontology' of the organism, which is also described, along with Gibson's (1979) concept of *affordance*, as "what the environment offers the animal for good or ill". Each species has its own ontology: the sun is in the ontology of a bee, but not of a bacterium, for example. We in fact learn that the various *affordances* of an *Umwelt* constitute what Dennett calls the *semantic information* available for a certain organism, defined as a 'distinction that makes a difference': any situation or state of affairs that elicits a differential response from the organism counts as information for it and its species.

Umwelts are not static, but they change over time due to the activity of the organisms and the changing environment: the more instruments are available for a certain being, the more semantic information becomes available, and with that come new differential responses and capacities to discriminate and individuate entities. While it is true that for Dennett the *Umwelt* comprehends the problems 'faced and solved' by the organism, this topic has a different ring than in DDI. We are in fact told that the *semantic information* is receiver relative and does not have independent measure (BB: 127), that it cannot be properly described in physical terms (BB: 134), and that it arises in the relationships between organism and environment, which should be conceived as a 'virtuous circle' (BB: 120).

Furthermore, in the same environments there can be very different niches, since what counts for an organism as information can be useless for another. Dennett is brilliant at thematising how the same physical medium can count as a completely different 'signal' depending on the organic 'threshold' it passes through. He uses the concept of *soft-inheritance* and openly speaks of behavioural traits that lead genetic development and of the role of organisms in building their own environment. As we have seen, these conceptual features of the concept of *Umwelt* are very close to Lewontin's idea that we should not see the organism as receiving a set of problems from a preformed environment considered independently of its inhabitants, but that the environment exists only *with respect to* the organisms that inhabit it. The 'virtuous circle' that Dennett describes is also very close to the idea that it is not the environment per se, but the *organism-environment differential relationship* that defines the 'traits' being selected.

Could this endorsement of the concept of niche lead to a reconsideration of the role of selection? The answer seems, at least partially, yes; we can appreciate this feature if we look at Dennett's analysis of the phenomenon of 'de-Darwinization', to which he dedicates a whole chapter of the book. While in DDI he was fond of describing a single 'design space' that selection was responsible to explore, and marginalized any phenomenon that departed from the ubiquitous natural selection, now he utilizes Peter Godfrey-Smith's concept of 'Darwinian spaces' (Godfrey-Smith 2009) to present the evolutionary environment as a space with different degrees of closeness to the evolutionary 'norm' exemplified by the bacterium. He calls these departures 'de-Darwinizations'. We learn that these are present at many levels of the biosphere, not just in *Homo sapiens* but also in other animals: examples include human cells (less Darwinian that their prokaryotic 'ancestors') (BB: 142) and communities of bacteria.

When he deals with the de-Darwinization brought about by culture and socialization, we see a beautiful diagram in which humans occupy the higher part, but there also are many intermediate levels among which Dennett counts even mushroom groups and 'societies' of aspen groves (BB: 150). He also dedicates a decent amount of space to the phenomenon of 'animal traditions' (Avital and Jablonka 2000)[7].

Proceeding along these lines, Dennett asserts that instead of trying to draw bright lines that separate mere pseudo-Darwinian phenomena from phenomena that exhibit all three of the 'essential' features of natural selection, "we contrive gradients on which we can place things that are sorta-Darwinian in some regard or another" (BB: 139). It should not surprise, then, that here Dennett openly speaks of evolution as a phenomenon that can reach different 'peaks' of 'sorta-Darwinism' depending on the environment and on the starting conditions: the 'blind watchmaker' peak is seen as a case seldom reachable, while in more 'rugged' landscapes evolution admits only local peaks (BB: 139).

There is certainly a sharp contrast with DDI, where Gould was accused of advocating for *skyhooks* for having stressed more or less the same points. In fact, it is quite striking to notice that the examples of genetic drift and the role of chance that Dennett makes in these pages are almost identical to the ones presented by Gould and Lewontin in the *spandrels* paper.

5.2 Dennett's 'Conversion' on the Brain-Computer Metaphor

Finally, we arrive at what constitutes perhaps the most interesting development in Dennett's thought: his critique of a mechanical conception of the brain. He dedicates a whole chapter to illustrate this difference. He criticizes the conception that sees the brain as a rudimentary computer, and the functionalist assumption of AI (BB: 153)—that he himself used to defend, as he admits—according to which "any living organ is really just a very sophisticated bit of carbon-based machinery that can be replaced, piece by piece or all at once, by a non-living substitute that has the same input-output profile" (BB: 157).

He says that he has come to find problematic the solution that we have quoted above, proposed in *Brainstorms* (Dennett 1978b), on how to handle the 'homunculus temptation' or, as described here, the *Cartesian Theatre*. Now Dennett states that new developments in various fields of science led him to reformulate a key part of his thought to the point where he wants to "emphasise the conversion" (BB: 161). He openly rejects the terms 'committee' and 'machine' since they suggest a "profoundly unbiological sort of efficacy" (BB: 162), and prefers to describe neurons as competent agents, playing enterprising roles, capable of a form of nano-intentionality (Fitch 2008). While machines are 'parasitic' on external energy, living things provide energy for themselves and are made of parts (like cells) that are themselves alive. They can

[7]It should be noticed that the authors here are critical of the concept of 'meme' as presented by Dawkins and explicitly link their work to Lewontin (1983a); they are also critical of a 'first problem-then solution' model of natural selection advocated as prime agent, and of the gene as 'recipe' to build something (Avital and Jablonka 2000: 68–78).

defend and repair themselves, constituting a system of units, which is open to the environment in which its body situates it.

Concerning the brain, the difference between neurons and circuits is that the former are in key respects autonomous on their own. Furthermore, the brain's most important feature is its plasticity: its capacity to reassign functions to different areas and to repair itself (BB: 159). Plasticity is important because it shows that the reassignment of functions is not 'imposed' by a 'politburo' form of top-down control, but by a bottom-up coalition of living entities. For this reason, the model previously endorsed by him applied "the wrong kind of hierarchy" (BB: 165), like a bureaucracy that suppresses innovation and exploration of possibilities (we have seen how seminal the concept of 'hierarchy' has been in Gould's reflections).

We have a significantly different Dennett here, with relevant philosophical consequences. This is a radical conversion: if our reconstruction is right, it touches more than a few of Dennett's key concepts and problems. His new concept of hierarchy is very close to the Gouldian one, insofar as it shows that in many cases a flexibility between structure and function is the preferable condition. Ever-changing environments call for 'incomplete designs' that can be 'tuned to the circumstances' (BB: 164), whereas the previous mechanical model (based on optimality and specialization) could have been a bad evolutionary strategy in many cases. This necessity of local adaptations calls for a plurality of levels of learning, some of which can be in the genes and others behavioural, as we have seen. Dennett's reformulation of the organism-machine metaphor even leads him to accept the "undeniable message of evo-devo", according to which

> the production of the next generation of any organism is not a straightforward matter of following a blueprint or recipe laid down in the genes; it is a construction job that must rely on local R&D that depends on the activity of (myopic) local agents that conduct more or less random trials as they interact with their surroundings in the course of development (BB: 164–165).

Summing up our analysis so far, we have seen that Dennett allows for brain plasticity and for a flexibility in the structure-function mapping. He rejects now the conception of genes as blueprints, calling instead for complex developmental processes. He puts in question the mechanical metaphor to a certain degree, preferring to refer to hierarchies of interrelated systems. He stresses that in the same environment there can be both different niches and different selective forces, acting at the same time with different degrees of efficacy.

As we tried to show, these arguments have philosophical consequences and are very close to the ones Gould used, namely against adaptationism and its functionalist metaphor of selection as a 'universal algorithm', as the reader can see in Gould (1997a). No wonder that, while in DDI Dennett criticized the 'Burgess Shale' argument for contingency (Gould 1989), contending that it would have been possible to rewind the tape of evolution 'algorithmically' with Alife models (DDI: 212), now he denies that a 'master algorithm' could exist since what the 'algorithm' of selection can act upon is only the "adjacent possible" (BB: 365), an expression (coined by theoretical biologist Stuart Kauffman) that ironically captures very well Gould's conception of the role of contingency in evolutionary history.

As a concluding remark, it is interesting to note that in the article that started the whole debate, Dennett referred polemically to Lewontin's review of *The Mismeasure of Man* (Gould 1981), where Lewontin claims that

> It is not easy, given the analytic mode of science, to replace the clockwork mind with something less silly. Updating the metaphor by changing clocks into computers has got us nowhere. The wholesale rejection of analysis in favour of obscurantist holism has been worse. *Imprisoned by our Cartesianism*, we do not know how to think about thinking (Lewontin 1981: 16)

Dennett suggested that Lewontin's opposition to the 'clockwork model' of mind was only due to his lack of interest in computer science. Now, after more than a few years of reflection on both artificial intelligence and evolutionary theory, Dennett has ended up doing exactly the same.

6 Conclusion: Homo Sapiens as an Exaptive Species

It is not by chance that Dennett's position gets closer to Gould's when it comes to the analysis of the evolution of culture. The concept of exaptation proves, in fact, to be very useful in those fields where it is hard to individuate a specific function for the objects studied, like, for example, in the study of the complex evolution of culture and technology (Larson et al. 2013: 498). In these cases, an adaptationist approach runs the risk of missing the intrinsic complexity of the phenomenon studied, since the most peculiar trait about human culture is its capacity to modify its own nature and its aims, adapting to phenomena of its own creation.

This is especially true in the case of technology. As William B. Arthur notes in an informative book dedicated to the evolution of technology (Arthur 2009), the system of technologies that a certain 'age' makes use of constitutes a complex structure, made by interrelated parts. Each instrument or set of instruments are built from preexisting technologies that are put to new uses, in a cumulative and continuous process that has many similarities with the evolution of species. Everything starts with the discovery of a natural phenomenon that is firstly studied and put under control (from the use of fire to the electromagnetic field): this first step is often rudimentary but then a new space is open for a technological development that proceeds by 'combinatory evolution' (Arthur 2009: 12).

The author stresses that technology always has a hierarchical structure, similar to that of a tree (Arthur 2009: 33): the heart of a certain system of instruments is the one put to the 'main' use (e.g.: the control of a certain phenomenon), but it is always accompanied by auxiliary parts that have themselves a certain set of autonomous applications, and so forth. In this regard, the functional organization of interrelated parts is a property that biological structures have in common with technological ones. As in the case of biological organisms, this hierarchy makes very likely that in any given technological system there are subparts that can be dissociated and put to a separate use, or that have no use at all.

According to Arthur's reconstruction, the first technology is described by a more or less abstract principle and is then developed and perfected by combining already existing instruments, in a sort of 'hybridisation' that proceeds by adding always new principles of use. This sort of 'evolutionary bricolage' is for Arthur the basis of technological evolution, as a sort of *working architecture* being modified from inside out by playing with constraints and preexisting features, in a continuity of change arising from the creative use of what already exists. This is what the author calls *adaptive stretch* (and that we could call 'technological exaptation' (Pievani and De Biase 2016: 31). This implies that deliberate projects are bound to be just *a* part of the development of new technologies: an equally and perhaps more important part is given by the creative use of the already existing items in a different way by changing the context of use.

In this sense, the phenomenon of exaptation can be seen as almost ubiquitous in the history of technology. From the phonograph to GPS, from the Internet to the radio, it is rare that an invention maintained the use that its creators had in mind, to the point that the uses of a given technology with regard to different contexts are bound to give birth to unpredictable exaptations (Dew et al. 2004).

This 'exaptive' view of technology is particularly fruitful if applied to the concept of niche construction, since *Homo sapiens* can be seen as the constructor of techno-cultural niches, experiencing and promoting gene-culture coevolutionary processes (Laland et al. 2010; Fisher and Ridley 2019). More generally, we could speak of a *gene-technology coevolution*, seeing *Homo sapiens* as an essentially techno-symbiotic species (Pievani and Di Biase 2016: 60). This concept of niche is a good instrument to weaken the image of a 'clockwork mind', to use Lewontin's expression: the fault of many socio-biological reconstructions is that they have a mechanical model of behaviour that turns human beings into 'adaptive automata' with Palaeolithic 'behavioural modules' in the brain.

As John Dupré rightly notes, this model that takes an element out of its context and makes it the 'cause' of behaviour is still a 'Cartesian' account that simply replaces the duality of body and soul with that of brain and behaviour (Dupré 2010: 297). The fault of this model is to see human beings as mechanical systems in which information is embedded from outside. As even Dennett admits today, a more fruitful strategy is to see our behavioural capacities as being proper of an 'open' (and hence 'living') system. In this way, we can accept a circular causality where the 'machinery' of the organism is both *caused* by the environment but is also an *effect* of its own behaviour.

Our genome did not change much from the time of our ancestors, and neither did our brains: what did evolve was our technological capacity that moved evolution to the level of culture[8]. In this regard, we can conclude by saying that all the factors that we mentioned, which enlarge the neo-Darwinian 'core' based on genetic variation and

[8]Due to their plasticity and the fact that their development continues for almost two-thirds after birth, an 'alphabetized' brain that has grown up in a certain technological environment can be proved to be biologically different from a brain that did not (cfr. Dehaene et al. 2015): this very capacity of the brain can be seen as the source of numerous 'neural exaptations' or neural recycling that start from the technological niche and act upon it.

selection, seem useful to better understand the evolution of the human species: epigenetics, phenotypic plasticity, developmental constraints, functional shifts, macroevolutionary factors that happen on a large scale, the interplay between the different levels at which the evolutionary process happen, and especially the study of how organisms construct their own niches. This extended and more ecological evolutionary theory, faithful to Darwin's pluralistic spirit (Eldredge et al. 2016), is what we need in order to understand the co-evolution of technologies and human beings. For a fruitful scientific comprehension of both biological and cultural evolution, the concept of exaptation still stands out as a pillar of the most updated evolutionary approach.

7 Attributions

Both authors are responsible for the content of this paper. Particularly, Telmo Pievani is the author of Chaps. 1, 3 and 5. Filippo Sanguettoli is the author of Chaps. 2 and 4.

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