Applied Evolutionary Epistemology: A new methodology to enhance interdisciplinary research between the life and human sciences

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1. Introduction and outline

An increasing amount of scholars that work within the human sciences are turning to evolutionary theory to find explanations for various aspects of human behavior. This has lead to the rise of a variety of new evolutionary sciences such as evolutionary epistemology (Campbell 1959, 1960, 1974), evolutionary psychology (Barkow, Cosmides & Tooby 1992; Barrett, Dunbar & Lycett 2002; Buss 1995, 2000; Cosmides & Tooby 1994; Tooby & Cosmides 2005), evolutionary linguistics (Christiansen & Kirby 2003; Dunbar 1996; Hurford, Studdert-Kennedy & Knight 1998; Knight, Studdert-Kennedy & Hurford 2000; Pinker & Bloom 1990) evolutionary anthropology and evolutionary archeology (Bar-Yosef et al. 2007; McBreaty & Brooks 2000; Mellars & Stringer 1989). All endorse an inter- and transdisciplinary approach: rather than adhere to classic, domain- and field specific methods, scholars working within the new evolutionary sciences are working from within the premise of evolution. Evolution is a fact of nature, and consequently, all natural beings, and also the behavior portrayed by these natural beings, can only be made sense of in light of evolutionary theory. They therefore investigate how evolutionary theory can be applied to study the knowledge process, cognition, language and culture.

Evolutionary theory was first formulated in the field of biology. Applying evolutionary theory to the human sciences implies that we must find ways in which evolutionary theories can extend the biological realm. Scholars working within both evolutionary epistemology (Campbell 1974; Hull, Langman & Glenn 2001; Plotkin

1994) and the units and levels of evolution debate (Lewontin 1970; Brandon 1982) have therefore sought systematic ways in which evolutionary mechanisms can be "universalized' in order for these to be applicable to a wide variety of traits that extend the gene; and they have sought ways to identify universal levels and units of selection such as the replicator (Dawkins 1976), interactor (Hull 1981), reproducer (Griesemer 2000) or manifestor (Sober 1980).

The way in which evolutionary epistemologists have tried to universalize evolutionary theory can set the example for the newly emerging evolutionary fields. Evolutionary epistemology can be understood as a new interdisciplinary method and it can be applied by all evolutionary disciplines. This method is called Applied Evolutionary Epistemology in order for it to be distinguishable from the field of evolutionary epistemology (that investigates how knowledge evolved).

This paper is outlined as follows. Firstly, we examine the methodology used by the new evolutionary sciences. It will be demonstrated that, contrary to early evolutionary biologists and ethologists, who endorsed a more pluralistic view of evolution, the scholars working within the newly evolving evolutionary sciences primarily endorse a selectionist approach. Secondly, we look for the roots of the selectionist approach. It will be proven that scholars active in the fields of evolutionary epistemology, philosophy of biology, together with scholars who engaged in the units and levels of selection debate, are mainly responsible for the idea that all and only selectionist accounts of sociocultural behavior are valid. Thirdly, we examine the validity of this claim made by universal selectionists in light of the extended synthesis. Finally, it is examined how other evolutionary theories, besides selectionist accounts, can contribute to research on the evolutionary origin of sociocultural behavior. In this latter part, Applied Evolutionary Epistemology is introduced as a method to examine the universality of evolution.

2. The new inter- and transdisciplinary evolutionary sciences

Within the last couple of decades, the Humanities have undergone considerable restructuring. Besides the classic departments of Philosophy, Linguistics, Anthropology, Archeology, or Psychology, interdisciplinary research units and even new departments are rising up that try and study problems set out by the classic disciplines from within an evolutionary approach. Knowledge, language, cognition and culture are studied as outcomes of biological evolution. Biological evolutionary theory is therefore indicated to provide better explanatory frameworks for the origin of these phenomena, and the classic synchronic and diachronic epistemological frameworks have come into disuse.

These new fields are also associated with the rise of new interdisciplinary-focused research associations that unite scholars by organizing international conferences and by introducing new scholarly journals.

Examples in evolutionary psychology are the Human Behavior and Evolution Society (founded in 1989 by sociobiologists and evolutionary psychologists and associated with the journal *Evolution and Human Behavior*) and The European Human Behavior and Evolution Association (founded in 2006). Other journals associated with evolutionary psychology are *Behavioral Ecology and Sociobiology*, *Behavioral and Brain Sciences*, *Journal of Evolutionary Psychology* and *Journal of Social, Evolutionary and Cultural Psychology*.

Evolutionary linguists organize themselves around biannual meetings called EVOLANG, the Evolution of Language conferences. Proceedings of the EVOLANG conferences go under the same name and are published by World Scientific. Additionally, both Cambridge and Oxford now host book series on the origin of language called *Approaches to the Evolution of Language* and *Oxford Studies in the Evolution of Language*. EVOLANG is also associated with the journal *Interaction Studies: Social Behavior and Communication in Biological and Artificial Systems* which is published by John Benjamins.

Institution-wise, evolutionary anthropologists and evolutionary archeologists are connected to the Evolutionary Anthropology Society (EAS), a society that organizes annual conferences on the theme. EAS was founded in 2004 as a section of the much older American Anthropological Association (AAA). In Europe, Germany pioneered with the Max Planck Institute for Evolutionary Anthropology (http://www.eva.mpg.de/) which was founded in 1997 and is directed by Bernard Comrie. Oxford University followed 10 years later, with the introduction of the Institute of Cognitive and Evolutionary Anthropology, directed by Robin Dunbar (http://www.icea.ox.ac.uk). Journals associated with the movement are *Human Nature*, founded in 1990 and published by Springer and *Evolutionary Anthropology, Issues, News and Reviews* printed by Wiley.

2.1 In search of a methodology

In this part, we focus on the methodologies these sciences use and how their explanatory framework differs from the classic human sciences. What distinguishes the new evolutionary sciences from the old fields is their overall inter- and transdisciplinary approach. As is the case with all transdisciplinary fields, neither the research fields, nor the scholars that form part of the new fields belong to a single discipline. Rather, what unites scholars is their adherence to a shared epistemological framework. In the case of the newly evolved evolutionary sciences, this framework endorses the premise that human behavior and culture needs to be studied from within Neo-Darwinian evolutionary theory (natural and sexual selection theory). Natural and sexual selection theory moreover are narrowly applied and reduced to the study of adaptation. Within the "canons" of the fields, and although they acknowledge that not all behavior is adaptive (see e.g. Buss et al. 2004), scholars argue that only selectionist accounts of human evolution and culture are valid (Barkow, Cosmides & Tooby 1992; Bar Yosef et al. 2007; Hurford, Studdert-Kennedy & Knight 1998; McBreaty & Brooks 2000; Pinker & Bloom 1990).

Of course, exceptions make the rule. In evolutionary archeology, Klein (2000) endorses saltational views of modern behavioral traits. D'Errico (2003, d'Errico et al. 2003) defends the view that the archeological record provides a pattern comparable to punctuated equilibria. In evolutionary linguistics, several authors object the view that language, or aspects thereof such as recursion, are an adaptation (e.g. Carstairs-McCarthy 1999, Chomsky 2005). Rather they contend that language might have co-evolved, or it might be an exaptation or "spandrel" of evolution. And also systems-theoretical and co-evolutionary inspired approaches are adhered to within both evolutionary linguistics (e.g. Jenkins 2000; Deacon 1997; Steels 2002) as well as evolutionary anthropology (e.g. Cavalli-Sforza & Feldman 1981; Lumsden & Wilson 1981). In evolutionary psychology too, several scholars have investigated how systems theory and exaptationist accounts provide alternative views on human cognitive evolution (e.g. Gould 1991). Nonetheless, these theoreticians have mostly been working from outside the new fields, and are fighting or are being criticized by an existing and expanding canon.

Mainstream evolutionary psychology, evolutionary linguistics, evolutionary anthropology and evolutionary archeology now endorse the selectionist, functional-adaptationist approach. This entails that cognition, tool-manufacture, parental investment, speech, rituals, emotions, etc. are understood to be functional adaptations. These traits are reasoned to have been selected in our hominin past because their functions provide their carriers with survival (in case of natural selection) and reproductive (in case of both natural and sexual selection) benefits. This also has consequences for the kind of epistemic questions that are raised by scholars working within the fields: when asking about the evolutionary origins of these traits, they refrain from the "how" question (for they take as premise that natural selection shaped the behavior) and exclusively focus on the "why" and "what for" questions (the reproductive and survival benefit of the evolved traits).

To understand what this epistemic shift from Neo-Darwinism to Selectionism entails, we need to go back to the origin of the fields of both Evolutionary Biology and Ethology.

2.2 Universal Evolution

The evolutionary origin of behavior was first examined by evolutionary biologists and ethologists. Contrary to the newly emerging evolutionary sciences who primarily focus on natural selection, the early evolutionary biologists and ethologists studied the origin of behavior from within a more heterogeneous and pluralistic research framework. The core question of this part is the following: How did early Neo-Darwinians and ethologists study the evolutionary origin of sociocultural behavior, and how does it differ from the selectionist approach endorsed by scholars working within the new evolutionary sciences?

2.2.1 Causation and epistemic questions in evolutionary biology

The classic field of Biology was introduced by the Natural History students of the 19th century. It outdates the introduction of evolutionary thought. It is only when the Neo-Darwinians founded the Modern Synthesis in the first half of the 20th century, that Evolutionary Biology became an independent science (De Laguna 1962; Mayr 1961). Besides courses on evolutionary biology, Biology departments would also continue to provide courses in developmental (ontogenetic and embryological) and functional (morphological or operational) biology. These latter fields would focus on "how" the various structures of the body function operationally or mechanistically, and "how" these functions develop during ontogeny. This functionalist approach must not be confused with the current functional-adaptationist approaches. Rather, the early biologists' methodologies relate more to the positivist, and function-structuralist approaches of the natural sciences (especially physics) and the classic human sciences such as sociology (e.g. the action theory of Talcott Parsons (1968)).

Following the operational turn induced first by Descartes and later by Newton, and inspired by system theoretical approaches, biologists examined how the different parts of the body function by themselves and how these parts enable the functioning of the whole. This approach implies a study of the mechanisms (the causes and effects) that underlie physiology ("how do we swallow", "how do we see", or "how do we breath"). These physiological mechanisms were not necessarily interpreted to be of an evolutionary nature, scholars merely endorsed a functionalist methodology that examined the operational physiology of traits.

When evolutionary biology was defined as an independent research discipline, scholars countered this purely functionalist, operationalist approach that exclusively focuses on the how question. The study of functionalism was now also asserted to relate to questions about adaptation and end-directedness of nature ("why did digestion or flying evolve?").

According to De Laguna (1962), the shift from mechanistic/ operationalistic approaches to evolutionary, adaptationist accounts took place in the late 1950s. She called it a debate of "mechanism" versus "teleology" and pinpointed the Darwin Centennial, held at the University of Chicago in 1959, as the place where the debate was introduced in the field of biology. This Conference also served as the impetus to give independence to the field of evolutionary biology. Initiator of the conference and its proceedings was Sol Tax (1960), who invited evolutionary biologists such as Theodosius Dobzhansky, Julian Huxley, Ernst Mayr, George Gaylord Simpson and Sewall Wright; but also ethologists such as Nikolaas Tinbergen; anthropologists such as Alfred Kroeber and Leslie White and several religious preachers. Tax also lay the foundation for the journal *Current Anthropology*.

The core questions tackled by the scholars who participated in the Darwin Centennial were (1) what is the depth of evolutionary theory: how does it influence theorizing on the inorganic, organic and super-organic; and (2) which epistemic queries are relevant for conducting evolutionary research.

In regard to the first question, participants in the Chicago Darwin centennial endorsed evolution as a fact of nature at all ontological levels: the inorganic, organic and post-organic (sociocultural) level. Especially Julian Huxley, according to De Laguna (1962, 117-8) pleaded for "universal evolution". Accepting that evolution occurs at all layers of reality, justified evolutionary research into sociocultural behavior, an endeavor ethologists and comparative psychologists had engaged in from the 1930s onwards.

But when studying sociocultural behavior, evolutionary biologists also needed to ask which epistemic queries are relevant to begin research into the evolutionary origin of the super-organic. This relates to the second theme of the Centennial. Huxley battled vitalism fiercely, but allowed for teleonomy in regard to post-organic evolution, even teleological approaches were considered valid. De Laguna (1962, 125) on Huxley:

> "'In man', he states, 'we have the beginning of a process that is, in the strict sense of the word, teleological, since purpose-consciously or unconsciously, but, in any case, subjectively, wanting to do something that is envisaged in the future-comes in. Thus

> you have a hangover from a teleonomic to a strictly teleological mechanism.' According to this view, organic evolution still goes on after man appears, although radically transformed and activated by new agencies and mechanisms."

In the natural sciences, physicists had replaced the Aristotelian, teleological world view with a mechanistic one. They rejected the scientific validity of inquiring into the causa materialis (what), formalis (what for) and finalis (why) of things. In short, they rejected teleology. Asking the what question results in essentialism. And as Aristotle already pointed out before them, asking the what for and why questions results in teleology. Instead, physicists and positivists endorsed that science must only inquire into the causa efficiens of phenomena. This implies that scientists need to ask how phenomena function, by identifying their operationalism, and by identifying the laws and mechanisms that enable phenomena to obtain their structure and function.

Functional and Evolutionary biologists had followed their lead. They subscribed to this mechanistic approach, and rejected teleological approaches such as the ones defended by vitalists that postulate that evolution is directed by driving forces such as Bergson's élan vital or Driesch' entelechy (Mayr 1961). De Laguna (1962, 118-9):

> "But what they reject as 'teleology' is the doctrine that the results of evolutionary process, the production of the living cell, and later of intelligent man, are ends, or goals, to which these processes have been directed by some external or internal controlling agency. Thus the distinguished biologist, George Gaylord Simpson, speaks of teleology as the problem 'whether evolution has goals or ends and, if so, what those ends may be,' and rejects it in its 'classical meaning' of 'corresponding with a preordained plan, or with Divine Providence, or with purposes especially relevant to the human species.' To reject 'teleology' in this sense, however, is by no means to repudiate it in the wider sense as the problem set by the existence of ends in nature. For there is no denying that there is a sense in which ends are actually there in nature. We may well agree that man, as well as the living cell, is a result, but not the goal of the evolutionary processes which produced them; but we must also recognize that man has conscious purposes and acts to attain goals. Even though man is not himself an end of nature, he brings ends into nature. … these evolutionists argue that it is the coming into existence of man with his purposeiveness that marks the critical transition from biological evolution to the human or psycho-social phase."

Although both functional and evolutionary biologists reject that evolution is directed and purposeful, this does not imply that the products of evolution, such as organisms and their physical or behavioral traits, cannot introduce purposeful behavior. And also morphological and behavioral traits are end-directed.

Against the physicists, the attendants of the Darwin Centennial validated the research into end-directedness. In Sol's proceedings, especially Simpson would adopt Collin Pittendrigh's notion of teleonomy (a term also used by Talcott Parsons), to delineate the study of these functional, end-directed, adaptive traits and behaviors. De Laguna (1962, 119) cites Pittendrigh (1958) as follows:

> "The biologist's long-standing confusion would be more fully removed if all end-directed systems were described by some other term, like 'teleonomic', in order to emphasize that the recognition and description of end-directedness does not carry a commitment to Aristotelian teleology as an efficient [sic] causal principle."

The *sic* is hers, and is there because biologists confused Aristotle's efficient cause with his final cause. The point was, as De Laguna (1962, 119) points out, that the Centennial biologists asked the question "to what end is the organization of the living being directed?". The answer they gave was "to the end of reproduction, self-replication". It is here that the adaptationist account, and its related discussions to fitness, questions that require an answer to the "what for" question, come into play.

Mayr (1961) also commented on Pittendrigh's work on teleonomy in a paper on causality called *Cause and Effect in Biology*, published in the journal *Science*. In his analysis, Mayr found inspiration in the works of Ernst Nagel (1961). The latter maintained a naturalist-positivist, systems theoretical-functionalist approach. Nagel defended the idea that the natural sciences can take on the study of any type of phenomenon, and every phenomenon needs to be understood as an independent system that functions as a whole through the mechanical workings of its parts. This approach is characterized as reductionist, because it declares that all and only natural, physicalist accounts are valid. Following Nagel, Mayr (1961, 1501) maintained that in science, matters of causality contain 3 elements: explanation, prediction and teleology:

> "(i) an explanation of past events ("a posteriori causality"); (2) prediction of future events; and (3) interpretation of teleological—that is, "goal-directed"—phenomena".

It was also Mayr who distinguished the field of biology into functional (to be understood as operational, not adapatationist) and evolutionary biologists. He claimed that:

> "The functional biologist is vitally concerned with the operation and interaction of structural elements […]. His ever-repeated question is 'How?' How does something operate, how does it function? […H]is approach is essentially the same as that of the physicist and the chemist." (Mayr 1961, 1502)

According to Mayr (1961, 1502), evolutionary biology differs from functional biology because it also asks about the "why" of behavior.

> "His basic question is Why?'. […] It may mean 'how come?' but it may also mean the finalistic 'what for?'. It is obvious that the evolutionist has in mind the historical 'how

> come?' when he asks 'why?' Every organism, whether an individual or a species, is the product of a long history, a history that dates back more than 2000 million years".

This why question is a historical question that is directed towards the past. It asks how traits, including adaptive ones, come into existence. The answer requires an evolutionary account.

Mayr argued that evolutionary biology differs from physics because biology needs to focus on history. Physicists can predict the future of the universe because the natural laws are constant and static, but there are no "absolute phenomena" in biology which is why the field finds it difficult to make predictions. Biologists deal with phenomena that are the result of contingent historical events. Biologists therefore also need to ask the "how come" question, which inquires into the causes of the origin of mechanical functions through time.

This question, according to Mayr, is raised within the domain of evolutionary biology, not within functional biology. Answers need to take into account how the functional units and goal-directed behavior portrayed by humans evolve. This in turn is done by investigating how the traits benefit the organism in its struggle for existence, i.e. it needs to be examined how functional units enhance successful survival and reproduction. This is the stuff natural selection works on:

> "Natural selection does its best to favor the production of programs guaranteeing behavior that increases fitness." (Mayr 1961, 1504)

Especially Mayr emphasized that this "how come" differed from finalistic "what for" questions. The main reason for that is that natural selection does not work with foresight. Variation is blind. Even though something might have been naturally selected for the function it performs, it cannot be foreseen that it will remain purposeful in the future, although it might be more probable. Selection works on existing traits, not future ones. That something is an adaptation therefore needs to be reinforced, via successful survival and reproduction. Contingent events such as random genetic mutations or changes in environmental conditions might make previously adaptive behavior maladaptive. For Mayr, adaptation is simply "an a posteriori product of natural selection", we cannot attribute cause to it.

He agreed with Huxley (1957), who defined teleonomy as "the apparent purposefulness of organisms and their characteristics", and affirmed that it is a phenomenon worthy of study in and of itself. But contrary to Pittendrigh, Mayr stressed that teleonomic phenomena cannot themselves be attributed causation. That behavior is teleonomic is the result of ontogeny, and the latter can be subjected to natural selection because it is partly underlain by biological determinants such as genes whereupon natural selection works.

> "Such a clear-cut separation of teleonomy, which has an analyzable physicochemical basis, from teleology, which deals more broadly with the overall harmony of the organic world, is most useful because these two entirely different phenomena have so often been confused with each other. The development or behavior of an individual is purposive, natural selection is definitely not." (Mayr 1961, 1504)

In other words, for Mayr, adaptation is first and foremost an *outcome* of natural selection working on phenotypic features: it favors those traits that enhance successful survival and reproduction. It does not work directly on adaptations. Adaptation is a status or condition with hindsight attributable to these phenotypic features.

But when studying the evolution of functional behavioral or physical traits by making use of terms such as adaptation and fitness, evolutionary biologists began to find it difficult to refrain from questions about goal-directedness and purposefulness.

Mayr's ideas on teleonomy and teleology would become countered by Christopher Williams (1966). Asking why a functional trait came into existence during the course of evolution requires studies into the success in survival (adaptedness to the environment) and reproductive success (fitness) the trait gives to its carrier. Williams therefore stated that functional-adaptationist accounts, that ask the "what is a trait for" question, need to be raised, and it was he who popularized the term teleonomy to study these adaptations. As such, he introduced a shift from the study of the origin and evolution of physical traits (that can possibly be adaptive) to the study of adaptations in and of themselves. Causation, he reasoned, can also be attributed to the functions of traits: they can influence the course of evolution. Maynard Smith (1968) followed his lead, and endorsed that evolutionary biology primarily needs to focus on the explanation of adaptive complexity. Both authors would highly influence Richard Dawkins (1976; 1983) who further reduced natural selection to the study of apparent "design". Natural selection was no longer understood as a mechanism that passively weeds out maladaptive organisms, but became understood as mechanism that actively "designs" adaptive traits. Terms like "pre-adaptations" and "accumulative selection" were introduced to facilitate such a view.

> "I agree with Maynard Smith (1969) that 'The main task of any theory of evolution is to explain adaptive complexity' ... We concur with Paley that adaptive complexity demands a very special kind of explanation: either a Designer, as Paley thought, or something such as natural selection that does the job of a designer. Indeed, adaptive complexity is probably the best diagnostic of the presence of life itself." (Dawkins, 1983, 16)

2.2.2 Causation and epistemic questions in Ethology

Julian Huxley was a close friend of both Konrad Lorenz and Nikolaas Tinbergen. How did these ethologists respond to the plea for evolutionary studies of teleonomy (a question especially relating to problems of adaptation and fitness) and the change it brought about in epistemic research questions?

Nikolaas Tinbergen (1963) wrote a paper entitled *On aims an methods of Ethology*. He dedicated the paper to Konrad Lorenz and regarded it as both a homage and an elaboration of Lorenz' article *Biologische Fragestellungen in der Tierpsychologie* (Biological questions in animal psychology) written in 1937. Tinbergen's paper would set the basis for what became known as the 4 questions of ethology. These 4 questions would later become the dictum of sociobiology (Wilson 1975).

Julien Huxley had distinguished between 3 problems of evolutionary biology: the problem of causation, survival value and evolution. Tinbergen (1963, 411) followed his lead and added ontogeny as a fourth problem. In ethology, aside from the usual "how" questions asked in matters of determining causation, also "why" and "what for" questions need to be raised in order to understand both behavior and its evolutionary origins. Let's turn to these problems one by one.

A first problem ethologists find themselves faced with is that of causation. Following Lorenz (1958), Tinbergen (1963, 413-416) argued that behavioral patterns need to be studied like functional organs that require a causal analysis of their "machinery". Just as functional biologists investigate what causes an organ to form and function, so ethologists need to ask "What causes this behavior"? Answering this question requires asking the "how"-question: we need to determine the causes and effects of the behavior, from the level of "supra-individual societies all the way down to Molecular Biology". In other words, the problem of causation is properly dealt with by asking how genes, proteins, cells, the brain, the body with its hormonal and muscular systems, and even society shapes behavior. Causation therefore asks about the "Physiology of Behavior", and behavior is treated as an organ that can be a unit of evolution at many hierarchical levels.

A second concern of the ethologist is the problem of survival value (in current literature often designated as the problem of adaptation). Ethologists, according to Tinbergen (1963, 417-423), need to ask "what" a behavior "is good for". That is, a cost-benefit equation needs to be made to examine how the behavior contributes to an organism's chances of survival. We can however only indirectly examine how behavior portrayed today contributed to past survival chances, and therefore, investigating the adaptive value of a trait often involves observing the current function of the behavior. Different from the physiologists, the ethologist

> "… too studies cause-effect relationships, but in his study the observable is the cause and he tries to trace the effects. Both types of worker are therefore investigating cause-effect relationships, and the only difference is that the physiologists look back in time, whereas the student of survival value, so-to-speak, looks "forward in time": he follows events after the observable process has occurred." (Tinbergen, 1963, 418)

Adaptationists study the outcome, the functions or effects of behavior. According to Tinbergen, one can also add causation to survival value (that something enables survival and reproduction and thus is adaptive might be the reason why it evolved). The problem is that the use or function of many of the current behaviors under study remains unknown. In order to know the use and survival benefit of a behavioral trait, we need to observe the present behavior (Tinbergen, 1963, 423). In sum, according to Tinbergen, adaptationist studies differ from physiological ones in that the former study the outcome of evolution and inquire about the present function of a trait (what it is good for), while physiologists examine how the trait was able to evolve and become functional and consequently how it became the subject of positive selection.

The third problem concerns ontogeny, or the "change of behavioral machinery during development". Question raised are: How does the functional behavior develop during the course of an organism's lifespan (developmental causes), and how does the environment change the behavior (environmental causes)? According to Tinbergen (1963, 424-426), answers firstly relate to determining whether the behavioral trait under study is innate or acquired (is the behavior a learned habit or an acquired instinct), which again requires insight into how physiological mechanisms cause the behavior to be produced. Secondly, ecological studies need to determine how the environment molds the behavior. Finally, Tinbergen points out that one can also add causation to ontogeny itself: the way in which behavior develops and gets molded by the environment, can cause an organism to have more or less survival value.

The final problem involves that of evolution. Why did the behavioral trait evolve in the way that it did? Tinbergen (1963, 428) wanted nothing less than that ethologists would develop a "taxonomy of behavior" that maps the "hereditary behavioral blueprints". He wanted the field to delineate the course of evolution of a behavioral trait just as systematics delineates a species' course of evolution. These variational behavioral blueprints are the subject of natural selection. In his view, natural selection is not necessarily the cause of the origin of the behavior. Physiological or ontogenetic causation might underlie the behavior and this behavior can then possibly become favored via natural selection. This is an important nuance.

Tinbergen maintained that all questions are of equal importance. Nonetheless, the current functions of behavioral traits, as well as the mechanisms that cause them are in both Tinbergen's as in our time, often unknown. Moreover, some traits, even though they function physiologically, and even though they undergo change during ontogeny due to an organisms' individual learning skills or due to environmental conditions, often do not contribute to the direct survival of a species. He therefore favored empiricist approaches over deductionist approaches. That is, he emphasized the importance of observation of current behavior in both natural and artificial settings, to understand how behavior develops and changes through time, how-questions that relate to the problem of causation and ontogeny.

2.2.3 Causation and epistemic questions of the newly evolving evolutionary fields

Current textbooks on ethology and evolutionary psychology (Buss 1995, 2004; Confer et al. 2010; Gaulin & McBurney 2003, 15) often rearrange the order in which Tinbergen formulated the questions. Epistemic queries about the physiological causation and ontogeny of behavioral traits are grouped as *proximate* causes of the behavior. The quest for the adaptive function and the evolutionary advantage this function might provide are understood as inquiries into the *ultimate* causes of the behavior. It is important to note that in his 1963 article, Tinbergen made no such distinction. Who did make the distinction between proximate and ultimate causes was Mayr (1961, 1503), in his previously discussed paper on *Cause and effect in biology*. It was he who stated that operational, mechanistic explanations lend insight into the proximate causes of traits while ultimate causes explain teleonomic inquiries (the study of adaptation and fitness through time). And it was Mayr who declared that structure-functional biologists studied the proximate causes, and evolutionary biologists the ultimate ones.

Evolutionary psychological textbooks further indicate that what sets their field apart from classic ethological approaches is their exclusive focus on the ultimate causes of behavioral traits (Gaulin & McBurney, 2003, 1-24). This implies that evolutionary psychologists take a more deductive approach to human behavior. Contrary to the early observational, inductive approaches taken by ethologists, evolutionary psychologists often exclusively focus on finding the functions of behavioral traits and why these functions evolved (for what reason). That behavioral traits are adaptations, and that they evolved by means of natural selection is often taken for granted. The epistemic concern lies with answering the "what" and "what for" questions. What is the adaptive function of a behavioral trait and is this function the ultimate reason why it evolved?

The new evolutionary sciences partly find their roots in classic human sciences such as anthropology, sociology and linguistics, wherein a structural-functionalist, synchronic approach was often favored. Herbert Spencer (1976), Emile Durkheim (1982) and Talcott Parsons (1968) in sociology, Malinowski (1944) and Kroeber (1963) in anthropology, or de Saussure (1972) or Chomsky (1965) in linguistics, respectively argued that society, culture or language need to be understood as closed systems, bodies composed of functional organs, wherein the different parts function together to create the whole. Focus should therefore lie on finding out how the functional parts work together to produce the whole.

Although the newly evolved sciences set themselves off against this synchronic structural-functionalist approach, they nonetheless primarily focus on the functions of behavioral traits. Although they claim to take an evolutionary, and therefore, diachronic approach with their focus on the ultimate causes that underlie modern behavior, they often remain stuck in the present. The reason for this is that studies about the adaptive value, as Tinbergen already pointed out, are directed to the present or the future. We can only examine the evolutionary, biological function of a trait once it evolved and serves its purpose.

The new sciences also lack an academic background in the methods of natural and evolutionary theory. This is probably one of the reasons why these scholars tend to refrain from the how question, a question that asks about the genetic, ontogenetic and physiological mechanisms that both constrain as well as enable the evolution of certain traits.

Following the popular writings of Dawkins (1974; 1982; 1983), Pinker and Bloom (1990) for example, in their seminal article on language evolution, stated that language shows design, and therefore it must be an adaptation that evolved by means of natural selection. Evolutionary linguists (Christiansen & Kirby 2003; Hurford, Studdert-Kennedy & Knight 1998) therefore tend to focus on what language evolved for (a common answer being given is that it evolved for better communication), but they refrain from examining how exactly the supralaryngeal vocal tract, breathing patterns, facial muscles, or the genes that encode for these physiological features, evolved through time. The latter physiological questions mostly remain studied by paleontologists, physical anthropologists, anatomists, geneticists, and so on. Granted, these latter scientists are getting more and more involved within the newly evolving evolutionary sciences, but it is no understatement that they do not make up the hard core of scholars working within the new evolutionary sciences. The core is made up of people that populate the humanity departments, and the latter merely acquire their “data” from these sciences.

When the theory of natural selection got first formulated, it was understood to explain the selective favoring of existing variation (Darwin 1859; Dobzhansky 1973; Mayr 1961). The selective favoring of adaptive organisms over maladaptive ones cause for descent with modification, evolutionary change through time. Darwin, and also the early Neo-Darwinians, never understood variation itself to be the outcome of natural selection. Variation, according to Neo-Darwinians, was caused by random mutations and genetic recombinations. Both are stochastic events: no selection occurs for a certain mutation, but once a mutation evolved stochastically, it can become the subject of positive selection, provided it gives an adaptive advantage. In a real sense, adaptation is merely a state an organism can be in. As such, it has no causal influence on evolution, it provides no mechanistic explanation, it is merely the outcome of evolution. Alternative outcomes or states an organism or its traits can be in is that it is either neutral (Kimura 1976), maladaptive or an exaptation (Gould & Vrba 1998).

Tinbergen and other early ethologists also understood the behavioral repertoire of organisms as “blind variation”. Behavioral variation is caused by ontogeny, physiology and phylogeny, and it can be adaptive, neutral or maladaptive, and it is exactly for this reason that it is blind. Although behavior might be the outcome of positive selection in the past, it remains a problem of the future whether these traits will still be beneficial and favored in times to come. Natural selection works on this blind variation and selects the adaptive ones indirectly, by weeding out the maladaptive ones. Moreover, conflicting evolutionary pressures often disable adaptive traits to evolve. And even if traits are favored in the future, that does not mean that they are the product of past positive selection. Other mechanisms (ontogenetic, chemical, physiological or ecological) might lie at their evolutionary origin. Finding out how the traits evolved or how traits develop during an organism’s lifespan, the question concerning the mechanisms that underlie current behavioral physiology, therefore was understood to stand apart from the problem of positive selection. Natural selection could of course have been the underlying mechanism, but the how questions in regard to physiological and ontogenetic causation needed to prove that. Behavior might have equally come into existence through trial and error learning, imitation, or conditioning.

2.3 The methodology used by the new evolutionary sciences: from Universal Evolution to Universal Selectionism

Evolutionary psychologists today work within the premise that all and only selectionist approaches can explain both the proximate and ultimate causes that underlie the evolution of behavior. To cite just once pioneering scholar in the field:

> "Evolution by Natural Selection is *the only known* causal process capable of producing complex physiological and psychological mechanisms." (emphasis mine, Buss, 1995, 2)

This is intriguing. Surely, no scholar today will disagree that ontogeny or learning, physiology or ecology can influence and cause certain behavior. Yet they argue that only selectionist accounts of behavior are valid. Why? If we acknowledge that ontogeny, physiology and ecology can also influence the evolution of behavior, then it is impossible to claim that only selectionist accounts are valid to explain behavior unless we assume that natural selection is responsible for all ontogenetic, physiological or ecological causes. But this is not the case, we cannot attribute such powers to natural selection.

Scholars working within the new evolutionary sciences often lack professional training in evolutionary biology and the nature of evolutionary methodology. They neither received proper training in all the evolutionary mechanisms currently studied by biologists, nor are they adequately aware of the explanatory powers of certain of these evolutionary theories.

Another example that illustrates this comment is the following. Evolutionary psychologists (Tooby & Cosmides 2005) claim that human behavioral traits are adaptive, and that they adapted to the Pleistocene environment, somewhat 2 million years ago. But given the fact that we do not live in the Pleistocene anymore, but inhabit the modern day world that differs greatly from the original environment, we have to conclude that our behavior is not adapted to the present environmental conditions we live in. However, if we are maladapted, it begs the question why we humans are still alive today, and why we are so good at propagating and populating this modern world. If we are maladapted to the modern world because we are adapted to our environmental past, it makes adaptive explanations of current behavior oblivious, thereby annihilating the necessity of the field of evolutionary psychology and all newly evolving evolutionary fields inspired by the former's premises.

I do not wish to make this claim. Rather, it needs to be pointed out that evolutionary psychologists often make category mistakes. They often attribute causation to adaptations, forget to attribute causation to ontogeny, physiology or ecology, don't have a clear view on what evolutionary mechanisms are, and how they can inflict change. Insight into the latter can only be acquired by focusing on the how of it all.

Today, it is an unspoken truism that the theory of natural selection can explain both the ultimate as well as proximate causes of behavior. The hope is cherished that the life sciences (molecular biology, anatomy, evolutionary biology, etc.), by making use of their field-specific methods, will eventually provide theories on how natural selection caused both the origin and evolution of every behavior. The assumption that the life sciences will outline the proximate causes, allows the new evolutionary sciences to focus on the ultimate causes.

The consequence is that scholars today are trying to run when they can't walk. As early ethologists rightly pointed out, we first need to understand the "proximate" causes of behavior, before we can tackle the "ultimate" ones. It might very well be that the proximate causes of behavior require selectionist explanations, but this still needs the burden of proof. And this proof can only be found by focusing on evolutionary history.

Arguing that culture, or society, parental investment or sense of beauty are adaptations does not explain how these features evolved genetically, ontogenetically, physiologically or ecologically. That tool manufacture is an adaptation does not explain the evolutionary origin of the cognitive mechanisms required to manufacture tools. The functionalist approach remains focused on the present. Yet evolutionary research is first and foremost a historical discipline: it focuses on the natural history of species and their behavioral traits. The newly evolving evolutionary sciences focus on only half the story. Quite contrary to their original goal, they leave out a major part of evolutionary history (the question of origins) and merely focus on building a new methodological framework to examines the ultimate causes. No general and universal methodological framework currently exists to study the proximate causes. In the last part of this paper, a methodology is introduced that does focus on the how of it all.

But first, we need to dive once more into academic history, and search for the roots of the claim that the theory of natural selection *alone* can lend insight into both the proximate and ultimate causes of evolution.

3. The roots of the selectionist approach

Scholars that work within these newly emerging evolutionary fields can best be understood to be in Kuhn's paradigmatic stage (Kuhn 1996). They do not question the validity of their epistemic framework, rather, they are confident that the methodologies used (i.e. the selectionist approach) will be able to provide adequate answers to the problems set out in the research program. Because they take their epistemic framework as a given, they also often don't know where the theoretical premises of their field stem from. Rather, they execute the existing epistemic program.

In this part, we focus on the root of the overall turn towards Neo-Darwinian theory as an explanatory framework for all aspects of human behavior. Where does the overall selectionist approach stem from? What is the epistemological framework that first allowed scholars to emphasize the validity of the selectionist approach? And what underlies the hope that selectionist accounts will succeed there where other methodologies have failed in explaining the full range of sociocultural behavior?

It will be demonstrated that the route taken by the new evolutionary sciences is a route laid out by early naturalized epistemologists, evolutionary epistemologists, and philosophers and biologists who engaged in what became known as the "units and levels of selection debate".

3.1 Evolutionary Epistemology

Inspired by Hume and Kant, who endorsed that we cannot directly gain knowledge of the world in itself, but rather that we gain knowledge of the world as it appears to us, Quine (1969) asserted that epistemology (the study of how we gain knowledge of the world) needs to be naturalized. Contrary to analytical philosophers who turned post-modern and introduced the field of Sociology of Knowledge, Quine positivistically argued that we need to understand the knowledge-gaining process as a psychological trait. As such, it needs to be studied from within the natural and life sciences. By redefining epistemology as a research topic of psychology, he annihilated the validity of epistemology as a philosophical discipline that stands on its own and classified it as part of the life sciences.

This in turn would inspire the early ethologists and experimental psychologists who investigated the knowledge that animals have about their environment. By examining the instincts and learning mechanisms in poultry and other animals, Lorenz (1941) would suggest that certain innate knowledge can be understood as *synthetic a priori* claims. The behavior is phylogenetically acquired, but ontogenetically innate. What does this mean? Throughout evolutionary time, organisms become molded by natural selection and as a consequence, they fit their environment. The selective favoring of the fit over the unfit organisms, as well assumed mechanisms such as habit-to-instinct processes, result in organisms that are born with mental (e.g. instincts that enable them to engage in mating behavior) and physical (e.g. a breathing apparatus that enables one to live in an oxygen-rich environment) predispositions of the environment they live in. This knowledge is ontogenetically innate, but phylogenetically acquired through natural selection. With its biological make-up, a fish is born to live in the water, it can therefore even be reasoned that the fish provides a trial or theory about its environment in which it will be born, that can be either confirmed or rejected by that environment via natural selection (Munz, 1993, Gontier, 2006a, b).

In his later life, Skinner (1974), would assert that trial and error learning is comparable to evolution by means of natural selection: both mechanisms were understood to be the same because of their selective nature. Inspired by the behaviorist learning approach in psychology that emphasized the importance of trial and error learning in all animals, including humans, evolutionary epistemologists started to regard evolution by means of natural selection as a selective mechanism that works by means of trial and error. Even natural selection itself became regarded as a knowledge process. And also human (innate or acquired) knowledge, cognitive features that underlie the knowledge-acquisition process, or behavior were understood to be the outcome of selective, trial and error processes.

In the 1950s, one of those psychologists that studied the human knowledge-acquisition process, Donald T. Campbell (1959; 1960; 1974; 1997), would lay the foundation of the field of Evolutionary Epistemology. Campbell was especially interested in human creativity, and suggested that it ontogenetically developed through trial and error learning, and phylogenetically evolved by means of natural selection. By doing so, Campbell, as well as the early ethologists, would start to undue of the distinctions between ontogeny (development) and phylogeny (evolution), the innate versus acquired dichotomy, and the nature/culture divide. Natural selection was proposed to work on both innate as well as acquired, natural and cultural traits, because they follow a trial and error heuristic. Rather than claim that natural selection merely works on whole organisms at the level of the external environment, as early Neo-Darwinians such as Mayr did, natural selection became internalized and was said to work on behavior as well.

Evolutionary epistemologists such as Hahlweg (1989), Riedl (1984) or Wuketits (1985) stated that the way in which an organism develops is the result of the way it evolved. This does not necessarily imply that ontogeny recapitulates phylogeny, as Haeckel (1912) assumed. It means that past selective processes have shaped as well as constrained the behavioral repertoire and physical features that are available to the organism during its lifespan. Humans can walk and run, but we can't fly, and we can see solid objects but not gasses. Development therefore needs to be understood as the outcome of evolution by means of natural selection, and developmental processes themselves are indicated to be of a selective nature. Natural selection theory was synthesized with systems theory: the organism, species, culture and society became defined as partly open, and partly closed systems, that all evolve by means of natural selection.

Especially in Germany this evolutionary epistemological research also went hand in hand with systems theoretical and cybernetic concepts of nested hierarchies, where each level in the hierarchy is considered to be autonomous, self-maintaining and self-regulating. This would lead to non-adaptationist (Gould & Lewontin 1979; Wuketits 2006), constructivist (Vollmer 1984) approaches. Self-regulation (Hahlweg 1989) or niche-construction (Lewontin 2000) might enable an organism to self-maintain, even though it is not adapted to its environment. This also relates to the concept of adaptability. Traits or behavior can be adjusted (through processes such as phenotypic plasticity) so that it becomes adaptive.

Biologically inspired system theoreticians (contrary to sociologists such as Talcott Parsons or anthropologists such as Mead) would hold that each level of organization can be regarded as an independent unit of evolution.

As a field, Evolutionary Epistemology (Lorenz 1985) regards all features (both cognitive as well as physical) portrayed by all organisms as knowledge processes: trials that are prone to positive or negative selection by the environment. They therefore investigates how knowledge-acquisition-processes evolve in various animals (both onto- as well as phylogenetically) by means of natural selection and by means of other "evolutionary" mechanisms such as trial and error learning. Bradie (1986) would dub this line of work the EEM program.

Moreover, evolutionary epistemologists assert that also cognition, culture (including scientific theories), society and language are phenomena that are the direct creations of animals. They are evolved learning programs (learned through trial and error) that can in turn also be regarded as evolving systems in and of their own. Culture, language or society are not, as many structural-functionalists assumed, static systems or phenomena that have independence of man. All these phenomena need to be studied as the outcome of evolution. Bradie (1986) would dub this line of thought the EET program. Originally, EET especially focused on how the growth of human (academic) knowledge could be modeled to evolve by analogy with biological evolution, but the EET-program rapidly included the study of all aspects of culture.

Finally, especially Campbell (1959; 1974; 1997), would suggest that all these knowledge-gaining processes (positive selection of genes, vision, echo-location, but also language and culture) themselves work selectively.

How is this possible? Natural selection is a mechanism first formulated by Darwin to explain the evolution of biological species. Evolutionary epistemologists endorse that natural selection not only works upon the evolution of organisms, also trial and error learning became understood as an instance of natural selection. Natural selection was thus said to work on non-biological phenomena. Classic neo-Darwinian scholars had come to define natural selection as a mechanism that works upon the whole organism (its genotype and phenotype) at the level of the environment. In order to be able to expand natural selection to non-biological phenomena, Campbell had to undue of the genetic requirements demanded by biologists.

He therefore unstrapped natural selection to its core. Basic to both cultural as well as biological selection, he reasoned, was that blind variation becomes selectively retained. Variation might be the outcome of genetic mutations, but also cognitive propositions or cultural traits can function as raw material whereupon selective retention is active. Campbell thus abstracted a template or heuristic of natural selection, which he called "blind variation and selective retention". Biological evolution was merely one phenomenon that was the outcome of selection, blind variation and selective retention could also underlie cultural, linguistic, and cognitive evolution. As such, Campbell provided more insight into "how" natural selection works: it selectively retains adaptive variation from of pool of blind variation. But variation itself is not necessarily caused by natural selection.

It is also for this reason that he claimed that knowledge-gaining processes themselves work selectively. Inspired by systems theorists, and a direct implication of assuming that natural selection is active on all natural as well as cultural phenomena, Campbell proposed that biological reality is layered, and processes such as upward and downward causation as well as vicarious selection shape that reality. This means that genes, themselves the result of natural selection, i.e. a blind variation and selective retention process, can determine the way in which an organism evolves (upward causation), but also culture, itself the result of selective processes (trial and error learning), can determine which genes can serve as raw material in future generations by retaining organisms with a genetic make-up fit to live in cultural society (downward causation).

The latter example can also illustrate vicarious selection: cultural selection might provide a stronger selection force on genes than physical-environmental selection. As such, cultural selection can substitute, much like a vicar substitutes and hence the word, physical-environmental selection. The concept of vicarious selection therefore strongly relates to the concept of multilevel selection.

3.2 The units and levels of selection debate

From the 1950s onwards, and mostly without being aware of the work of evolutionary epistemologists, evolutionary biologists too had contemplated the explanatory power and application range of natural selection, especially in regard to issues such as altruism, group and kin selection (Haldane 1955; Hamilton 1964;

Maynard Smith 1964; Trivers 1971; Wyne-Edwards 1962). Could there be a genetic basis for social behavior such as altruism? They reasoned that this might be possible, if organisms can contribute to the successful propagation of the genes of their conspecifics. They introduced inclusive fitness theory: through social behavior such as food sharing, organisms can contribute to their own fitness by increasing the fitness of organisms that share their genes.

These debates would first and foremost tackle the problem of fitness. Fitness is measured by the number of offspring an organism can produce, and fitness therefore can be used to quantify adaptation; adaptation is often measured by an organism's fitness. Theories about group and kin selection ultimately ask what the fitness is good for (Lloyd 1986). Who benefits from survival and successful reproduction? The organism, its genes, its kin, the group, or even the species? These questions would further spark debates over nested hierarchies and different levels of selection. Williams (1966) opposed the idea of higher-order selection, and contended that only genes are the true units of selection.

In the 1970s, Richard Lewontin wrote an article called "The units of selection" wherein he dealt with these issues of group and species selection, and the possibility that also culture evolves by means of natural selection. Independent from the earlier published work of Campbell, he further introduced "a logical skeleton" of natural selection (Lewontin 1970). This skeleton (phenotypic variation, differential fitness and hereditability of fitness) too can be regarded as a template or heuristic of natural selection: i.e. it explains how natural selection can proceed.

But because Lewontin focused on fitness, and thus the problem of adaptation (Tinbergen's problem of survival value), evolutionary biologists started to focus much more on the what of selection than the how of selection. Primary questions became: What is the unit of selection? Whereupon does selection work? Who's fitness increases?

Dawkins (1976) proposed that the ultimate and only survivors or beneficiaries of selection are the genes. Organisms or even groups are mere vehicles that house the true units of selection. Vehicle selection can occur, but needs to be explained through the differential survival of their genes. A gene became defined as a replicator, "any entity in the universe of which copies are made", and these replicators posses fecundity, longevity and copying-fidelity, which is why they can be units of selection. If such replicating entities exist in culture, then culture too might be argued to evolve by means of natural selection. Not because culture would increase the fitness of entities such as kin or groups (which are mere vehicles), but because replicators, and errors during replication, provide the variation whereupon selection acts. Dawkins would introduce the concept of a meme to characterize these hypothetical units of cultural evolution, a concept that would be further developed by the evolutionary psychologist Susan Blackmore (1999), when she introduced the field of memetics.

From the 1980s onwards, philosophers of biology would join the debate over the units of selection. Hull (1980, 1981) contended that Dawkins' vehicle selection was best characterized by a selection of interactors rather than replicators, and interactors too could function as units of selection. Wimsatt (1981) would also plead in favor of the existence of "higher-level biological units of selection".

Brandon (1982) emphasized that these different units of selection often evolve at different levels, and he therefore pleaded for an independent study of the levels of selection. Brandon's paper on levels and Lewontin's paper on units would inspired the scholars involved to designate the ongoing debates as "the units and levels of selection debate".

3.3 Philosophy of biology as an academic discipline

It is by engaging in the units and levels of selection debate, and by subscribing to the claims made by evolutionary epistemologists, that from the 1980s onwards, the field of philosophy of biology would originate. The research agendas of both evolutionary epistemology and the units and levels of selection debate became synthesized: it was investigated how not only genes, organisms, groups, or species can possibly be units of selection, but how also language, culture, social behavior, and scientific theories evolve by means of natural selection. And it was examined how natural selection can be universalized to take on the evolutionary study of all these phenomena.

On the one hand, philosophers of biology would join the sociobiological debates over cultural evolution. This gave rise to Dual Inheritance theories. Originally, these scholars would try and model cultural evolution by analogy to biological evolution. It was reasoning based upon finding analogies because they would assert that although the biological capacity to have culture is a biologically acquired trait, cultural evolution occurs at a different pace and often by different means than natural selection (Gould 1991; Lumsden & Wilson 1981). In line with Huxley's plea for Universal Evolution, cultural evolution was considered to be enabled by biological evolution, but it also stood apart from it because both variation and selection could be more directed and goal-oriented (Boyd & Richerson 1985). In culture, transmission and retention can result from intentional, purposeful learning. Information can be passed on both vertically and horizontally (Cavalli-Sforza & Feldman 1981; Feldman & Cavalli-Sforza 1976), and culture was also argued to evolve by drift (Koerper & Stickel 1980). Therefore, these scholars introduced the idea of gene-culture co-evolution: humans and intelligent animals are subjected to a dual system of inheritance, one biological, one cultural. Because they took biological evolution as a model for cultural evolution, they would look for cultural analogues of the gene (the unit of selection) and the physical environment (the level of selection). But what characterizes these scholar's theories the most, is their multi-mechanistic approach.

On the other hand, philosophers of biology would, on a more theoretical and even metaphysical level, contemplate on the general nature of units and levels of selection. Besides replicators and interactors, terms such as manifestors, reproducers and beneficiaries, would be introduced to characterize the unit of selection (Dawkins 1976; Griesemer 2000; Hull 1981; Lloyd 1986; Sober 1980). And the units and levels of selection would also become modeled by the system theoretically inspired field of artificial intelligence (Szathmáry, 2002, 2006), where questions on hierarchies and the major transitions of evolution arose.

Characterizing the nature of units went hand in hand with characterizing the level, the locus of selection. By analyzing the debates over group and kin selection, the possibility of multilevel selection would become investigated (Brandon 1982; 1988; Sterenly & Kitcher 1988; Vrba & Eldredge 1984; Vrba & Gould 1986; Wimsatt 1981). Campbell, with his notion of vicarious selection raised the possibility that a higher system (e.g. teaching) can alter or substitute selection at lower levels (e.g. individual trial and error learning). Philosophers of biology and evolutionary biologists together would further suggest that a unit can simultaneously be subjected to selection at various levels. A gene can be subjected to natural selection at the level of the physical environment, but also at the level of the genome, or the level of culture. The locus or level of selection was therefore broadened to include the internal, physical and cultural milieu of an organism. And a new question was introduced: where does selection occur?

As can be deduced from its name, the theoretical considerations on the units and levels of selection primarily focus on the units and levels of natural selection. The possibility that other evolutionary mechanisms, such as drift or symbiogenesis, might also identify units and levels of evolution was rarely examined. This primary focus on natural selection helped lay the foundation for universal Darwinism (Dawkins 1983; Dennett 1995) and universal selectionism (Cziko 1995). Huxley's idea that evolution was universal got reduced to the idea that natural selection is the *only* evolutionary theory available to evolutionary scholars, and that *only* natural selection can explain teleonomy or "purposeful design". Universal selectionists thereby set themselves off from the earlier discussed evolutionary epistemologists and evolutionary biologists who had come to investigate how also (developmental) systems-theory, neutral theory, processes of horizontal transmission and directed selection underlie cultural and biological evolution. Popular authors such as Richard Dawkins, Daniel Dennett and Gary Cziko declared that *all and only* selectionist accounts are valid because only they explain adaptations or apparent design. Proof for this claim:

> " [Natural selection] … is probably the only theory that can adequately account for the phenomena that we associate with life." (Dawkins, 1983, 15).

> "Only a theory with the logical shape of Darwin's could explain how designed things came to exist, because any other sort of explanation would be either a vicious circle or an infinite regress ... .' (Dennett, 1995, 70)

> "Let us recall that Dawkins' conclusion is based on the argument that the process of cumulative blind variation and selection is the only currently available scientific explanation that is in principle capable of explaining the emergence of the adapted complexity required for life" (Cziko, 2005, 303).

These three authors would further start a crusade against non-selectionist theories. Cziko (2005: 315) would go so far as to state that "punctuated equilibrium, direct mutation, exaptation, symbiosis and self-organization" are merely "would-be challengers to natural selection". Without providing proof, they belittled the possibility that other evolutionary theories might also be able to explain the how and why of evolution, and these theories became antithetical to the new canon.

In philosophy of biology, focus has therefore also been reduced to the study of adaptation (survival value) and fitness. Primary questions are what evolves, where does it evolve, and what does it evolve for?

> "One of Darwin's most fundamental contributions is showing us a new way to make sense of 'why' questions". (Dennett, 1995, 25)

The how and why of evolution is assumed to only be explicable by natural selection theory. It is here that the new evolutionary sciences got their confidence that the selectionist account is both necessary and sufficient to explain all of life and behavior.

4. Problems with universal selectionism in the old and new evolutionary sciences

Evolutionary psychology, linguistics, anthropology and archeology follow the philosophers and biologists who introduced the universal selectionist account. Different for the scholars engaged in Dual inheritance frameworks, the new evolutionary scientists (e.g. Cosmides & Tooby 1994; Pinker & Bloom 1990) argue that rather than co-evolve, both natural and sociocultural evolution are the outcome of evolution by means of natural selection. They further narrow down their research program to identifying which aspects of the sociocultural realm are adaptive rather than the result of by-products or random noise, and what these adaptive traits evolved for (their functions as well as selective pressures). As such, the researchers involved primarily use a theoretical, deductive approach. They assume that most behavior is adaptive and that natural selection will be sufficient to explain both the origin and evolution of these adaptations.

Establishing their own research program has disabled them to keep track of advances made in other research programs, including the ones they first consulted to establish and justify that program. This is especially the case with regard to the field of evolutionary biology, wherein the whole of the evolutionary process is no longer understood to be the sole result of natural selection.

Evolutionary biology has now demonstrated that adhering to an evolutionary account of all of nature in no way justifies the claim that only natural selection can provide adequate explanations for the full range of evolutionary phenomena under study. Natural selection is an important evolutionary mechanism, and it is able to explain adaptations, but biologists have come to the conclusion that evolution can also proceed by mechanisms such as drift (Kimura 1976), symbiogenesis (Margulis 1998), horizontal gene transfer (Zhaxybayeva & Doolittle 2011), hybridization (Arnold, 2006, 2008; Ryan 2006; Sapp 2009), niche construction (Lewontin 2000), self-organization (Kauffman, 1995) or epigenetic mechanisms that are studied by developmental systems theoreticians (Haig 2004; Oyama 1985; 2000; Pigliucci, 2009; Robert 2004; Waddington 1942). Causation can be attributed to every single one of these mechanisms.

Not all phenomena are adaptations. Traits can be exaptations (Gould & Vrba 1998), they can be neutral, or even maladaptive, and they still evolved. Natural selection is a good theory to explain adaptations, but it cannot account for the evolution of all traits. Natural selection theory can explain the ultimate causes of *adaptive* traits, but other evolutionary mechanisms can also explain both the proximate as well as ultimate causes of *adaptive as well as non-adaptive* traits. The claim that natural selection suffices to be explain both ultimate and proximate causes is unwarranted.

And even if selection occurs, it does not exclusively occur in the way in which Darwin predicted it to take place. Punctuated equilibria theory (Eldredge 1971; Eldredge & Gould 1972) has demonstrated that evolution does not always proceed gradually, rather long periods of stasis are often punctuated by periods of rapid evolutionary change. The Baldwin effect (Baldwin 1896) and advances made in the field of developmental biology and epigenetics or evo-devo, sometimes also called eco-evo-devo (Goodman & Coughlin 2000), have demonstrated how ontogeny and the environment can influence the future course of evolution.

Finally, the fact that evolution can occur by many different means, and the acceptance of the view that evolution acts upon many units, at many levels, necessitate the acceptance of nested hierarchy theory (Eldredge 1985; Vrba & Eldredge1984; Vrba & Gould 1986). An organism is understood to be heterogeneous. It is made up of different elements and systems that often evolve at different paces, according to different (sometimes contradicting) mechanisms, and at different or multiple levels simultaneously. Nonetheless, the organism as a whole also evolves as a unity. Nested hierarchy theories therefore need to be developed that explain how the various elements evolve and influence the evolution of higher and lower elements through processes of upward and downward causation.

There is no reason whatsoever for these new evolutionary sciences not to take into account the advances made in current evolutionary biology. In fact, adhering to the view that evolution is a universal phenomenon, and endorsing the naturalistic claim that the same mechanisms underlie both biological as well as cultural evolution, necessitates that we take on the study of how these new biological theories can also help explain cultural evolution.

Indeed, such enterprises have been made. The dispersal of certain language families, and the successive appearance of cultural artifacts have been proposed to portray a pattern of punctuated equilibria (Atkinson et al 2008; Eldredge & Tattersall 1982; d'Errico 2003; Pagel, 2009). And drift theory (Bentley, Hahn & Shennan, 2004; Bentley & O'Brien, 2011; Koerper & Stickel 1980), hybridization and symbiosis (Gontier 2007, Hird, 2008; Shijulal et al, 2010), horizontal cultural transmission (Borgerhoff Mulder, Mace & Jordan, 2011; Nunn & Towner, 2006; Knappett, 2009, 2011; Franz & Bunn, 2009), niche construction (Day, Laland & Odling-Smee 2003; Deacon 1997), and self-organization have been used to explain certain aspects of cultural evolution. And also complex adaptive system theory (Holland, 2006), although it mostly works from within adaptationist frameworks, are tackling problems of nested hierarchies, and how a variety of mechanisms are active at different levels of complex systems. These endeavors look promising. But we have to be honest and acknowledge that they remain a marginal activity, conducted by scholars who often do not form part of the newly emerging, selectionist-inspired, evolutionary sciences. Scholars that work from within non-selectionist and non-adaptationist evolutionary frameworks have also been known to either be perceived as "old school", or critics of the selectionist approach, or they have been criticized by the selectionist approach for not being adequate or even unscientific and not in line with the naturalistic approach set forth (e.g. Dennett 1995, Cziko, 2005).

Why do we meet such resistance? Why, in a time where biologists plead for an extended synthesis, do the new evolutionary sciences remain so exclusively focused on the selectionist approach?

Are we faced with an emerging "politics of science"? Perhaps. Money does seem to flow more towards selectionist studies. For a large part however, it is insufficient knowledge of the extended synthesis that disables its application. Keeping busy with establishing their own research field has made them lose sight of the advances made within biology. And even if scholars know of the new theories, it is not so much a critique as a mere observation that they often don't have a clue of the implications these new findings have on cultural evolution or how we can integrate these new findings when studying cultural evolution.

In sum, the newly evolving evolutionary sciences lack sufficient knowledge of the overall evolutionary process. They have insufficient knowledge of the various mechanisms by which evolution can proceed, and they don't know how to use the currently existing evolutionary theories to fully explain cultural evolution.

Moreover, sociocultural phenomena have proven to be very complex, for they range from the individual level all the way up to the societal, and they are induced as well as constrained by genetic, developmental, environmental and even physical factors. This often makes it difficult to simply identify the elements and levels of inquiry, let alone develop theories on their evolutionary origin. Indeed, how does one take on the study of the evolutionary origin of monetary systems, technologies, or parental investment strategies? Is there such a thing as the evolution of one monetary system, or do we need to investigate the emergence of different monetary systems independently from one another? Does such an account start at the cognitive level, where mathematical skills develop? Are the latter genetically or modularly determined, or the result of learning and conditioning? And given that learning and modules are both the outcome of selective processes, is the latter distinction valid? Do we need to take into account the rise of societies or language and altruism, to give a comprehensive account on the evolutionary origin of monetary systems? Where do we turn our research focus to?

At present, we have a hard time seeing the forest with the trees. These questions prove very difficult to answer. Arguing that these elements are adaptive and functional does not enable us to identify the various units and levels that lie at their formation. Identifying either of them as "replicators", "interactors" or "reproducers" (if we would in fact be able to do so), doesn't really advance our insight either. At best, these labels provide us with a description of the nature of these elements. But it is highly unlikely that, from this nature, we can deduce just how it was that they originate, combine and evolve through time.

We therefore have to conclude that currently, no universal evolutionary methodology or methodologies exist that allows us to build universal evolutionary theories that explain both biological as well as sociocultural evolution, and that, while doing so, take into account the full spectrum of evolutionary theories and sociocultural phenomena. What's worse, no clearly defined research programs delineate how we can overcome these obstacles, which makes one wonder whether it is even acknowledged to be a problem.

5. Including the how of it all: Applied evolutionary epistemology

Solely adhering to a selectionist account is, due to advances made in both biological as well as cultural evolution studies untenable, and the methodologies put forward to study sociocultural evolution so far have been proven to be either inapplicable or insufficient to explain the full range of evolutionary events. The result of all this is that, at present, we don't really know how to identify the various units, levels and mechanisms of biological and sociocultural evolution and how they together, explain evolution at all ranks of life.

This observation does not overrule the necessity of the naturalistic approach. The selectionist approach, that searches for the units and levels of selection, and the means by which natural selection operates, is not wrong. In fact, this approach is highly necessary. But taken on its own, it is insufficient to conduct what it sets out to do: namely to explain the evolution of the sociocultural realm as an outcome, continuation and expansion of biological evolution.

What we need to do to succeed in our task, is expand the existing research program. We need to identify the variety of elements and phenomena involved in sociocultural evolution; we need to examine both their proximate as well as ultimate causes; and for that we need to examine how a multitude of evolutionary mechanisms induce the sociocultural realm.

How can we proceed in doing just that?

In this part it will be proposed that the way in which evolutionary epistemologists and philosophers of biology have engaged in finding the units and levels of natural selection, and the conditions under which natural selection operates (the logical skeletons and heuristics), can set the example. We can universalize the evolutionary epistemological tenets and deduce from them a methodology that enables us to identify the units, levels and mechanisms that underlie all sorts of evolution. This methodology is called Applied Evolutionary Epistemology (AEE) to distinguish it from the classic field of evolutionary epistemology that solely focused on the evolution of knowledge and the theory of natural selection to explain the evolution of knowledge. Applied evolutionary epistemology or applied evolutionary methodology (epistemology is a word used to denote both knowledge as well as methodology) holds that a method of inquiry can be deduced from the evolutionary process itself. In other words, the way in which evolution proceeds, can function as the basis for theory formation about that phenomenon.

5.1 Premises of AEE

Applied Evolutionary Epistemology rests on 6 premises.

5.1.1 Universal evolution

AEE sides with Darwin who declared that evolution is a fact of nature. Following Huxley, it premises that evolution is universal: not only nature, but everything in the universe, is the outcome of evolution (not merely natural selection). And everything continues to evolve. It therefore agrees with Dobshansky (1973); that nothing makes sense except in light of evolution.

This also means that it undoes of the classic divides between the natural, life and sociocultural sciences, nature/culture, ontogeny/phylogeny, physical (external)/physiological (internal) environment, history/change/evolution, inorganic/ organic/superorganic. Everything evolves and evolution occurs everywhere.

The only alternative to something not having evolved is that is has been created. There is no natural proof of the latter, so AEE does not endorse this view.

5.1.2 Naturalism

AEE pars with evolutionary epistemologists and evolutionary biologists and endorses that all and only evolutionary accounts of phenomena are valid.

5.1.3 Positivism

AEE endorses that naturalistic accounts can be provided, and that they will lead to objective knowledge. It accepts that our human nature, our equipment, and politics of science might induce theory-biases and might constrain how much we can come to know. To find and overcome these biases, scholars need to turn to naturalistic approaches. Increased insight into human nature and the way in which other animals perceive nature, and how our human nature causes for politics of science, will enable us to better deal with them.

5.1.4 The basic mode of evolution

Evolution occurs when something (the unit) evolves somewhere (the level) somehow (according to a certain mechanism). In agreement with premise 1, AEE therefore suggests that as soon as either a unit, a level, or a mechanism can be identified, that unit or level or mechanism evolved.

This also enables one to define these elements by ostensively pointing out the presence of the other ones. X is a unit of evolution if we can identify a level where it evolves, and a mechanism according to which it evolves. X is a level of evolution if we can identify a unit that evolves at that level and a mechanism according to which that unit evolves at that level. X is a mechanism of evolution if we can identify a unit upon which it is active, and a level where it is active on that unit.

AEE therefore refrains from exclusively identifying units as “replicators”, levels as “the environment”, and mechanisms as “natural selection”. It is first and foremost a pragmatic approach that acknowledges our lack of knowledge of what exactly the various units, levels and mechanisms of sociocultural and biological evolution are, and seeks ways to discover all of them.

5.1.5 Plurality of units, levels, mechanisms and kinds of evolution

Evolution itself is a heterogeneous phenomenon. Life evolved, but so did the universe, or culture. On a theoretical level, we can therefore distinguish between different kinds of evolution (the evolution of the brain, or language, or technology). Advances made in evolutionary biology and evolutionary epistemology have made us come to realize that a multitude of units (genes, physiological systems, organisms, …) evolve at a multitude of different levels (the physical environment or cultural environment) according to a multitude of evolutionary mechanisms (drift, selection, symbiogenesis, trial and error learning, …), and that they often do so simultaneously. Multicellular organisms, for example, are true chimeras, where elements such as mitochondria, nucleic genes, hormonal systems, and behavioral traits evolve at various levels (such as the genome, the cell, the body, the brain, the sociocultural environment), by a multitude of mechanisms and at different paces.

5.1.6 Nested hierarchy

Given the plurality of units, levels and mechanisms of evolution, we need to conclude that there exist different layers of reality. And our theories too, therefore need to take into account how these different layers come about and interact through processes such as upward and downward causation.

5.2 The AEE methodology: 3 heuristics

At present, we only have partial knowledge of what the different units, levels and mechanisms are and how they together form the reality of evolution. In order to overcome this obstacle, 3 heuristics are introduced that allow one to *identify*, *examine* and *evaluate* the different units, levels and mechanisms of evolution. The methodology can be used within the various sciences, as a pragmatic means to identify the elements under study as units, levels or mechanisms. And it can be used on a meta-level, by philosophers of science, because the heuristics also deal with issues such as proof, validation and justification. As such it is a tool to investigate theory formation. For a more elaborate explanation of the heuristics, I refer the reader to Gontier, 2010a, and for some examples in regard to language evolution, see Gontier 2010b).

5.2.1 The unit heuristic

By endorsing a naturalistic framework, we assume that organisms, memory, language, kinship, society, etc. are the outcome of evolution: they must be units *in* evolution, and *of* certain kinds of evolution (the evolution of humans, of culture or society, hence the dots in the title of table 1).

How can we proof this claim to be true on a meta-level, and how does AEE allow scientists to examine these units and evaluate the results from such a study (table 1)?

Units are *identified* as such if we can point out the level where it evolves and the mechanism according to which it evolves. The epistemic questions that enable us to answer these questions are “what”, “where” and “how”. Asking about the function of these units (“what for”) might be relevant to identify them as units of natural selection, but this step is unnecessary for identifying them as units of evolution. It is likely that behavioral units evolve at many levels, according to many different mechanisms.

If we are able to point out the levels and mechanisms where behavioral and other traits evolve, we can *examine* the unit more closely. In order to gain more knowledge of the unit, we need to examine "when" the unit first evolved, and when it became a unit in a certain kind of evolution. The *FOXP2* gene for example might have first evolved in multicellular animals (as a unit), but only became a unit in language evolution when humans and perhaps other hominins evolved. If anything, evolution concerns the study of natural history. Answering the "since when" question, should therefore be of primary concern to any naturalist.

The unit is also more closely examined by investigating "how it interacts" with other units of evolution. It is highly likely that the units under study can themselves be subdivided into subunits and superunits. The evolution of language for example contains elements such as pointing, speech, cognition, Machiavellian intelligence and altruism. Emotions, facial expressions and co-verbal gesturing can be grouped together as "non-verbal behavior". These elements might have evolved independently, or they might have evolved as a whole, not all at once, but through processes such as co-evolution. These different units might also be units in other kinds of evolution, such as the evolution of intelligence or foraging behavior. If such sub- and superunits can be identified, we can theoretically study each and every single one of them as possible units of certain kinds of evolution. The quest for sub- and superunits also enables us to outline the nested hierarchy. Insight into the nested hierarchy in turn will enable us to more clearly demarcate the trait or behavior under study, and this delineation will provide us with insight into which fields need to be consulted to answer our quest.

Because units are not defined by their traits, but by the levels where they evolve and the mechanisms according to which they evolve, they might also be levels or mechanisms of evolution. Culture is the outcome of evolution, and as such it is a unit, but it can also serve as a level where elements such as art evolve.

Having thus examined the unit will allow us to better *evaluate* the relevance this unit has in evolution, and the weight scholars should give to the unit in their theories.

Note that the "what for" and "why" question are not raised at this point in analysis, there is no need for teleonomy. Yet, I'm sure you will agree with me, that if we could answer these questions, we would know a great deal more about the phenomena we study than we do now.

5.2.2 The level heuristic

How do we proof, identify, examine and evaluate elements of study such as culture or the environment as levels of evolution (table 2)?

Levels are *identified* as such if we can point out units that evolve at that level and mechanisms according to which those units evolve at those levels. Questions that need to be raised are “how many” levels are there, and “how” do they evolve.

After the identification of a certain x as a level of evolution, we can begin the *examination* of the level. Specific to the level heuristic is that we need to ask about the ontological status of the level. If we indicate that something as culture can serve as a level for something like cognition to evolve, then we need to ask ourselves how real culture is. Do we use it as a theoretical concept to facilitate theory formation, or is it real and does it form part of a nested hierarchy of reality?

Afterwards, we can, quite recursively, ask “when” the level evolved, and whether the level itself can be divided into different sub- and superlevels. The latter enables us to establish the nested hierarchy.

Only then, can we *evaluate* how relevant the level is in the kind of evolution we study, and the theory we develop to explain that kind of evolution.

5.2.3 The mechanism heuristic

How can we proof and examine that natural selection, drift, symbiogenesis, or any other evolutionary mechanism is involved in the kind of evolution we study (table 3)?

Mechanisms of evolution are *identified* by pointing out units upon which they act and levels where they are active upon those units.

Specific to the examination of evolutionary mechanisms is that we need to ask ourselves the question “How does the mechanism work?”. Which conditions need to be met in order for a certain mechanism to occur?

Answering this questions requires that we abstract the “logical skeletons” or “templates” of all known evolutionary mechanisms. Natural selection, for example, as Campbell (1997) asserted, occurs when blind variation is selectively retained. Punctuated equilibria occurs when long periods of stasis are intermitted by short periods of rapid change (Eldredge & Gould 1972). A variety of mechanisms can lead to stasis (such as stabilizing selection or drift), and numerous mechanisms can explain rapid change (such as symbiogenesis). Universal symbiogenesis occurs when independently evolved structures irreversibly merge, and lead to the emergence of new stable structures (Gontier 2007). Again, the “what for” question will do us no good when asking about “how” natural selection as a mechanism functions.

We can also ask when the mechanism originated in time (for it must itself be a unit of evolution) and when it became relevant for a certain kind of evolution. Finally, we can ask how the mechanism interacts with other mechanisms. Drift and natural selection for example, often alternate. And it can be defended that the Baldwin effect or ratchet effect are submechanisms of natural selection. This too will enable us to form the bigger, hierarchically-nested picture of evolution.

Afterwards, and only then, can we evaluate the *relevance* of, and the explanatory power that a certain mechanism has in evolution.

6. Conclusion

Turning naturalistic is the way to go. However, naturalizing the sociocultural sciences implies more than merely turning to natural selection theory and asking about the adaptive status of traits. It is simply wrong to assume that all and only selectionist accounts are valid.

Our top priority is to first get a grip on the phenomena we study when we study language, culture and cognition. Which elements are involved? Identifying these elements as units, levels and mechanisms, and placing them in the nested hierarchy they form, will help us a long way.

The methodology proposed here is of an inductive and pragmatic nature. It is inductive because it requests that one ostensively points out the what, where and how of evolution. It is pragmatic, because it first and foremost wants to clean house and give every aspect of cultural and biological evolution its proper place in both theory and reality. The focus lies not on contemplating the metaphysical nature of units, levels and mechanisms of evolution. AEE focuses on identifying the aspects under current study as either one of them. Emphasis therefore lies on the how and when of evolution, not on the what for.

The AEE heuristics will enable scholars working within the different sciences to unite and delineate a shared research program and theoretical framework.

Acknowledgements

This paper was written with the support of the European Marie Curie Actions (project number EU 332 EEUSUP).

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Tables

<table>
<tr><th colspan="4">Table 1. Is x a unit in/of ... evolution? (read from left to right and top-down)</th></tr>
<tr><td>?</td><td colspan="3">Try to prove that it is a unit of evolution (1 example suffices). Thus go to yes.</td></tr>
<tr><td rowspan="7">YES</td><td rowspan="2">Where?
At which level is x the subject of evolution.</td><td colspan="2">Not one level found? X is not a unit, go to no.</td></tr>
<tr><td>One/multiple level(s)? Identify them all. (Justifies that x is a unit.)</td><td>Via which evolutionary mechanism(s)? How? Identify them all.</td></tr>
<tr><td>Since when?</td><td colspan="2">When did x first originate in time and when did it become a unit of evolution?</td></tr>
<tr><td rowspan="2">How does this unit x interact with other units?</td><td colspan="2">Can this unit be divided into one or several subunits?
If so, are they also units in evolution?</td></tr>
<tr><td colspan="2">Can this unit be absorbed into one or several superunits? If so, are they also units in evolution?</td></tr>
<tr><td>Can this unit also be regarded as a level and/or mechanism of evolution?</td><td colspan="2">? & yes: try and treat the unit as a level and/or a mechanism, go to level and/or mechanism.</td></tr>
<tr><td>Relevance?</td><td colspan="2">Is the unit x sufficient and/or necessary for evolution?</td></tr>
<tr><td rowspan="2">NO</td><td rowspan="2">Level and/or mechanism?</td><td colspan="2">? or Yes: go to level and/or mechanism.</td></tr>
<tr><td colspan="2">No: treat x as irrelevant for evolution until proven otherwise.</td></tr>
</table>

Table 2. Is x a level in/of ... evolution? (read from left to right and top-down)

?	Try to prove that it is a level of evolution (1 example suffices). Thus go to **yes**.	
YES	How many/which **units** evolve at this level?	Not one unit, x is not a level of evolution, go to **no**.
		One/multiple unit(s)? Identify them all. (Justifies that x is a level.)
	How many **evolutionary mechanisms** are active at (not on) this level?	Equals the question: how many evolutionary mechanisms are active upon the units that evolve at this level. (testing device)
	What is the **ontological status** of the level?	The level is an **abstract notion** that facilitates theory formation/ an **existing entity**.
	Since **when**?	Locate the origin of x in time or when it becomes necessary to invoke x as an abstract notion in the theory of evolution
	How does this level x **interact** with other levels?	Can this level be divided into **sublevels**? If so, are they also levels in evolution?
		Can this level be absorbed into s**uperlevels**? If so, are they also levels in evolution?
	Can this level also be regarded as a **unit** and/or **mechanism** of evolution?	? & yes: try and treat the level as a unit and/or mechanism, go to **unit and/or mechanism**.
	Relevance?	Is the level x **sufficient** and/or **necessary** for evolution?
NO	**Unit** and/or **mechanism**?	? or Yes: go to **unit** and/or **mechanism**.
		No: treat x as irrelevant for evolution until proven otherwise.

<table>
<tr><th colspan="3">Table 3. Is x an evolutionary mechanism involved in/on ... evolution?
(read from left to right and top-down)</th></tr>
<tr><td>?</td><td colspan="2">Try to prove that x is an evolutionary mechanism involved in evolution. Thus go to yes.</td></tr>
<tr><td rowspan="11">Y
E
S</td><td rowspan="2">On how many units is this evolutionary mechanism working?</td><td>Not one unit: x is not an evolutionary mechanism involved in evolution.</td></tr>
<tr><td>One/multiple unit(s). Identify them all.
(Justifies that x is an evolutionary mechanism involved in evolution.)</td></tr>
<tr><td>At (not on) how many levels of evolution is this evolutionary mechanism active?</td><td>Equals the question: the units that are subjected to this evolutionary mechanism, at how many levels are they subjected to it?</td></tr>
<tr><td colspan="2">How does the mechanism work? Which conditions need to be met in order for the evolutionary mechanism to occur? Answer requires (universal) EE formulas of the workings of the mechanism.</td></tr>
<tr><td>Since when?</td><td>Locate in time when these conditions are met regarding each unit and each level = when the evolutionary mechanism became a mechanism involved in evolution at that unit and/or level.</td></tr>
<tr><td rowspan="2">How does this mechanism x interact with other mechanisms?</td><td>Can this mechanism be divided into sub-mechanism(s)? (Depends on the presence of sub conditions.) If so, are they also mechanisms of evolution?</td></tr>
<tr><td>Can this mechanism be absorbed into a super-mechanism(s)? (Depends on the existence of a mechanism that allows to combine different mechanisms into one single mechanism.) If so, are they also mechanisms of evolution?</td></tr>
<tr><td>Can this mechanism also be regarded as a unit and/or level of evolution?</td><td>? & yes: try and treat the mechanism as a unit and/or level, go to unit and/or level.</td></tr>
<tr><td>Relevance?</td><td>Is the mechanism x sufficient and/or necessary for evolution?</td></tr>
<tr><td rowspan="2">N
O</td><td rowspan="2">Unit and/or level?</td><td>? or Yes: go to unit and/or level.</td></tr>
<tr><td>No: treat x as irrelevant for evolution until proven otherwise.</td></tr>
</table>