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TARGET ARTICLE

Is Evolutionary Psychology a Metatheory for Psychology? A Discussion of Four Major Issues in Psychology From an Evolutionary Developmental Perspective

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Evolutionary psychology has been proposed as a metatheoretical framework for psychology. We argue that evolutionary psychology should be expanded if it is to offer new insights regarding the major issues in psychology. Evolutionary developmental biology can provide valuable new insights into issues such as the domain-specificity of the human mind, the nature–nurture debate, stages in development, and the origin of individual differences. Evolutionary developmental biology provides evidence for the hypotheses that domain-general and domain-specific abilities co-occur, that nature and nurture interact in a dynamic and nonadditive way, that stages occur in development, and that individual differences are the result of pleiotropic effects during development.

Evolutionary psychology has been advanced as a metatheory for psychology, that is, as a unifying theory that can accommodate a diversity of facts and findings from all fields within psychology (Buss, 1995; Cosmides, Tooby, & Barkow, 1992). The general idea is that psychological characteristics (e.g., sex-specific mate preferences), like biological characteristics, have evolved over a long period and should be seen as adaptations to the social and ecological circumstances that characterize human existence. The main tenet of evolutionary psychology is that the human mind comprises a collection of psychological adaptations, which arose through the process of natural selection. Another tenet is that humans have encountered distinct problems in different evolutionary periods and that the specific solutions to these problems have resulted in a multitude of functionally specialized, domain-specific mechanisms in the brain. This is known as the *massive modularity assumption* (Sperber, 1994).

Since the rise of evolutionary psychology, many hypotheses about evolved psychological mechanisms have been derived and tested. Buss and Reeve (2003) pointed out that evolutionary psychologists have made many discoveries that had eluded other psychologists. These discoveries mostly concern issues related to social exchange, mate choice, sexual behavior, relationship maintenance, and parental care. The interpretative framework and the possibilities of making new discoveries offered by the evolutionary perspective have certainly been fruitful.

However, to function as a metatheory in psychology, evolutionary psychology should both identify important research questions that are often missed in other perspectives and address the current major issues in psychology. In this article, we consider the present contribution of evolutionary psychology to four major issues in psychology:

- Does the human mind consist mostly of domain-specific abilities, or is the mind domain-general?
- What is the influence of nature and nurture on the human mind?
- Does development proceed in stages or gradually?
- How do individual differences arise?

As our point of departure, we examine three approaches to evolutionary psychology. Tooby and Cosmides (1992) presented a comprehensive framework for the field of evolutionary psychology. Buss (1995, 2003) presented a similar framework, in terms more suitable for a general audience. Pinker (1997), working within this same framework, provided evolutionary explanations for many psychological phenomena. To ease presentation, we refer to the general framework of these researchers as mainstream evolutionary

psychology. This should not be taken to imply that all evolutionary psychologists subscribe to this framework, but most, if not all, do take this framework as a point of reference.

We contend that mainstream evolutionary psychology at present is not sufficiently elaborated to address the major issues in psychology. We show that certain tenets and ideas of mainstream evolutionary psychology are inconsistent with certain empirical facts pertaining to these issues. However, we maintain that these inconsistencies do not disqualify evolutionary psychology as a metatheory for psychology. We attribute these inconsistencies to the fact that mainstream evolutionary psychology embraces a limited subset of ideas from evolutionary biology and is therefore lacking in scope. We argue that the inclusion of theoretical concepts and empirical findings from the field of evolutionary developmental biology can remove these inconsistencies and broaden the scope of evolutionary psychology such that it can serve as a proper metatheoretical framework for psychology.

This article is organized as follows. First, we present a brief introduction to mainstream evolutionary psychology. Second, we describe evolutionary developmental biology. Third, we discuss the implications of both views for four major issues in psychology.

Mainstream Evolutionary Psychology

Mainstream evolutionary psychology starts with the tenet that evolution by natural selection is at present the only viable scientific explanation of the existence of complex biological and psychological mechanisms (Buss, 1995, 2003; Pinker, 1997). Hypotheses derived from the theory of evolution by natural selection have been confirmed many times, and so this theory is generally considered to be well established (e.g., Dawkins, 1986; Mayr, 1982; Williams, 1966). As discussed in the next section, evolutionary developmental biologists do not disagree with this tenet, but argue that it is incomplete; they maintain that there are additional processes that influence the evolution of complex traits (Müller & Wagner, 1991, 2003).

The second tenet of mainstream evolutionary psychology is that psychological theories imply psychological mechanisms, for example, information-processing devices and decision rules (Buss, 1995). For example, Skinner's behaviorist theory implies a very general learning mechanism. This mechanism must have evolved in some way. Mainstream evolutionary psychologists define a psychological mechanism as a set of processes within an organism that exists because it solved a particular problem of survival or reproduction in ancestral times (Buss, 2003). Examples of putative evolved psychological mechanisms are the male's desire for sexual variety (Schmitt & 118 Members of the International Sexuality Description Project, 2003), male sexual and female emotional jealousy (Buss, Larsen, Westen, & Semmelroth, 1992), and child-directed speech (Fernald, 1992).

For example, Schmitt et al. (2003) offered an evolutionary explanation for the finding that men, in general, express greater desire for sexual variety than women. This universal sex difference can be explained in terms of differential reproductive success: Men who have sex with many different women will have on average more offspring than men who have sex with few women. Women do not tend to have more offspring by having sex with many different men, because they experience relatively long periods of infertility due to pregnancy and breastfeeding. For them, it is more important to have a stable relationship for keeping protection and resources.

The third tenet of mainstream evolutionary psychology is the so-called massive modularity assumption. This tenet holds that the human mind consists of many different domain-specific psychological mechanisms. It is based on the idea that the confrontation in the evolutionary past with domain-specific problems gave rise to domain-specific, functionally specialized psychological mechanisms (Buss, 1995; Tooby & Cosmides, 1992). Therefore, many different psychological mechanisms are supposed to exist, just like many organs exist in the body that perform specific functions. Although the ultimate criterion is fitness, no general mechanism for fitness exists, because environmental conditions change over time and differ from place to place (Symons, 1992). In other words, there is no such thing as a "general solution," because there is no such thing as a "general problem" (Buss, 1995). The massive modularity assumption is important in the debate on the domain-specificity of the mind, which we discuss next. First, we provide a brief account of evolutionary developmental biology.

Evolutionary Developmental Biology

In the wake of the synthesis of Darwin's theory of natural selection and genetics, most biologists have come to consider themselves to be neo-Darwinians. The central tenets of the neo-Darwinian theory are that evolutionary change occurs because of genetic mutations and that adaptive variants get "fixed" in the population through natural selection. Although neo-Darwinian theory enjoys a considerable following (e.g., Dennett, 1995), it is not free of controversy (e.g., Gould, 2002). One controversy concerns the role of natural selection, which is, in the neo-Darwinian approach, the most important force in evolution. Neo-Darwinians argue that complex biological forms and organs arise as a result of the retention, by natural selection, of genetic changes that cause small gradual

changes in phenotypic features, which in turn increase the individual's fitness to procreate in its environment. The transmission of these genetic changes from parents to offspring increases the frequency of these phenotypic features in the population. Because of the accumulation of small advantageous features, complex forms and organs, such as the eye, evolve.

Mainstream evolutionary psychologists adhere to the neo-Darwinian approach. In their theorizing, they neglect another important approach in evolutionary biology, namely, the evolutionary developmental approach. This is defined as a "synthesis of those processes operating during ontogeny with those operating between generations (during phylogeny)" (Hall & Olson, 2003, p. xiii). The starting point in evolutionary developmental biology is the thesis that new variants emerge before natural selection can do its work. The relevance of natural selection is not disputed, but evolutionary developmental biology provides a better account of the evolutionary origin of new forms than does neo-Darwinian theory (Müller & Wagner, 1991, 2003). Natural selection does not explain how individual variants arise or how they evolved. Here, knowledge about development may help us address these issues (S. B. Carroll, 2005).

Several evolutionary developmental biologists have argued that individual development and behavior can be viewed as the initiator of evolutionary change (Gottlieb, 2002, 2003; Weber & Depew, 2003). Developmental change leads to new behavior, which may be better suited to certain environmental conditions. The new behavior brings out latent possibilities for physiological or morphological change. As was put forward by Gottlieb (2003), the issue is whether the original change in behavior requires a genetic mutation. Neo-Darwinian theory is guided by the tenet that only a change in genetic structure can be the initiator of evolutionary change (Crick, 1970). Gottlieb (2002, 2003) used the study of the evolution of the apple maggot fly (*Rhagoletis pomonella*) to illustrate that a genetic mutation is not required to produce new behavior. Originally, the female apple maggot fly laid her eggs on hawthorns. When domestic apple trees were introduced, females started to lay their eggs on these as well (a phenotypic change). At present, there are two variants of the apple maggot fly, one that lays its eggs on apples and the other on haws. The two variants no longer mate with each other, because apples mature earlier than haws, so the mating seasons are different. This change in developmental timing has given rise to genetic changes (i.e., differences in gene frequencies) in the two populations (Feder, Roethele, Wlazlo, & Berlocher, 1997).

Note that these genetic changes occurred after the new phenotypic behavior emerged, that is, the phenotypic behavioral change provided the impetus for the genetic change. Note also the clear difference with Lamarckian theory, which states that acquired characteristics are transmitted biologically to the offspring. The evolutionary developmental point of view is that new behaviors (phenotypic changes) create new possibilities to deal with environmental conditions, which set the stage for later genetic change.

Another issue that requires an evolutionary developmental solution is the origin of novelties. For example, consider the origin of eyespots on butterfly wings, a relatively recent evolutionary novelty, which serve to deter predators. 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, as Wagner (2000) stressed, we do not learn from this account how the eyespots arose in the first place. An evolutionary developmental study offered new insight in the developmental mechanisms that cause the emergence of eyespots (Keys et al., 1999). This study showed that eyespots evolved as new patterns that develop from special organizers called foci. An organizer is a signaling center that directs the development of parts of the body. Formation of these organizers is associated with novel expression patterns of a signaling protein, its receptor, a transcription factor, and a related gene. These novel expression patterns break the existing regulatory circuits of the butterfly wing. The general message of this study is that the redeployment of pre-existing regulatory circuits may serve as a general mechanism underlying the evolution of novelties. This study provides an example of how the evolutionary developmental biology approaches the developmental mechanisms that underlie evolutionary change. The neo-Darwinian approach in contrast can tell us only about the selection of existent traits.

It is important to emphasize that the neo-Darwinian and the evolutionary developmental approaches are complementary rather than opposite. Most evolutionary biologists cannot be classified as either neo-Darwinian or evolutionary developmental. Although we recognize that the two approaches are largely complementary, in the remainder of this article we emphasize their differences, to accentuate the different contributions the two approaches can make to four major issues previously mentioned.

Evolutionary Biology and Four Major Issues in Psychology

This section contains four parts, each addressing a major issue in psychology. The issues are concerned with the domain-specificity of the mind, nature and nurture, stagewise versus gradual development, and individual differences. We discuss each issue from the perspective of mainstream evolutionary

psychology and the perspective of evolutionary developmental biology.

Domain-Specificity Versus Domain-Generality of the Mind

The issue of the domain-specificity of psychological abilities has been discussed intensively, both in psychology in general, and in the field of evolutionary psychology. Domain-specificity refers to the extent to which a mechanism is tailored to handle some particular and narrow range of inputs. One view emphasizes domain-specificity of the brain, that is, the view that different brain regions work more or less independent from each other (e.g., Gazzaniga, Ivry, & Mangun, 2002). Another view emphasizes domain-specificity of cognition, that is, the view that knowledge about someone's ability for a specific aspect of cognition tells you little about other specific cognitive abilities of that person (e.g., Carey, 1985). Still another view emphasizes the domain-specificity of innate bodies of knowledge, for example, the knowledge that newborns possess about physical entities of the world (e.g., Gelman & Williams, 1998; Spelke, 1994). Finally one view emphasizes the domain-specificity of processes that solve a particular psychological problem (e.g., Buss, 1995).

In this last view, a domain-general process is viewed as one that plays a role in a wide range of domains and is independent of the content of the domain involved. The processes of assimilation and accommodation as proposed by Piaget (1952) are examples of domain-general abilities. Assimilation is a process by which a new experience is perceived in accordance with existing knowledge. Accommodation is a complementary process by which a new experience can no longer be perceived in accordance with existing knowledge, resulting in a change in the existing knowledge. The two processes are independent of the kind of experience or the kind of existing knowledge. In contrast, a domain-specific process solves problems only in a single domain and is dependent on the content of the domain. For example, Cosmides and Tooby (1992, 2005) proposed a cheater detection ability, which is functionally specialized to help people to detect cheaters. When people have to solve logical problems in the form of "If P then Q," they perform best if the logical problem consists of a situation in which a cheater has to be detected. Cosmides and Tooby concluded that humans do not have a domain-general logical-problem-solver ability that is independent of the content of the problem but do have a cheater detection ability, which solves a specific adaptive problem.

Mainstream evolutionary psychologists are not always clear about the particular kind of domain-specificity to which they refer (see Samuels, 1998, and Fodor, 2000, for an analysis of this problem). However, in general they refer to domain-specificity in the last sense (i.e., domain-specificity of processes that solve a particular psychological problem). In the remainder of the article, we refer to this meaning of domain-specificity.

Mainstream Evolutionary Psychology's View

An important tenet of mainstream evolutionary psychology is the massive modularity assumption. This tenet holds that our minds consist of many domain-specific devices to solve domain-specific adaptive problems that human beings have encountered in their evolutionary past. This tenet does not exclude the possibility of the existence of some domain-general abilities. It asserts only that we should expect many domain-specific abilities. However, Cosmides and Tooby (1994) advance three reasons that domain-general processes that solve adaptive problems are unlikely. First, what counts as the best solution differs from domain to domain. There is no domain-general criterion for what generates an adaptive or maladaptive outcome. What counts as a success or a failure in terms of fitness depends on the specific domain. Second, individuals, equipped only with domain-general problem-solving mechanisms initially have to treat all perceptual information equally, as they have no specific prior knowledge about the information. It is impossible for an individual to learn all necessary specific knowledge in one lifetime. In this connection, Cosmides and Tooby referred to Chomsky's (1975) theory, which states that it is impossible for a child to learn a language by trial and error. Third, because organisms with only domain-general abilities 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 a long time before one can act is not adaptive. This line of reasoning has given rise to the massive modularity assumption, which states that the human mind consists of many functionally specialized, domain-specific mechanisms.

Empirical Evidence for Domain-General Abilities

The massive modularity assumption of mainstream evolutionary psychology has given rise to an intense debate (for an overview and references, see Barrett & Kurzban, 2006). Although mainstream evolutionary psychologists argue that the evolution of domain-general abilities is unlikely, there is ample empirical evidence for the existence of domain-general abilities. Bjorklund and Pellegrini (2002) mentioned speed of processing, working memory, inhibition, and general intelligence as possible domain-general abilities. Habituation, statistical learning, associative learning, and metacognition are other examples. We present empirical evidence for the existence of these putative domain-general abilities in the remainder of this section. This

evidence does not exclude the existence of domain-specific abilities, but it suggests that domain-general abilities also exist.

Speed of processing. The amount of time that people need to perform distinct tasks show developmental similarities across those tasks. For example, Hale (1990) compared performance on four different tasks (choice reaction time, letter matching, mental rotation, abstract reasoning) and found that it is possible to predict the response latencies of the younger children from the response latencies of the older children, no matter which task was involved (for similar research, see Kail, 1986, 1991). Other evidence for the domain-generality of speed of processing comes from studies in which factor analysis revealed a higher-order general mental speed factor (Danthiir, Wilhelm, Schulze, & Roberts, 2005; Roberts & Stankov, 1999).

Working memory. The hypothesis that working memory is domain-general has been tested with a so-called latent variable approach (Kane et al., 2004). In this approach, multiple tasks are used to measure the putative construct to statistically remove the irrelevant variance (e.g., due to measurement error) of individual tasks. Kane et al. found that verbal and visual-spatial working memory share about 80% of their variance, leaving little room for variance that can be attributed to domain-specific components (see also Hambrick, Kane, & Engle, 2005). Swanson and Sachse-Lee (2001) found that children with and without reading disabilities who were matched on central executive processing did perform similarly on all domain-specific working memory tests (e.g., verbal, visual-spatial). These results imply that reading disability is the result of impaired domain-general executive processing and not the result of domain-specific impairment in verbal working memory (see also Swanson, Howard, & Saez, 2006).

Inhibition. Inhibition has also been proposed as a domain-general ability (Bjorklund & Kipp, 2002). It is argued that inhibition, like other domain-general abilities, plays a facilitating role in cognition. That is, without a certain amount of inhibition, people would not be able to perform higher-order cognitive tasks. Band, van der Molen, Overtoom, and Verbaten (2000) found that individuals of several ages performed equally well on inhibition tasks in different domains. A general ability to inhibit responses seems to be present at the age of 5 (for similar results, see van den Wildenberg and van der Molen, 2004).

General intelligence. The construct of general intelligence ("g") is based on the finding that an individual who has a high score on a specific test (e.g., a verbal test), will, in general, get a high score on another specific test (e.g., a mathematical test). The idea of general intelligence is an old one (Spearman, 1904) and has received a lot of attention (Jensen, 1998). General intelligence has also been discussed from an evolutionary perspective. From this perspective, general intelligence is required for dealing with variant patterns in nature and for integrating information across different domain-specific abilities (Geary, 2005). Recent evidence for the existence of general intelligence is provided by a study in which a large sample was tested on three well-known batteries of intelligence tests that cover different aspects of cognitive ability (Johnson, Bouchard, Kreuger, McGue, & Gottesman, 2004). The main result was that the correlations among the second-order g-factors of the three different test batteries were very high, ranging from .99 to 1.00. Based on this study, and several other studies (for a review, see J. B. Carroll, 1993), it can be concluded that there is ample evidence for general intelligence.

Habituation. Habituation involves a decreased strength of a response as a result of repeated presentation of a stimulus. Habituation occurs regardless of the nature of the stimulus, for example, in the language domain (e.g., Bijeljac-Babic, Bertoncini, & Mehler, 1993), the visual domain (e.g., Kirkham, Slemmer, & Johnson, 2002) and the music domain (e.g., Hannon & Trehub, 2005).

Statistical learning. Statistical learning takes place in both children and adults when they try to structure information from the environment. Human beings, as well as nonhuman primates (Newport, Hauser, Spaepen, & Aslin, 2004), quickly discover statistical regularities of their environment. For example, when visual stimuli are presented in pairs, infants quickly discover this statistical regularity, as measured by habituation studies (Kirkham et al., 2002). Infants can also detect statistical patterns in musical stimuli (Hannon & Trehub, 2005), and language (Bijeljac-Babic et al., 1993; see Saffran, 2003, for a general overview of research on statistical learning and language).

Associative learning. Associative learning is the ability to learn connections between stimuli that often occur together. Most research on associative learning concerns infants' ability to learn categories. Infants as young as 3 months can form categories when presented with different visual stimuli (see Quinn & Eimas, 1996, for an overview). Networks in which these results are simulated are based on a single domain-general associative learning mechanism (Mareschal & French, 2000). These networks can also be used for video image compression (Cottrell, Munro, & Zipser, 1988), text compression (Schmidhuber & Heil, 1996), and the detection of fault diagnoses in marine diesel engines

(Sharkey, Sharkey, & Chandroth, 1996), showing the domain-generality of the networks.

Metacognition. Metacognition is the ability to evaluate and change one's own performance. Schraw, Dunkle, Bendixen, and Roedel (1995) tested undergraduates in five different domains (knowledge of U.S. presidents, geographical distances between American cities, vocabulary, prominent sport figures, and popular music stars). Participants were asked to provide a confidence rating for each test item, immediately after completing each of the five tests. The confidence rating is supposed to express metacognition. Partial correlations among confidence scores on each of the five tests, with performance covariation statistically removed, were all significant. This result is inconsistent with the hypothesis that metacognition is based on knowledge and expertise in a particular domain (see also Veenman & Verheij, 2003).

Conclusion. The presented research findings are consistent with the view of speed of processing, working memory, inhibition, general intelligence, habituation, statistical learning, associative learning, and metacognition as domain-general abilities. These are abilities that help human children and adults to deal flexibly with varying environmental conditions (Geary, 2005). These research findings suggest that evolutionary psychologists' massive modularity assumption is incorrect.

Evolutionary Developmental Biology's Contribution

Modularity is a central theme in evolutionary developmental biology (e.g., Callebaut & Rasskin-Gutman, 2005; Schlosser & Wagner, 2004). Modularity is defined as "the properties of discreteness and dissociability among parts and integration within parts" (West-Eberhard, 2003, p. 56). The concept of modularity in evolutionary developmental biology usually refers to morphology, that is, the form and structure of an organism. This may seem removed from the discussion in psychology, in which modularity usually refers to functions (i.e., cognitive abilities). However, morphology also includes the structure of the brain and the functions that accompany the different parts of the brain (for an evolutionary developmental perspective on the modularity of functional modules in the brain, see Redies & Puelles, 2004). So the discussion about modularity in evolutionary developmental biology is certainly relevant to the discussion in psychology.

An ongoing discussion in evolutionary developmental biology, related to the discussion on domain-specific versus domain-general abilities, concerns the coexistence of modularity and pleiotropy. Pleiotropy refers to cases in which a single gene has effects on more than one phenotypic trait. Wagner (1996) argued that a module has the following properties: (a) It serves a particular functional role, (b) it is relatively independent from other modules, and (c) pleiotropic effects are more frequent within a module than across modules.

Wagner (1996) argued that the elimination of pleiotropic effects is a necessary condition for evolution, that is, modularity is a necessary condition for evolution. Evolution is only possible if one module can be changed without changing the whole organism. However, Hansen (2003) disagreed with this. He argued that the elimination of pleiotropic effects reduces the number of genes that can influence the module and thereby reduces its mutational target size. According to Hansen, modularity is beneficial for the individual modules but not beneficial for the whole organism. He hypothesized that evolvability (i.e., the capacity to respond to a selective challenge) is maximized by variable pleiotropic effects. Eliminating pleiotropic effects may increase the evolvability of one module but reduce the evolvability of another. Thus, Hansen concluded, "It has been almost universally accepted that biological organisms are 'modular', but the fact remains that pleiotropy across characters is a ubiquitous property of biological variation" (pp. 91–92).

Griswold (2006) showed with simulation experiments that under some conditions an increase in pleiotropy enhanced evolvability, whereas under other conditions an increase in modularity enhanced evolvability. The condition that is probably found most often in nature is that some traits are under stabilizing selection, whereas other traits are under directional selection (Wagner, 1988, 1996). Stabilizing selection occurs when individuals with an average value for a trait have higher fitness than individuals with an extreme value; under stabilizing selection, the trait will remain constant. Directional selection occurs when individuals with an above- or below-average value for a trait have higher fitness than individuals with an average value. For example, Darwin's famous finches were adapting their beak shape (i.e., directional selection) while conserving other body parts (i.e., stabilizing selection; Grant, 1986). Griswold found that evolvability is enhanced when an increase of pleiotropy is associated with traits that are under directional selection but not under stabilizing selection. When a mutation is beneficial for two or more traits, which only occurs when the mutation has pleiotropic effects, then the increase in fitness is larger and the mutation gets fixed faster.

Hansen (2003) and Hansen, Armbruster, Carlson, and Pélabon (2003) proposed a model to explain the relationship between modularity and pleiotropic effects and how this relationship affects the evolvability of a system. It is beyond the scope of this article to discuss this technical model in detail, but an example illustrates the idea. It has been found that the lens of the eye, commonly seen as a clear example of a separate

module, has pleiotropic links with other traits. For example, in amphibians, the lens is formed by interactions with tissues from the retina and even heart mesoderm. Furthermore, crystalinnes, proteins that make up 30 to 40% of the mass of the lens, are not specialized for their role in lens formation, because they also have functions in other cells. In other words, crystalinnes are domain-general. The process where a single gene has pleiotropic effects in that it produces a protein that has several different functions, is called co-option, and this process is regarded as fundamental to the evolution of new traits (e.g., Gerhart & Kirschner, 1997; Raff, 1996; True & Carroll, 2002).

Other evolutionary developmental researchers also conclude that modularity is not the only path to evolvability. Evolutionary developmental biologist West-Eberhard (2003) criticized mainstream evolutionary psychology explicitly for its rigid use of the concept of modularity. She argued that modularity and connectedness or integration are two sides of the same coin. Biological modules, such as body parts, are never pure modules, because they are always connected to some degree to other body parts. She preferred to refer to biological entities or behavioral traits in terms of their modular properties, not in terms of actual separate modules.

Ancel and Fontana (2000) presented results of simulation studies which show that strong modularity leads to a strong decline in variation, and finally to an evolutionary dead end. We discuss their research more extensively in the section on individual differences. Nagy and Williams (2001) presented experimental support for the idea that organisms possess both modular and nonmodular developmental mechanisms. They stated that there is ample evidence for the modularity of the segments that make up the principle body axes of vertebrates and for the modularity of the major body parts that arise from the segments (e.g., the limbs). That is, the genes that underlie the segments of the body axes, and the development of each particular body part can be specified. The body parts themselves can be divided into smaller units, but the genes underlying these smaller units are not specific, that is, there is no one-to-one relation between specific genes and specific parts of the limb. That is, the genes that underlie the smaller parts of limbs are domain-general.

Simulation studies by Kauffman (1993) support the idea that organisms have both domain-general and domain-specific properties. Kauffman described the capacity of a system to evolve in terms of fitness landscapes that are characterized by a degree of ruggedness. Fitness landscapes are used to describe the relationship between genotypes and their fitness. Fitness landscapes are two-dimensional representations, with genotypes on the x-axis and the degree of fitness on the y-axis. Genotypes that resemble each other are close together on the x-axis, whereas genotypes that are very different are far away from each other on the x-axis. Genotypes with a high fitness have a high value on the y-axis, whereas genotypes with a low fitness have a low value on the y-axis. The ruggedness of the fitness landscapes is indicative of variation in the fitness conferred by similar genotypes. A smooth landscape expresses the similar fitness conferred by similar genotypes.

Kauffman's (1993) simulation study revealed that very smooth landscapes and very rugged landscapes lead to low evolvability. An intermediate degree of ruggedness results in optimal evolvability. In terms of domain-specific and domain-general abilities, we may explain this as follows. A very smooth landscape represents a system with stable fitness. Such a system consists of domain-specific modules that have proved to be adaptive. There are few pleiotropic effects across the different modules, so the modules will not easily break down because of negative pleiotropic effects. As long as there are no significant environmental changes, such systems do well. However, when the environment changes significantly, these modules are inflexible and cannot improve by means of positive pleiotropic effects. Such a system has low evolvability. In terms of domain-specificity, systems with only domain-specific abilities have low evolvability. On the other hand, a very rugged landscape represents a system with a single domain-general ability. In this kind of system, a small change affects the fitness of the whole system, resulting in many different peaks and valleys in the fitness landscape. This system also has a low evolvability, because a single negative change in the system can reduce the fitness of the system as a whole dramatically. A system with both domain-specific and domain-general abilities has the greatest evolvability.

Conclusion

We showed that there is ample empirical evidence for the existence of several domain-general abilities. In addition, we showed that the evolutionary developmental approach provides models that can explain the existence of both domain-specific and domain-general abilities. We conclude that, if evolutionary psychology is to provide a metatheoretical framework for psychology that can address the existence of both domain-specific and domain-general abilities, it will have to include elements of the evolutionary developmental approach.

Nature and Nurture

Present-day psychologists subscribe neither to the idea that the mind is a tabula rasa nor to the idea that the mind is completely genetically determined. Today, the nature–nurture debate is about how genetic and environmental influence interact in the development of phenotypes (e.g., Li, 2003), or about the question whether it makes sense to break up the environmental

and the genetic in separate components (Lickliter & Honeycutt, 2003; Oyama, 2000).

Mainstream Evolutionary Psychology's View

Mainstream evolutionary psychologists proposed the integrated causal model to explain the interaction between nature and nurture (Tooby & Cosmides, 1992). This model contends that the human mind consists of a set of evolved functionally specialized content-specific information-processing mechanisms that generate human culture. Thus, Tooby and Cosmides regard evolved psychological mechanisms as the basis of human culture: "Content-specific information-processing mechanisms generate some of the particular content of human culture, including certain behaviors, artifacts, and linguistically transmitted representations" (p. 24). According to mainstream evolutionary psychology, evolved psychological mechanisms and the environment cannot be split up in two different components: Because of their evolved psychological mechanisms, humans create an environment that reflects the operation of their evolved architecture. Thus, mainstream evolutionary psychology rejects the dichotomies of the genetic and environmental, the biological and social, and the nativist and environmental. In general, mainstream evolutionary psychologists have little to say about the relation between their proposed evolved psychological mechanisms and genes. They study the mechanisms at the behavioral and the cognitive level and leave the question open about how the mechanisms actually develop.

Evolutionary Developmental Biology's Contribution

Evolutionary developmental biologists hold the view that there is a dynamic interaction between genes and environment. As Sterelny and Griffiths (1999) stated, "No one supposes that a plant will grow in just the same way no matter what sort of light or nutrients it receives" (p. 13). Sterelny and Griffiths distinguished two kinds of interaction. The first kind of interaction is additive: A small genetic change will result in a small change in the outcome, and a large genetic change will result in a large change in the outcome (i.e., a linear relationship between genetic change and phenotypic change). This kind of interaction is referred to in statements such as, "If we keep the environment equal, then differences in outcomes are attributable to differences in genes (and vice versa)."

The second kind of interaction is nonadditive, which means that a small genetic change may lead to a large difference in outcome (i.e., a nonlinear relationship between genes and outcomes). The phenotypic expression of some genes can be strikingly different in different contexts. This can be illustrated in depictions of identical twins with obviously different lengths and weights (Gottlieb, 2000, p. 96). Sterelny and Griffiths (1999) stated that most scientists think of interactions between genes and environment in an additive way, although it is most likely that interactions happen in nonadditive ways.

Gaertner (1990) provided empirical evidence for the existence of nonadditive interaction. He noted that efforts to standardize laboratory animals so far have been unsuccessful. He found that when genetic variability is reduced by using inbred strains, and when the amount of food is held constant, the weight of mice is still highly variable. It is estimated that 70 to 80% of the range of body weight is due to a third source (i.e., in addition to genetic and environmental sources) of variability. Archer et al. (2003) compared variability in phenotypic traits between cloned pigs (Duroc swines) and noncloned controls. Remarkably, for many traits variability was equal for cloned and noncloned pigs—for example, body weight, number of teats, skin type, hair growth, and several blood parameters such as calcium. For some blood parameters, variability was even larger for cloned pigs than for noncloned controls.

Molenaar, Boomsma, and Dolan (1993) argued that this third source probably comprises self-organizing processes. The process of self-organization is often recognized in evolutionary theorizing that is strongly related to evolutionary developmental biology (e.g., Camazine et al., 2001; Kauffman, 1993, 1995; Solé & Goodwin, 2000). It has also been recognized in psychological theorizing (Kelso, 1995; Lewis, 2000; Smith & Thelen, 1993; Thelen & Smith, 1994), but, as Kenrick (2001) pointed out, it is mostly ignored in mainstream evolutionary psychology. In self-organizing systems, patterns appear through interactions internal to the system, without intervention of external directing influences. In technical terms, self-organization refers to "a set of dynamical mechanisms whereby structures appear at the global level of a system from interactions among its lower-level components" (Solé & Goodwin, 2000, p. 151). This means that patterns appear without a blueprint of the patterns themselves.

From an evolutionary point of view, we arrive at the concept of self-organization to explain recurrent patterns in nature. Kauffman (1993, 1995) noted that the patterns on the trunk of a tree, the patterns on shellfish, and the stripes on the skin of the zebra or the tiger look so alike, whereas neo-Darwinists claim that evolution takes place based on random mutations and the selection of good variants. Based on the neo-Darwinist idea, one would expect much more variant patterns in nature. However, to the contrary, there is increasing evidence for extreme homology, that is, extreme conservation of ancient patterns (Gerhart & Kirschner, 1997; Gould, 2002). Random mutations and natural selection are not sufficient to explain these recurrent patterns. Models that include the concept of self-organization, however, can do so.

Conclusion

We showed that there is empirical evidence for the existence of a third source of variance that can be explained neither by genetic nor by environmental influences.

It has been proposed that self-organization plays an important role in creating variance. Mainstream evolutionary psychologists and the neo-Darwinian approach to evolution, at least at present, have yet to develop explicit models for nonadditive interaction and self-organization. Because evolutionary developmental biology provides these models, we argue that we need this approach to achieve a metatheoretical framework based on evolutionary psychology, which can bring new input into the discussion about the role nature and nurture in explaining the human mind.

Stagewise Versus Gradual Development

A third major issue in psychology is whether children's development proceeds in a stagewise or in a continuous fashion. A stage is defined by a discrete period of time, in which the child is characterized by a qualitative different functioning compared to the functioning in other periods. Piaget was the major proponent of stagewise psychological development (Piaget & Inhelder, 1969). He proposed a theory in which development includes four major stages. As described by Flavell (1982), a developmental period is called a stage, if the child's cognition is homogeneous at any point during that period. That is, the mind operates consistently at a single, uniform level of complexity and cognitive developmental maturity. Thus, one of the questions concerning stages is whether children possess homogeneous cognitive abilities over extended periods. Another question is whether the transition from one period to the next is abrupt, rather than continuous or gradual.

Mainstream Evolutionary Psychology's View

Mainstream evolutionary psychologists have not addressed the issue of stagewise development. However, it is possible to give an evolutionary interpretation of stagewise development by comparing the development of humans with the development of primates. For example, Bjorklund and Pellegrini (2002) mentioned Piaget's work in reference to Parker and McKinney's (1999) view on primate cognition. Piaget (1952) distinguished six substages in the sensorimotor period, the first stage of development. Parker and McKinney studied the existence of these six sensorimotor substages in humans, great apes, and monkeys. They concluded that all primates follow the same sequence of sensorimotor stages. Bjorklund and Pellegrini related this finding to the issue of domain-specific versus domain-general abilities. They contended that "intelligence is multifaceted, and that a Piagetian-like domain-general intelligence exists alongside other more domain-specific abilities, which have their own phylogenetic history" (p. 143). This suggests that there is a relation between the debate on the domain-specificity of the mind and the debate on stagewise development. Stages, as defined by Piaget, are domain-general. From the discussion on domain-specific versus domain-general abilities, we doubt that mainstream evolutionary psychology will subscribe to this aspect of Piaget's theory. Another part of Piaget's stage theory concerns the existence of abrupt transitions from one stage to the other. Because mainstream evolutionary psychologists have not addressed this issue, we cannot evaluate their point of view.

Empirical Evidence for the Existence of Stages in Development

The first question is whether there is empirical evidence for homogeneity of cognition in children's development. This is one of the most controversial aspects of Piaget's theory (see Feldman, 2004, for a review). Piaget (1950) acknowledged the fact that children at a single point in development show different levels of cognitive skills on different but also on highly similar tasks. He called this phenomenon *horizontal décalage*, referring to the inability of the child to solve a particular problem, although the child can solve a similar problem involving the same operations. For example, the ability of conservation—that is, the ability to understand the permanence of the quantity of a substance in spite of changes of the form—is highly variable depending on what kind of substance is used. Conservation of number, mass, and length is reached between the age of 7 and 8, conservation of weight between the age of 9 and 10, and conservation of volume between the age of 11 and 12.

However, infants and older children differ both quantitatively and qualitatively. Current researchers in the Piagetian tradition have tried to reconcile the research findings of general qualitative differences between children of different ages, and the findings of specific abilities that can differ remarkably from domain to domain (Case, 1991; Feldman, 2004; Karmiloff-Smith, 1992). As explained in the discussion of domain-specificity of abilities, empirical evidence favors a position in which both domain-specific and domain-general abilities are admitted. In relation to the stage debate, this means that we have to adapt Piaget's strict idea of domain-general stages to an idea of stages that contain both domain-specific and domain-general elements (see Feldman, 2004, for a similar view).

The second question is whether abrupt transitions from one stage to another take place. Because the idea of domain-general stages is controversial, this question is hard to answer. It is impossible to study transitions from one stage to the other without clearly

defined stages. However, if we abandon the idea of strict domain-general stages, we can ask whether the development within a domain is continuous or discontinuous. We need no longer to speak of stage transitions, because we do not exactly know how to define a stage, but we can speak of phase transitions.

Phase transitions are defined as points of instability and turbulence, where old patterns break down and new ones appear (Lewis, 2000; van der Maas & Molenaar, 1992). The concept of a phase transition is derived from dynamic systems theory and has its roots in physics. In physics, a phase transition is the observation of sudden changes in physical properties, for example, the transitions between solid (e.g., ice), liquid (e.g., water), and gaseous (e.g., steam) phases. Note that the independent variable (i.e., temperature) changes continuously, whereas the dependent variable changes discontinuously. The concept of a phase transition can be applied to cognitive development as well. In child development, a phase transition is the observation of sudden changes in cognitive properties (e.g., knowledge or skills). There is ample evidence for the existence of phase transitions in cognitive development.

For example, Jansen and van der Maas (2001) showed that a phase transition takes place in the development of proportional reasoning as measured by the balance scale task (Siegler, 1981). In the balance scale task, children are confronted with a scale and asked to predict the side to which it will tip, in view of a given configuration of weights. Clearly this movement depends on the number of weights that is put on either side and on the distance between the weights and the fulcrum. Children use several different rules to solve items of the balance scale task. Initially, they focus mostly on the number of weights (Rule 1). Later, they focus only on the distance between the weights and the fulcrum (Rule 2). Finally, children use both dimensions to predict the movement (Rule 3, i.e., adding distance and weights, and the correct Rule 4, i.e., multiplying distance and weight).

Jansen and van der Maas (2001) tested 6- to 10-year-olds on the balance scale task to study the phase transition from Rule 1 to Rule 2. They hypothesized that children who do not spontaneously use Rule 2 can be encouraged to adopt this rule by making the distance dimension more salient. The salience of the distance dimension increases, as the distance between one of the weights and the fulcrum increases. Children received a series of five distance items, in which the distance between one of the weights and the fulcrum gradually increased. A phase transition was observed: Some children who initially used only Rule 1 switched to using Rule 2 when the distance between the weight and the fulcrum increased.

Phase transitions have also been observed in the domains of language development (Dromi, 1987; Ruhland, 1999; Ruhland & van Geert, 1998), motor development (Smith & Thelen, 1993; Vereijken & Adolph, 1999; Wimmers, Savelsbergh, Beek & Hopkins, 1998), analogical reasoning (Hosenfeld, van der Maas, & van den Boom, 1997) and physical growth (Hermanussen & Burmeister, 1993; Lampl, 1993; Lampl & Johnson, 1993). Thus, although there is little empirical evidence for the existence of strict Piagetian stages, there is ample evidence for the existence of phase transitions occurring within more specific domains.

Evolutionary Developmental Biology's Contribution

The main question in evolutionary developmental biology regarding the stage debate is how stagewise development is related to the evolvability of populations. As previously defined, evolvability is the ability to respond to a selective challenge (Hansen, 2003). This ability requires the capacity to produce the variation that can serve as the input for natural selection. Evolutionary developmental biologists would like to know whether evolvability is dependent on the nature of development, that is, whether development proceeds in a stagewise or continuous fashion (Stadler, Stadler, Wagner, & Fontana, 2001).

Kauffman (1993, 1995) has contributed to this issue. As described in the discussion on the domain-specificity of abilities, his simulation studies provided evidence for the idea that a system with both domain-specific and domain-general abilities has the greatest evolvability. Of interest, these simulation studies also provided evidence for phase transitions in evolution. The simulations are built on the idea of random graphs. In a random graph, a set of dots, or nodes, is connected at random with a set of lines. Imagine that we have 100 nodes and that only a few nodes are connected by lines. Then imagine that we increase the number of lines, so more and more nodes become interconnected. After a while the nodes start to become interconnected into larger clusters. With up to 50 lines, the number of nodes that are interconnected within a single cluster is relatively limited. However, when the number of lines exceeds 50, a "giant cluster" suddenly forms. Kauffman's simulation studies revealed a general finding: As the ratio of lines to nodes passes 0.5, a phase transition happens from relatively small clusters to relatively large clusters of interconnected nodes.

According to Kauffman (1993, 1995), this kind of phase transitions always occurs when individually simple elements get connected and start to form more meaningful complex wholes. As evolution is mostly about the formation of complex systems composed of simple elements, Kauffman claimed that phase transitions are at the heart of evolution. Kauffman's model has enjoyed a lot of attention in the literature. Many specific changes of his model have been proposed, but phase transitions remain central to all variations of this

model (e.g., Aldana, 2003; Solé, Salazar-Ciudad, & Garcia-Fernández, 2002).

Why would this theory be of interest for psychology? In the section about nature and nurture, we explained why self-organization is an important concept in the explanation of development. Kauffman's (1993, 1995) simulation studies demonstrated that complex wholes start to form when individually simple elements are connected. We have seen that self-organization (i.e., the nonlinear interaction among small-scale elements) plays an important role in this process. Kauffman's work also demonstrated that phase transitions characterize the process of interacting individual elements, which result in complex wholes. The emergence of self-organization from phase transitions, often called phase shifts or bifurcations, has been demonstrated mathematically (Scheinerman, 1996) and applies to physical, chemical, and biological systems (Kelso, 1995; Nicolis, 1977; Prigogine & Stengers, 1983; Thelen & Smith, 1994). The general idea is that complex systems arise by means of nonlinear interactions among local elements, and these self-organizing processes always occur by means of phase transitions. So if self-organization is ubiquitous in nature, phase transitions are also ubiquitous.

If complex systems arise by means of self-organization, and thus by means of phase transitions, it would seem unavoidable that individual development is characterized by self-organization and phase transitions. We illustrate this idea with an example concerning infant kicking (Thelen & Smith, 1994). During the 1st year of life, infants kick their legs in rhythmic succession, seemingly caused by nonspecific behavioral arousal. The traditional explanation of this kicking is that it is controlled by a Central Pattern Generator (CPG), a group of neurons in the spinal cord that could generate locomotion without sensory input (for references, see Thelen & Smith, 1994). An important aspect of the CPG is that it leads to precise alternation between flexor and extensor neurons in the limbs. However, in studying the muscles in the infants' legs, Thelen and Smith did not find this pattern of alternation. Instead, they found that at the initiation of the flexion movement, both the flexors and the extensors of the hip, knee, and ankle joints contracted simultaneously. Moreover, they observed no muscle contraction at the initiation of the extension part of the kick.

According to Thelen and Smith (1994), the leg completed the kick, not because of a CPG prescribing how to end the kick but because of the spring qualities of legs. That is, legs store elastic energy during the flexion movement. Combined with the pull of gravity, this energy caused the leg to extend. Because there is no agent that prescribes the kicking trajectory, the cyclic kicking movements can be viewed as self-organized. In addition, because of the recurrent nature of this cyclic movement, it can be said to be a stable pattern. Infants must overcome this pattern to learn to crawl, stand up, and walk. Specifically, to execute these movements, infants must be able to move the joints of the knee, ankle, and hip independently.

Thelen (1985) found that the pairwise correlations between knee–ankle, hip–ankle, and hip–knee movements were moderate to high up to about Month 8. In the last months of the 1st year, this coupling decreased dramatically, indicating strong individual actions of the different joints. A phase transition occurred from strong interlimb coupling to independent action of the joints. This research shows that self-organization in development is amenable to empirical study and that phase transitions from relatively simple behavior to more complex patterns take place, as a consequence of interactions among local elements.

Conclusion

Empirical evidence for the domain-generality of Piagetian stages is lacking, but we showed that there is ample evidence for phase transitions occurring within specific domains of development. Evolutionary developmental biologists relate phase transitions to the evolvability of traits, making phase transitions an important subject for both researchers in the domain of evolution and researchers in the domain of development. They also show, along with mathematicians and physicists, that self-organization and phase transitions go hand in hand, putting the concept of phase transitions in a larger framework. We conclude that if we want to arrive at a metatheoretical evolutionary psychology, we must be able to give an evolutionary rationale for the occurrence of phase transitions in development.

Individual Differences

The study of individual differences is a major part of psychological research. Most studies focus on individual differences in intelligence and personality. The question that remains unresolved is, How do individual differences arise?

Mainstream Evolutionary Psychology's View

Mainstream evolutionary psychology studies the universal architecture of the mind. Regarding individual differences, Tooby and Cosmides (1990, 1992) emphasized the distinction between evolved mechanisms and manifest behavior. Although there are individual differences in manifest behavior, the underlying set of evolved psychological mechanisms is universal. Individual differences are due to different environmental input, not differences in the cognitive architecture. For example, children raised in England speak English and children raised in the Netherlands speak Dutch, but the underlying ability to learn language is the same in all children. To know how the mind works, we have

to unravel the common cognitive architecture. Thus, we have to identify and explain the universals, not the individual differences.

Tooby and Cosmides (1990) argued that genetically based individual differences are an unrepresentative subset of human features and are only quantitative variation of domain-specific psychological mechanisms. There must be enough variation in the population to combat parasites[1] and to be able to react to changes in the environment, but this variation must be superficial from the point of view of the functional design of the organism, so as not to interfere with it. Tooby and Cosmides also argued that human groups do not differ substantially in the genes they possess. Natural selection is a process that eliminates variation. They stated, "Those interested in studying complex psychological mechanisms should be most interested in design features that are inherited, but not heritable" (p. 38). They followed with

> From the point of view of natural selection, it does not matter whether an alternative strategy is activated in an individual by a gene, an environmental cue, or a cognitive assessment of the situation. All that matters is that the innate mechanism is designed such that the right alternative is activated under the right circumstances. (p. 43)

But if there is little room for variation, how can people adapt to changing environments so well? Where does this plasticity come from? Tooby and Cosmides (1992) argued as follows:

> The solution to the paradox of how to create an architecture that is at the same time both powerful and more general is to bundle larger numbers of specialized mechanisms together so that in aggregate, rather than individually, they address a larger range of problems. Breadth is achieved not by abandoning domain-specific techniques but by adding more of them to the system. (p. 113)

In sum, mainstream evolutionary psychologists' point of view is that plasticity is the result of massive modularity, not of large differences between individuals.

Evolutionary Developmental Biology's Contribution

The discussion of individual differences in evolutionary developmental biology centers around the study of mutation-selection balance, that is, the balance between the number of mutations (i.e., variation or individual differences) and the number of adaptations within a system (e.g., Turelli, 1984; Zhang & Hill, 2005). The conflicting fitness effects (i.e., sometimes positive, but often negative) of mutations suggest small genetic variation, but the opposite is true. In natural populations, variation is typically large and attributable to genes at 20 to 60% (i.e., heritability is .2 to .6; Mousseau & Roff, 1987).

An appealing idea is that the loss of variation due to natural selection is compensated for by many new mutations (i.e., the mutation-selection balance). Different models for this balance have been proposed, but some of them have assumptions that predict much higher mutation rates than are observed in nature (Kimura, 1965), and some of them predict less variation than is observed (Turelli, 1984). Recently a model was proposed that can account for the observed mutation rate (Zhang & Hill, 2005; Zhang, Wang, & Hill, 2004a). Recall that all genes have pleiotropic effects (i.e., they have an effect on more than one trait). It is not feasible to describe all pleiotropic effects of any gene on all traits. However, it is possible to assess the effects of a gene on the focal trait (i.e., the trait that is influenced by that particular gene mostly) and the effects of a gene on fitness. The latter effect includes all pleiotropic effects. These two effects of genes are the basis of Zhang et al.'s (2004a) model, called the joint stabilizing and pleiotropic selection model. Predictions derived from this model fit well to empirical observations (Zhang, Wang, & Hill, 2004b). Thus evolutionary developmental biologists have recently developed a model that can explain the balance between the generation of individual differences and the elimination of individual differences by natural selection. So far, empirical results that fit well within the model are often based on studies of the fly *Drosophila*. The next step is to study whether the same results can be found in other species, including human beings.

Another issue that evolutionary developmental biology addresses is how people, or organisms in general, are able to adapt to changing environments. Mainstream evolutionary psychologists suggested that plasticity is the result of massive modularity, not because of large individual differences (Tooby & Cosmides, 1992). However, they did not provide empirical support for this statement. Can evolutionary developmental biology provide this support? West-Eberhard (2003) argued that modularity can contribute to the emergence of plasticity. For example, a multisegmented leg is more flexible than a single-segment, or a less segmented leg. She followed the same line of reasoning in relation to behavioral flexibility: "Modularity in behavioral sequences permits a great diversity of combinations to characterize the flexible repertoire of an individual" (p. 59). She referred to a model of courtship behavior of grasshoppers, in which courtship is organized in more or less independent modular phases.

[1]Species that reproduce asexually, and thus have offspring that are genetically identical, are vulnerable to parasites. Once parasites "crack" their genetic code, all of their offspring and kin will also pass away. Asexually reproducing species have a short life, so parasites do not have enough time to crack the genetic code.

This organization permits sensitivity to environmental conditions (Otte, 1972).

Research by de Kroon, Huber, Stuefer, and van Groenendael (2005), focusing on plasticity in plants as the result of modularity, is consistent with West-Eberhard's theory. De Kroon et al. showed that plasticity in plants is the result of changes at the modular level, that is, at the level of structural and functional subunits of the plant, rather than changes that influence the whole plant. Chipman (2002) presented similar results in a study of different anuran species (i.e., tailless amphibians, frogs, and toads). He showed that the plasticity of anuran development is attributable to the modular nature of anuran development. Modules can shift in time and space, without affecting other modules. Different arrangements of modules give rise to a large degree of plasticity.

Of course, the step from plants, grasshoppers, and frogs to human behavior and cognition is large, but these species can be used as models for studying the relation between modularity and plasticity. Another way of studying this relation that has been used by evolutionary developmental biologists is by means of simulation experiments. Ancel and Fontana (2000), using this method, showed that natural selection leads to a decrease in plasticity, which as a side effect results in modularity. They used an empirically simple model of RNA sequences folding into different shapes to illustrate their ideas about the relation between natural selection, plasticity, and modularity. In this model, the RNA sequence represents an individual's genotype and the folded shape represents an individual's phenotype. The RNA sequence can fold into several different RNA shapes under environmental fluctuations (i.e., temperature fluctuations).

In the simulation experiments it was assumed that the fitness value of a particular RNA shape is reflected by the amount of time the RNA sequence spends in it. The RNA sequence was regarded as plastic if it can fold into many different shapes. However, when the RNA sequence folded quickly into many different shapes, it did not spend much time in each shape individually. The more alternative shapes were possible, the less time the RNA sequence spent in each shape, including the advantageous ones. When the RNA sequence stayed in the advantageous shapes for extended periods, the simulation studies revealed that the number of possible shapes (under different environmental circumstances) was reduced very quickly (i.e., there was a rapid loss of plasticity). As a side effect, the advantageous shapes appeared to show great modularity (i.e., they contained several structural units that are thermophysically and genetically independent). To summarize, optimal structures have low plasticity and show strong modularity. Although modularity leads to quantitative improvement of a trait, it also prevents significant structural modifications of that trait. Once modules are available evolutionary novelty is reduced to combinatorial arrangements of the modules.

Thus, according to Ancel and Fontana (2000), the emergence of modularity implies a reduction of evolvability because it leaves little room for significant structural changes that improve the phenotype. This finding is consistent with the proposal of Hansen (2003), which was discussed in the section on domain-general versus domain-specific abilities. Hansen advanced, and provided evidence for, the view that modularity is not the best evolutionary solution; it reduces the mutational target size.

Based on these results, it is unlikely that plasticity is the result of extreme modularity, as this would reduce the mutational target size considerably. Conversely, it is also likely that plasticity is only possible given a certain degree of modularity. Modules can be changed without affecting other modules, leaving room for plasticity within a module. As was discussed in earlier sections, the results of Kauffman's (1993, 1995) simulation experiments offer a compromise that explains the existence of both stability and plasticity within a single system. In his random networks, plasticity depends on the degree of connectedness among the elements of the network. If the network is sparsely connected, the system exhibits clear order. The network quickly falls into very short cycles and is very stable. Although stable behavior emerges, this behavior is very simple. When the degree of connectedness is very high, the network behaves in a chaotic way. There is a certain order, but when the network is very dense, this order cannot easily be detected. The network is too plastic and clear patterns are not discernible. This behavior also is not very interesting. Only when the network has an intermediate density, discernable interesting patterns emerge. Kauffman claimed that networks at the edge of chaos behave in a realistic manner, that is, they serve as a model for life processes. Only systems with an intermediate degree of connectedness of elements can evolve.

To illustrate the relevance for psychology, this idea of connectedness plays an important role in a new model for general intelligence proposed by van der Maas et al. (2006). Van der Maas et al. explain general intelligence with a nonlinear dynamic model adapted from mathematical ecology. Simulation experiments show that the positive correlations between scores on cognitive tasks are not caused by a single underlying biological or cognitive source but by the positive mutual interactions between cognitive modules during development. It appears that such a developmental process results in the same pattern of positive correlations between tasks on which the famous g-factor is based. The dynamic model, however, also explains additional phenomena in the development of intelligence, such as the hierarchical factor structure of intelligence and the increase in heritability of "g." Thus, simulation studies

such as Kauffman's (1993, 1995) have also been shown to be successful in a psychological context.

Conclusion

Mainstream evolutionary psychologist have argued that to unravel our cognitive architecture, we have to study universals rather than individual differences. The evolutionary developmental approach provides detailed models about the mutation-selection balance, which predict the genetic variation for different traits in different populations. Another contribution of this approach is that it provides some evidence for the hypothesis that modularity increases plasticity. However, it also shows that massive modularity does not necessarily do so; systems with a moderate degree of modularity have the greatest evolvability.

Discussion

The first aim of this article was to evaluate the role of evolutionary psychology as a metatheory for psychology. We argued that mainstream evolutionary psychology, as advanced by Tooby and Cosmides (1992), Buss (1995, 2003), and Pinker (1997), will have to address the major issues in psychology if it is to fulfill this role. Here we considered four such issues. We judge mainstream evolutionary psychology to be deficient in this respect. The discussed deficiency should not be construed to imply that evolutionary psychology has no role to play in the general discussions in psychology. As discussed by Buss and Reeve (2003), evolutionary psychology certainly has identified important research questions, which were largely missing in the general research agenda of psychology. However, we do contend that the scope of mainstream evolutionary psychology requires broadening, if it is to contribute to the solution of the major issues in psychology. We judge the present strict adherence of mainstream evolutionary psychology to the neo-Darwinian approach to be overly restrictive. The neo-Darwinian approach is undoubably indispensable, but it does not represent the whole field of evolutionary biology. We argued in favor of expanding the scope of mainstream evolutionary psychology to include the theory of evolutionary developmental biology.

The second aim of the article was to demonstrate how the inclusion into mainstream evolutionary psychology of concepts and findings from the field of evolutionary developmental biology does result in the desired metatheory. So far, alternatives to mainstream evolutionary psychology, such as developmental dynamics (Lickliter & Honeycutt, 2003), have not been welcomed with open arms. For example, Buss and Reeve (2003) judged Lickliter and Honeycutt's proposal to be "obscure" (p. 851) and stated that they failed to provide clear hypotheses. Although Lickliter and Honeycutt's proposal may have not included specific hypotheses or predictions, it is not true that evolutionary developmental biology cannot furnish these. We derived several hypotheses, which are relevant to the major issues in psychology. The first hypothesis is that domain-general and domain-specific mechanisms coexist and that the ability to evolve requires both classes of mechanisms. The second hypothesis is that the interaction between nature and nurture is largely nonadditive and that self-organization constitutes an important third source of variance. The third hypothesis is that development is characterized by phase transitions. The fourth hypothesis is that individual differences are largely attributable to pleiotropic effects that are incorporated in recent models that describe the balance between selection and mutations. As discussed, these hypotheses are consistent with many empirical results.

One might argue that research in the field of evolutionary developmental biology is concerned mainly with nonhuman organisms and that the link with human development is therefore tenuous. Certainly most research in evolutionary developmental biology is not concerned with humans, but this does not mean that this research cannot provide input that is relevant to the study of human development and evolution. Moreover, for ethical reasons many hypotheses about the relationship between genetics and development cannot be tested on human beings, so animal research is the only way to get a better insight into this relationship. Another possible objection against the inclusion of concepts and findings from evolutionary developmental biology in mainstream evolutionary psychology might be that the former is relatively new and therefore characterized by a lack of general consensus (e.g., this is the case with respect to the issue of modularity). Evolutionary developmental biology cannot be expected to provide clear-cut answers to all the unresolved questions in psychology. However, a clear contribution can be made, because evolutionary developmental biology provides other, potentially fruitful, perspectives on the major debates. For example, in evolutionary psychology the discussion concerning the issue of modularity often takes the form of a philosophical debate, in which logical arguments are advanced concerning the likelihood of the evolution of domain-specific (modular) versus domain-general structures (e.g., Cosmides & Tooby, 1994; Fodor, 2000). In evolutionary developmental biology, this discussion takes the form of a biological debate about how modules actually develop and evolve and how these modules are biologically related to each other (e.g., Griswold, 2006; Wagner, 1996). In contrast to the philosophical debate, this biological debate is more strongly embedded in empirical findings. Thus evolutionary developmental biology can provide an empirical basis for the various arguments in the philosophical debate and thus bring the debate closer to a resolution. Moreover, evolutionary

developmental biologists have used a wider diversity of research methods to study basic issues, such as modularity. For example, simulation experiments and mathematical modeling are often used as research tools by evolutionary developmental biologists (e.g., Hansen, 2003; Kauffman, 1993, 1995). Such tools have hardly been explored by evolutionary psychologists.

Another advantage of the evolutionary developmental approach is that its incorporation in the metatheoretical framework will free evolutionary psychology from the accusation of simply providing "just-so stories," that is, ad hoc functional explanations of current cognition and behavior. Evolutionary developmental biology provides theory and empirical findings concerning the actual development and evolution of structures. It also lessens the emphasis of evolutionary psychology on the end-products of development (i.e., the final adaptations that help human beings to survive and reproduce). The perspective of evolutionary developmental biology includes the role of evolution in the ontogenesis of adaptations. Specifically, evolutionary developmental biology provides psychology with a general framework concerning development and the interaction of ontogenesis and evolution. This general perspective emphasizes the roles of self-organization and phase transitions, which give rise to partly modular structures with a balanced number of pleiotropic connections between them. This creates a greater mutational target size, and so greater evolvability.

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