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Approaching a semiotics of exaptation: At the intersection between biological evolution and technological development

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Abstract. This paper recognizes a specific correspondence between biological evolution and technological development and on this basis tries to set up a semiotic approach to the evolutionary phenomenon of exaptation. To do this, the existence of a historical-structural and pragmatic analogy between organs and tools is shown, which in turn implies on a communicative ground the dissolution of some of their traditional distinctive attributes. Finally, a philosophical-analytical approach to natural and cultural functions is applied to define three types of exaptations.

Keywords: action, combination, exaptation, function, organs, selection, semiotics, technology, tools.

1. Introduction

For Stephen Jay Gould and Elizabeth Vrba the notion of exaptation defines those biological traits that "are fit for their current role, hence *aptus*, but they were not designed for it, and are therefore not *ad aptus*, or pushed towards fitness. They owe their fitness to features present for other reasons, and are therefore *fit* (*aptus*) *by reason of* (*ex*) their form, or *ex aptus*" (Gould, Vrba 1982: 6). As a classic example, birds do not have feathers because they were originally designed to perform the function of flight, rather they were co-opted from the original use they had in dinosaurs, where they served as means of thermoregulation.

Since the concept was proposed as a response to the predominance of adaptation in the neo-Darwinian paradigm for evolutionary change, this article follows the same

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critical approach and the theoretical framework of reference adopted to address its analysis is the research program of *biosemiotics*, namely a semiotic science whose paramount heuristic principle consists in the view that a sign-based modelling of living organism can provide a better understanding than traditional (physicalist or neo-Darwinian) approaches within mainstream biology (Kull *et al.* 2008).

This said, what would it mean to work out a (bio)semiotic model of exaptation? On one side, a model is a "form of meaning" that stands for something else (Sebeok, Danesi 2000: 2), namely a system of ordered elements conveying some kind of information about a specific reality; on the other side, by being "a trait [...] that confers *performance advantage* in a particular way at a specific time but *was not produced by natural selection for that use*" (Arnold 1994: 126; emphasis mine), exaptation covers a specific subset of instances of functional change in the relational properties of a character. Hence, a semiotic account of exaptation is based on the schematic representation (Krampen 1997: 248) of the factors involved in the non-selective and non-adaptive (in Gould and Vrba's sense) evolutionary generation of new connections within the organism-environment dynamics.

This project is grounded on the idea of an analogy between different objects of analysis: in order to take a model developed within a specific discipline – semiotics – and exploit it in a different one – biology – the existence of common features between their respective domains must be assumed preliminarily. When it comes to exaptation, a commonsensical assimilatory comparison is often advanced to illustrate what the shift in the performance of a biological structure might look like; at the end of the exposition it will appear clear how deep and striking this insight is and its value in the detection and adoption of a concrete model.

In his study on the evolution of complex organs, and to facilitate the reader's understanding, T. Ryan Gregory (2008) draws a parallel between the mechanism of biological functional shift and the way a common everyday object – a coin – has been given a new use in recent years. If the primary function of a coin was and still is as currency, the appearance of a new conditioning situation (lottery tickets covered by removable coating) has turned it into a lottery tickets scraper as well. Moreover, because of the difficulty to scratch just by holding it between the thumb and index finger, the coin has being integrated in a keychain that ensures a better grip. This exemplification is remarkable in two ways.

First of all, it allows of a handy and concrete translation of Edwin Nicholas Arnold's conceptual terminology adopted in his important contribution (Arnold 1994) on exaptation. With this term he refers to traits that "arose in some other way, and only subsequently acquired the performance advantage and use under consideration, usually as a result of change in the selective regime" (Arnold 1994: 126). Similarly, some properties of the coin, including the abrasive nature of its edges, had not been conceived to perform the scraping function, but the interest in this function is what became relevant additionally as soon as they were differently exploited in a new context.

Besides, Arnold articulates different kinds of exaptations: *first use exaptations*, where "a trait has no performance advantage at its origin, gaining one only when subsequently coopted to the use in question" (Arnold 1994: 137); *extra-use exaptations* (the trait is already performing a function before change), divided into *addition exaptations*, "when the new use is merely added to the first" (Arnold 1994: 138), and *transfer exaptations*, "involving a shift to a new use with loss of the original one" (Arnold 1994: 138). Back to Gregory's example, before becoming useful in the construction of human tools, metal (which also coins are made of) had not had any peculiar workable function and only later was recruited for currency exchange. All the same, its scratching use in the form of a coin is an additional function that by no means substitutes its monetary value. The choice of the coin is particularly interesting because, as for the material employed, it presupposes the succession of three historical moments: tool production, monetary value (maintaining that currency and work instruments are different kinds of tools) and scraping utility. And such alternate phases characterize exaptation as well.

Coming to the second benefit of Gregory's example, it offers the opportunity to highlight two other important points made by Arnold. In the first instance, "although the evolutionary role of first-use exaptations has been emphasized [...] these appear to be relatively rare. [...] Extra-use exaptations, on the other hand, seem to be far more common...they may be a more immediately effective source of aptations in many situations than adaptations" (Arnold 1994: 144). In the second instance, "[f]eatures of organisms that become exaptations are often quite complex and have not arisen from a single evolutionary event. Not infrequently, they are the result of a series of likely adaptations often widely separated in time" (Arnold 1994: 137), which has to be interpreted not only singularly, in the sense of multiple functional shifts and adaptive refinements of a single trait, but also collectively, since its cooption can be caused by an ensemble of elements that all together perform a definite function, as in the case of the eye described by Gregory (2008: 372). That is, sometimes "existing components, be they functional for something else or nonfunctional initially, are brought together or rearranged to form a new, more complex combination with a novel function" (Gregory 2008: 364). This is another way to say that the performance of a trait is a *systemic property* depending on the whole (in which it happens to become a part), where the requirements demanded by the general function of the latter specify the particular usefulness of the former.

Extra-usage and complexity are also key features of technology production and tools manufacturing closely resembles the occurrence of some exaptations: the coin was already at hand before being exploited for a new use and the innovative functions was what caused the recruitment of the keychain, which before had never meant to be a coin-holder. The following quotation by Deborah A. McLennan suitably summarizes this general idea of a resemblance between the way instruments are assembled and the evolutionary process by which nature produces some of its creations:

> The co-option of traits to serve new functions is not a difficult concept to understand. In fact, we ourselves do it all the time [...]. We are forever finding new functions for old devices, using an old boot as a planter, a fishing rod to fly a kite, a magnifying glass to start a fire, a shell as currency, a berry or a root to dye cloth. The only difference between human and evolutionary co-option is that we purposefully change an object's function, while evolution simply takes advantage of an opportunity with no direction, purpose, or forethought. (McLennan 2008: 257)

This analogy places itself within a complex multidisciplinary context where similar unitary interpretations of seemingly different phenomena have already been suggested. Therefore, before moving on, a brief outline of the background panorama from which it stands out is needed; moreover, this sketch will clarify with more precision the specific contribution made by my research.

The current topic is part of a wider debate on the parallelism between biology and culture and, strictly related, between biological and cultural evolution. With respect to the latter there are as many subcategories of development – and accordingly as many analogies to the organic evolutionary process – as there are distinct interconnected subsystems that make up culture itself, such as for instance scientific progress, conceptual turn, language change and technological innovation. Besides, an appropriate typology of these possible interactions should carry out a whole series of distinctions: between the source and target spheres of assimilative interpretation; whether the comparison has to be understood literally or just hints to an analogy; whether it concerns the functional status of the elements at stake or just their development; eventually, it should take into account possible mutual interactions within the cultural sphere in general.

As a first qualification, my reasoning focuses its attention on the affinities detectable between biological evolution and technological innovation, with three distinctive points: firstly, it interprets the former on the basis of the latter; secondly, it is limited to the recognition of an analogy between the two spheres; thirdly, it splits the comparison up into a twofold similarity concerning the constitution and function of organs and tools.

As a second qualification, it adopts what it is generally considered and defined as a *post-Darwinian approach*, since it places adaptation by means of natural selection side by side with complementary processes eliciting micro- and macro-evolutionary transformations. In this way, it anticipates and possibly counters one probable objection: if technological innovations fall under the rubric of non-random intelligent design, how can they be compared to a process triggered by casual variations? The existence and description of mechanisms of evolution both escaping the paradigmatic neo-Darwinian sequence (chance variation, inheritance, differential reproduction and adaptation) and implying the evolutionary effectiveness of the environmental responsiveness of organisms provide a more suitable biological-theoretical background for the analogy to be drawn. In this respect, Hoffmeyer (1996, 2008), Hoffmeyer, Kull (2003), Markoš (2002), Markoš *et al.* (2009) and Kull (1998; 1999; 2004) are essential references to frame the issue. Besides, an extensive work thereupon is provided by West-Eberhard (2003).

Such a tension between neo- and post-Darwinism can already be sensed within existing reflections. The idea that new technologies arise as a result of variations of old ones and selective pressure against their diverse effectiveness, so as to yield differential spreading, is supported for instance by Basalla (1988) and Constant (1980) (further references for a Darwinian approach are: Gilfillan 1935; Mokyr 1990; Saviotti, Metcalfe 1991; Metcalfe 1998). However, Arthur (2007; 2009) is more relevant here, since he agrees only in part with these interpretations and introduces a key distinction: "I do not want to dismiss variation and selection in technology. [...] But when we face the key question of how radically novel technologies originate [...] we get stymied. Darwin's mechanism does not work" (Arthur 2009: 18). Besides, as for the introduction of novel solutions, he detects a mechanism quite similar to exaptation: "This lock-in of an older successful principle causes a phenomenon I will call adaptive stretch. When a new circumstance comes along or a demand for a different sphere of application arrives, it is easier to reach for the old technology – the old base principle – and adapt it by "stretching" it to cover the new circumstances" (Arthur 2009: 140). Scholars who have focused expressly on framing and modelling technical progress from the viewpoint of an exaptation-based evolutionary theory are Allen and Andriani (2007) and Cattani (2005).

As a third qualification, my approach stands in continuity with previous linguistic and semiotic interpretations of technological change. For Arthur (2009: 76) a "domain" or body of technologies "forms a language; and a new technological artifact constructed from components of the domain is an utterance in the domain's language. [...] the key activity in technology – engineering design – is a form of composition. It is expression within a language (or several)". Since the domain/artefact distinction resembles the *langue/parole* opposition, technology appears as a system whose single concretizations obey its grammatical rules of combination (Arthur 2009: 77). Similarly, Lotman (1991) takes a semiotic perspective on the issue and his contextualization of technological progress within culture theory and semiotics of cultural points indirectly to a biosemiotic interpretation as well, by virtue of the well acknowledged analogy between the notions of biosphere and semiosphere (see for instance Markoš 2004; Kotov, Kull 2011; Lotman 2005). Finally, Innis (2009) claims for the application of different semiotic conceptual tools and frameworks – Jakob von Uexküll's biologically based theory of meaning, Charles Sanders Peirce's typology of signs, Ferdinand de Saussure's model of language as a dynamic system of differences and Ernst Cassirer's model based on the triadic schematization of the forms of sense – to highlight quite different, but nevertheless complementary, features of technology.

2. The analogy of production

In order to develop the argument, this section is providing some definitions of technology and taking into account, as concrete examples of comparison, a light bulb on one side and the case study of exaptation described by Gregory – the evolution of the eye – on the other side. The central idea can be summarized as follows: instruments and organs are similar in the way they are produced by, respectively, man and nature.

Firstly, since designed as a tool to satisfy or support human intentions, "[a] technology fulfills some expressed purpose – some *need* – personally or socially perceived" (Arthur 2007: 278; my emphasis): a technological artifact, or, better, its process of realization, always proceeds from a need and ends up finding a solution for a problem. It does not matter whether it is the case of a new economic chance or an emerging market to be exploited: a requirement and its fulfillment are always at stake. This clearly holds for the light bulb: thanks to the progress in the knowledge of electric phenomena, man was able to get rid of previous constraints (day-night alternation and usage of oil lamps) and secure a stable and versatile source of artificial light for daily activities. But a similar reasoning can be applied to the eye as well: once appeared in the form of simple photo-pigment, it increasingly enabled its carriers to better fulfill their needs for food identification, locomotion, predator avoidance, and so forth. Hence, both historical processes can be classified as problem-solving situations, which can be addressed with or without the participation of anticipatory intentionality.

Secondly, "[a] technology is built always around the reliable exploitation of some base phenomenon as envisaged through some principle of use" (Arthur 2007: 278), that is, technological artifacts are based upon one or more natural effects, whether they be chemical, physical, magnetic or electrical. As for the incandescent light bulb, among various phenomena it harnesses the (physical) Joule effect, concerning the ratio between the intensity of current flow through a conductor and the heat generated, and the (chemical) property of argon gas to be inert, namely not to take part in the reactions occurring in the same environment where it is. But the same is also true of the eye and several interconnected facts are required for its functioning: the property of a molecule (chromophore) to change its physical conformation when interacting with light; the involvement of a protein (opsin) “in the chemical cascade that transduces the incoming light to an electrical signal” (Gregory 2008: 372); the convergence of light rays towards the photoreceptors, which is accomplished by exploiting their refracting and reflecting capacity; and so on. As before, natural organs and artificial instruments can be categorized together as solutions to problems that both take advantage of one or several natural phenomena.

Thirdly, “[a] technology requires other sub-principles (and therefore sub-components) for its practical working. It consists of components that are themselves technologies [...] the whole arranged in a recursive hierarchy” (Arthur 2007: 278). On one side, the already existing components are thought of as *functionalities*, namely “generic actions or operations that *lie at hand*” (Arthur 2007: 283; emphasis mine); on the other side, they enter as building blocks in to a *combinatorial procedure*. Hence, “we think of new technologies [...] as *combination of existing technologies* possibly going on to become building blocks for future descendant technologies” (Arthur 2007: 284; emphasis mine).

Looking at the elements that make up the light bulb, before this particular application the glass had always been used as a means to fulfill other needs thanks to its optic and chemical natural properties; as such, it was a previous existing technology in respect to its following adaptation to the function of gas container. The same holds for the wires employed to transport the current flux or the screw shape of the bulb base: before their recruitment, both were there for other reasons. Above all, the respective functional shifts occurred by means of their recombination in a new ensemble, so that what was actually new in the invention of incandescence light bulb was the arrangement of components and their relations.

The evolution of the eye can be described in the same technological terms, namely as the manifold re-functionalization of previously used elements. For instance, the first photo-pigment arose from the combination of two preexisting molecules (retinal and opsin) that, in addition to the eye, can be found elsewhere in the organism and serve several non-visual functions: they “predate the origin of vision, and their merger and subsequent specialization in visual systems represents an important example of evolution through collage, exaptation, and secondary adaptation” (Gregory 2008: 372). All the same, refractive proteins (crystallins) located in the lenses “are not only similar but *identical* to proteins that serve other functions in the eye and elsewhere in the body” (Gregory 2008: 376) and became co-opted and refined for the new role in association with photoreceptors, to which they had now to redirect and focus sunlight.

On this basis, it is possible again to associate organic and artificial objects and link them in this case to the concept of combination: the reuse of the old can happen in isolation, but it often involves the assembly of many elements, each of them solving a 'minor' sub-problem in a parts-whole recursive way, functional to the overall systemic working.

Before turning to the next analogy, a final comment is necessary on Arthur's reasoning about the differences between technological and biological evolution. While critically discussing the assumption that a novel technology might arise from a process of variation and selection of old technologies, Arthur stresses that "[t]his idea has a certain Darwinian appeal, and it has validity with respect to *improvements* in technology. But it does not hold up for what interests us here: *radical invention* by deliberate human design" (Arthur 2007: 275; emphasis mine). Since they are thought of as complementary phenomena – "while I talk here about the creation of radically novel technologies, I recognize that the step-by-step improvement of existing technologies is economically just as important" (Arthur 2007: 276) – the main problem regards their distinction: "[w]hat, in our context, allows one new technology to qualify as radically novel, and relegates another to be a mere improvement on or variation of some standard design?" (Arthur 2007: 277). The answer is the following: "I will therefore define a new (radically novel) technology as one that achieves a purpose by using a new or different base principle than used before" (Arthur 2007: 278).

However, from a post-Darwinian viewpoint, Arthur's idea of a "Darwinian appeal" insofar the perfecting of existing technologies is concerned is half true and betrays a partial consideration of the biological evolutionary process. Small, continuous and inheritable chance variations of a functional trait and its better adaptation to the environment by means of natural selection are but one way through which evolution acts to transform species. Exaptive phenomena prove that relatively radical novelties do occur in nature and therefore the complementarity of re-functionalization and improvement, ascribed by Arthur just to technological development, can be extended to the organic domain as well. Going back to the eye, once crystallins became coopted to perform the new function of refraction in association with photoreceptors, then there occurred a "[g]radual evolution of lens crystallin concentrations resulting in evolution of graded refractive index lenses in aquatic animals" (Gregory 2008: 374). Just as the different level of efficiency between ancient and contemporary forms of light bulbs, so in biological history "any coopted structure (an exaptation) will probably not arise perfected for its new effect. It will therefore develop secondary adaptations for the new role" (Gould, Vrba 1982: 12).

3. The pragmatic analogy

Along with the acknowledgement that complex organic units and instrumental artifacts come into existence following a common historical path of production, the previous section has also implicitly shown that, beyond the specific function to be executed, they both represent at large forms of action and mediation characterizing the relationship with the environment. In order to better understand the nature of this common performance, special attention can be paid to a curious coincidence in the history of ideas: when it comes to the issue of identifying and explaining the main features of human perception, different thinkers resort to a comparison with the situation of the blind man and his aid stick. Take for instance Descartes and his famous passages from the *Dioptrics*:

> By means of his stick a blind man observes differences between trees, stones, water, and so on, apparently just as great as those between red, yellow, green and other colors, and […] there is nothing in these various bodies to make the differences except their different ways of moving the stick or resisting its movements. (Descartes 1971[1637]: 241–242)

> When our blind man [holding two sticks and crossing them in front of him, the contact point being E] […] turns his hand A towards E, or again his hand C towards E, the nerves inserted in the hand cause a change in his brain, and this enables his soul to know not only the places A or C, but also any other places lying on the straight line AE or CE. […] Similarly, when our eye or head is turned in a given direction, our soul is made aware of it by the change in the brain that is produced by the nerves inserted in the muscles that execute the movement. (Descartes 1971[1637]: 248–249)

Or consider Donald T. Campbell's quotation, always in a context of analysis focused on visual perception:

> Blind locomotor search is the more primary, the more direct exploration. A blind man's cane is a vicarious search process. The less expensive cane movements substitute for blind trials and wasted movements by the whole body, removing costly search from the full locomotor effort […]. The substitutability of cane locomotion for body locomotion, the equivalence of opaque-to-cane and opaque-to-body, is a contingent discovery, although one which seems more nearly "entailed", or to involve a less complex, a less presumptive model of the physical world than does the substitutability of light waves or radar waves for body locomotion. (Campbell 1987[1974]: 60)

This is instead how Maurice Merleau-Ponty (2005[1945]: 165–166) uses the same example while addressing the psychological issue of habit:

> The blind man's stick has ceased to be an object for him, and is no longer perceived for itself; its point has become an area of sensitivity, extending the scope and active radius of touch, and providing a parallel to sight. [...] The position of things is immediately given through the extent of the reach which carries him to it, which comprises besides the arm's own reach the stick's range of action. If I want to get used to a stick, I try it by touching a few things with it, and eventually I have it 'well in hand', I can see what things are 'within reach' or out of reach of my stick. [...] To get used to a hat, a car or a stick is to be transplanted into them, or conversely, to incorporate them into the bulk of our own body. Habit expresses our power of dilating our being-in-the-world, or changing our existence by appropriating fresh instruments.

Again, while questioning the inside/outside physical dichotomy with respect to a communication system, Gregory Bateson (2000[1972]: 251) claims the following:

> It is not communicationally meaningful to ask whether the blind man's stick or the scientist's microscope are "parts" of the man who uses them. Both stick and microscope are important pathways of communication and, as such, are parts of the network in which we are interested; but no boundary line – e.g., halfway up the stick – can be relevant in a description of the topology of this net.

Finally, a passage taken from Michael Kubovy (1988: 152; emphasis mine) makes explicit the kernel of the whole issue:

> If you are walking in the dark feeling your way about with a cane, you are unaware of the pressure of the cane on the palm of your hand; all your attention is focused on the nature of the obstacles revealed by the of the cane. *Under these circumstances, if you had to classify the cane as part of the world or part of your body, you would most likely say that it was part of your body. This is true of all tools.*

On one side, the first two quotations suggest the possibility of replacing our organs with vicarious technologies, but two different things can be substituted one for the other if they fulfill the same needs and their functions get enough closer so as to allow them to perform more or less identical actions in respect to the environment. On the other side, the last three quotations point to the meaninglessness of such distinctions as in/out and organic/inorganic, which lose value exactly when the pragmatic analogy holds true, since what really matters is the fact that both organs and tools, by being interchangeable, share the same significance for the organism, regardless of their material constitution or physical collocation. Though an absolute or literal identity between sticks and eyes cannot be established, all authors seem thus to share the presumption that objects and instruments (in a word, technology) are *exosomatic organs* mediating between human body and outside world.

Such an interpretation already follows quite naturally from the observation that several living organisms other than man do use *devices* or *means* (terms to be preferred here to human *tools* or *instruments*, so as to keep the discourse on an analogical plane). As a first example, the weaver ant (*Oecophylla smaragdina*) is an arboreal species whose adults are able to roll up leaves and piece them together by softly squeezing the larvae with their jaws, so that they release a drop of silk to be used as a kind of glue. Thus, "the ants then carry the larvae along the entire length of the leaf edges, squeezing as they go, using the larvae like living bottles of glue, until the edges of the leaves are stuck together from end to end" (Shuker 2001: 191).

As a second example, the diving bell spider (*Argyroneta aquatica*) is a species that can live under water by building "diving bell" webs or air bubbles, anchoring them through silk threads to support materials like water plants, filling them with air and, eventually, using them as submarine houses where to eat, molt, mate and raise offspring. The overall apparatus allows a process of gas exchange (carbon dioxide with oxygen) that is driven by differences in partial pressure and water solubility of the components and serves as an underwater gill; in fact, the system has been referred to as a sort of 'aqualung' (Flynn, Bush 2008).

The technological metaphors (glue and aqualung) used by scientists relate these behaviours to the case of the blind and the cane and suggest a specific sense of the concept of *mediation* between organisms and environment. By relying on the work of Arnold Gehlen about the essential connection between instruments and human body features, in his article on exosomatic organs Robert E. Innis states that the formers "can be analyzed under the threefold rubric of compensation, extension, and substitution" (Innis 1984: 68). A hammer, for instance, extends the power of the hand for pounding and compensates for the relative fragility of human tissues and bones; similarly, wheels (and the apparatus they belong to) substitute feet and other locomotive structures, extend the distance that can be traversed and compensate for the limited speed achievable just through organic movement. In this respect, the performances of organs, non-human devices and tools can all be interpreted as extensive, substitutive and compensative actions.

To understand the assumptions underlying such a generalization, it can be assumed the schematic model of a living being proposed by Bateson (2009[1951]) as a minimal system consisting of a self-corrective internal causal circuit, acting on the environment and upon which the environment itself acts. External influences are perturbations of the systemic self-organization of the components (homeostasis) from which the entity is constituted; at the same time, the environment is a source of preservation for the living system and hence the latter accomplishes several transformative operations on the former. It follows that coordination between internal and external processes of different types is required and the institution of this correspondence is called by Bateson (2009[1951]: 169) "codification". Specifically, the congruence between inside and outside is pursued by the system through the attempt to *operate* (or act) on objects and events.

This understanding of the notion of action encompasses all the aforementioned examples: the reconnoitering movements of the eye and the stick are not passive processes, but active operations to collect information that, despite not actually changing the environment, are in any case meant to modify the relations between it and the organism, so as to fulfill its requirements; the percussion movements of the fist and the hammer are transformations of the physical status of reality so as to make it congruent with internal needs; the foot and the wheel, the air bubble and the aqualung, the silk and the glue are all devices and instruments through which a certain kind of action – functional to the type of organism/environment congruence that is looked for – is made possible.

Besides, in his analysis Bateson maintains that, as for the organic model, the boundary between what can be said to belong to the self or the environment is *arbitrary*: "the organism includes within the self *various objects* and events outside its skin but intimately connected to him, while he labels as parts of the environment certain of his own body parts or functions" (Bateson 2009[1951]: 189; emphasis mine). This means that as long as certain elements, whether they be internal (endosomatic) or external (exosomatic), promote homeostasis, they can be defined as systemic or belonging to the set of perceptive-active operations of the living unity. Any component that is, to say, 'caught' in this net of relations and proves to be useful is subjected to an operation of meaning attribution that selects some of its properties and makes it a part of a whole: it becomes thus functionalized or re-functionalized, indeed something akin to the core of exaptation.

What was just said applies to the typology of exaptations articulated by Telmo Pievani (2003). Whether the factor at stake is a constraining developmental path that encounters differential environmental conditions, or a single (or a set of) gene whose expression (protein) undergoes a change in time production or localization, or a whole organ that becomes useful for a new use because of ethological and ecological transformations, always the same occurs: a component is inserted in a new relational web, thereby becoming functional to the homeostatic working of a single system or a set of subsystems and, in turn, to the entire organism.

To conclude, this application of Bateson's perspective is, first of all, a strong counter-argument to possible critiques directed against the recognition of similarities between organs and tools: if one adheres to a systemic view of living beings, the organic/inorganic dichotomy blurs (without considering the fact that the intracorporeal exploitation of inorganic compounds is already a constitutive aspect of life as such). Secondly, tools and devices themselves, intentionally and naturally produced by means of selective and combinatory operations, seem to reflect the very nature of the agents that make use of them, in a twofold sense: on one side, they enable them to perform actions, in this being 'active' like their utilizers; on the other side, they exhibit systemic properties, exactly as organisms do. Thirdly, since the whole reasoning is constitutively based on a broad interpretation of the concept of communication, it immediately takes on a quasi-semiotic dimension. Finally, the very terminology adopted ("pragmatic") is fully semiotic to the extent that the underlying argument consistently fits Peirce's pragmatic maxim, where the meaning of concepts (in our case, organs, devices and tools) consists in the practical-experiential consequences they entail for the subject of action.

4. Functions and definitions of exaptations

In the previous analysis the notion of *function* has come to have a central role: organs and tools follow similar directions in the historical and structural process leading them to the acquisition of a general function of action towards the environment. This imposes a requirement on the modelling attempt, that is the adoption of an as general as possible schematization of what it means to perform a function, able to encompass satisfactorily both biological and technological instances.

Despite the fact that a "history of attempts by philosophers to clarify the notion of function exhibits all the strengths and weaknesses of this sort of undertaking" (Hull 1998: 223), Larry Wright's article "Functions" (1973) is appropriate for a number of reasons: firstly, it has been considered to stand out as "seminal" (Hull 1998: 224) and hence is an authoritative reference; secondly, it explicitly offers a unifying view on biological and technological functions; thirdly, the formula it proposes can be applied, with opportune modifications, to the types of exaptations described by Arnold; eventually, the distinction it draws between functionality and usefulness, by avoiding to directly call into question phenomena of adaptation, is well suited to some interpretations of Darwinism and parallels an almost identical critique in the context of evolutionary biology.

As for the last point, Wright complains about those accounts that fail to handle what he claims to be one of the most important distinctions to be concerned with when reflecting on functions, namely accidental versus non-accidental situations. In his words: "Something can do something useful purely by accident, but [...] something that I does by accident cannot be the function of I. [...] Buckles stop bullets only by accident. Blowouts only accidentally keep us off doomed airplanes. Sweep hands only accidentally brush dust, if they do it at all" (Wright 1973: 147).

The incapacity of some theories to embrace this distinction reminds of the dispute on the extension of such notions as adaptation and natural selection that sees the opposition between neo- and post-Darwinism, a debate from which exaptation itself derives. This similarity clearly appears from the following quotation:

> Following Williams, we may designate as an *adaptation* any feature that promotes fitness and was built by selection for its current role (criterion of *historical genesis*). The operation of an adaptation is its *function*. We may also follow Williams in labeling the operation of a useful character not built by selection for its current role as an *effect*. [...] Adaptations have functions; exaptations have effect. (Gould, Vrba 1982: 6)

The exaptive switch is the final outcome of a process through which something, originally useful in some respect just accidentally (it is not a function, neither in Williams nor in Wright's sense), ends up taking on that usefulness as its own function, therewith turning an incident into the very reason of its maintenance. Hence, Wright's criticism is indirectly and negatively referring to mechanisms also at work in the production of exaptations.

Such a coincidence between analytic philosophy and evolutionary biology regards the examples adopted as well: as for Wright "it is absurd to say with Pangloss that the function of the human nose is to support eyeglasses" (Wright 1973: 148), so for Gould and Richard C. Lewontin (Gould, Lewontin 1979: 581–585) "the adaptationist programme is truly Panglossian" because of "its failure to distinguish current utility from reasons for origin". There is no proof that the latters got acquainted with the former; it might simply be that Voltaire did go at the heart of our cognitive attitude, touching a common epistemological issue. Whatever the case, Wright's article appears to be born out of similar problems and distinctions to those that later led to the precise identification of exaptation.

Coming to the point, this is how the results of his analysis are summarized (Wright 1973: 161):

> The function of X is Z means
>
> (a) X is there because it does Z;
>
> (b) Z is a consequence (or result) of X's being there.

This formula is meant to represent a necessary and sufficient condition for something to be a function and, by taking into account the past causal background of the phenomena under consideration, allows to rule out accidental instances. It includes both conscious and natural cases: "[t]he reason the sweep-secondhand is there is that it makes seconds easier to read. It is there *because* it does that". Moreover, "[w]e can say that the natural function of something – say, an organ in an organism – is the reason the organ is there by invoking natural selection. […] we can say animals have kidneys *because* they eliminate metabolic wastes from the bloodstream" (Wright 1973: 158–159).

Before modifying the formula so as to make it apt to define what *is not* the consequence of selection and thus at the beginning merely fortuitous, a clarification about the evolutionary connection between adaptation and exaptation is required. A character with a previous function (adaptation) can begin for a number of reasons to bring about accidental effects; when these, because of changes in the selective regime, become the grounds for its utility from that moment onwards, two things can happen: either the character undergoes modifications that transform it entirely and give rise to a secondary adaptation; or small (or not at all) subsequent refinements occur, so that the character continues to be identifiable as basically the same, thereby acquiring the logical status of exaptation. The situation can be ambiguous and poses a problem of distinction: "[i]nevitably, there will be borderline cases where the term exaptation is hardly worth employing because the original trait has changed so much that it is scarcely recognizable" (Arnold 1994: 127). That is, something can be both an adaptation and an exaptation simultaneously or one before the other sequentially.

Both aspects are acknowledged by Gould and Vrba: on one side, if an "aptation" is defined as the general phenomenon of being fit, then "the set of aptations existing at any one time consists of two partially overlapping subsets: the subset of adaptations and the subset of exaptations" (Gould, Vrba 1982: 6); on the other side, when considering for instance the evolution of feathers and wings from dinosaurs to birds, "[w]e see, in this scenario, a sequential set of adaptations, each converted to an exaptation of different effect that sets the basis for a subsequent adaptation" (Gould, Vrba 1982: 7). The last point is implicitly contained in Wright's account as well: though "this analysis makes a clear and cogent distinction between function and accident", nevertheless "it is worth noting that something can get a function – either conscious or natural – as *the result of* an accident of this sort" and, in agreement with the words of Gould and Vrba, "that only disqualifies an organ from functionhood for the first – or the first few – generations. If it survives by dint of its doing something, then that something becomes its function on this analysis" (Wright 1973: 165).

However, even though one sequence (adaptation/exaptation/next adaptation) parallels the other (function/effect/next function), there is not a perfect coincidence: an exaptation (or effect, in Williams' terminology) is accidental just in respect to the previous selective regime that shaped the character and made it an adaptation; but it is not an accident at all insofar the new context of significance is concerned, that cooperates in the production of the exaptation or effect by selecting functionally the old trait (and hence promoting fitness), but with no further or substantial modifications of its shape (that is, differently from Wright, you have a function that is not an adaptation).

This said, to apply the original formula to Arnold's typology, firstly, it has to be considered valid to characterize functions as adaptations; secondly, its wording must be revised so as to refer to effects of unmodified traits after the change of selective regime; thirdly, the temporal dimension needs to be properly signaled grammatically (simple present is substituted with present continuous, which implies a stronger conceptual differentiation from past events). Accordingly, the definition of a *first-use exaptation* is the following:

> The effect of X is Z means
> > (a) X is there because it is doing Z;
> > (b) X was not there because of Z;
> > (c) Z is a consequence (or result) of X's being there.

[*Sutures in the skulls of young birds and reptiles probably has arisen from the laws of growth, with no specific function, and only later where coopted because of their advantage in the parturition of higher mammals*; example taken from C. R. Darwin and quoted in Gould, Vrba 1982: 5.]

By accepting Wright's indication – "the notion of something having more than one function is derivative. It is obtained by substituting something like 'partly because' for 'because' in the formula" (Wright 1973: 166) – this is instead the definition of an *extra-use addition exaptation* in respect to the most recent usefulness:

> The effect of X is Z
> > (a) X is there partly because it is doing Z;
> > (b) X is there partly because it does Y;
> > (c) Z and Y are consequences (or results) of X's being there.

[*Feathers began to allow birds to fly from a certain historical moment onwards, but this effect did not supersede the previous function of thermoregulation; therefore, both thermoregulation and flying are now causes and consequences of their being there;* example taken from Gould, Vrba 1982: 7.]

The complete interchange between two subsequent utilities promoting fitness, namely an *extra-use transfer exaptation*, can be finally expressed as follows:

The effect of X is Z means
(a) X is there partly because it is doing Z;
(b) Z is a consequence (or result) of X's being there;
(c) X is there partly because it did Y;
(d) Y was a consequence (or result) of X's being there.

[*The shell of chelonians performs the main role of skeletal support of the trunk from the vertebral column and this consequence is the reason why it is now selected; however, the shell owes its existence also to the fact that once was probably performing the function of external protection, which is no more something it does and hence cannot currently be the consequence for which it is selected*; example taken from Arnold 1994: 144.]

For Wright's analysis has been pursued to come up with a unifying view, this classification pertains also to technological-conscious phenomena of re-functionalization. Besides, further grounds for the construction of a general framework are provided by his interpretation of the notion of *selection*.

After agreeing with the standard view, which identifies selection with conscious choice, Wright claims that other uses of the notion can be understood as extensions of this definition, namely by "drawing attention to specific individual *features* of the paradigm which occur in subconscious or nonconscious cases" (Wright 1973: 163). Within the conscious cases, it is possible to distinguish between "mere discrimination" (selection without any apparent reason) and "consequence-selection" (selection by virtue of resultant advantage). In the latter, "the consequence is the function" and "it is specifically this kind of selection of which *natural* selection represents an extension" (Wright 1973: 163). The parallel Wright is drawing is the following (Wright 1973: 164): just as in biological evolution, given the trait X, the causal consequence Z and the environment, X will be selected *automatically* (to be read not in a necessary-deterministic fashion, rather as absence of intentionality), so in our conscious behaviour, given the object X, the causal consequence Z and our criteria (corresponding to the 'human environment'), X will be selected automatically. Thus, "consequence-selection, by contrast with mere discrimination, de-emphasizes volition in just such a way as to blur its distinction from natural selection on precisely this point" (Wright 1973: 164).

Two remarks are worth making. On the one hand, though Wright's theory accounts for functions and adaptations, it is applicable to exaptations as well once the addition or transfer performance, originally fortuitous, becomes the new consequence Z for which X is selected from that moment onwards according to a given environmental situation. On the other hand, despite Wright's intentions, the selecting process might have nothing to do with natural selection: both in biological evolution and technological development there actually happen co-options of incidental consequences of traits and tools *without substantial optimizing modifications of their features*, hence not becoming adaptations, which on the contrary is by definition a process whereby "the average state of a character becomes improved with reference to a specific function" (Futuyma 2005: 544).

Before turning to the conclusions, it must be noticed that if the *consequence* Z of an entity X is the *cause* of its selection – "Z must be or create conditions conducive to the survival or maintenance of X" (Wright 1973: 164) – and any X, by performing different actions, can take part into several connections, then any exaptation of X is definable as the *selection of one or more causal consequences, induced by contextual variation, within a set of possible actions realizable by X*. Since such a reading of the phenomenon discloses a systemic perspective, biosemiotics – the semiotic modelling of systemic relations – provides therefore an adequate theoretical framework for its treatment (Eder, Rembold 1992; Kull *et al.* 2008; Favareau 2010).

5. Conclusions and research prospects

Three conclusions have been reached by the present research. Firstly, there exists an analogy of production between organs and tools. At least in some cases, they resemble each other in the way they originate and change, since both fulfill needs, exploit natural phenomena, arise through the combination of pre-existing elements and can undergo subsequent phases of functional shift and refinement or improvement.

Secondly, there is a pragmatic analogy between organs, animal devices and human tools. In some instances all are means of mediation, to be understood as a compensative, extensive and substitutive action meant to transform favourably the set of relations established between a living subject and its environment. Above all, a communication-based approach to the topic blurs and eventually proves as misleading, if not totally wrong, such historical (and still on) distinctions as in/out, organic/inorganic, natural/artificial, and so forth (for the philosophical relevance of this theme, see postmodernism and cyborg theory, for instance Haraway 1991)[1].

Thirdly, the notion of function, implicitly operating throughout the twofold analogical comparison and essential to the very definition of exaptation, has been analysed from an analytic-philosophical perspective, where Wright's theory, able to unify natural and conscious functions, has allowed a definitional schematization of Arnold's classification of exaptations. The resulting formulation of general types of functionalization (first-use and extra-use) is both extendable to the technological

[1] I thank scholar Tiina Pitkäjärvi for making me notice the connection.

dimension and developable into a *semiotic typology of exaptations* (for a biosemiotic notion of function, see for instance Emmeche 2002; cf. also Weible 2012).

Besides, two notions (logically complementary) have been a background theme of the whole reasoning: on one side, the concept of *selection* runs in parallel to that of combination, since the consequence of a trait is selected on the basis of its arrangement with other elements; on the other side, both functionalization and re-functionalization are processes of the *system* to which the trait happens to start belonging.

As far as modelling is concerned, a further similarity is decisive at this point, since there exists another reality that, as much as technology and close to semiotics, behaves like a system, develops through selection and combination of already existing elements and performs actions. As a matter of fact, several authors have thought of *language as a technology*:

> Language – and its extensions in script and print – is, by reason of its flexibility and reflexive structures, the most distinctive of all exosomatic organs. [...] if we look closely enough we can see that the structure of embodiment relations used to explicate probes and canes [...] perhaps applies also to language with a vengeance. (Innis 1984: 83)

> Consider a familiar tool or artifact, say a pair of scissors. Such an artifact typically exhibits a kind of double adaptation – a two-way fit, both to the user and to the task. On the one hand, the shape of the scissors is remarkably well fitted to the form and the manipulative capacities of the human hand. On the other hand (so to speak), the artifact, when it is in use, confers on the agent some characteristic powers or capacities which humans do not naturally possess: the ability to make neat straight cuts in certain papers and fabrics, the ability to open bubble packs, and so forth. This is obvious enough; why else would we value the artifact at all?
>
> Public language is in many ways the ultimate artifact. Not only does it confer on us added powers of communication; it also enables us to reshape a variety of difficult but important tasks into formats better suited to the basic computational capacities of the human brain. Just as scissors enable us to exploit our basic manipulative capacities to fulfill new ends, language enables us to exploit our basic cognitive capacities of pattern recognition and transformation in ways that reach out to new behavioral and intellectual horizons. Moreover, public language may even exhibit the kind of double adaptation described above, and may hence constitute a body of linguistic artifacts whose form is itself in part evolved so as to exploit the contingencies and biases of human learning and recall. (Clark 1998: 193–194)

According to the previous conclusions, language can thus be considered analogically both as an organ and a tool and the work of Lass (1990; 1997) in particular offers an appropriate conceptual apparatus to this comparative approach.

First of all, from the methodological viewpoint, he repeatedly stresses how the relation between organisms and languages must be properly understood: "[I]t is important to note that by comparing X and Y as terms of an analogy I am not saying that X=Y. [...] by saying that much of the methodology of historical linguistics is 'like' that of geology or evolutionary biology, one is not saying that languages are rocks or organisms" (Lass 1997: 293, fn 10). Hence, "on the tack I take here, the consilience is with what we know of the behavior of a *large class of non-linguistic system types*" (Lass 1997: 384; emphasis mine).

Secondly, he refers to examples, theories and metaphors taken from evolutionary biology and, particularly, from Gould himself. For instance, as the giant panda, at some point of his evolution, lost the digit corresponding to our thumb (Gould 1980) and later on co-opted another forelimb bone to make a new thumb – that is "[t]ypes of change can and do recur, and old types of objects (if in different shapes) may re-emerge" (Lass 1997: 298) – so "[l]ong-term cycles of change are familiar from the histories of many (I would suspect most) languages" (Lass 1997: 298). Similarly, in languages there happens something "not dissimilar to the picture of 'punctuated equilibrium' suggested by Eldredge & Gould (1972) [...]; evolution in their (controversial but arguable) view is not steady change, but shows stasis as a background, with fairly short bursts of dramatic speciation activity at odd intervals [...]. I think the evidence in the case of languages is as good as it can be" (Lass 1997: 304)[2]. Eventually, just as "natural systems like the genomes contain enormous amounts of non-functional material" (Lass 1997: 313–314) and this "non-expressed variability may eventually serve as a reservoir for evolutionary change", so "[t]he same seems to be true of linguistic junk" (Lass 1997: 314–315).

Thirdly and above all, *languages do evolve by means of exaptations*. Among Lass' examples (Lass 1997: 317–318) there are the development of the Germanic strong verb (when late Western Indo-European lost its aspect system, the old perfect and aorist morphophonology were redeployed as a marker of number) and, in English, the old number opposition "you" vs. "thou", that was pragmatically exapted to distinguish between an unmarked and an 'affective' pronoun. Moreover, grammaticization and new grammatical categories can occur and develop through new functional co-options, as for instance in the development of grammaticized aspects in Germanic or the rise of marked progressive aspect in English (further references thereupon are Lass 1990; Traugott 2004; Fanego 2004; Narrog 2007).

Lass' understanding of language change, founded on the images and terms of complexity, chaos and systems theories ("phase-space", "epigenetic landscapes",

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[2] Lass refers to Eldredge, Niles; Gould, Stephen J. 1972. Punctuated equilibria: An alternative to phyletic gradualism. In: Schopf, Thomas J. M. (ed.), *Models of Paleobiology*. San Francisco: Freeman, Cooper, 82–115.

"attractors", "chreods", and so on; cf. Lass 1997: 293–303; for a description of his model, Lass 370–383), provides a very comprehensive framework which it is worth working on:

> I am convinced [...] that there is such a thing as a theory of 'historically evolved systems', and that virtually any such system that meets certain criteria is going to show phenomena that look like junk-deposition. In other words, human cultural evolution (or the *evolution of human cultural artifacts*, which is almost certainly not the same thing), like the *evolution of biological systems*, is based at least partly on *bricolage*, cobbling, jerry-building, whatever you want to call it; pieces of such systems are always falling off and if not lost are recycled, often in amazingly original and clever ways. (Lass 1998: 316; emphases mine)

This contribution to already existing viewpoints on language change based on systems theory (for a review, see Nöth 1990: 202–204) establishes the centrality of exaptive phenomena for language and, in turn, for semiotics, thereby determining the plausibility to set up a provisional research plan for the proper development of a semiotic model of exaptation.[3]

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К семиотике экзаптации: в точке соприкосновения биологической эволюции и технологического развития

В статье отмечаются точки соприкосновения между биологической эволюцией и технологическим развитием, и на этой основе делается попытка выработать семиотический подход к явлению экзаптации в эволюции. Для достижения этой цели сначала описывается историко-структурная и прагматическая аналогии между человеческими органами и орудиями труда, что на коммуникативном уровне, в свою очередь, указывает на присоединение некоторых им традиционно свойственных для них характеристик. Затем применяют аналитико-философский подход к природным и культурным функциям, чтобы определить три типа экзаптации.

Eksaptatsiooni semiootikast: bioloogilise evolutsiooni ja tehnoloogilise arengu lõikumispunktis

Artiklis täheldatakse konkreetset vastavust bioloogilise evolutsiooni ning tehnoloogia arengu vahel ning püütakse sellelt aluselt lähtudes luua semiootilist lähenemist eksaptatsiooninähtusele evolutsioonis. Et seda teha, näidatakse ajaloolis-strukturaalset ja pragmaatilist analoogiat elundite ning tööriistade vahel, mis kommunikatiivsel pinnal omakorda osutab mõnede nende traditsiooniliselt eriomaste omaduste kokkusulamisele. Lõpuks rakendatakse filosoofilis-analüütilist lähenemist looduslikele ja kultuuriliste funktsioonidele, defineerimaks kolme tüüpi eksaptatsiooni.