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Evo-devo and Cognitive Science

Annemie Ploeger and Frietson Galis

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Abstract

Evo-devo is an approach that integrates knowledge on evolution and development. Cognitive science is a research field that tries to unravel the functioning of the mind and the underlying processes. In this chapter, the main subfields within cognitive science that have contributed to a better understanding of the evolution and development of the mind are discussed. Highlighted are the subfields of evolutionary cognitive science, developmental systems theory, genes × environment interaction research, epigenetics, comparative cognitive science, and

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cognitive neuroscience. Finally, the question what cognitive scientist can learn from research in evolutionary developmental biology is addressed. Many evo-devo biologists study morphogenesis, which is relevant for cognitive development, but it is not always straightforward how to apply their knowledge to cognitive science research. Interdisciplinary research is strongly recommended, so scholars from different fields such as morphology, genetics, neuroscience, primatology, and psychology can learn from each other and contribute to the unraveling of the working of the mind.

Keywords

Evo-devo • Cognitive science • $G \times E$ interactions • Epigenetics • Developmental systems

Introduction

Cognitive science is a broad, interdisciplinary research field that tries to unravel the functioning of the mind and the underlying processes. It includes the study of perception, motor control, attention, consciousness, learning, memory, representation of knowledge, language, problem-solving, creativity, decision-making, reasoning, and intelligence (e.g., Newell 1990). The emergence of cognitive science has been called the cognitive revolution, which started in 1959. Linguist Noam Chomsky argued that language acquisition cannot be explained by simple stimulus–response associations proposed by behaviorism, which was the dominant paradigm in psychology at that time. Behaviorists, amongst others their famous proponents Ivan Pavlov, Edward Thorndike, John B. Watson, and B. F. Skinner, argued that mental processes cannot be scientifically studied and that psychologists should restrict their research to observable behavior. Chomsky's discussion preluded the rise of cognitive science.

Cognitive science has become a successful field, partly because of the development of new research tools, such as brain imaging techniques and computer simulations. Cognitive neuroscience is a rapidly growing subfield in which concepts such as attention and memory are linked to specific brain areas and neural activity. Artificial intelligence is another subfield that uses insights from cognitive research to create computer models of the mind. In huge programs such as the *Human Brain Project*, headed by physiologist Henry Markram (see Markram et al. 2011), knowledge on cognitive architectures, brain simulations, high-performance computing, neuroinformatics, neurorobotics, and other disciplines is combined with the aim to simulate the whole human brain. Results from this kind of projects show the fruitfulness of cognitive science and also how important technological progress has been.

The first aim of this chapter is to provide an introduction of the history of the attempts of cognitive scientists to integrate their work with developmental and evolutionary approaches. After the cognitive revolution, the study of cognitive

development started to grow. Jean Piaget, with his stage theory of cognitive development, became the major proponent of this field. Later, in the 1990s, the study of the evolution of cognition arose under the flag of evolutionary psychology. Major proponents of this field in the 1990s were cognitive psychologist Leda Cosmides, anthropologist John Tooby, linguist Steven Pinker, and social psychologist David Buss. In the first years of the new millennium, the first attempts were made to integrate developmental and evolutionary approaches to cognitive science by developmental psychologists David Bjorklund and David Geary, among others. Only lately, attempts have been made to integrate evo-devo biology and cognitive science.

The second aim is to show the importance of evo-devo research for cognitive science. Evo-devo is an approach that integrates knowledge on evolution and development (see chapter on the "▶ History of Evo-devo"). Evolutionary biologists study evolutionary change of organisms over generations; developmental biologists study the development of organisms within a single lifetime. Evo-devo researchers try to unravel the interaction between these two processes – evolution and development, to obtain a fuller understanding of each of these processes.

Before the contribution of evo-devo research to cognitive science is described, first the contributions of developmental cognitive science and evolutionary cognitive science are explained separately.

Developmental Cognitive Science

Developmental cognitive science is the study of cognitive development, from prenatal development to cognitive aging. The study of prenatal cognitive development is limited, because it is hard to study the cognition of fetuses in the womb. Most of this research is focused on the senses, especially the visual and auditory system. Vision research with premature infants revealed that they can distinguish between light and dark at 28 weeks after conception, and that they can distinguish different patterns at 30 weeks. Considering the auditory system, fetuses start to react with movement to acoustic stimulation between 23 and 25 weeks. It is also well known that newborns remember sounds they heard during their last month in the womb. In addition, newborns show a preference for their mother's voice compared to a stranger, and they can discriminate between their mother's and a foreign language.

In general, developmental cognitive scientists study the same topics as cognitive scientists, but they emphasize differences between children and adults by conducting longitudinal or cross-sectional studies. An example of a topic that recently has attracted a lot of attention is the development of executive functions. This is an umbrella term for all processes necessary for cognitive control, such as inhibition, task flexibility, planning, and working memory. Researchers generally agree that normal or good development of executive functions is required to be able to deal with daily-life problems in our complex society. Many common psychiatric disorders, such as ADHD, autism, and anxiety, are associated with atypical development of executive functions.

As was mentioned in the introduction, the theory on cognitive development developed by Jean Piaget has been most influential. He argued that cognitive development proceeds stagewise, with children acquiring knowledge by changing their cognitive structures by the processes of assimilation and accommodation. When children encounter new situations, they try to assimilate their experiences into their existing cognitive structures. Only when they find out that the existing structures fail to explain the new situation, they will build new cognitive structures (a process called accommodation). New approaches that arose out of Piaget's theory are neuroconstructivism (e.g., Karmiloff-Smith 2006), which combines Piaget's theory with recent neuroscientific findings and dynamic systems theory (e.g., Thelen and Smith 1994). Adherents of the latter approach argue that development can be best described by differential equations, where development is modeled as a trajectory through state space. Following this approach, children learn by discovering that available patterns of knowledge are incomplete, leaving them in a state of disequilibrium, after which a new equilibrium can be reached, when new patterns of knowledge are formed. The process of breaking down old patterns and establishing new ones occurs by means of phase transitions. This process is considered to be selforganized, because there are no control parameters that govern it. This approach has been specifically successful in explaining motor development, but also other areas of cognitive development.

Evolutionary Cognitive Science

Evolutionary cognitive science is the study of the evolution of cognition, with the expectation that knowledge about the evolution of cognition improves our understanding of the working of the human mind (Barkow et al. 1992). Evolutionary cognitive scientists try to discover cognitive adaptations that have been under natural selection or cognitive fitness indicators that were sexually selected. Well-studied examples of cognitive adaptations are language, face recognition, color perception, cheater detection, and spatial abilities that are related to hunter-gatherer skills (see the chapter on "▶ Evo-devo of Language and Cognition"). Geoffrey Miller (2000) has argued that many aspects of human cognition are sexually selected, such as art, music, humor, and science. Empirical support for this hypothesis is provided by studies that showed an association between these phenomena and measures of fitness, e.g., health and symmetry, and levels of estradiol (in females) and semen quality (in males). Other evolutionary cognitive scientists have used a comparative approach. For example, psychologist and primatologist Michael Tomasello (2014) has compared the cognition of human children and chimpanzees and concluded that their physical cognition (e.g., knowledge about quantities) is similar, but that 2-yearold humans already have a better developed social cognition (e.g., empathy) than adult chimpanzees.

Evo-devo and Cognitive Science

Evo-devo research in cognitive science can be carried out in many different ways. Several subfields that combine an evolutionary and a developmental approach in the study of cognition are outlined. First, the work of evolutionary developmental cognitive scientists is discussed. Second, the work of developmental systems theorists is discussed. Third, studies on the interaction between genes and environment by cognitive scientists are discussed. Fourth, research on epigenetics in cognitive science are discussed. Fifth, comparative evo-devo studies by cognitive scientists are discussed. Sixth, the studies on cognition by evolutionary developmental neuroscientists are discussed. Finally, the work of evo-devo biologists extrapolating results on evolutionary developmental mechanisms to the field of cognition are discussed.

Evolutionary Developmental Cognitive Science

Evolutionary developmental cognitive scientists are usually trained as developmental psychologists and try to understand the origin of the behavior and cognitive abilities of children. Evo-devo psychologist David Bjorklund (2009) has studied the adaptive role of cognitive immaturity. Children are often viewed as "unfinished adults," but Bjorklund showed that children's failures on cognitive tests are sometimes adaptive. For example, young children often overestimate their cognitive abilities. It was found that this overestimation was associated with better cognitive performance at a later age, probably because overconfidence leads to more exploratory behavior. This suggests that overestimation is functional. Evo-devo psychologist David Geary (2005) has addressed educational psychology from an evo-devo perspective. He argued that children learn some abilities naturally, such as language and simple counting. Also children that are not stimulated by their parents or formally educated will learn these. He called these primary abilities. Other abilities are secondary, such as higher-order mathematics, which require formal instructions to be learned. He argued that children will be better motivated to learn secondary abilities when they are coupled to primary abilities.

Developmental Systems Theory

Developmental systems theorists argue that organisms do not only inherit the DNA of their parents but a whole developmental system, which includes the environment in its full spectrum – at the cellular, tissue, body, family, and ecological level (Oyama et al. 2001). They argue that the scope of some evolutionary cognitive scientists is too limited. For example, developmental psychologist Elizabeth Spelke has argued that human babies are born with core knowledge about objects, social agents, numbers, and geometry (Spelke and Kinzler 2007). Her conclusions are based on empirical results that revealed that newborns, even on the first day after birth, show different responses (e.g., different looking times) to different situations, even though

they have no prior experience with these situations. Spelke argues that, based on her data, the inevitable conclusion is that some basic knowledge is innate. Developmental systems theorists tend not to agree with this conclusion. Nonetheless, they agree that a functional perspective is necessary to get a better understanding of the mind, but they highlight the importance of ecologically relevant conditions to study cognition, in agreement with evolutionary ecologists.

Another illustration of the sometimes limited scope of evolutionary cognitive scientists was put forward by developmental psychologist Annette Karmiloff-Smith (2006). She criticized some of the arguments put forward by Steven Pinker in the discussion on language evolution. Pinker argued that the gene *FOXP2* is "the language gene." Research revealed that members of a family with severe language problems showed mutations in *FOXP2*, suggesting that it is a crucial gene in language development. Later research revealed that *FOXP2* is not specifically involved in language development but in multiple processes that are associated with producing sequential movements. Karmiloff-Smith argued that the effects of many genes are associated with general processes and that specific complex traits, such as language, are the result of several developmental pathways, with no simple relationship to a specific DNA sequence.

Some researchers have tried to bridge the gap between evolutionary cognitive science and developmental systems theory. For example, David Bjorklund (2015) has proposed the concept of an evolved probabilistic cognitive mechanism. He argued that it is inevitable that natural selection has selected cognitive adaptations to deal with problems related to survival and reproduction. However, these adaptations will not develop when individuals are placed in an environment that is not species typical (e.g., for humans an environment without spoken language). Therefore, he argued that all evolved cognitive mechanisms are probabilistic, with their development being dependent on the right environmental input.

Genes X Environment Interactions

The discussion on the interaction between the influence of genes and that of the environment on the development of phenotypes goes back to the seventeenth century when philosopher John Locke started the nature-versus-nurture debate. Nowadays most psychologists and biologists agree that both nature and nurture are important, with some researchers pointing to the importance of culture (e.g., Richerson and Boyd 2005; see also the chapter on " \blacktriangleright Evo-devo and Culture"), next to nature (genes), and nurture (parenting). Recently, a wide array of new discoveries has been made in studies that examine the interaction effects between specific genes and specific environmental input (i.e., G×E studies) on specific behavioral outcomes (e.g., aggression, depression, etc.). The paradigm case is a longitudinal study performed by Avshalom Caspi and colleagues (2002). They followed a large sample of boys from birth to adulthood in order to study the development of antisocial behavior. Data on individual differences at a polymorphism in the promoter of the *MAOA* gene and maltreatment were collected. It was found that the interaction

between maltreatment and having a genotype associated with low levels of MAOA expression resulted in a high risk of developing antisocial behavior. This was the first study that showed a significant G×E interaction. Many other studies followed.

Interesting theoretical contributions were made by psychologists Bruce Ellis, Jay Belsky, and colleagues. Ellis et al. (2011) reviewed several $G \times E$ studies and observed that some genotypes are associated with a vulnerability to develop psychopathology in interaction with a negative environment (such as maltreatment), but that the very same genotype is also associated with positive outcomes in interaction with a positive environment (such as the absence of maltreatment). They prefer to call these "plasticity genes," rather than "vulnerability genes." An appealing comparison with orchids and dandelions has been made. Orchids are beautiful flowers when they are taken good care off, but nothing but a boring empty stem remains when they are maltreated. In contrast, dandelions are arguably not that beautiful, but they can grow everywhere, even at a roadside or a dumping ground. Thus, some people are more susceptible to specific environmental influences - based on their genotype – and can be regarded as orchids, whereas other people are less susceptible to these influences and can be regarded as dandelions (although, naturally, plants that are more tolerant to environmental conditions are not necessarily less beautiful than those that are less tolerant). This is called differential susceptibility theory and has received considerable empirical support in the past decade.

A hypothesis derived from this theory is that orchids benefit more from psychotherapy than dandelions. It is well known that the success rate of psychotherapies is variable - some individuals improve considerably, while others do not. Where do these large individual differences come from? Part of the answer may be that individuals with a genotype that makes them more susceptible for environmental influences – the orchids – benefit more from specific therapies, because they are more susceptible to both positive and negative environmental influences than dandelions. A study on the interaction effect of an intervention and a genotype (the polymorphism in the promoter of the DRD4 gene) on problem behaviors in children provided support for this hypothesis (for this and other interesting references, see Ellis et al. 2011). It was found that the positive effect of the intervention was largest in the group of children with DRD4 genotypes associated with low levels of dopamine reception efficiency. This study provided experimental support for the hypothesis that children are differentially susceptible to intervention effects based on genetic differences. More studies on different types of differential susceptibility, age effects, and the relationship with therapy success are necessary.

In sum, this work shows the importance of studying both genetic and environmental differences to explain the development of phenotypical outcomes. The biological mechanisms underlying these processes remain unknown. Studies on epigenetics (see next section) should contribute to the understanding of these mechanisms.

Epigenetics

Recently, new discoveries have been made under the umbrella of epigenetics. Epigenetics refers to changes that influence how genes are expressed, other than changes in the DNA sequence (e.g., Masterpasque 2009). Two major epigenetic mechanisms are DNA methylation (the attachment of methyl molecules to cytosines, which switches off the expression of the gene) and histone modification (a change in the histone proteins around which DNA is wrapped, which causes the expression of the gene to switch on or off). Research relevant for cognitive science comes from two main sources: studies on the effects of early caregiving on later development and studies on the role of epigenetics in psychiatric disorders. Famous work was carried out on the effects of licking and grooming by the mother on later behavior, physiology, and epigenetics of newborn rats (for relevant references, see Masterpasque 2009). They found differences in the reactivity of the hypothalamicpituitary-adrenal (HPA) axis of offspring raised by either high licking/grooming or low licking/grooming mothers. High HPA reactivity is associated with stress responses and psychiatric disorders in humans. The decrease in HPA reactivity in high licking/grooming offspring of rats is directly linked to decreased methylation of glucocorticoid receptor genes in the hippocampus. Cross-fostering experiments showed that the individual differences in reactivity were the result of licking and grooming patterns and not of differences in genotype of the mother. Performing similar experiments in humans is not possible, but postmortem studies with maltreated versus nonmaltreated humans revealed similar epigenetic patterns as were found in rats.

It is now well known that epigenetic processes play an important role in the development of psychiatric disorders. For example, research in mice has revealed that social stress leads to low levels of brain-derived neurotropic factor (BDNF) in the hippocampus due to histone modification. Similar patterns have been found in humans diagnosed with major depression disorder. Considering schizophrenia, postmortem studies revealed low concentrations of reelin in the brains of patients, which were associated with hypermethylation of the reelin gene. With regard to autism, studies were performed on a monozygotic twin, of which one was diagnosed with autism, while the other was not, despite their identical DNA sequence. Results revealed that the individual with autism showed methylation-dependent silencing of the *BCL-2* and the *RORA* gene.

Only a few of the many recent studies on epigenetics that are relevant for cognitive science have been described here. The studies on epigenetics are at the heart of evo-devo research: how do inherited DNA sequences interact with developmental processes that vary under the impact of environmental influences to form constant or novel phenotypes.

Evolutionary Developmental Comparative Cognitive Science

Evolutionary developmental comparative cognitive scientists compare the cognition of nonhuman primates and human children. The book The Origins of Intelligence (Parker and McKinney 1999) is a hallmark in this field. In this book, the development of different primate species was compared, following the theory on cognitive development by Jean Piaget, as mentioned above. However, the choice to test children is usually not made because researchers are interested in a developmental perspective; often adult nonhuman primates and young human children (2–3-yearsolds) are compared because their cognitive levels are similar. For example, the Primate Cognition Test Battery has been developed in order to have tests that both adult nonhuman primates and young human children can perform. Recently, a first large study was published where young chimpanzees and bonobos (together called Pan infants) and human children were followed longitudinally for 3 years with a new test battery, the Comparative Developmental Cognitive Battery (for relevant references, see Tomasello 2014). Individuals were tested on social cognition (e.g., gaze following, imitation, goal understanding), physical cognition (e.g., discriminating different quantities, tool use, understanding of object permanence), attention, and motivation. Results revealed that over all tasks, the rate of improvement is slower in Pan infants than in human children, and that abilities that require cooperative motivation do not emerge at all in *Pan* individuals. This is useful research, because it provides us insight in the differences and similarities between three closely related species, including two sister species of humans, and thereby also in the cognitive evolution of humans.

Evolutionary Developmental Cognitive Neuroscience

Evolutionary developmental cognitive neuroscientists study how brains change, both from an evolutionary and a developmental perspective. Two general models about brain evolution and development have emerged. One model emphasizes the relative independence and modularity of different brain structures, assuming that, for example, the auditory system requires different neural networks from the olfactory system. From an evolutionary perspective, it is argued that most brain areas are functionally specialized, and hence selection pressures will differentially affect brain areas (Barrett 2012). The other model assumes that the entire brain will change in response to selection pressures, and that architectural and functional constraints ensure that brain size as a whole will change.

Four types of brain growth have been observed in the evolution of mammals (Finlay et al. 2001). First, brain growth that is associated with body growth; when the body grows, the brain grows accordingly. Second, the brain can grow while body size remains constant; this kind of brain growth is associated with enhanced behavioral and cognitive capabilities in the course of evolution. Third, the limbic system, the part of the brain associated with emotion, motivation, memory and olfaction, grows independently of overall brain and body size. Fourth, other individual brain

parts may vary in size independently of overall brain and body size. For example, prefrontal gray volumes are 4.8 times larger in humans compared to chimpanzees (for a review, see Schoenemann 2006). In addition, the relative size of the neocortex and striatum is positively correlated with tool use, innovation, and social learning. These four different types of growth indicate that both independent evolution of different brain structures and size changes of the entire brain have been important for brain evolution and development.

Evolutionary Developmental Biology and Cognitive Science

The last subject addressed is the question what cognitive scientists can learn from evo-devo research in biology. Many evo-devo biologists study morphogenesis, and it is not immediately obvious how to relate their research findings to cognitive science. This issue has been addressed in an earlier paper (Ploeger and Galis 2011; relevant references can be found in this paper). A first conclusion was that some of the main issues in evo-devo biology and cognitive science overlap and that tools can be used profitably by both types of scientists. For example, modularity is a main topic in both evo-devo biology and cognitive science (see chapter on "> Modularity in Evo-devo"). Evo-devo biologists study the modularity of developmental and genetic pathways as well as that of body parts, whereas cognitive scientists study the modularity of the human mind. Evo-devo biologists have developed tools to study modularity that have been largely unnoticed by most cognitive scientists. It was argued that cognitive scientists can benefit from these tools. Another example is the issue of plasticity. Both evo-devo biologists and cognitive scientists are interested in the question how plasticity is important in an individual life time and how it evolved over generations. It was also argued in this case that evo-devo biologists have developed tools that should benefit cognitive scientists.

A second conclusion was that evo-devo biology research can provide new insights in the evolution and development of psychiatric disorders. One example is research on developmental constraints. For example, it was proposed that mutations that give rise to the positive aspects of the savant syndrome, i.e., the impressive memory capacity, cannot spread in the population, due to a developmental constraint that has its roots in low modularity. This developmental constraint is thought to result from the high interactivity (low modularity) among body parts during early organogenesis (i.e., the phylotypic stage). The interactivity during this stage involves all components of the embryo, and as a result mutations that affect one part of the embryo also affect other parts (pleiotropic effects or side-effects), with almost inevitably negative effects among them. As a result of the sheer unavoidable deleterious side-effects, there is strong selection against mutations with an effect on this stage, presumably leading to the extremely strong conservation of the entire stage. The low modularity of this embryonic stage has implications for the conservation of many traits of the body plan and is for example at the root of the strong developmental constraint against changes of the number of cervical vertebrae in mammals. The same hypothesis was proposed for the savant syndrome. Mutations,

which give rise to the development of the positive aspects of the savant syndrome, i. e., an impressive memory capacity, will virtually always have deleterious sideeffects on the development of other phenotypic traits. The support for such strong deleterious side-effects that are associated with the savant syndrome (e.g., autism and/or impaired motor coordination) was discussed. One of the new insights that were reported is that psychiatric disorders that result from brain deviations usually appear to start to develop as early as during the phylotypic stage, due to the general instability and vulnerability of the stage that results from the intense inductive interactivity. Another example is research on epistatic interactions between the effects of different genes. It is a paradox why psychiatric disorders, such as schizophrenia and autism, are common, why they are highly heritable, and why they still persist. Why did natural selection not wipe out these disorders? The answer lies in the polygenic nature of most psychiatric disorders. When multiple genes are involved, the effects of these genes will interact during development, sometimes resulting in positive but sometimes in negative outcomes. Interdisciplinary approaches in which insights from evo-devo research on morphogenesis have shown to yield new hypotheses about the evolution and development of psychiatric disorders.

Conclusion

Evo-devo in cognitive science consists of a wide array of subfields, including evolutionary developmental cognitive research, developmental systems theory, genetic research ($G \times E$ interactions), epigenetic research, comparative research, neuroscientific research, and applications of evo-devo biology in cognitive science. Interdisciplinary research is strongly recommended, so that scholars from different fields such as theoretical biology, morphology, embryology, genetics/genomics, neuroscience, primatology, and psychology can learn from each other and contribute to the unraveling of the working of the mind.

Cross-References

- ► Epigenetic Innovation
- Evo-devo and Cognitive Science
- ► Evo-devo and Culture
- Evo-devo of Language and Cognition
- Evo-devo of Social Behavior

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