Evolutionary Systems Theory: A Unifying Meta-Theory of Psychological Science

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Psychology is a theoretically heterogeneous discipline seeking a single, cohesive framework to unite the subdisciplines. To address this issue, I propose a hierarchical metatheory of psychological science that synthesizes neo-Darwinian selectionist thinking and dynamic systems theory by organizing evolutionary psychology, evolutionary developmental biology, developmental psychobiology, and the subdisciplines of psychology around four specific, interrelated levels of analysis: functional explanations for evolved, species-typical characteristics; explanations for between-groups differences arising from phylogenetic mechanisms; explanations for individual differences resulting from ontogenetic processes; and mechanistic explanations for real-time phenomena, respectively. Informational exchange between these levels advances their integration and facilitates important innovations, and the nonsubstantive metatheories of general selection and self-organization interpenetrate all four levels to promote consilience. I conclude by discussing the implications of this model for theory and research.

Keywords: dynamic systems theory, evolutionary developmental biology, evolutionary psychology, evolutionary systems theory, general selection, the hierarchically mechanistic mind, self-organization

In the spirit of dialectics (Peng & Nisbett, 1999; Sameroff, 2010), this article introduces a hierarchical metamodel of psychological science that draws from evolutionary system theory (EST) in an attempt to capitalize on metatheoretical juxtapositions (i.e., theses vs. antitheses) to create a synthesis of traditionally competing paradigms within our discipline. EST appeals to an emerging, transdisciplinary body of literature that unifies neo-Darwinian selectionist principles and dynamic systems theory (DST). As a general principle extending across the sciences, it assumes a complementary, inextricable relationship between the processes of general selection (of which natural selection is a special case) and self-organization (Rocha, 1998; Swenson, 2010; Weber & Depew, 1996). Given that humans are biological systems, it further predicts that psychologists should attend to distinct (albeit interrelated) levels of analysis rallied around Timbergen’s (1963) four broad questions pertaining to the scientific study of any species: (adaptive) function, phylogeny, ontogeny, and mechanism. Specifically, I propose a model that organizes these levels of explanation around evolutionary psychology, evolutionary developmental biology, developmental psychobiology (which incorporates EST with developmental psychology), and psychology’s collective subdisciplines, respectively. To build this model, I begin by highlighting core theoretical tenets, supportive empirical work, and important debates at each of these levels, and outline key conceptual distinctions that emphasize their commensurability. Finally, I conclude by elucidating the implications of EST for psychological theory and research.

While I fully acknowledge the importance of skepticism concerning “grand unifying theories,” this should not obstruct our pursuit of consilience (Caporaal, 2001; Sheldon, 2011). Consilience entails the synthesis of research across all scientific disciplines to unify knowledge and create a common information base, forcing professional researchers to consider key theoretical constraints imposed by other disciplines (see Wilson, 1998). By adhering to this principle, I hope to introduce an approach to psychological inquiry that contributes meaningfully to the advancement, scientific legitimacy, and unity of our tenaciously divided field.

Evolutionary Psychology

EP has long been heralded an integrative paradigm to unite the subdisciplines (Buss, 1995, 2004; Cosmides, Tooby & Barkow, 1992; Crawford & Krebs, 2008). It centers on the massive modularity hypothesis (MMH). This maintains that instead of being a general purpose problem-solver, the human mind comprises a large collection of species-typical, domain-specific, functionally specialized mechanisms (Buss, 1995). These respond to only certain types of proximate input (gleaned from an external environment or other internal processes); and once activated, transform this information into output by influencing physiological activity, activating other mechanisms, and/or producing manifest behavior

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1 Given the sheer extent of empirical support for the ideas discussed herein, please note that I have necessarily omitted a discussion of particular studies. For relevant details, the interested reader is directed to the major volumes and more specific sources referenced throughout.
Psychological mechanisms are adaptations: they have evolved, through the process of natural selection, because they increased the likelihood of reproductive success and/or survival throughout human evolution. Any hypothesis concerning such mechanisms must therefore be stated in terms of their consequences for inclusive fitness (Cosmides & Tooby, 1992). Note that these mechanisms may not predict survival and reproductive success in proximate contexts, but influence behavior in ways that were likely to have performed an adaptive function over evolutionary time. Consequently, EP differs from sociobiology (Buss, 1995).

To translate the MMH into research, evolutionary psychologists combine evolutionary computational theories with algorithmic models (Cosmides & Tooby, 1994). Evolutionary computational theories concern the functional (i.e., ultimate/adaptive) properties of psychological mechanisms, while algorithmic models concern the mechanistic (i.e., proximate) level of explanation by articulating the input and output criteria that characterize the mechanism in question (Scott-Phillips, Dickins & West, 2011). Knowing why a phenotypic feature exists imposes strong constraints on how it operates, and by using computational theories to restrict theoretical possibilities, one can derive a limited number of testable hypotheses (Cosmides & Tooby, 1994). Thus, the locus of EP is not behavior per se, but identifying, explaining, and describing the properties of specific psychological mechanisms.

The MMH continues to attract strong theoretical support (e.g., Barrett & Kurzban, 2006; Dewsbury, 2009; Ermer, Cosmides & Tooby, 2007; Frankenhuysen & Ploeger, 2007; Machery & Barrett, 2006; Okasha, 2003) and has generated a wealth of testable hypotheses backed by an impressive body of empirical work (see Buss, 2004; Crawford & Krebs, 2008; Dunbar & Barrett, 2007). However, many remain skeptical of the MMH and some reject it altogether (e.g., Fodor, 2000; Greenberg, Partridge, Mosack, & Lambdin, 2006; Jablonka & Lamb, 2007; Karmiloff-Smith, 2000; Panksepp & Panksepp, 2000). Chiefly, it is criticized for promoting human essentialism and genetic determinism, producing overly conjectural hypotheses, and failing to account for neural plasticity, individual differences, and domain-general cognitive processes (Buller, 2005).

Arguably, evolutionary psychologists stand to benefit from addressing these critiques. Assuming this approach in the following section, I submit a refinement of the MMH that attends to its strengths and echoes proposals by Barrett and Kurzban (2006), Cosmides & Tooby (2000), and Merritt (2008). The idea that human psychological and behavioral processes rely on hierarchical message passing is also consistent with accepted models in neuroscience, where the output of one neural level is seen to provide input for the next, with sensory data representing the lowest level and higher cortical activity the highest (Friston, 2010). Further, this model aligns with empirical work highlighting specific cognitive capacities that process information across a range of subdomains (e.g., working memory, general intelligence, inhibition, habituation, associative learning, metacognition; Penn, Holyoak & Povinelli, 2008; Ploeger et al., 2008a). Finally, the HMM is widely supported by anthropological literature, which suggests that human ancestral (particularly social) conditions were likely to have fa-
vored flexible mechanisms that are highly dependent on social learning, able to manage context-dependent analysis, and integrate information gleaned from more primitive, lower-order domain-specific mechanisms (see Flinn, 1997).

**Evolutionary psychology reconsidered.** I propose here that evolutionary psychologists recast the MMH in terms of the HMM: a model that resolves the domain specificity/generality debate, allows for developmental plasticity, and accords with theoretical and empirical advances within and beyond EP. Arguably, this furthers the scientific legitimacy of the paradigm.

There are compelling reasons to absorb EP into psychological theorizing. First, natural selection is a fully accepted explanation for the functional properties of all biological systems (Tooby, Cosmides, & Barrett, 2003). Moreover, EP conforms to consilience by drawing heavily from anthropology, evolutionary biology, evolutionary ecology, genetics, paleoanthropology, philosophy, sociobiology, and zoology (Caporael, 2001; Frankenhuiss & Ploeger, 2007; Machery & Barrett, 2006).

Acknowledging the influence of evolved mechanisms on psychology and behavior is far from trivial. To date, EP has produced a wealth of empirically supported theories generating unique, testable predictions relevant to manifold psychological subdisciplines (see Buss, 2004; Crawford & Krebs, 2008; Dunbar & Barrett, 2007; Ellis & Bjorklund, 2005; Pinker, 1997). The search for relatively universal psychobiological features has also inspired extensive cross-cultural investigations, producing a representativeness largely unrealized by other psychological paradigms (Tooby et al., 2003). Finally, evolutionary models provide insights into biological, psychological, and social phenomena not afforded by other social scientific theories (e.g., Figueredo et al., 2006). Thus, by neglecting EP, one also runs the risk of neglecting a key resource for addressing important individual, social and political problems (Crawford & Krebs, 2008).

It should also be recognized that EP is a heterogeneous paradigm encompassing a range of selection theories (e.g., sociability theories, multilevel evolutionary theories and systems theories; see Caporael, 2001). All of these models draw from the nonsubstantive metatheory of general selection, involving three interacting principles of change: variation, selection, and retention (Caporael, 2001). It has long been established that this process not only applies to organisms, but acts (e.g.) on molecules, neural synapses, behaviors, cultural beliefs, technological products, and scientific theories (Czik, 1995). This has two implications. So long as Darwinian principles and methods are adapted to suit the subject matter, they can be extended beyond the analysis of psychobiological adaptations to include other phenomena relevant to psychological inquiry (Mesoudi, Whiten, & Laland, 2006). Second, EP is best considered a theoretically diverse field that has, at its core, inclusive fitness theory (Hamilton, 1964), but also encompasses sociability, multilevel, and systems approaches. Arguably, the capacity of such a substantive body of theory and research to advance our understanding of human psychology and behavior ought not to be ignored.

Nevertheless, EP cannot explain everything. Not all phenotypic features are adaptations, a sentiment expressed by evolutionary psychologists themselves (Barrett, 2008). Furthermore, while evolutionary psychologists focus on the functional (i.e., ultimate) properties of phenotypic features, EP does not necessitate research into the developmental or physiological (i.e., proximate) mechanisms responsible for producing them (Kenrick, 2001; Lickliter & Honeycutt, 2003). In a related vein, EP generally centers on species-typical or population-level traits fixed by selection, leading to claims that it tends to overlook the influence of the environment and the ways in which developmental plasticity produces substantial variations between groups and individuals (Buller, 2005; Lickliter & Honeycutt, 2003). Last, EP has yet to fully encapsulate another fundamental mechanism which revises the idea that evolution occurs solely through natural selection (i.e., self-organization; see Kaufmann, 1993). Arguably, a fully integrative theory of psychological science demands recourse to fields that explicitly address such issues. I turn now to two other paradigms that do so.

**Evolutionary Developmental Biology**

Evolutionary development biology (EDB) examines the relationship between ontogenetic and evolutionary processes (see Hall, 1999; Oyama, 2000; West-Eberhard, 2003). Proponents maintain that instead of occurring through random mutations alone, new variants impacting on fitness often emerge during ontogeny before natural selection has a chance to operate. Thus, to explain the evolution of a morphological, physiological, or behavioral trait, one needs to consider the developmental processes contributing to its construction (Ploeger et al., 2008a). Research in EDB is ideally suited to the study of phylogeny—eliciting mechanisms responsible for the emergence of important novelties in evolution which then become subject to selection (Ploeger et al., 2008a).

EDB promotes consilience by incorporating botany, biological systematics, ecology, genetics, paleontology, and zoology, alongside cell, comparative, developmental, and evolutionary biology (Jablonska & Lamb, 2007; McCain, 2010). It also provides evolutionary explanations for the plasticity of the organism and variability in populations, while extending the traditional subject matter of neo-Darwinian thinkers from relatively species-typical features to include group- and individual-level differences (Ploeger et al., 2008a). Minimally, it does so via two avenues.

First, it explains the maintenance of genetic variation and individual differences in fixed populations. Because natural selection eliminates phenotypes that deviate from the optimal adaptive value of a trait, explaining high levels of genetic variance in natural populations is problematic for classical Darwinian models (Ploeger et al., 2008a). A solution lies in mutation-selection balance: the balance between the number of mutations and the number of adaptations within an evolved system (Turelli, 1984). In particular, Zang and Hill (2005) have proposed a model that successfully explains the high mutation rates observed in nature. Their joint stabilizing and pleiotropic selection model is predicated on pleiotropy, where a single gene has effects on more than one phenotypic trait. Specifically, they point out how a mutant gene with deleterious effects upon the adaptive value of a focal trait can still be preserved by natural selection because of the neutralizing influence of its pleiotropic effects upon fitness.

Second, EDB accounts for stable patterns of plasticity in populations. Of particular relevance, Lam and Jablonka (2008) describe how plasticity (the capacity of a genotype to produce several phenotypes) contributes directly to evolvability (an organism’s capacity to produce heritable, selectable phenotypic variation;
Kirschner & Gerhart, 1998). To do so, they explore the notion of epigenetic inheritance systems.

**Epigenetic inheritance systems.** Jablonka and Lamb (1995, 2005, 2007) propose three important, nongenetic pathways of inheritance likely to have played a crucial role in evolution. The first refers to *cellular epigenetic inheritance*, where adaptive phenotypic responses to environmental conditions affect particular aspects of gene regulation, resulting in equivalent phenotypic characteristics in an organism’s offspring despite the absence of conditions that led to the development of the parental trait. These intergenerational modifications are not necessarily permanent—when the conditions remain absent for several generations, the trait is expected to decay (Harper, 2005).

The other two epigenetic systems include *socially mediated learning* and, with particular respect to humans, *symbol-based information transmission* (Jablonka & Lamb, 2005, 2007). Socially mediated learning occurs through an animal’s exposure to selective cues and learning opportunities provided by its social environment (e.g., imitation) (Jablonka & Lamb, 2007). This can lead to behavioral responses that reinforce each other and create a stable complex of behaviors that have important ramifications for survival and reproductive success (Jablonka & Lamb, 2007). Symbol-based transmission systems (e.g., language) enable humans to reason deductively and hypothesically and transmit information to conspecifics. This is likely to profoundly expand the potential for transmitting information and affecting behavior in ways that differentially affect fitness (Jablonka & Lamb, 2007).

While many transgenerational epigenetic effects are unlikely to be adaptive or attributable to chromosomal modifications passed through gametes (Youngson & Whitelaw, 2008), mounting evidence for epigenetic inheritance from research involving protozoa, plants, and animals suggests that evolution has favored the intergenerational transmission of certain adaptive phenotypic modifications without altering the genome itself (see Avital & Jablonka, 2000; Bonduriansky & Day, 2009; Jablonka & Lamb, 1995; Ros-siter, 1996). The critical point here is that epigenetic inheritance reflects, in itself, an adaptation: compensating for the limitations of genetic inheritance by allowing traits acquired during the lifetime to be transmitted to offspring, permitting the transmission of favorable trait combinations across generations, and enabling environmental heterogeneity to generate heritable phenotypic variation (Bonduriansky & Day, 2009).

Crucially, epigenetic inheritance systems are capable of effecting evolutionary change. In novel environments, all organisms are able to make developmental adjustments through cellular epigenetic changes; animals can make behavioral modifications through socially mediated learning; and humans can solve abstract problems through symbolic systems (Jablonka & Lamb, 2007). If conditions persist, selection will favor the most well adjusted phenotypes and the genes underlying them: either those leading to a faster, more reliable developmental adjustment, or those with fewer detrimental side effects (Jablonka & Lamb, 2007).

The notion of epigenetic inheritance therefore illustrates how plasticity and evolvability are complementary and continuous. Epigenetic inheritance can produce adaptive phenotypes through *transgenerationally extended plasticity*; and *developmentally induced heritable variations* generate additional foci for selection capable of producing evolutionary change (Lamm & Jablonka, 2008). Epigenetic mechanisms can therefore lead both to ontoge-

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2 Proposed mechanisms of cellular epigenetic inheritance include the following: 1) self-sustaining metabolic loops; 2) structural inheritance; 3) chromatin marking; and 4) heritable RNA-mediated variation in gene expression (see Jablonka & Lamb, 2007).
the mechanisms responsible for the origin and development of adaptations over evolutionary time (Müller & Wagner, 2003). In terms of research, Ploeger et al. (2008a) discuss how contemporary EP fails to adequately address some of the major issues in psychology and should therefore integrate alternate models from EDB providing unique, empirically supported predictions about key psychological phenomena. Finally, EDB encompasses a suite of promising research methods, such as data-rich longitudinal designs (Harper, 2005); animal work providing insight into relationships between human genetics, development, and evolution while maintaining ethical research practice; statistical modeling and computer simulation studies; as well as empirical approaches in biology and zoology that lend scientific scrutiny to philosophical debates about how different modular processes have evolved and are biologically related (Ploeger et al., 2008a).

Despite these distinctions, inconsistencies between EDB and EP are arguably more apparent than real. As Barrett (2008) points out, the idea that events initiating evolutionary change occur before the actions of natural selection, and include more than random mutations, has long been recognized. Thus, EDB does not reflect a paradigm shift in evolutionary theorizing per se, but advances relevant knowledge by identifying additional mechanisms responsible for phylogenetic change. Second, the use of evidence for the existence and evolvability of “domain-general” mechanisms to undermine EP (e.g., Jablonka, 2007; Ploeger et al., 2008a) misconstructs the paradigm. As discussed, the HMM readily accommodates “domain-general” (i.e., more inclusive) processes, and EP simply suggests that dedicated adaptations result from evolutionarily persistent selection pressures with specific, reliable solutions. This does not preclude the evolution of heterogeneous types of adaptations in the absence of such pressures (Barrett, 2008). Third, critics commonly misrepresent EP as reducing the mind to a rigid set of logical propositions (Barrett, 2008). The MMH is not seen as an unalterable truth but as a set of heuristics to generate testable hypotheses. Rather than invalidating this position, discoveries furnished by EDB refine our knowledge about the nature and evolution of psychological adaptations, contributing useful additions to our understanding of the intersection between biology and psychology (Barrett, 2008). Ultimately, the two paradigms should be seen as synergistic, not contradictory or competitive.

This is well illustrated by evolutionary developmental psychology (Bjorklund & Pellegrini, 2002; Causey, Gardiner & Bjorklund, 2008; Geary & Bjorklund, 2000). This is a sister discipline of EDB that uses evolution by natural selection to explain the ontogeny of species-typical physical, social, and cognitive capacities as well as the epigenetic processes that adapt such competencies to local environments, with a particular emphasis on how such capacities vary between developmental stages (i.e., infancy, childhood, juvenile-nility, adolescence, and adulthood) (Causey et al., 2008). Researchers examine how evolved genetic systems are expressed during ontogeny and emphasize plasticity by exploring how ecological mechanisms influence developmental processes to produce variable phenotypes adapted to local conditions (Geary & Bjorklund, 2000). Arguably, this subsidiary paradigm also falls under the rubric of EP. It likewise acknowledges that evolutionary processes produce certain phenotypes common to most human beings, incorporates many of the core tenets of EP, and is included in major edited volumes on the field (e.g., Buss, 2004; Ellis & Bjorklund, 2005; Geary, 2005). Evolutionary psychologists also recognize the complex, bidirectional nature of gene-environment interactions and that local conditions instantiate deviations from species-typical developmental trajectories (Barrett & Kurzban, 2006).

The fact that evolutionary developmental psychologists amalgamate key principles from both paradigms is unsurprising. As Barrett (2008) reminds us, EP represents a union of psychology and evolutionary biology, not a subset of them. Because it does not demand revision of evolutionary biology, EDB can be incorporated into EP as providing important, theoretically consistent explanations for phenomena such as modularity, plasticity, development and individual differences. I have separated the two fields here because EDB can be identified with a distinct body of theories, predictions, and findings extrinsic to psychology that promise to advance psychological knowledge, not to reinforce misleading divisions between them.

Similarly, EDB has recently incorporated an important theory from another paradigm: self-organization. While portrayed by Ploeger and colleagues (2008a) as synonymous with EDB (e.g., Ploeger, 2010; Ploeger et al., 2008a, 2008b), next, I explore its origins in DST: the basis for my penultimate tier of psychological analysis.

### Dynamic Systems Theory

In this section, I discuss a level of psychological analysis that肩膀s the ambitious burden of explaining phenotypic variations at the level of the individual. To derive models capable of capturing the complexity of the dynamic, multilevel system represented by the developing human, an increasing number of researchers have turned to DST. Rooted in computer science, ecology, mathematics, and physics (particularly nonequilibrium thermodynamics; see Prigogine & Stengers, 1984), DST has since expanded into a diversity of disciplines, ranging from biology and genetics through to anthropology, economics, and psychology (Kenrick, Li & Butner, 2003; Lansing, 2003). DST entails the study and modeling of complex multicomponent systems as they change over time. The core premise of this approach is self-organization, referring to the spontaneous emergence of coherent, higher-order patterns resulting from recursive interactions among simpler components intrinsic to a complex, dynamic system (Lewis, 2000). Lewis (2000, 2005) outlines four key properties of self-organizing systems. First, following some sort of (internal or external) environmental perturbation or trigger, microscopic coordinations emerge between different components that lead to new macroscopic patterns, which are recruited for unique functions that entrain and reinforce certain lower-order patterns over time (a process of circular causality between different levels of the system). Second, they become progressively complex and ordered, producing increasingly sophisticated arrangements of coordinated processes to subserve increasingly functional forms. Third, global reorganizations toward increasing complexity occur at phase transitions: points of turbulent instability where old patterns break down to be replaced by new ones. Fourth, they are both stable and sensitive to change: emergent change is stabilized through negative feedback loops and the coordination of functional patterns, while an interconnectedness with other systems and propensity for positive feedback favors sensitivity to environmental conditions,
particularly during phase transitions. Thus, self-organizing processes tend toward nonlinearity.

Clearly, self-organizing systems change over time. Given that dynamic activity within any one timescale (e.g., neural activity) is continuous with, and nested within, the dynamics of all other timescales (e.g., growth, learning, development and evolution), another critical feature of DST is the study of how activity across different timescales interacts (Smith & Thelen, 2003).

The application of DST to human ontogeny is unsurprising. Developing organisms are composed of multiple individual elements that interact with each other and a complex, external environment (Smith & Thelen, 2003), making them ideal targets for dynamical analyses. Second, self-organization supplies a conceptual framework to explain the appearance of true novelty within developing systems, the emergence of order and increasing complexity over time, transition points that permit both structural advances and individual diversification, and the capacity for self-correcting stability alongside sensitive adaptation to the environment (Lewis & Granic, 1999). Much like EP then, DST has been proposed as an interdisciplinary paradigm to unite psychology’s subdisciplines (Lewis, 2000; Witherington, 2007).

Research in this area lends itself to a variety of methods. In psychology, the analysis of self-organization suits fine-grained, real-time, and small-N longitudinal designs (Lewis & Granic, 1999). Behavior is seen to move toward attractors in real time, while over developmental time, attractors reflect patterns of interactions that eventually stabilize and become increasingly predictable (Granic, 2005). The stronger the attractor, the more likely it is that behavior will tend toward it and become increasingly resistant to environmental perturbations, with bifurcation points providing opportunities for substantial developmental repatterning. To map such processes, researchers use descriptive analyses, hybrid designs combining micro- and macrodevelopmental processes, state space descriptions combined with statistical approaches, and other methods borrowed from biology and physics, particularly mathematical modeling and computer simulations (Lewis & Granic, 1999).

A prevailing criticism of DST is that it fails to produce testable predictions (Dunley & Buss, 2008). However, an increased understanding of the relevant perturbations, trajectories, and attractors for a given system arguably assists in gauging the sorts of outcomes that are probable versus those which are not. Indeed, by adopting DST, developmentalists have already contributed a substantive body of empirically supported hypotheses in a range of areas, including cognitive, emotional, language, neurological, personality, social, and motor development (Kelso, 1995; Lewis, 2000; Ploeger et al., 2008b; Thelen & Smith, 1994; Witherington, 2007).

Finally, by focusing on interactions between different timescales, DST can also be applied to the brain and behavior operating in real-time, allowing developmental analyses to be incorporated into other subdisciplines. This is superbly exemplified by the free-energy principle of the brain (Friston, 2010, 2011; Friston, Kilner & Harrison, 2006), which builds on a core distinction between biological agents and other self-organizing systems. Friston’s free-energy formulation stems from statistical thermodynamics, where it is used as a measure of probability distributions. Specifically, free-energy refers to an information theory quantity that limits (by being greater than) the entropy of a generative model entailed by the state of an agent (e.g., a brain). A generative model is a probabilistic mapping from causes in the environment to observed consequences (e.g., sensory data); while entropy refers to the (long-term) average of surprise: the negative log-probability of sensory experiences encountered by an agent (Friston, 2010).

Friston (2010) points out that unlike other self-organizing systems, biological agents can avoid critical phase transitions that lead to decay by minimizing the entropy of their physiological and sensory states. Because the repertoire of functional/adaptive states occupied by an organism is limited, mathematically, the probability of these states have low entropy: there is a high probability the organism will occupy a small number of states. Ergo, an organism’s distal imperative of maintaining functional states within physiological bounds (i.e., homeostasis) translates into a proximal avoidance of surprise (Friston, 2010).

While surprise itself cannot be evaluated, given that free-energy imposes an upper bound on surprise, biological systems can minimize surprise by minimizing their free-energy, which basically equates to the amount of prediction error. To evaluate prediction error, an organism depends on the following: (a) its sensorium, and (b) predictions based on its generative model encoded by its internal states (e.g., neuronal activity and connection strengths). This means that biological agents minimize free-energy by reducing prediction errors—either through changing the sensory input predicted by acting on the environment (i.e., action), or changing predictions by altering internal states (i.e., perception).

Although initially proposed to explain human action, perception, and learning (Friston, 2003, 2005; Friston et al., 2006), this theory has since been lauded as a unifying theory for neuroscience (Huang, 2008). It has been recruited to account for the evolution, development, form and function of the brain (Huang, 2008; Friston et al., 2006); generates testable, empirically supported hypotheses (Harrison, Stephan, Rees & Friston, 2007; Friston et al., 2006; Marta, Garrido, Kilner, Kiebel & Friston, 2007); and synthesizes manifold global brain theories (see Friston, 2010).

As well as shedding light on hierarchical message passing and the functional role of specific neurons, microcircuits, and their associated dynamics, more broadly, this theory also promises important insights within engineering, robotics, embodied cognition, and evolutionary biology (Friston, 2010). Thus, Friston’s extension of principles derived from DST not only proffers a unifying theory for neuroscience, it informs multiple psychological subdisciplines (especially cognitive psychology and neuropsychology) and has the potential to further the integration of psychological inquiry with the sciences at large.

Developmental psychobiology: Integrating DST with developmental psychology. Many of the ideas captured by DST have been expressed by developmentalists for years (e.g., Bronfenbrenner, 1977; Greenberg et al., 2006; Lickliter & Honeycutt, 2003), but this has been coupled with a tendency to downplay the
importance of evolutionary influences (e.g., Greenberg et al., 2006; Kar miloff-Smith, 2000). Emphasizing such (biological) attractors in developmental models (hence the emphasis on developmental psychobiology) is crucial, because it explains the homologous characteristics of human phenotypes and therefore avoids a core pitfall of pure constructivism. Moreover, to fully incorporate DST into developmental psychology, we require a cohesive account that follows the principles of the former and adapts them to the study of human ontogeny in particular. DST is not a substantive theory, but it provides a set of tools and principles to analyze a given system and allow substantive theories about that system to be constructed (DeLancy, 2005). Dynamic system modeling therefore demands information about the system under scrutiny, including the ways in which particular elements of that system interact. This requires recourse to the wide range of fields relevant to developmental psychology, an idea elegantly expressed by Sameroff’s (2010) dialectical unified theory of development and the multilevel personality in context model advanced by Sheldon and colleagues (Sheldon, Cheng, & Hilpert, 2011).

By imposing a top-down assumption that researchers only examine part of a larger whole comprising multiple interacting dynamic systems, these theories encourage cooperative attempts to combine different research streams targeting specific mechanisms behind the dynamic, developmental system of the individual (Sameroff, 2010). Advances in fields such as molecular genetics, endocrinology, and neurology are being increasingly recruited in psychological research. These involve multidirectional models emphasizing gene–environment interactions, epigenome–experience transactions and neural plasticity, and require increasingly complex dynamic systems analyses to encompass the part–whole processes responsible for developmental change (Sameroff, 2010). Importantly, modeling environmental influences should also highlight key social processes impacting on development, such as the opportunity structure concept from sociology and economics (i.e., individual development is constrained by social relationships, institutions, and availability of resources) and the meaning making construct from anthropology (i.e., individual differences are constrained by cultural differences in prohibitions, values, mores, and norms) (Sameroff, 2010). In short, promoting dynamic, multilevel biopsychosocial models of ontogeny facilitates the unification of theory and research across the social, biological and physical sciences.

This is also likely to maximize scientific and practical outcomes. Consider, for instance, contributions from genetics and epigenetics, which have contributed substantially to our understanding of individual differences in personality, cognitive abilities, behavior, psychopathological development, and disease (Plomin, 1994; Plomin & Davis, 2009; Tsankova, Renthal, Kumar, & Nestler, 2007) and stand to inform targeted prevention, early intervention, and treatment strategies in psychology, psychiatry, and public health (Handel et al., 2009; Masterpasqua, 2009).

The relationship between DST and EDB. DST is well suited to EDB for a number of reasons. First, self-organization provides a scientifically validated mechanistic account for important sources of developmental and subsequent phylogenetic change: self-organization successfully explains the plasticity of organisms (Lewis, 2000), and selection can act on variants produced by self-organization as well as those arising from genetic mutations (Ploeger et al., 2008b). As explored below, DST also extends evolutionary theory by introducing a key evolutionary mechanism beyond natural selection alone (Kauffman, 1993; Hozier, Smith & Pepper, 2006), while Ploeger and colleagues (2008a, 2008b) have already incorporated self-organization into the rubric of EDB to explain key aspects of human development.

At one key juncture, however, they traditionally diverge. Evolutionary developmental biologists tend to privilege the causal role of genes in ontogeny, retaining a gene-centered view of natural selection by differentiating between genes as units of inheritance; and units of transmission of information, such as cells, cytoplasm, organelles, and the extracellular environment (Jablonska & Lamb, 2002). However, because non-DNA units of information transmission can transmit variations to subsequent generations—and may therefore be relevant to evolutionary change—drawing a distinction between these and genes as units of inheritance is misleading (Jablonska & Lamb, 2002). Similarly, Caporael (2001) has synthesized selection theory and dynamic systems approaches by arguing that inheritance is based on the repeated assembly of reliably recurrent resources: evolutionary theorists should seek to understand the system dynamics that result in the variation, retention, and selection of the component parts of repeated assemblies rather than genes alone (Caporael, 2001). These contributions explain how adaptive phenotypic features reliably develop in each generation, synthesize DST and EDB, and solve the problem of genetic determinism (Caporael, 2001; Jablonska & Lamb, 2002).

The relationship between DST and EP. Much like EDB, EP is frequently criticized for imposing a gene-centered view of development (Buller, 2005; Jablonska & Lamb, 2007; Greenberg et al., 2006). Evolutionary psychologists disagree. Given that EP represents an interactionist theory, the type of either/or model critics attribute to it is logically impossible (Krebs, 2003). Indeed, many have pointed out that understanding the ways in which gene expression is modified by life experience, and how social and physical ecologies impact on brain development and organization, is a core commitment in EP (Badcock, 2000; Barrett, Dunbar & Lycett, 2002; Buss, 2009).

Nonetheless, evolutionary psychologists tend to overlook the ways in which complex interactions between evolved, genetic programs and epigenetic processes are actually realized (Kenrick, 2001). DST assists in exploring how genetically based dispositions reliably and consistently emerge across individuals, as well as vary substantially in response to local ecological conditions (Kenrick, 2001). Dynami cal approaches also offer methods to model biopsychosocial systems far too complex for the human mind to analyze (Kenrick, 2001); mathematical modeling and computer simulations enable researchers to explore the implications of theoretical propositions concerning complex probabilistic systems, examine specific processes in isolation from extraneous sources of influence (much like experiments), reduce these processes to clean mathematical rules, and allow the use of real world data to affirm the accuracy of simulation outcomes (Holland, 1998).

Most importantly, DST adds significantly to our understanding of selection and evolution. While recognized by Eigen and Schuster (1977) more than 30 years ago, this idea has more recently captured widespread attention through Kauffman’s (1993) work, which synthesizes DST with the theory of natural selection in three main ways. First, he uses statistical analyses to illustrate that much like natural selection, self-organization influences the trajectory of a population through a state space of possible genotypes or phe-
notypes that vary in degrees of fitness. Second, he uses computer simulations to show that the most adaptive self-organizing systems tend toward the edge of chaos: a dynamic, intermediate state that optimizes problem-solving by being caught between completely ordered, stable cycles of activity and complex, highly chaotic ones. This means that (a) systems are likely to evolve toward the edge of chaos because it optimizes evolvability (i.e., inheritable solutions to adaptive problems), and (b) the edge of chaos is actively maintained by natural selection (i.e., it is, in itself, an adaptation). Finally, he uses random graph models to demonstrate how phase transitions characterize the progression from random connections between individual elements toward more functional, complex wholes. Because evolution concerns the formation of complex systems comprising simple interacting elements, he argues that phase transitions likely reflect a core mechanism in evolution.

The complementary relationship between natural selection and self-organization is also considered by Hoelzer and colleagues (2006). While the former maximizes fitness and the latter maximizes the rate of energy flow across a gradient (i.e., a fuel source), they describe how selection typically results in more efficient energy processing at any level of biological organization (the cell, multicellular organism, population or ecosystem). Thus, the maximization criteria of both are highly complementary. They also assert that because the origin of life reflects the emergence of higher-scale functional structures from smaller sets of interacting, prebiotic chemical particles (e.g., RNA, DNA and proteins), natural selection is an emergent process based on the thermodynamically driven origin of the birth/reproduction/death cycle. This denotes that ultimate explanations based on natural selection are more proximate than thermodynamic explanations (e.g., self-organization) and that natural selection is one of many thermodynamic processes involved in the higher order processing of energy (Hoelzer et al., 2006).

Nevertheless, this should not obscure the essential role of selection entailed by all forms of self-organization (Swenson, 2010). This represents the very core of EST; given that optimal adaptive/functional (macroscopic) patterns of interacting (microscopic) components are necessarily selected over competing alternatives, both self-organization and general selection represent the two fundamental, mutually reinforcing, and inextricable processes driving any evolving system (Eigen & Schuster, 1977; Schneider & Kay, 1994; Weber & Depew, 1996). Arguably, consilience demands that psychologists adopt this idea. It enables evolutionary theorists to merge a theory of inheritance with a theory of the transmutation of form (Pigliucci, 2007) and is predicated on a wealth of literature across the physical, biological, and social sciences (Depew & Weber, 1995; Eidelson, 1997; Lansing, 2003; Lesne, 2008; Schneider & Kay, 1994).

Crucially, this tenet is remarkably consistent with evolutionary models of the brain. As noted, biological systems are distinguishable from other self-organizing systems because they can preclude deleterious phase-transitions by minimizing the entropy of their sensory states. This property is, in itself, the result of natural selection: self-organizing systems that can avoid such phase-transitions will be selected above those that cannot (Friston et al., 2006). With particular respect to the brain, Friston (2010) describes how both the free-energy principle and neural Darwinism explain neurobiological changes in terms of evolutionary processes. The brain only labels a sensory state as valuable if it leads to another valuable state, and selection ensures that an organism moves through a succession of states with genetically specified (i.e., innate) adaptive value. Because minimizing free-energy (and therefore entropy) ensures that organisms spend most of their time in a small number of valuable (i.e., adaptive) states, value in this context is inversely related to surprise (i.e., entropy). Natural selection therefore reduces surprise by specifying the value of sensory states through genetic and epigenetic mechanisms, prescribing a small number of attractive states with innate value that minimize prediction error by optimizing an organism’s prior expectations and ensuring that they are consistent with its phenotype and environment (Friston, 2010). Most critically, this unifies the ultimate/functional account of the HMM described above and the proximate/mechanistic account proffered by the free-energy principle (for ease of reference, this model is abbreviated hereafter as the HMM).

Finally, it must be recognized that the complementary relationship between selection and self-organization has long been recognized by evolutionary psychologists themselves. In their development of dynamical evolutionary psychology, Kenrick and colleagues (2002) illustrate how DST elucidates the processes responsible for the properties of psychological systems as they emerge and change over time, while EP targets the specific function (i.e., content) of these systems. Dynamical analyses of psychological, behavioral, developmental and social patterns can therefore be informed by specific evolutionary predictions concerning those patterns more likely to emerge in human populations than others. Kenrick and colleagues translate this approach into a structured set of testable hypotheses (Kenrick et al., 2002) and demonstrate its empirical utility by using simulation experiments to support key predictions about gene-culture interactions (see Kenrick et al., 2003).

Summary

In this article, I have described three paradigms that furnish crucial insights into psychological phenomena. Historically, the validity of developmentalist versus evolutionary approaches has attracted ardent debate. Given the complexity of the human condition, I suggest that this stems chiefly from the fact that they target different questions. By doing so, they must neglect others (Krebs, 2003). Ultimate (why) versus proximate (how) questions should be differentiated, resultant conclusions must be appropriate for the sorts of questions being posed, and undermining a useful approach at one level because it does not attend to another is misguided (Dewsbury, 2009; Scott-Phillips et al., 2011).

So in what way might a holistic model draw these paradigms together? Psychological theorists need to commit to cooperation, not competition. It is vital for theoretical approaches not to confuse one level of analysis with another, and while standing alone, neither EP, EDB nor DST can explain the full host of interacting factors producing human phenotypes, psychology and behavior, the fruits of hybrid (e.g., biopsychosocial) models amalgamating explanations from two or more levels should not go ignored (Barrett et al., 2002). In this tradition, I propose in the following

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4 Other variations of this theme have been expressed by others (e.g., Bak, 1997; Carlson & Doyle, 1999; Levin, 2002).
section a heuristic for psychological science that relies on all three of the paradigms explored above to develop a hierarchical approach to psychological inquiry that bridges the gap between ultimate, evolutionary theories and proximate/mechanistic explanations, and tackles one of the core challenges in the field by encompassing relatively universal human characteristics as well as the enormous variability presented by the developing individual situated in real-time contexts.

An EST of Psychology

An evolutionary systems model of psychology comprises four interrelated levels of analysis centered on distinct problem areas that, when taken together, attend to the four areas of biological inquiry articulated by Tinbergen (1963): function, phylogeny, ontogeny, and mechanism. These levels entail both a temporal domain (i.e., evolutionary, intergenerational, developmental, and real-time processes, respectively) and a domain of diversity (i.e., species-typical characteristics, between-groups differences, individual differences, and the individual-in-context, respectively). My EST organizes these levels around EP, EDB, developmental psychobiology and the subdisciplines, respectively, which each correspond with a range of associated disciplines, core hypotheses, and sets of research methods. Crucially, a synthesis of the non-substantive metatheories of general selection and self-organization (i.e., EST) interpenetrates all four levels to promote consilience and impose exclusion criteria on the model: theories across all levels should stray from violating these principles. A schematic of this approach is presented in Figure 1.

As shown in the figure, first-level explanations are attributed to EP, a paradigm producing testable, functional explanations for species-typical traits, and ubiquitous dimensions of individual differences. Given that it explicitly targets homologous biological characteristics, cross-cultural, comparative, and genetic research are key methodologies for this heuristic.

The second level is devoted to EDB, which explores how ontogenetic mechanisms and phenotypic variability emerged from, and interacted with, the evolutionary processes highlighted by EP. EDB extends evolutionary explanations by shifting the focus from species-typical characteristics to the developmental plasticity of the organism and group-level variations, concentrating explicitly on key points of intersection between functional explanations and ontogenetic ones.

The third level is assigned to developmental psychobiology, involving the study of ontogenetic mechanisms producing individual differences. By incorporating evolutionary as well as developmental factors into their analyses, researchers can explore how they interact with proximate variables to shape phenotypic expression. This crosses the divide between ultimate and proximate explanations; those for species-typical traits and those for individual differences.

The fourth level of analysis comprises subdisciplinary content. This addresses the highest level of variability and fuses developmental psychobiology with the subdisciplines by analyzing the effects of unique developmental outcomes (i.e., the individual) interacting with unique environments in real-time. This variability is captured implicitly by all psychological research, which involves the collection of chosen data on particular individuals in a specific context at a given point in time. This tier of analysis therefore addresses the most proximate/mechanistic level of explanation and allows for the highest degree of specificity in the model.

Finally, the HMM provides an integrative hypothesis of psychological and behavioral processes that applies EST to the evolution, development, and mechanistic properties of the human psyche.

Importantly, the model presented here promotes consilience (Wilson, 1998): each level relies on theories and research emerging from specific paradigms and other scientific disciplines relevant to its problem area, and disciplines, theories, and research methods associated with adjacent levels tend to overlap.

In closing, there are two addenda. First, the associated disciplines, core hypotheses and research methods in Figure 1 are illustrative, not exhaustive. Second, the dashed lines in Figure 1 indicate that the boundaries between levels are not discrete. While each level of analysis is best captured by its corresponding field(s), this does not preclude informational exchange between them. As discussed, EP, EDB, and developmental psychobiology are complementary, and using theory and research from one level to inform theory and research in another is arguably essential for quickening knowledge and a unified psychological science.

Now, I will turn briefly to the implications of this model for theory and research.

EST: Implications for theory and research. The ramifications of EST for psychological science are potentially threefold. This article attends to the first, exploring theoretical relationships between major paradigms to provide a unifying, internally consistent metatheory that organizes and reconciles the diversity of paradigms and hypotheses that constitute our discipline.

Second, it can be used as an integrative heuristic for theory and research. As a nonsubstantive principle that extends across all fields of psychological research, it encourages the use of dynamic systems analyses to investigate the ways in which general selection and self-organization affect the evolution of particular psychological, behavioral, and developmental phenomena across different time-scales. Of particular importance, it can also be recruited to develop substantive hypotheses about specific phenomena, motivating researchers to build models that integrate all levels of inquiry identified by the model. Consider, for example, depression, a phenomenon that will be explored through an EST framework by my colleagues and me (see Badcock, Allen & Spry, in preparation). Specifically, a number of functional (i.e., first level) explanations suggest why depression has evolved as a species-typical phenomenon. A promising model is the social risk hypothesis, which suggests that depressed states evolved to facilitate a risk-averse approach to social interaction when individuals were typically under threat of exclusion from social contexts (i.e., dyads or groups) that, over the course of evolution, had a critical impact on inclusive fitness (Allen & Badcock, 2003). Consistent with this view, numerous lines of evidence suggest that epigenetic inheritance (a second level explanation) is implicated in familial variations in the sensitivity and severity of depressogenic responses, highlighting the intergenerational transmission of susceptibility to depression attributable to deficiencies in the social environment (e.g., low maternal care; Champagne, 2008). A third level analysis builds on the above work by illuminating likely ontogenetic mechanisms responsible for individual differences in depressogenic responses. Relevant research includes DST approaches emphasiz-
ing how exposure to detrimental (e.g., social) real-time experiences produces and strengthens the development of stable, resilient attractor states (e.g., depression) which influence and constrain real-time behavior (Granic, 2005); work in behavioral genetics indicating that depression is both highly heritable and under environmental control (Rutter, Moffitt & Caspi, 2006); and studies in molecular genetics identifying specific gene-(socio-)environment interactions contributing to depressive onset and severity (e.g., Caspi et al., 2003; Zalsman et al., 2006). Fourth, subdisciplinary content canvasses a surfeit of empirically supported hypotheses about the proximate (especially psychosocial) mechanisms involved in depression (see Allen & Badcock, 2003; Gotlib & Hammen, 2009). Finally, explanations can be integrated within and across levels, such that hypotheses at any one tier (e.g., the social risk hypothesis) can be used to inform theory and research at another (e.g., hypotheses for depressogenic phenomena at the subdisciplinary level; see Allen & Badcock, 2003; Badcock, Allen, & Spry, in preparation).

While ESTs of specific psychological phenomena are undoubtedly complex, hybrid models that integrate multiple levels of

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**Figure 1.** An evolutionary systems theory of psychology.
explanation are already evident in the literature (e.g., Sameroff, 2010; Sheldon et al., 2011) and promise to generate a suite of novel, testable predictions that, when taken together, capture a greater diversity of phenomena than explanations at any one level alone (Barrett et al., 2002).

The third, presently more speculative research avenue emerging from EST concerns the empirical assessment of its own metatheoretical models. A crucial shortcoming of metatheories is that they rely on extensive qualitative literature reviews but are seldom operationalized as quantitative hypotheses amenable to empirical assessment. Indeed, the validity of the EST I propose here rests on three premises: as a unifying metatheory, it should be applicable to all fields of psychological science; as a scientific theory, it should be testable; and given that psychology—like any other scientific discipline—represents a dynamic, evolving (sociocultural) system (Leydesdorff, 2001), it should be reflexive. All three criteria can be addressed by adopting a scientific approach to the metatheory itself.

To this end, the model can be translated into three principal hypotheses. The first is that EST (i.e., a synthesis of the metatheories of selection and self-organization) will continue to gain prominence in psychological research, within and across the subdisciplines. The second predicts the division of psychological and behavioral phenomena into four interconnected levels of analysis (i.e., functional, phylogenetic, ontogenetic, and mechanistic models, respectively). The third is that the explanatory power of EP, EDB, developmental psychobiology, and the collective subdisciplines will vary differentially according to the different levels of analysis identified in the second hypothesis: EP will tend to target ultimate and species-typical phenomena; EDB phylogenetic and intergenerational group-level phenomena; developmental psychobiology ontogenetic and individual-level phenomena; and the subdisciplines individuals acting in real-time contexts.

These hypotheses can be tested through recourse to scientometricics. This field defines science as the subject of its own inquiry, assumes that the evolution of different theories and paradigms is amenable to measurement, and maps the systematic processing of information within science that reduces uncertainty about the environment (Leydesdorff, 1995). Chiefly relying on quantitative approaches, scientometricians have developed a wealth of models and methods to analyze scientific change, including citation and text analysis, sets of scientometric indicators (e.g., numbers of publications and citations), computerized techniques to analyze scientific revolutions, and models of growth, mobility, and problem-solving processes (Bruckner, Ebeling, & Scharnhorst, 1990). Conceivably, the abovementioned hypotheses might be tested using scientometric methods that capture the proportion of psychological scientists, journals and/or key citations associated with different research fields; the growth and decline of particular theories and paradigms both within and across different fields of inquiry; and/or the temporal development of new fields. Analyses could be restricted to comparisons between particular psychological subdisciplines, encompass the discipline as a whole, or involve the sciences at large. Thus, while as yet unrealized in the psychological literature, existing empirical analyses of scientific/theoretical relationships and developments in other disciplines (e.g., Bruckner et al., 1990; Leydesdorff, 1995; McCain, 2010) suggest that metatheoretical models like the one proposed here can, in principle, be subject to scientific scrutiny.

Conclusion

This treatise represents the first of two founded on the metatheory of EST. My aim here was to propose a logical (internally consistent) notion of synthesis of psychological paradigms to resolve persistent theoretical divisions in our discipline, and promote consensus by introducing a singular model of the human mind (i.e., the HMM) that unites ultimate and proximate explanations of evolutionary, developmental, psychobiological, and behavioral phenomena. In a second, forthcoming treatment, I aim to build on this foundation by elaborating upon the empirically supported theoretical premises of the HMM, expressing it formally (i.e., mathematically), and exemplifying its capacity to generate testable predictions with respect to specific psychological phenomena (e.g., depression).

References


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