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Towards an integration of evolutionary psychology and developmental science : new insights from evolutionary developmental biology

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GENERAL INTRODUCTION

It was in 1996 during my stay at the Florida Atlantic University (FAU) in the USA, that I first learnt about evolutionary psychology. As a student of developmental psychology, I started working on my Master's thesis in the lab of Howard Hock, who is a renowned professor in the field of visual perception. I arrived at FAU to investigate experimentally dynamic aspects of vision, as I was interested in a dynamic systems approach to development. Dynamic systems theory is a mathematical theory that describes the behavior of complex dynamical systems, such as the behavior of human beings. Within this theory, developmental outcomes are explained as the spontaneous emergence of coherent, higher-order forms through recursive interactions among lower-level components (Lewis, 2000). The emergence of higher-order forms occurs by phase transitions, and visual perception was an excellent subject to study such phase transitions.

In Florida, I hoped to meet people with whom I could discuss the dynamics of development, and to develop a new research program on how to study the dynamical aspects of the human mind. With the presence of the Center of Complex Systems at FAU, at the time directed by Scott Kelso, I certainly met those people, and I had a very inspirational time. Rather coincidentally, I took a course on evolutionary psychology, taught by the professors David Bjorklund and Robin Vallacher, and this course influenced my scientific thinking more than any other course I had taken in Florida or at home in Amsterdam. This was quite surprising, because at high school I was a *gymnasium-alpha* student, without biology in my curriculum, and my knowledge of evolutionary theory was vague at best, as was my understanding of the relevance of evolution for psychology. The book we read for the course was *The Adapted Mind: Evolutionary Psychology and the Generation of Culture*, edited by Barkow, Cosmides, and Tooby (1992). From the very first sentence I read in the book, to the very last, I was overwhelmed by all the new theories and new experiments, all following from evolutionary thinking. As many students in psychology, I had always been displeased by the fragmentation of the research in the field: many interesting experiments and findings, but all quite isolated and lacking a unifying view on how the mind works. Dynamic systems theory was one way to

integrate different areas in psychology, and evolutionary psychology appeared to be another way to integrate the diverse array of facts and findings in psychology and other social sciences.

Evolutionary psychology

In *The Adapted Mind*, evolutionary psychology is defined as ‘simply psychology that is informed by the additional knowledge that evolutionary biology has to offer, in the expectation that understanding the process that designed the human mind will advance the discovery of its architecture’ (Cosmides, Tooby, & Barkow, 1992, p. 3). It continued with: ‘It unites modern evolutionary biology with the cognitive revolution in a way that has the potential to draw together all of the disparate branches of psychology into a single organized system of knowledge’ (p. 3). During the aforementioned course, we also read an article by Buss (1995), who stated that ‘although psychologists assume that the human mind is a whole and integrated unity, no metatheory subsumes, integrates, unites, or connects the disparate pieces that psychologists gauge with their differing calipers. An important new theoretical paradigm called *evolutionary psychology* is emerging that offers to provide this metatheory’ (p. 1). I was thrilled by the possibility of evolutionary psychology as a metatheory for psychology. Actually, it was not the first time that I was thrilled by a theory. From the very first start of my study in psychology, I liked the developmental theory of Jean Piaget.

Jean Piaget

Piaget, the father of developmental psychology, proclaimed that children’s development proceeds in stages, each stage characterized by qualitatively different kinds of behavior and cognition. The differences in behavior and cognition arise because underlying each stage is a domain-general structure that constrains the way the child thinks and explores its environment at a certain age. Interestingly, Piaget used to be a biologist. Only after finishing his dissertation on mollusks, did he embark on his studies in psychology. However, his interest in biology remained, leading him to write books, among many others on child development, entitled *Biology and Knowledge* (1971), *Behavior and Evolution* (1978), and *Adaptation and Intelligence* (1980a). In 1983 Piaget wrote that his theory of development ‘is impossible to understand if one does not begin with analyzing in detail the biological presuppositions from which it stems and the epistemological consequences in which it ends’ (p. 103). Thus, Piaget can be viewed as an evolutionary psychologist *avant la lettre*.

But do Piaget and the well-known evolutionary psychologists such as Cosmides, Tooby, and Buss, agree with each other on the implications of evolutionary theory for psychology? To answer this question, we first need to acknowledge that Piaget does not play a role in the work of the main evolutionary psychologists. In *The Adapted Mind*, a book of 666 pages, Piaget is only mentioned twice, and in the other works of the main evolutionary psychologists, he is not mentioned at all. So in some way, Piaget has not inspired the main evolutionary psychologists with his writings on evolution. Why not?

Integrated Causal Model

To understand this, we first need to know a bit more about the principles of evolutionary psychology. As our starting point, we take the *Integrated Causal Model* as proposed by evolutionary psychologists Tooby and Cosmides (1992). The tenets of this model are:

1. 'the human mind consists of a set of evolved information-processing mechanisms instantiated in the human nervous system;
2. these mechanisms, and the developmental programs that produce them, are adaptations, produced by natural selection over evolutionary time in ancestral environments;
3. many of these mechanisms are functionally specialized to produce behavior that solves particular adaptive problems, such as mate selection, language acquisition, family relations, and cooperation;
4. to be functionally specialized, many of these mechanisms must be richly structured in a content-specific way' (Cosmides & Tooby, 1992, p. 24).

In a later paper, Cosmides and Tooby (1994) gave some additional reasons why functionally specialized mechanisms are more likely to evolve than a single domain-general mechanism. First, what counts as the best solution differs from domain to domain. There is no domain-general criterion for what is right or wrong. For example, someone with a domain-general learning mechanism succeeds to find out that intercourse is necessary for reproduction. He has sex with everybody he meets. This strategy will not be optimal, because, for instance, having sex with one's relatives is counterproductive. Suppose the person finds out with his domain-general learning mechanism that having sex with relatives is not a good strategy. He now may conclude that all interaction

with relatives is wrong. This behavior would also be selected out, because helping relatives favors the survival of one's own genes. What counts as a success and failure in relation to fitness, depends on the specific domain.

Second, someone with a single domain-general learning mechanism has, initially, to treat all perceptual information equally, as he has no specific knowledge about the information. It is impossible for an individual to learn all specific knowledge in one life-time. For example, it is impossible for a child to acquire a complex skill such as language so quickly only by trial and error. The child must possess some functionally specialized mechanism(s) that facilitates language acquisition.

Third, as organisms with a single domain-general learning mechanism have no specific knowledge, they have to evaluate all possible alternatives in every situation, which leads to a combinatorial explosion of possibilities. Having to think that long before one can act, is unlikely to be very adaptive.

In short, Cosmides and Tooby (1994) proclaim that in the course of evolution, human beings have encountered a diverse set of specific psychological problems, and it is likely that specific psychological mechanisms to solve these problems emerged through natural selection. Therefore, it is likely that our mind is composed of a multitude of specialized psychological mechanisms, like our body has different organs that are functionally specialized. There is no such thing as a general solution, because there is no such thing as a general problem (Symons, 1992; Buss, 1995).

Structuralism

It is interesting to note the difference between the Integrated Causal Model and Piaget's theory on child development. Piaget's theory has been called structuralism, because he believes that there are *domain-general* homogeneous structures which are characterized by laws that pertain to all cognitive, social and moral aspects during a given developmental epoch (Piaget, 1970). This theory appears to contradict the Integrated Causal Model, which claims that the human mind consists of evolved *domain-specific* mechanisms to solve recurrent problems encountered in the evolutionary past. According to Piaget, the only innate abilities are reflexes (Piaget & Inhelder, 1969). For example, sucking is behavior that the infant shows spontaneously, which does not have to be learned. Piaget states that abilities that require experience are not innate; the child learns these by an active exploration of the environment. By

exploring the environment the child constructs schemata, i.e., mental representations of external events. By encountering a new event, the child will first try to assimilate the environmental information in existing schemata. If the information does not fit into a present schema, the child has to accommodate to the environment by constructing a new schema. Piaget called the process of assimilation and accommodation *adaptation*. The purpose of adaptation is to reach a balance of assimilation and accommodation, which is called *equilibrium*.

Piaget and evolutionary psychologists agree that the child is not born as a blank slate, but this is where the agreement ends. According to Tooby and Cosmides (1992), cognitive psychologists replaced the blank slate metaphor with 'blank cognitive procedures' (p. 29). Piaget claimed that the infant's ability to assimilate and accommodate is innate, but he also proclaimed that these abilities are content-free and general-purpose. As Piaget (1980b) stated: 'Fifty years of experience have taught us that knowledge does not result from a mere recording of observations without a structuring activity on the part of the subject. Nor do any a priori or innate cognitive structures exist in man; the functioning of intelligence alone is hereditary and creates structures only through an organization of successive actions performed on objects' (p. 23).

Annette Karmiloff-Smith

Piaget died in 1980, so unfortunately we shall never witness a debate between him and evolutionary psychologists. However, it is clear that they would have had much to disagree about. Fortunately, Piaget had many followers, and many of them are active researchers at the moment. One of them, Annette Karmiloff-Smith, trained as a developmental psychologist in Piaget's lab in Geneva, recognized that Piaget put too little emphasis on innate abilities: 'Why would Nature have endowed every species except the human with some domain-specific predispositions?' (Karmiloff-Smith, 1992, p. 1), but she also contended that evolutionary psychologists put too much emphasis on domain-specific innate abilities. The position of evolutionary psychologists on evolved domain-specific psychological mechanisms, in the literature often referred to as *modules*, has been called the *massive modularity thesis* (Sperber, 1994), because evolutionary psychologists believe that the mind consists of many different evolved domain-specific psychological mechanisms, or modules. Karmiloff-Smith (1992) believes that the adult mind consists of many modules, a belief based on brain studies that show modularity of different brain regions.

But she does not believe that infants are born with a modularized brain. She proclaims that children develop by *gradual modularization*, i.e., by actively exploring the environment children gradually develop neural circuits that are modular in nature. For example, it is possible to develop a ‘piano play module’, a neural circuit that specializes as the result of intensive piano playing. It is self-evident that this is not an evolved module, but a module developed by experience. With her theory, Karmiloff-Smith reconciles Piaget’s idea that development requires an active exploration by the child with the idea of modularity of the adult brain, but she does not believe that infants are born with a modular mind. She recognizes the role of some domain-relevant biases, but considers the massive modularity position of evolutionary psychology as too strong (Karmiloff-Smith, 1998). This is just one example in the literature that shows that there is quite a big gap between evolutionary and developmental psychology.

David Bjorklund

There have appeared two ways to deal with this gap. The first approach, as advocated by David Bjorklund, was to adopt the framework as defined by evolutionary psychologists, and to propose new hypotheses related to developmental psychology derived from this framework (Bjorklund & Pellegrini, 2000). Central in this approach, named evolutionary developmental psychology, is the idea that there were different adaptive pressures at different times during individual development. The fruitfulness of this approach was shown in a special issue of the *Journal of Experimental Child Psychology* in 2003, which covered tests of evolutionary hypotheses over the whole lifespan, with topics such as infants’ ability to detect and act upon the direction of eye gaze of another human face (Farroni, Mansfield, Lai, & Johnson, 2003), strategies of control, aggression, and morality in preschoolers (Hawley, 2003), children’s impaired performance on false-belief tasks with a predator-avoidance content (Keenan & Ellis, 2003), sexual segregation and integration in early adolescence (Pellegrini & Long, 2003), and mechanisms of inbreeding avoidance (Weisfeld, Czilli, Phillips, Gall, & Lichtman, 2003).

Lickliter and Honeycutt

The second approach, as advocated by Lickliter and Honeycutt (2003a), took the opposite direction. They denied that evolutionary psychology, as proposed by Cosmides, Tooby and Buss, has any value, because it is an approach that ignores development. They proposed an alternative, the developmental

systems approach: 'Development is not the result of the interaction of genetic and environmental factors, as neither operate as independent causes; rather, development results from the bidirectional and dynamic transaction of genes, cells, tissues, organs, and organisms during the course of individual ontogeny' (Lickliter & Honeycutt, 2003b, p. 869). Lickliter and Honeycutt argued that evolutionary psychology is too much a gene-centered, predeterminedistic approach to the study of the human mind. The gene-centered approach should be replaced by the probabilistic epigenesis approach, i.e., the idea that each level of an organism (e.g., genetic, neural, behavioral, social) is influenced by, and interacts with each adjacent level (see also Gottlieb, 2000).

As expected, evolutionary psychologists were not very pleased with this criticism. Buss and Reeve (2003) demonstrated the ongoing success of evolutionary psychology by providing a long list of new empirical discoveries made by evolutionary psychologists. In addition, they argued that the developmental systems approach is rather vague and obscure, and does not give rise to testable predictions. Cosmides, Tooby and Barrett (2003) countered Lickliter and Honeycutt (2003a) by arguing that evolutionary psychology does acknowledge the important role of development in phenotypic outcomes.

Evolved probabilistic cognitive mechanisms

The only researcher among the commentators who tried to reconcile the two approaches was Bjorklund (2003). He argued that developmental systems theorists perceive an incompatibility of evolved psychological mechanisms, as proposed by evolutionary psychologists, and probabilistic epigenesis, as proposed by developmental systems theorists. In the view of developmental systems theorists, the idea that the human mind consists of many evolved psychological mechanisms leaves too little room for environmental and developmental influences, whereas evolutionary psychologists argue that developmental systems theory cannot predict species-typical behavior and cognition. Bjorklund, Ellis, and Rosenberg (2007) tried to reconcile these opposite views by proposing the concept of evolved probabilistic cognitive mechanisms, defined as 'cognitive mechanisms that are functionally organized to solve recurrent problems faced by ancestral populations, are highly probable when species-typical environments are encountered (i.e., when developmentally relevant features of the environment are in the range typically encountered during a species' evolution), and are products of emerging developmental systems that have evolved over the course of the ontogenies of

our ancestors'(p. 22). This definition acknowledges that natural selection played a role in the evolution of species-typical traits, but it also acknowledges that development is always an interaction among different levels of organisms. Evolved probabilistic cognitive mechanisms *prepare* an organism for life in a species-typical environment, but they are not *performed* (Bjorklund et al.).

Evolutionary developmental biology

Despite the attempts of Bjorklund and colleagues to bridge the gap between evolutionary psychology and developmental systems theory, there is still a long way to go to reconcile these positions. Interestingly, one approach in evolutionary biology, the evolutionary developmental (commonly abbreviated as evo-devo) approach, has, so far, been ignored in the debate about evolutionary psychology. Evo-devo biology 'forges a synthesis of those processes operating during ontogeny with those operating between generations (during phylogeny)' (Hall & Olson, 2003, p. xiii). It includes topics such as the processes leading to the rise and evolution of embryonic development, the role of embryonic development in evolutionary modification and evolutionary novelties, the origin of life history stages, the interaction of genotypes and phenotypes, and the co-evolution of development and ecology. To appreciate the contribution of evo-devo biology, I first outline some history of evolutionary biology.

With the publication of his book *The Origin of Species* in 1859, Charles Darwin was among the first to recognize the importance of natural selection in evolution: the forms of organisms that are best adapted to the environment increase in frequency relative to less well adapted forms over a number of generations (definition by Ridley, 2004). However, he did not know the mechanism of inheritance, as was later revealed in the work of Gregor Mendel. Mendel's discovery of the laws of inheritance gave rise to the field of genetics. In 1942, Julian Huxley published a book called *Evolution: The Modern Synthesis*, which integrated the fields of evolutionary biology and genetics, by recognizing that evolution can be explained by small genetic changes that result in variable forms that are acted upon by natural selection. The Modern Synthesis has also been called the neo-Darwinian evolutionary theory.

With the Modern Synthesis, we know that forms do change, and that natural selection is a force, but we do not know *how* forms change (S.B. Carroll, 2005). In order to understand this, we have to know how forms develop. This was

studied by embryologists, but researchers in the fields of evolutionary biology and embryology did not join forces until the 1970s. Stephen Jay Gould's book *Ontogeny and Phylogeny*, published in 1977, was the first step towards an integration of the fields. In the 1980s, the two fields became inseparable in the light of the discovery of genes that controlled development. These genes appeared to be similar across a wide range of species (McGinnis, Garber, Wirz, Kuroiwa, & Gehring, 1984; McGinnis, Levine, Hafen, Kuroiwa, & Gehring, 1984). This research was the start of the field of evo-devo biology (S.B. Carroll, 2005).

Thus, evo-devo biologists take the neo-Darwinian evolutionary theory as a starting point, but they argue that it is not a complete theory of evolution (S.B. Carroll, 2005; Müller & Wagner, 1991, 2003). Evo-devo biologists want to understand both which variants were better adapted to local circumstances than others, and how variants arose in the first place. Neo-Darwinian theory does not provide an explanation for the latter, i.e., the origin of evolutionary novelty.

Wagner (2000) argued that the neo-Darwinian theory of evolution and evo-devo biology have different explanatory power, and showed this with two examples. The first example concerns the stable sex ratio; in almost every species, there are as many females as males (Bell, 1982). How can we explain this stable sex ratio? Wagner argues that the 1:1 sex ratio can best be explained by using the neo-Darwinian approach. Suppose that there are fewer females than males in a given population. Because the females are the rare sex, the average female will have more offspring than the average male. Any genetic variant that increases the offspring sex ratio in favor of the female sex, will be selected, leading to more females. This process is stable when there are as many females as males (Fisher, 1930). In this example, the occurrence of natural selection explains why there is a 1:1 sex ratio. Knowledge about developmental mechanisms determining the sex of organisms does not add much to the explanation of the stable sex ratio. Developmental mechanisms causing the sex of an organism (Bell, 1982) can be very different among species (e.g., dependent on environmental temperature). However, because the sex ratio is stable among many different species, none of these mechanisms causes a change in sex ratio. Thus, according to Wagner, in this example, the neo-Darwinian approach has more explanatory power than the developmental approach.

The second example concerns the origin of eyespots on butterfly wings. The eyespots are a relatively recent evolutionary novelty, which serves to deter predators. Evolutionary developmental biologists (Keys et al., 1999) found two developmental events that are necessary for the development of eyespots on the wings¹. The neo-Darwinian explanation for the emergence of the eyespots would be that butterflies with eyespots had a greater chance to survive, and hence eyespots were selected. However, we do not learn from this account how the eyespots arose in the first place. The evo-devo study of Keys et al. offers new insight in the developmental mechanisms that cause the emergence of eyespots. Thus, in this example, the developmental approach has more explanatory power, because it tells us something about the mechanisms that contributed to the origin of the novelty.

What is the crucial difference between the two examples? Wagner (2000) explained that sex ratio is a simple quantitative variable; in the evolution of sex ratio, there were no qualitative changes in genetic properties. In contrast, the origin of eyespots is a qualitative innovation, which goes together with a radical change in the genetic properties. An explanation in terms of population or quantitative genetics (i.e., the neo-Darwinian approach) is not informative. Evo-devo research is necessary to know how forms evolved.

Back to the metatheory

I started this introduction with a description of evolutionary psychology as a metatheory. What followed suggested that not all psychologists welcomed the ideas of evolutionary psychology with open arms. Especially developmental psychologists were critical, because evolutionary psychologists seem to discard the role of development in the unfolding of psychological mechanisms. If evolutionary psychology does not pay enough attention to development, what is left of the claim of evolutionary psychology as a metatheory?

As mentioned above, evolutionary developmental biology takes the neo-Darwinian evolutionary theory as its starting point. The neo-Darwinian theory is also the starting point for evolutionary psychologists, but for them it is also

¹ These developmental events are '1) a modulation of hh expression along the proximal-distal axis of the wing disc, and 2) a relaxation of ci repression by en' (Wagner, 2000, p. 96-97).

the endpoint. Their main research method is reverse engineering, which means providing an account of: (1) what counts as a biologically successful outcome in a given situation, (2) the recurrent structure of the ancestral world that is relevant to the behavior to be explained, (3) of the organization of recurrent features that comprise the suspected adaptation, (4) what happens when the suspected adaptation interacts with the world, and (5) how well the design in ancestral conditions resulted in a successful outcome (Tooby & Cosmides, 1992). As proclaimed by Buss and Reeve (2003), this approach has been quite successful in discovering mechanisms that had eluded other psychologists. However, the method of reverse engineering is not conducive to explanations of the development of a mechanism. One may contend that evolutionary psychology is a young field, and has yet to address development. However, given the metatheoretic ambition of evolutionary psychology, the present lack of a developmental perspective is undesirable. Although Piaget's theory did not turn out to be true on every count (Feldman, 2004), his theory was a true metatheory; it predicted behavior and cognition for different ages groups and different domains, and it predicted the developmental pathway of the behavior and cognition. The promise of evolutionary psychology as a metatheory has yet to be realized with respect to the explanation of psychological development.

With this statement, need we relinquish evolutionary psychology as a metatheory? In chapter 2 of this dissertation I will address to this question. In short, the answer to this question is 'no', but evolutionary psychology has to broaden its scope in order to become a fruitful metatheory for psychology. It has to include theories and facts delivered by evolutionary developmental biology and dynamical systems theory to be able to contribute to the main issues in psychology. Evolutionary developmental biology provides a rich array of theories and facts on modularity (Kreimer, Borenstein, Gophna, & Ruppin, 2008; Callebaut & Rasskin-Gutman, 2005; Schlosser & Wagner, 2004), phase transitions (Coveney & Fowler, 2005; Camazine et al., 2001; Stadler, Stadler, Wagner, & Fontana, 2001), novelties (Moczek, 2008; Osorio & Retaux, 2008; Müller & Wagner, 2003), individual differences (Allen, Beldade, Zwaan, & Brakefield, 2008; Hallgrímsson, 2003; Stern, 2000), and plasticity (Badyaev, 2007; Wagner, 2005), all subjects of major interest for evolutionary psychology and psychology in general. Without incorporation of these facts and theories within the metatheory of evolutionary psychology, it will remain wanting as a metatheory.

Testable predictions

Buss and Reeve (2003) have complained that developmental systems theory does not generate testable predictions. To show that this is not true for the application of evo-devo biology to psychology, we (Frietson Galis, Han van der Maas, Maartje Raijmakers, and myself) have tested three hypotheses derived from evo-devo thinking. In chapter 3, we provide evidence for the hypothesis that the savant syndrome, despite its positive aspects, did not spread in the population because of a developmental constraint. The savant syndrome is a condition in which individuals have one or more areas of expertise, ability or brilliance that is in contrast with the individual's general capacities (Treffert, 2000). A developmental constraint is a mechanism that limits the possibility of a phenotype to evolve (Maynard-Smith et al., 1985). The developmental constraint is the result of high interactivity among body parts during a particular stage of embryological development, called *early organogenesis*. During this stage, a mutation or an environmental disturbance does not only affect a single phenotypic trait, but several traits (Sander, 1983). A potential positive mutation, such as a mutation that causes the positive aspects of savant syndrome, is not naturally selected because of the negative side-effects (e.g., the development of mental retardation or autism). The finding that individuals with savant syndrome often have autism, mental retardation and several physical anomalies supports our hypothesis.

In chapter 4 we argue that schizophrenia is the result of disturbances during early organogenesis. Due to the high interactivity of body parts during this stage, we expect that individuals with disorders that originate from disturbances during this stage, have several physical and mental anomalies. During early organogenesis, all organs start to develop, including the brain, as well as the limbs and the vertebrae. We show that schizophrenia is not only a disorder of the brain, but a disorder that includes multiple anomalies, of body parts that become established during early organogenesis. In chapter 5 we show that the same results are found in individuals with autism. We show that concrete hypotheses can be derived from evo-devo thinking that are relevant to psychology. We conclude this thesis with a discussion of the value of the evo-devo approach for psychology.