Integrating Development and Evolution in Psychological Science: Evolutionary Developmental Psychology, Developmental Systems, and Explanatory Pluralism

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\textbf{Abstract}
New attempts in psychological science at integrating developmental (individual-level) and evolutionary (population-level) accounts of phenotypic stability and variability have achieved increasing prominence of late. Foremost among such attempts is the field of evolutionary developmental psychology (EDP). EDP proposes that selective pressures in evolution inform psychological development through a synthesis of the Darwinian/neo-Darwinian selectionist perspective embraced by evolutionary psychology and the developmental dynamics perspective endorsed by developmental systems theory. We examine the theoretical assumptions behind selectionist and developmental perspectives and argue that both perspectives are ontologically incompatible. We provide an alternative framework for integrating developmental and evolutionary explanations that transcend this ontological division of selectional and developmental perspectives. This framework promotes a pluralistic approach that moves beyond traditional antecedent/consequent, mechanistic views of causality and embraces both functional (part-to-whole) and structural (whole-to-part) modes of explanation as distinct, equally legitimate, and simultaneously applicable perspectives in understanding phenotypic stability and variability over time. © 2016 S. Karger AG, Basel

For much of the 20th century, it was common for biologists and psychologists to espouse the gene-centered view of neo-Darwinism – the “modern synthesis” – and regard development as having little to no relevance for evolution. Beginning in the
late 1970s, however, the importance of development and developmental theory for an understanding of evolution surfaced as a lively and controversial topic within evolutionary theory [e.g., Alberch, 1982; Bonner, 1982; Gottlieb, 1987; Gould, 1977; Oyama, 1985]. Subsequently, numerous proposals for reintroducing development into the study of evolution have arisen in both biology and psychology [e.g., Amundson, 2005; Gottlieb, 1992; Jablonka & Lamb, 2005; Lickliter, 2008; Robert, 2004; Sansom & Brandon, 2007; Stotz, 2014; West-Eberhard, 2003]. The majority of these proposals maintain conceptual grounding in Darwin’s idea of natural selection, as a creative or shaping force behind the phenotypic form, but add a significant role for developmental processes in the guidance of evolutionary change, challenging neo-Darwinism and its gene-centered focus. In brief, an “extended synthesis” has become commonplace in recent years, designed to amend the “modern synthesis” and its marginalization of development in evolutionary theory without abandoning commitment to the organizing force of natural selection [e.g., Pigliucci, 2007; Pigliucci & Müller, 2010; see Walsh, 2015, for further discussion].

Such attempts to integrate ontogenesis (developmental change in individual organisms) and phylogenesis (evolutionary change in populations – e.g., species – of organisms) routinely adopt a “middle-ground” position between what Sober [1984] has termed selectional and developmental forms of explanation. Selectional explanation – embodied in both Darwinian and neo-Darwinian perspectives – regards natural selection as the principal creative force behind all levels of organized complexity and relegates development to a subservient role of supplying the unoriented and undirected variation upon which natural selection acts [Depew & Weber, 1995; Hughes & Lamb, 1984]. In contrast, developmental explanation – with pre-Darwinian roots in both the functionalism of Lamarck and the rational morphology of Cuvier, Owen, and Goethe, among others – regards developmental processes as the constructive force behind all levels of organized complexity, generating both organization in phenotypic form and direction in evolutionary change such that natural selection is relegated to a negative role, that of “eliminating the unfit” rather than “constructing the fit” [Gould, 2002, p. 139; Russell, 1916; Smith, 1992; Webster & Goodwin, 1982].

In biological science, evolutionary developmental biology, or Evo-Devo, commands center stage as the most prominent middle-ground attempt to synthesize selectional and developmental forms of explanation. Evo-Devo seeks to reunite evolutionary and developmental biology and has enjoyed both wide-ranging application and considerable influence as an integrative framework [Arthur, 2002; Gilbert, Opitz, & Raff, 1996; Hall, 1999]. In psychological and developmental science, a similar middle-ground attempt has emerged: evolutionary developmental psychology, or EDP. Specifically targeting how natural selection informs psychological development, EDP focuses on merging the selectional focus of evolutionary psychology [e.g., Buss, 1999; Tooby & Cosmides, 1992] with the fundamental tenets of a developmental system (DS) approach to development [e.g., Gottlieb, 1992; Lickliter & Honeycutt, 2003a; Oyama, 1985] so as to embrace the dynamics of both development and natural selection in the construction of psychological organization [Bjorklund, 2015; Bjorklund & Ellis, 2005, 2014; Bjorklund & Pellegrini, 2002; Del Giudice & Ellis, 2016].

Both of these middle-ground syntheses are predicated on an assumption of ontological compatibility between the creative force of Darwinian natural selection and the developmental dynamics of a DS framework. Sober [1984], however, has argued that Darwin’s creative force argument for natural selection necessarily precludes a
developmental perspective on the emergence of form: “The Darwinian view of natural selection suggests that there can be no developmental theory of phylogeny … it admits no inherent tendency toward complexity or anything else” (pp. 153–154). Others have argued that once developmental processes enter the explanatory arena as legitimate sources of increasing organization and complexity of form, the argument for natural selection as creative force effectively collapses [e.g., Edelman & Denton, 2007]. And, as we shall argue, when focus turns specifically to the role of evolutionary change with respect to the individual-level dynamics of development, the “irreducibly population-level character” [Sober, 1984, p. 150] of Darwinian selectional explanation fundamentally misaligns with a developmental perspective, compromising the very conceptualization of development central to a DS perspective. These sorts of concerns about ontological incompatibility have already arisen within Evo-Devo circles [Ioannidis, 2008; Linde Medina, 2010]. Debates over whether to maintain conceptual grounding in natural selection as a creative force or to completely overhaul orthodox evolutionary theory in favor of conceptual grounding in the constructive dynamics of development speak to fundamental ontological division within the field [e.g., Amundson, 2005; Arthur, 2002; Gilbert, 2003; Hall, 2000; Winther, 2015]. Two Evo-Devo approaches, in fact, seem to currently exist: the mainstream Evo-Devo, which still fundamentally embraces a selectional explanatory perspective, and the alternative of Devo-Evo, which favors replacing selectional orthodoxy with a developmental explanatory perspective [Hall, 2000; Linde Medina, 2010; Robert, 2004].

In this article, we address questions of ontological compatibility between Darwinian natural selection and the dynamics of a developmental perspective with specific focus on EDP’s proposed synthesis for evolution-development interplay. We argue that Darwinian natural selection and the DS framework are, at their cores, ontologically incompatible with respect to conceptualizing the relation of evolutionary processes to developmental processes. We then offer an alternative framework for aligning population-level dynamics in evolution with individual-level dynamics in development that overcomes such an ontological incompatibility through an appeal to explanatory pluralism – an appeal grounded both in Rieppel’s [1990] call to diversify explanation in the biological sciences by reinstating Aristotle’s four causes, as well as in Overton and Lerner’s [2014] recent metatheoretical elaboration and extension of the DS approach, relational-developmental systems [e.g., Overton, 2010, 2015; Overton & Lerner, 2014].

The first third of this article examines the central tenets of both EDP’s framework and those of the DS approach to development. We argue that proponents of EDP’s framework and the DS framework are, at their cores, ontologically incompatible with respect to conceptualizing the relation of evolutionary processes to developmental processes. We then offer an alternative framework for aligning population-level dynamics in evolution with individual-level dynamics in development that overcomes such an ontological incompatibility through an appeal to explanatory pluralism – an appeal grounded both in Rieppel’s [1990] call to diversify explanation in the biological sciences by reinstating Aristotle’s four causes, as well as in Overton and Lerner’s [2014] recent metatheoretical elaboration and extension of the DS approach, relational-developmental systems [e.g., Overton, 2010, 2015; Overton & Lerner, 2014].

The first third of this article examines the central tenets of both EDP’s framework and those of the DS approach to development. We argue that proponents of EDP
fundamentally misconstrue DS’s emergence-oriented approach to ontogenetic processes and, in their notion of evolved probabilistic cognitive mechanisms, actively contradict the very concept of a developmental process in the DS approach that they purport to endorse. This yields a model in EDP that is decidedly selectional in its explanatory perspective, amounting to little more than a shallow mimicry of DS concepts. The second third of this article examines the ontological incompatibility between EDP and DS more broadly in terms of fundamental differences in how each approach conceptuallyizes the nature of living matter, the “force” dynamics of natural selection, and the relation between population- and individual-level dynamics. We argue that EDP mistakenly construes change in the distribution of phenotypes at the level of populations as a predisposing, antecedent force of influence in the ontogenetic construction of individual phenotypes, resulting in a conflation of individual- and population-level dynamics.

The final third of this article examines how the DS approach to development-evolution interplay neglects to adequately establish a role for evolutionary processes in the organization of individual development. We offer a potential remedy by building on Rieppel’s [1990] twofold contention that (a) conflict between selectional and developmental perspectives “largely results from the abolition of the four Aristotelian causes in favor of a unified concept of causality, the efficient cause” (p. 318) and that (b) transcending the opposition of these explanatory perspectives is most readily achieved by embracing an explanatory pluralism that moves beyond the antecedent-consequent mode of efficient cause to include other types of explanation, like formal and final causes [see also Walsh, 2013]. Specifically, we propose, in line with the metamodel of relational-developmental systems [Overton, 2015; Overton & Lerner, 2014], that conceiving of evolutionary change’s relation to developmental change requires an explanatory framework that captures the relation of a whole relative to its parts – that captures, in other words, the atemporal quality of organizational constraint via formal and final levels of explanation.

### Integrating Development and Evolution: The Proposed Synthesis of EDP

Proponents tout EDP as a major advance over evolutionary psychology in representing a truly developmental perspective [Bjorklund & Pellegrini, 2002; Frankenhuys, Panchanathan, & Barrett, 2013; Machluf, Liddle, & Bjorklund, 2014]. After all, evolutionary psychology’s self-proclaimed “interactionism” has been taken to task for promoting a predeterministic conceptualization of behavior and development wholly incompatible with the DS perspective on epigenesis [e.g., Lickliter & Honeycutt, 2003a; Nash, 2014]. However, as Lickliter and Honeycutt [2003b] began to explore over a decade ago, EDP’s efforts to take development seriously fall victim to the same criticisms leveled against evolutionary psychology. Expanding on Lickliter and Honeycutt’s [2003b] critique, we argue that proponents of EDP – despite couching their model in the developmental process terminology of DS approaches – remain committed to a view of developmental processes as the transmission and expression of preexisting information, not as the constructive emergence of new, irreducible organization from previous levels of organization [Oyama, 1985; Oyama, Griffiths, & Gray, 2001].
EDP’s model for understanding development-evolution interrelations revolves around the concept of evolved psychological mechanisms, or, in its more recent nomination, evolved probabilistic cognitive mechanisms [Bjorklund & Ellis, 2014; Bjorklund, Ellis, & Rosenberg, 2007; Bjorklund & Pellegrini, 2002]. Examples include “prepared” learning by means of biased selective attention and speech perception and production by means of language acquisition mechanisms [Bjorklund et al., 2007]. Routinely characterized as genetic dispositions, messages, and biases [Bjorklund & Pellegrini, 2002; Bjorklund et al., 2007], competencies [Hernandez Blasi & Bjorklund, 2003], epigenetic programs [Bjorklund & Pellegrini, 2002], and “rules that tend to guide development toward adaptive goals” [Del Giudice & Ellis, 2016, p. 4], evolved probabilistic cognitive mechanisms essentially serve as proxies in ontogeny for the “shaping forces” of natural selection across evolutionary time. “Crafted by natural selection” to solve problems in ancestral environments [Bjorklund et al., 2007, p. 7], these genetically founded mechanisms house information for creating species-typical development, but must interact with the environment (or, more generally, extragenetic factors) during development in order to generate actual psychological form and functioning from this information [Bjorklund & Ellis, 2005; Bjorklund & Pellegrini, 2002]. Under species-typical environmental conditions, evolved probabilistic cognitive mechanisms “express” their species-typical information [Bjorklund et al., 2007; Bjorklund & Pellegrini, 2000, 2002], with this genetic information becoming “translated into behavior” [Bjorklund & Pellegrini, 2000, p. 1691] through “bidirectional gene × environment × development interactions” [Bjorklund et al., 2007, p. 23]. Under species-atypical environmental conditions, however, new problem-solving behaviors may developmentally arise that depart substantially from the genetic disposition or ancestral competence (hence the probabilistic nature of the mechanisms’ expression), allowing for flexibility of behavior in individual ontogeny as competencies adapt to local circumstances [Bjorklund et al., 2007; Bjorklund & Pellegrini, 2002; Del Giudice & Ellis, 2016; Hernandez Blasi & Bjorklund, 2003].

For proponents of EDP, the concept of evolved probabilistic cognitive mechanisms bridges the gap between evolutionary psychology and DS approaches to development by addressing “how inherited genetic information becomes expressed in the adult phenotype” [Bjorklund et al., 2007, p. 16]. Absent from EDP’s developmental model is the genetic determinism language evident in many of evolutionary psychology’s core texts [for salient examples, see Lickliter & Honeycutt, 2003a]. In its stead, proponents of EDP emphasize the probabilistic quality of phenotypic outcomes in development and the developmental dynamics necessary for producing those outcomes. Though structured by natural selection and founded in transmittable genetic information, evolved probabilistic cognitive mechanisms do not exist in a developmental vacuum; in Del Giudice and Ellis’ [2016] words, “while evolved mechanisms prepare an organism for life in a species-typical environment, they are not preformed or specified in advance by a rigid genetic program” (p. 7). Instead, these mechanisms must themselves develop in ontogeny and must do so via bidirectional relations between genetic and extragenetic/environmental factors, with the environment necessarily playing an active role in influencing the nature of that development. Environmental information pertaining to species-typical conditions is necessary for an evolved mechanism to express its evolutionary heritage (e.g., a language learning
environment is necessary for language acquisition mechanisms to develop ontogenetically, but environmental information falling outside the species-typical purview can substantially modify the mechanism’s development [Bjorklund et al., 2007; Bjorklund & Pellegrini, 2002; Hernandez Blasi & Bjorklund, 2003].

As we shall demonstrate, EDP’s developmental model, founded as it is in the concept of evolved probabilistic cognitive mechanisms, is conceptually incompatible with the developmental focus of DS’s epigenetic framework. Take, as just one example, EDP’s routine framing of development as a process of expression, particularly in the context of explaining what takes place developmentally when evolved probabilistic cognitive mechanisms – or the genetic information for them – interact with species-typical environments. We shall show that arguments based on the expression of preexistent information in development actively conflict with the core tenets of the DS approach. Proponents of EDP point out that they emphasize the role of environmental information, not just genetic information, in shaping the development of evolved probabilistic cognitive mechanisms [Bjorklund et al., 2007; Hernandez Blasi & Bjorklund, 2003]. But, as we shall argue, adding another source of preexistent information to the mix, or emphasizing that development is the result of multiple informational “shaping forces” in interaction with one another, fails to embody the relational focus that DS approaches bring to bear on the study of development. Despite its proponents’ assertions to the contrary, EDP’s substitutions of “informational” for “instructional” language and “probabilistic” for “predetermined” language [Bjorklund & Ellis, 2005, 2014; Bjorklund et al., 2007; Del Giudice & Ellis, 2016] make no meaningful progress toward effectively incorporating DS’s epigenetic model. Before we delve more deeply into these arguments, however, a review of the central tenets of the DS approach to development is in order.

Central Tenets of the DS Approach

Numerous variants of the DS approach to development have emerged over the last few decades. In the biological sciences, the DS approach is often linked to the writings of Oyama [e.g., Oyama, 1985; Oyama et al., 2001] as well as those of Griffiths and Gray [e.g., Griffiths, 1996; Griffiths & Gray, 1994]. In developmental science, the writings of Gottlieb [e.g., Gottlieb, 1992; Johnston & Gottlieb, 1990], Lickliter [e.g., Lickliter, 2008; Lickliter & Berry, 1990; Lickliter & Honeycutt, 2013], and Oyama, as well as those of Lerner [e.g., Ford & Lerner, 1992; Lerner, 1978, 2002], have traditionally occupied center stage in discussions of the DS approach. All of these variants, whether in psychological or biological science, tend to agree on a number of central themes [Oyama et al., 2001; Robert, Hall, & Olson, 2001]. Furthermore, recent years have witnessed a substantive elaboration and extension of the DS approach in the form of relational-developmental systems [Overton, 2010, 2015; Overton & Lerner, 2014]. Relational-developmental systems provide a metatheoretical framework that explicitly marries DS’s particular focus on the bottom-up dynamics of the developmental process with a holistic structuralist emphasis on the explanatory significance of system organization in its own right, and we employ this framework in the last third of the paper when detailing our model of evolutionary change as organizational constraint relative to developmental dynamics. For the purpose of articulating the central tenets of the DS approach, however, here we rely heavily on the theoretical
and metatheoretical work of Gottlieb, Lickliter and Oyama, as it is their writings that are foundational to – and continue to figure most prominently in – both EDP’s characterization of the DS approach [e.g., Bjorklund, 2015; Bjorklund et al., 2007; Del Guidice & Ellis, 2016] and the general discussion of the approach within the biological sciences [e.g., Hochman, 2013; Robert et al., 2001]. It is also important to stress that our use of terms like “the DS approach” or “DS proponents” is a matter of convenience and should not imply a unanimity of thought within DS circles. On the contrary, considerable variation exists among those who espouse a DS approach, and although we will endeavor to abstract a prototypical characterization for the approach, we would be remiss not to acknowledge the rich variability that distinguishes DS proponents from one another [for some examples, see Oyama, 2009].

All versions of the DS approach commit to an emergentist philosophy – to the principle that development entails the emergence of new levels of organization in a system [Lerner, 2002]. These new levels of organization spontaneously arise, or self-organize, by virtue of the activities – the coactions – that comprise the nonlinear relations among components of the system and, as emergent properties of developmental processes, are irreducible to those components, as well as to all previous levels of organization that have characterized the system [Gottlieb, 1992; Oyama, 1985]. A recent illustration from Overton [2015] aptly captures what it means for emergent phenomena to be irreducible:

The unity exhibits systemic qualities that are different than any single part process or the sum of the part processes. Thus, these systemic qualities are emergent novelties. Consider the simple example of vision and the visual system: cornea, pupil, iris, lens, retina, optic nerve, lateral geniculate nucleus, optic radiation, primary visual cortex, and associative visual cortex: Where is vision? Vision does not reside in any of the part processes, nor is vision found in the aggregate sum of the parts. Vision is an emergent function of the whole organization; the pattern of coacting part processes. (p. 37)

Emergent qualities of a system are novel in at least two senses. First, as higher-order wholes relative to lower-order parts of a system, emergent qualities are not prefigured, informationally or otherwise, in any of the lower-order parts and processes that help to generate them and therefore represent qualitatively distinct outcomes of these lower-order parts and processes [Johnston & Gottlieb, 1990; Johnston & Lickliter, 2009; Lickliter & Berry, 1990]. Second, as the epigenetic hallmark of what it means for a system to develop, emergent qualities (e.g., different levels of organization, different skills, different forms, etc.) consistently and necessarily arise over the course of an organism’s development that did not previously exist for that organism and therefore constitute a novelty for that organism in its own developmental context.

Proponents of the DS approach argue that the key to the developmental emergence of structure and function is not in preexistent information, privileged levels of analysis, or processes of transmission but rather in the constructive activity of developmental processes themselves [Lickliter & Honeycutt, 2013; Oyama, 1985; Robert, 2004]. For example, Bard [2013] notes that the development of an embryo can be understood only with hindsight – there are no top-level rules that allow prediction of what will happen in a particular tissue, and there are no bottom-up rules that allow knowledge of a tissue’s gene expression profile to predict that tissue’s developmental trajectory. No “organizing factor” or “informational guide” defined separately from or in addition to the relational activity of the system itself is necessary for order to
emerge [Overton, 2015]. It is within the activity of local relations themselves that new levels of organization arise from previous levels of organization, with such relations operating as “sources of both stability and variability” [Lickliter & Honeycutt, 2003a, p. 828]. Thermodynamically, the recursive nature of living systems is such that system activity constantly feeds back to itself, both positively and negatively. As a consequence, more complex levels of organization in development arise in a genuinely novel fashion, without instruction or guidance, from the nonlinear coactions that obtain among the simpler component parts of the system – parts which themselves exist as parts only by virtue of their embeddedness within the system as a whole [Ford & Lerner, 1992; Overton, 2010].

The component parts of any living system, at any level of analysis (from gene-gene relations to organism-environment relations), are “internally” related such that the identity of each component part depends on its relation to other component parts (and to the whole of which it is a part). This, in fact, is what it means for relations in a system to be nonlinear, another central tenet of the DS approach and its holistic orientation [Kitchener, 1982; Lerner, 1978, 2002]. Components of the system are therefore what they are by virtue of their relations to other components (and to the system as a whole). They do not house an elemental identity independently of the relations in which they engage, for these relations involve “interpenetrations of co-acting parts processes” [Overton, 2015, p. 52] and are consequently essential to the components’ very identity [Lerner, 1978; Oyama, 1985]. Each component-to-component coaction in a system involves simultaneous influence between the components (e.g., component A is affecting, while simultaneously being affected by, component B, and vice versa), meaning that the system as a whole is multiply determined [Ford & Lerner, 1992]. Causality becomes distributed across all of the parts that make up the whole such that each part influences the emergence of the whole without determining it [Lickliter & Honeycutt, 2013; Oyama, 1985]. Thus, changes in the relational activity among component parts of a system constitute antecedent conditions for the consequent emergence of new levels of organization in the system.

Proponents of the DS approach additionally stress that the multiple levels of system structure (e.g., cellular levels, organ levels, organism-environment levels) that characterize a complex system synchronically (i.e., at any given point in time) involve a hierarchical structuring [Gottlieb, 1992; Lickliter & Honeycutt, 2013]. Genes comprise parts of the whole that is the cellular level of structure, cells comprise parts of the whole that is the tissue level of structure, organs comprise parts of the whole that is the organ system level of structure (e.g., the cardiovascular system), and organisms comprise parts of the whole that is the organism–environment level of structure, just to list a few. So even though genes, cells, tissues, organs, etc. are all components/parts of the organism as a whole, each of these parts is also a whole, or level of structure, in its own right, relative to its lower-order parts (e.g., the cell is a whole relative to genes but a part relative to tissues). Given that bidirectionality characterizes all coactions in a system, relations among the components of any system play out both horizontally, via part-to-part coactions, and vertically, via parts-to-whole and whole-to-parts relations, across all levels of structure, from the biological to the psychological and sociocultural [Overton, 2015]. And as we discuss in the final third of this paper, horizontal and vertical system relations constitute fundamentally different kinds of explanation [see also Craver & Bechtel, 2007].
Critically, to be hierarchically structured as a system means that the activity of any given component of the system under question is local to the immediate level of system structure to which the component belongs [Gottlieb, 1992; Johnston & Edwards, 2002]. Gene functionality, for example, is specific to the local context of the cell. When cells coact with other cells, however, such processes operate at the structural level of cells themselves. Thus, an understanding of tissue construction, which itself derives from cellular coactivities, cannot simply be reduced to the level of DNA-RNA-cytoplasm relations within the cell. As components of any system act locally, so the significance of their activity should be defined locally.

Viewing EDP from the Vantage Point of a DS Perspective

Despite assertions to the contrary [e.g., Machluf et al., 2014], EDP’s developmental model of interaction bears little more than surface resemblance to DS’s emergentist philosophy. With their explicit focus on “how evolved psychological mechanisms develop through bidirectional interactions between environmental and genetic factors” [Del Giudice & Ellis, 2016, p. 4], proponents of EDP are actually promoting a fundamentally different conceptualization of how phenotypic form is generated in ontogeny.

Consider the question of what develops in ontogeny with respect to evolved probabilistic cognitive mechanisms, the centerpiece of EDP’s model. Proponents of EDP assert that these psychological mechanisms develop through continuous, bidirectional interactions among multiple levels of organization both within the organism and between the organism and its environment – such that the mechanisms, although shaped via natural selection, must be constructed anew in each ontogeny – which would suggest a true process of emergence and construction consistent with the DS approach’s focus on relational activity [Bjorklund et al., 2007]. However, EDP proponents also assert that it is the expression of the evolved mechanism that actually develops, with the developmental process itself involving little more than the realization, or lack thereof, of a mechanism built from information that predates the mechanism’s ontogenetic manifestation [Bjorklund, 2015; Bjorklund & Ellis, 2005; Bjorklund et al., 2007; Bjorklund & Pellegrini, 2000, 2002; Del Giudice & Ellis, 2016]. In other words, information for constructing language acquisition mechanisms already inheres in the genome of the fertilized egg – all developmental processes do is translate this information into an ontogenetic reality.

If, as EDP proponents suggest, developmental processes involve the differential expression of “information,” can the outcomes of these processes be considered emergent and irreducible? Under species-typical environmental conditions, at least, the answer seems to be no. From all accounts, it would appear that the ontogenetic “expression” of evolved probabilistic cognitive mechanisms and the genetic information associated with the development of these mechanisms are structurally isomorphic in the sense that a blueprint’s structural layout is formally identical to the actual structural layout of the house that ends up being successfully built to match the blueprint’s specifications. Such structural isomorphism between genetic information and an associated phenotypic outcome suggests that a process of translation, not emergence, characterizes the developmental construction of evolved mechanisms.

The problem is that, for proponents of EDP, evolved probabilistic cognitive mechanisms exist in two forms or incarnations. These mechanisms are both (a) con-
solidated evolutionary adaptations – shaped by natural selection – from our ancestral past, the information for which is “built into the organism” to prepare organisms for certain kinds of environmental information processing [Bjorklund & Ellis, 2014, p. 228] and (b) developmental products of gene-environment interactions in individual ontogenies. As such, when development occurs in the context of species-typical environmental conditions, these mechanisms exist as both potentials for development and successful actualizations of such potential, organizationally prefiguring their very ontogenetic construction in the process. Where is there room for emergence in EDP’s account when, under species-typical conditions, the actual activity of development simply acts to translate form into ontogenetic content?

Perhaps the structure of the mechanisms that develop under species-atypical conditions is truly emergent in the sense of being irreducible to the “information” that precedes it. It remains unclear in EDP accounts whether environmental information essentially prescribes the properties of developing mechanisms under species-atypical conditions or whether genetic and environmental informations interact to give rise to something truly novel and irreducible. In the context of species-typical environmental conditions, however, the developmental processes behind the construction of evolved probabilistic cognitive mechanisms seem to involve little more than the transmission and expression of information to which the mechanisms are formally reducible, not the emergence of qualitatively new levels of organization from previous levels of organization. Proponents of EDP have essentially relegated the constructive activity of developmental processes – which constitutes the source of developmental organization for proponents of the DS approach – to a secondary role of expressing in content what already exists in form via information, genetic or otherwise.

Appeals to information are notoriously tricky in discussions of development [Oyama, 1985; Oyama et al., 2001], especially because the idea of information “is little more than a metaphor that masquerades as a theoretical concept” [Sarkar, 1996, p. 187]. In the context of the DS approach (and to the extent that DS proponents see fit to incorporate the notion of information into their accounts of development), the idea of information is necessarily wedded to local activity, for information is only meaningful as information in the context of activity [Oyama, 1985; Oyama et al., 2001; Thompson, 2007]. Thus, for example, genetic information – viewed from the vantage point of an emergentist framework – would remain wedded to the construction of RNA, possibly the construction of amino acid chains or, by liberal extension, the synthesis of proteins, but evolved probabilistic cognitive mechanisms are, presumably, a far cry from these much lower levels of system structure, given their status as psychological mechanisms and the intricate processes necessarily involved at multiple levels of systems structure for their construction. To suggest, as proponents of EDP do, that genetic information could possibly be of direct guidance for the construction of these psychological mechanisms – or for any lower-order perceptual biases that serve as foundations for them – is to suggest that the information contained in the genome substantially transcends the local activities with which genes are actually engaged. Viewing information as transcending its local activity – its local arena of system structure – violates both DS’s focus on local activity for its own sake and DS’s hierarchical conceptualization of integrated activities in the system.

Owing to this persistent tendency in conceptual models like EDP to view information (whether genetic or extragenetic) as going beyond the very activity to which
it is wedded, the information metaphor is wholly inadequate for capturing the centrality of constructive activity in the DS approach. As an alternative, Thompson [2007] has recommended the metaphor of *laying down a path in walking*, in which “there is no separation between plan and executed action” (p. 180). Such a metaphor grounds an understanding of development precisely in terms of relations and activity – local activities in relation to other local activities, constituting a network of local relations that gives rise to emergent organization in the system. No underlying facsimile or representation of order in the form of information need exist for local activities of a system to give birth to new levels of organization in the system from previous levels of organization; the new organization instead comes from the very network of activities themselves. Within this metaphorical framing, any conceptual division between preexistent information for an evolved probabilistic cognitive mechanism and the phenotypic “expression” of said mechanism in ontogeny collapses. This is because the local activities that combine to yield the developmental construction of the mechanism in any given ontogeny do not in themselves – that is, outside their collaboration in a system of relations – harbor any form of guidance or specification for the emergent mechanism itself.

In fact, adopting Thompson’s [2007] *laying down a path in walking* metaphor renders the notion of evolved probabilistic cognitive mechanisms explanatorily vacuous. What exactly could these mechanisms *be* independently of their phenotypic expression or in the absence of their developmental emergence? If, as a DS approach would suggest, an evolved probabilistic cognitive mechanism *is* its phenotypic form, then why treat the evolved mechanism as if it has any explanatory significance independent of its phenotypic form? Proponents of EDP routinely write that these mechanisms are “modified” when organisms encounter species-atypical contexts, but *what exactly* undergoes modification when the very mechanism itself is in the process of being actively constructed, anew for each individual ontogeny [Johnston & Gottlieb, 1990; Lickliter & Berry, 1990]? Again, terms like *expression* and *modification* indicate that the mechanism or the information for its construction predate the very processes that actually give rise to the mechanism in development.

For EDP proponents, organisms enter this world “prepared by natural selection” [Bjorklund, 2015, p. 14] to process certain aspects of their environment more readily than others, with such biological preparedness “built into the organism” via information apparently contained in the genome [Bjorklund & Ellis, 2014, p. 228]. From these lower-order information-processing biases develop more sophisticated evolved probabilistic cognitive mechanisms, with the actual phenotypic outcome of the evolved mechanisms dependent on developmental relations between genetic and environmental information. If, however, as DS proponents claim, information holds no explanatory value outside of local activity, then information cannot guide anything beyond local activity. Higher-order organization results from relations *among local, developmentally successive activities* and cannot be guided by the individual, local activities themselves. The higher-order organization is guided by the relational network (i.e., the system) of activities across developmental time. This is the essence of the distributed causality framework that DS proponents espouse. Interpreting causality as distributed does not simply entail adding more informational components to the mix (i.e., placing environmental sources of information alongside genetic ones). Distributed causality entails recognizing that developmentally emergent levels of organization are *irreducible* to these components. It entails recognition that the source of
emergent order, at all levels of organization, resides in the interdependent, nonlinear activity of relations among components of a system. Distributed causality means that any initial perceptual or other molar biases that an organism enters the world with are themselves the products of developmental activities at multiple levels of system organization and hierarchy – irreducible to, and therefore not guided by, the molecular levels of genetic or cellular activity to which EDP proponents appeal with phrases like “built into the organism” and “prepared by natural selection.”

An example from a recent paper by Bjorklund [2015] highlights how conceptually superfluous the notion of evolved probabilistic cognitive mechanisms becomes when considered within a DS account of developmental emergence. Bjorklund’s example concerns the development of face processing in human infants, which he employs to demonstrate how an evolved mechanism arises in ontogeny. After charting the robustness with which neonates attend to face-like stimuli, Bjorklund makes it clear that such an information-processing bias “does not imply that [neonates] understand the conceptual meaning of faces” (p. 26). He further asserts that this initial bias toward faces is not specific to faces but derives from domain-general, lower-order perceptual processing biases for stimulus properties like up-down asymmetry, vertical symmetry, and high contrast [e.g., Turati, 2004]. Nonetheless, because faces routinely feature properties consistent with these initial processing biases, young infants strongly orient to them and, with experience, develop more finely honed skills for discriminating among faces. In other words, skilled face processing – as a prototypical evolved probabilistic cognitive mechanism – develops out of “initial perceptual and information-processing biases interacting with species-typical environments to produce patterns of behavior that yield, more often than not, adaptive outcomes” [Bjorklund, 2015, p. 23].

To the extent that evolved probabilistic cognitive mechanisms reflect an outcome of developmental processes via organism-environment relations, Bjorklund’s [2015] example establishes a perfectly reasonable emergence account for the development of these mechanisms. However, the more his developmental account of face processing aligns with a DS approach, the more superfluous the notion of evolved mechanisms becomes. If this evolved mechanism is nothing more than an emergent product of developmental processes, how is it any different from every other new level of functioning and organization that emerges over the course of development? Why attach the qualification of “evolved” to the mechanism of face processing when its phenotypic existence is fully explicable in terms of the activity of developmental processes?

Presumably, skilled face processing is considered an “evolved” mechanism because it derives, in part, from early information-processing biases such that “babies enter the world prepared to make sense of at least one important social stimulus: faces” [Bjorklund, 2015, p. 28]. Bjorklund clearly argues that evolved mechanisms emerge from these information-processing biases in interaction with environmental conditions and that the information-processing biases in themselves are not specific to faces. As a result, evolved mechanisms seem truly emergent from prior developmental activity. However, Bjorklund [2015] presents the early biases from which evolved mechanisms arise as being “influenced by the genome” (p. 25), and, significantly, he does not couch them in terms of developmental relations between gene and environment, strongly implying that the biases are genetically “prepared” biases, a product of natural selection. The biases, in other words, amount to a type of evolved
mechanism themselves. If these initial processing biases are genetically prepared biases, built into the organism by natural selection, then Bjorklund’s account ignores the developmental activities that must necessarily take place to construct the biases themselves, because such organismic biases – like the evolved mechanisms that derive from them – are irreducible to the local activities of genes and other molecular developmental resources. Alternatively, his account could posit genetic activity as providing a “guiding force” behind the developmental activity, but a guiding force, helping to direct (in “entelechy” fashion) the actual process of developmental activity itself, moves us no closer to a developmental emergence account for these biases. True, a guiding force is not a determining force – as Bjorklund [2015] notes, “prepared is not preformed” (p. 28) – but it is also antithetical to a process of true emergence; guiding forces assume the role of organizer or central executive, transcending local activities and smacking of instructional foresight for something as yet undeveloped [Oyama, 1985].

Whatever the case may be, the notion of biases built into the organism by natural selection is fundamentally inconsistent with a DS approach. And if, in all of this discussion of information-processing biases, Bjorklund is not suggesting the operation of a guiding force and is, in fact, recognizing the various levels of formative developmental activity that intercede between gene and basic organismic “biases,” then his account is perfectly consistent with a DS approach – but the notion of an information-processing bias, prepared by evolution, becomes superfluous in the process. How are these initial biases any different from simply positing, at birth, a certain level of developmental organization in behavior that necessarily derives from previous levels of developmental organization prenatally and constrains the possibilities for future levels of developmental organization? Calling it an information-processing bias is fine, but it has its own developmental history, one from which it developmentally emerged, just like evolved mechanisms have a developmental history from which they emerged, and the origin of any organismic bias or evolved probabilistic cognitive mechanism is the activity of developmental processes themselves, at least from the vantage point of a DS approach.

In our view, a basic, ontological incompatibility clearly exists between EDP and DS approaches. It is an incompatibility that plumbs the very conceptualization of what development entails and precludes any meaningful rapprochement between the developmental principles of DS and the evolutionary principles of Darwinian theory. In fact, as we argue in the section to follow, it is an incompatibility that arises precisely because of EDP’s fundamental allegiance to Darwin’s mechanistic view of phenotypic construction. Given Darwin’s entrenchment in a Newtonian world view, in which organisms are treated “as material objects whose design and functioning must be imparted to them” [Oyama, 1985, p. 12], and his conceptualization of natural selection as an external, shaping force creatively generating phenotypic organization [Depew & Weber, 1995; Lewontin, 1983], the very idea that an orthodox Darwinian perspective could support “a truly developmental approach to human behavior” [Del Giudice & Ellis, 2016, p. 4] seems doomed from the start.

In shifting an understanding of biological diversity to an “irreducibly population-level” [Sober, 1984, p. 150] analysis, Darwin revolutionized the study of evolution, and his insight has unquestionably advanced our understanding of evolutionary change in a most profound fashion. Modern developmental science itself owes enormous debt to Darwin’s visionary argument against design – his “dangerous idea” that
all levels of organized complexity in living systems can be explained from the bottom-up, without recourse to a “designer” on high [Dennett, 1995]. Furthermore, it should also be stressed that Darwin’s writings are both complex and richly nuanced enough to afford different readings and interpretations. Nonetheless, the seeds of the modern synthesis’ full-blown exclusion of development from the story of evolutionary change were sowed by Darwin’s own marginalization of developmental process [Depew & Weber, 1995; Gould, 2002; Russell, 1916; Sober, 1984], and so it is to these Darwinian foundations that we now turn.

**EDP and DS as Ontologically Incompatible**

Employing the notion of information, in either genetic or extragenetic sources, to explain the driving force behind the activity of development, as EDP proponents do [e.g., Bjorklund & Ellis, 2005, 2014; Bjorklund et al., 2007], presupposes that the activity of development needs to be driven, but DS proponents conceptualize the “driving force” behind the emergence of developmental structure and function as the very activity of developmental processes themselves – eschewing, in effect, the whole idea of postulating a driving force to begin with. And therein lies the crucial ontological incompatibility between EDP and DS approaches to development: in the conceptual framework of EDP, consistent order and stability in development cannot arise simply from ontogenetic processes in the absence of some kind of guiding force. Bjorklund et al. [2007], for example, argue that “although we concur that all traits are generated in ontogeny … developmental systems theory fails to address how the range of alternatives becomes limited … if not via some genetic ‘prespecification’” (p. 21). For EDP’s proponents, components of a system could, in theory, combine in so many different ways that the phenotypic forms generated through the dynamics of developmental processes across individual ontogenies will be wide-ranging and show no signs of converging on any common forms – that is, unless these combinatorial possibilities are subject to the structuring constraints of a shaping force, namely natural selection.

Such an argument springs directly from EDP’s conceptual adherence to Darwin’s evolutionary approach [e.g., Bjorklund & Pellegrini, 2002; Del Giudice & Ellis, 2016]. Organization, from a Darwinian perspective, does not “naturally” inhere in developmental activity – it must be imparted to that activity, first by the selective pressures of the environment, then by the heritable (genetic) information that reliably transmits the results of those selective pressures to future ontogenies. Thus, without some kind of prespecification, some kind of organizing factor, either genetic or environmental, developmental activity will generate nothing but free-ranging variability, unoriented and undirected. The same concern over specification has been raised by Gilbert [2003] – one of the architects of Evo-Devo – in the context of distinguishing mainstream Evo-Devo from its DS-inspired, revolutionary alternative, Devo-Evo:

[DS theory] has, generally, made the error of not assigning instructive or permissive influences in the interactions… However the specificity of the reaction (that it is a jaw that forms and not an arm; that it is a salamander jaw that forms and not a frog jaw) has to come from somewhere, and that is often a property of the genome…. Instructive partners provide specificity to the reaction, whereas permissive partners are necessary, but do not provide specificity. (p. 349, italics added)
Like mainstream Evo-Devo, in EDP the nature of developmental interaction requires “instructive” and “permissive” partners, with one partner contributing the specificity necessary to guide the undirected and unoriented variation of developmental processes.

Neither proponents of mainstream Evo-Devo nor those of EDP take seriously the possibility of “specifications as emergent from developmental processes” [Derkesen, 2010, p. 482], revealing the substantial ontological divide that exists between EDP and DS with respect to “the nature of matter” itself [Linde Medina, 2010, p. 7]. The Darwinian focus of EDP envelops its proponents in a view of living matter as “more acted upon than acting” [Depew & Weber, 1995, p. 71; see also Walsh, 2015], inherently variable but incapable of its own organization, requiring instead the relentless shaping pressures of the external world to forge its undirected variability into systematic, reliably ordered biological form, heritable from one generation to the next [Gould, 2002; Lenoir, 1987; Lewontin, 1983]. This view centrally conditions EDP’s model of developmental processes. For EDP’s proponents, genes and environment constitute separate sources of information for the specification of biological form and serve as antecedent causal forces interacting with each other on the developing organism to implement transfer and expression of the said information, much as the kinetic energy of one billiard ball is imparted to another by spatiotemporal contact. Each individual ontogeny starts with the developing organism’s “original nature” – that is, the innately given genetic code and the information it contains, born of natural selection – and proceeds, via the environmental information to which the developing organism is exposed, to either the facilitation and elaboration of or the inhibition and alteration of the information set forth in the genome [see the following for critiques of such an approach: Derksen, 2010; Ingold, 2004; Schneirla, 1960; Walsh, 2015]. The developing organism thus emerges as a byproduct of preexistent information transferred from more elemental causal sources, “the passive object of autonomous internal and external forces” [Levins & Lewontin, 1985, p. 89].

For proponents of the DS approach, in contrast, living matter, far from needing to be acted upon, is inherently active and self-organizing [Ford & Lerner, 1992; Gottlieb, 1992; Lickliter & Honeycutt, 2013; Overton, 1976, 2015; Oyama, 1985]. Matter, at whatever level of analysis, is always actively situated in the context of other matter and definable in terms of its relational activity, with the coactivity of matter-to-matter relations as the ground out of which the very idea of matter as a thing in itself emerges [Brinkmann, 2011]. DS’s conceptual framework, beholden to activity and relations, departs from the atomistic cosmology of Darwin’s evolutionary stance, in which organization in the biological world is cobbled together out of independent, isolable elements under the sway of the external shaping force of natural selection [Kauffman, 1985; Smith, 1992; Webster & Goodwin, 1982]. Instead, DS proponents take as their ontological starting point systems of relations among components of matter born of the inherently active (and reactive) status of the components themselves, with components necessarily defined in terms of relations with other components and with the system as a whole, not as isolable elements whose interactions must be imparted to them by an external force. Thus, the interdependence of matter – parts of the world depend on other parts for their very existence and identity such that their definition as parts necessarily stems from the relational activity in which they are embedded – constitutes a precondition for understanding the very nature of matter itself. This, in brief, entails DS’s ontological commitment to holism [Overton, 2015].
further establishes organization as an ontological category of necessity, not contingency; under the principle of holism, organization is fundamental to all living matter, at all levels of analysis, not contingently imposed from without [Overton, 2015].

The relational, activity-based focus of DS grounds the approach’s conceptualization of development squarely within the domain of self-organization and the dynamics that characterize nonlinear, complex systems [Lerner, 2002; Lickliter & Honeycutt, 2003a, 2013]. As a process, self-organization characterizes the emergence of new, irreducible forms in a system through the lower-order fluctuations and nonlinearity of relations among the components that comprise the system, with more complex levels of organization in systems arising in novel fashion from the nonlinear dynamics that obtain among the simpler component parts of the system [Lewis, 2000; Thelen & Smith, 1994]. Evident in the generation of higher-order organization across both the inorganic and organic world (from the dynamic construction of convection cells in heated liquid and the Belousov-Zhabotinskii chemical reaction to that of protein folds and cellular membranes in living systems, to identify just a few), self-organization has emerged as a viable candidate “for generating robust adaptive complexity – at all levels of the biological hierarchy, from the molecular to the organismic” [Edelmann & Denton, 2007, p. 580; see also Batten, Salthe, & Boschetti, 2008; Depew & Weber, 1995; Kauffman, 1985; Swenson, 2010].

Critically, major advances in the mathematical understanding of self-organization over the last few decades – springing from the multidisciplinary approach of nonlinear dynamical systems theory [Guastello, 1997; Molenaar & Raymakers, 1998] – have revealed that a relatively limited set of stable patterning in macrolevel organization can and does repeatedly emerge from dramatically varied microlevel relations. This demonstrates that the dynamics of self-organization delimit the combinatorial possibilities available to a developing system [Edelmann & Denton, 2007; Ho, 2010; Lickliter, 2008; Saunders, 1984]. In other words, restrictions on what kinds of organized forms in biology can and do exist spring from the very activity of developmental processes, reflecting the developmental principles that govern how organisms develop in context [e.g., Alberch, 1982; Thompson, 1942]. Thus, the reliable and stable generation of a relatively restricted range of organized forms at all levels of complexity, both within and across generations, need not require an external organizing force like natural selection.

In their search for the basic principles of developmental organization within the self-organizing dynamics of developmental processes themselves, proponents of the DS approach adopt a thorough-going developmental explanation for the nature of the interrelation between ontogenesis and phylogenesis, not a selectional explanation, as proponents of EDP do. Although DS proponents recognize a role for selectional explanation in the context of population-level change – as we discuss in the next section – their orientation is strictly developmental in the context of individual ontogeny and the emergence of organized complexity. DS proponents readily acknowledge the historical roots of this approach in the work of developmental psychobiologists such as Schneirla [1960], Kuo [1967] and Lehrman [1970] and, more generally, in the evolutionary embryological work of Garstang [1922] and de Beer [1958], among others [Gottlieb, 1987, 1992; Lerner, 2002; Lickliter & Honeycutt, 2015]. Equally important, however, are the decidedly pre-Darwinian roots of the DS approach’s developmental focus, traceable to aspects of the structuralist orientations of early rational morphologists like Goethe and Cuvier who sought to establish laws of biological organization.
by examining regularities in how parts of different complex systems interdependently relate to one another in the service of the systems as unified wholes [Hughes & Lambert, 1984; Lenoir, 1987; Saunders, 1984; Webster & Goodwin, 1982]. These pre-Darwinian roots – actively extended and elaborated in modern days through the DS-related discipline of process structuralism2 [Goodwin, 1982; Ho & Saunders, 1984; Webster & Goodwin, 1982] – further highlight the basic ontological division that exists between DS and Darwinian-inspired approaches to the construction of organized complexity. At the heart of such division lie opposing conceptualizations of natural selection itself.

**Natural Selection, Individual- and Population-Level Dynamics**

The concept of natural selection – which we identify broadly with the process dynamics of differential survival and reproduction in a population – actually predates Darwinian theory [Gould, 2002]. Under the auspices of pre-Darwinian evolutionary thought, however, natural selection operated solely to weed out phenotypic variation, with the real motor of evolutionary change inhering in the transformative powers of organismic development [Gould, 2002; Ho, 2010]. The significance of Darwin’s conceptualization was to elevate natural selection from this negative role to “the creative force of evolutionary change,” establishing it as a “positive force” behind the construction of organized complexity [Gould, 2002, p. 139; Ho, 2010; Sober, 1984]. This elevation, however, arrived entirely at ontology’s expense. Darwin’s Newtonian, mechanistic focus – external forces confer order and direction upon unoriented, inert matter – removed the origins of organized complexity from development (and, by extension, developmental processes) in individuals over ontogenetic time and situated these origins, instead, in the realm of cross-generational, evolutionary time, with the shaping forces of natural selection working on unorganized variability in populations to slowly build up, across generations, systematic, organized complexity in form and function [Depew & Weber, 1995; Gould, 2002; Russell, 1916; Linde Medina, 2010].

Proponents of EDP uphold this Darwinian, positive view of natural selection, evident in repeated references to natural selection as “shaping” human functioning and development, and to human functioning and development as “products” of selec-

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2 Adopting “a more European view of scientific metatheory” [Smith, 1992, p. 433], the biological sciences’ discipline of process structuralism actively embraces the explanatory significance of a time- and history-independent taxonomy of forms; in this, proponents of process structuralism revive the efforts of early rational morphologists and argue for the scientific legitimacy of structural explanation [e.g., Goodwin, 1982; Ho & Saunders, 1984; Saunders, 1989; Webster & Goodwin, 1982], a mode of explanation to which we appeal later in this paper as a complement to the bottom-up, temporal dynamics of self-organization and developmental construction. The extent to which process structuralism dovetails with the DS approach of biological science has been a point of contention for both Oyama [1985] and Griffiths and Gray [Griffiths, 1996; Griffiths & Gray, 2005]. Oyama [1985], for example, while praising process structuralists’ emphasis on developmental process, has criticized their emphasis on “necessary and universal forms” (p. 119). Griffiths [1996; see also Griffiths & Gray, 2005] has further critiqued process structuralism for marginalizing the worth of historical explanation (e.g., common ancestry and lineage) in an understanding of evolutionary change. It remains unclear, however, whether either of these DS proponents actually accepts the scientific legitimacy of structural explanation or whether they simply object to a perceived elevation of one mode of explanation (structural) over another (functional, historical) and the potential for structural reification that such an elevation might entail.
tion pressures [Bjorklund & Ellis, 2005; Bjorklund et al., 2007; Bjorklund & Pellegrini, 2000, 2002; Del Giudice & Ellis, 2016]. Though they admit that “it is the developmental plasticity of an organism that provides the creative force for evolution” [Bjorklund & Pellegrini, 2002, p. 52], such admissions merely acknowledge the role of developmental processes in the creation of variability; from the vantage point of EDP; it is natural selection that shapes this ontogenetic variability into serviceable form and mechanism over evolutionary time, producing “incremental modifications in existing phenotypes, leading to an accumulation of characteristics that are organized to enhance survival and reproductive success” [Del Giudice & Ellis, 2016, p. 5]. Proponents of the DS approach, however, espouse more of a pre-Darwinian, negative view of natural selection, as eliminator of the unfit but as neither creator nor modifier of phenotypic organization itself [Ho, 2010; Johnston & Gottlieb, 1990; Lickliter & Honeycutt, 2003a; Oyama, 1985]. In Lickliter’s [2008] words, “natural selection cannot serve as a creative generator of phenotypic form or phenotypic change. Natural selection is simply the filter that preserves reproductively successful phenotypes, which themselves are products of individual development” (p. 362).

This modern divide with respect to the conceptualization of natural selection is not as clearcut, however, as a simple pre-Darwinian/Darwinian contrast might suggest. In particular, DS proponents stress the need to demarcate individual organism-level and population-level dynamics when discussing what exactly it could mean for natural selection to “shape phenotypes” [Johnston & Gottlieb, 1990; Moore, 2008]. At the population-level of analysis, for example, DS proponents fully endorse the explanatory significance of natural selection as an antecedent process behind changes in the distribution of phenotypes across evolutionary time. The nature of phenotypic change at the level of populations, however, concerns the characteristic distribution of phenotypes in the population qua population, with natural selection acting to increase or decrease the frequency with which an individual phenotypic variant (e.g., a long neck) characterizes the population as a whole [Lickliter & Honeycutt, 2013, 2015]. To the extent, for example, that a population changes from a thoroughly heterogeneous mix of many different phenotypic variants (e.g., varying sizes of neck, from short to long) to a grouping that revolves around one of those phenotypic variants (e.g., a long neck, now represented in the majority of the population), natural selection would be a viable candidate as an antecedent process for having creatively engineered this “transformation” in the phenotypic character of the population itself. In this way, natural selection can “influence the distribution of existing phenotypes in a population by reducing the number of unsuccessful phenotypes” [Lickliter & Honeycutt, 2003a, p. 827], answering the question of why a particular phenotype persists in a population or why one phenotype rather than another characterizes the population as a whole [Olson, 2012]. However, DS proponents restrict the creative dynamics of natural selection exclusively to the distribution of phenotypes in populations. Natural selection, in other words, can only account for the persistence and spread of a particular phenotypic character in a population, not for its existence as a form to begin with, in any given individual, or for its developmental stability in individuals across generations [Johnston & Gottlieb, 1990; Lickliter & Honeycutt, 2003a; Sober, 1984]. The question of why any given phenotypic form exists at all, in fact, resolves not to population-level dynamics but to the developmental dynamics of individual organisms, for every form must first exist at the level of the individual before it can exist at the level of the pop-
ulation (and thus be subject to the selective pressure of natural selection). After all, individual phenotypes and the developmental processes that generate them necessarily precede whatever distribution of phenotypes eventually comes to characterize the population as a whole via a population-level mechanism like natural selection. Furthermore, any transformative changes that arise with respect to existing phenotypes must first take place in the developmental arena of individual ontogeny before such changes can begin to play out at the population level in terms of changes in the distribution of the newly formed phenotype [Johnston & Gottlieb, 1990; Lickliter & Berry, 1990; West-Eberhard, 2003]. This principle is embodied in the emphasis that many biologists currently place on genes as “followers, not leaders, in adaptive evolution” [West-Eberhard, 2005, p. 6547; see also Pigliucci & Müller, 2010].

Thus, proponents of the DS approach regard population-level, evolutionary changes as “the outcome of a process that begins with organismic change, rather than as a mechanism for explaining organismic change” [Johnston & Gottlieb, 1990, p. 490]. Individual-level dynamics in the form of ontogenetic processes, not the process dynamics of natural selection, assume the explanatory task of generation, maintenance, and transformation of phenotypic organization itself, with every form that develops in an individual ontogeny being novel and truly emergent for that individual, “constructed anew in each generation” [Johnston & Gottlieb, 1990, p. 480]. Natural selection and the dynamics of population-level change can “describe existing variation in a population of organisms, but not potential variations of one organism” [Gabora, 2006, p. 446]. As Sober [1984] has succinctly articulated:

Natural selection does not explain why I have an opposable thumb (rather than lack one)…. It may account for why particular organisms survive and why they enjoy a particular degree of reproductive success. But phenotypic and genotypic properties of individuals – properties of morphology, physiology, and behavior – fall outside of natural selection’s proprietary domain. Yet at the population level, these limitations disappear…. The frequency of traits in a population can be explained by natural selection, even though the possession of those traits by individuals in the population cannot. (p. 152)

This means that adaptationist explanations in evolutionary theory, which focus on the adaptive value of a trait – its fitness and functional significance – and which appeal to the antecedent mechanics of natural selection, specifically explain why a given phenotype has persisted in a population across evolutionary time. Such explanations, however, are routinely employed in the literature as if they explained why a given phenotype “should exist at all” or why it “exists in the first place” [Scott-Phillips, Dickins, & West, 2011, p. 40, 41], promoting confusion over what natural selection can actually account for. Employing natural selection as a mechanism for phenotype construction, in fact, constitutes a fundamental error of application, confusing functional consequence with antecedent cause [Bateson, 1988; O’Grady, 1984]. As Jamieson [1986] emphasized, adaptationist mechanisms like natural selection “can only account for the relative distribution of epigenetically produced behavioral phenotypes in local populations, but they do not explain the evolution of forms of the behaviors” (p. 205, italics added).

Of course, altering the compositional make-up of a population through the dynamics of natural selection delimits the kinds of phenotypic form likely to arise in those individuals who subsequently develop within the context of the population. Developmental resources – genes, cytoplasm, cells, and various facets of their intra- and extraorganismic environmental surround – pass from one generation to the next...
[Griffiths & Gray, 1994; Jablonka & Lamb, 2005; Johnston & Lickliter, 2009; Oyama, 1985], and as the distribution of phenotypes in a population changes over evolutionary time, via selective pressures, so the developmental resources available to that population necessarily change. To the extent, then, that natural selection eliminates certain phenotypes and preserves others in a population, its population-level effects translate into changes in developmental resources, which, in turn, directly influence, in antecedent-consequent fashion, the construction of future individual ontogenies. Does this not suggest that natural selection – via its direct effect on the availability of developmental resources in a population – exerts some measure of creative influence over the construction of individual development?

For DS proponents, developmental resources, as heritable qualities, are not recipes – i.e., informational, directive sources – but ingredients for the emergence of phenotypic organization in ontogeny [Griffiths & Gray, 1994; Griffiths & Stotz, 2013; Oyama, 1985]; the source of reliability in the “construction and reconstruction” of phenotypic organization, from generation to generation, resides within the self-organizing dynamics of developmental processes themselves [Oyama et al., 2001, p. 1; Robert, 2004]. Nonetheless, if the dynamics of natural selection act to cobble together (over evolutionary time) specific ingredients within a population and filter out other ingredients, then one could argue for a “creative” role of natural selection in ontogeny, at least to the extent that selective pressures are responsible for having assembled the collection of ingredients currently available to any developing member of a population. This line of reasoning presupposes that selective pressures can operate independently on different parts of organisms – different facets of phenotypic variability within organisms – such that tiny bits of incremental variation in various phenotypic properties of organisms could be cobbled together over extended time by the inexorable force of natural selection. Such assumptions undergird both Darwinian and neo-Darwinian treatments of natural selection.

However, from the vantage point of DS approaches, systematic regularities in how parts of different complex systems relate to one another derive from developmental dynamics – from the laws of developmental organization [Hughes & Lambert, 1984; Saunders, 1984; Webster & Goodwin, 1982]. Natural selection, in selecting for outcomes in organisms as wholes, operates on systems of relations, not on isolated parts of systems. Developmental resources, in other words, are not isolated elements to be combined in whatever fashion natural selection “chooses.” Natural selection can only increase or decrease the frequency of representation in a population of systems of components that are already stably established at the individual, ontogenetic level. For natural selection to play a creative role of any kind in ontogeny requires selective pressures to affect the developmental dynamics of processes or the developmental resources available for interaction. But natural selection does not do anything to the dynamics of ontogeny and does not assemble developmental resources – it does not even introduce regulatory or stabilizing mechanisms. It simply increases the likelihood that certain already stable systems of developmental resources will be represented in the population relative to other already stable systems of developmental resources. Selective pressures do not consolidate, stabilize, or fine-tune developmental variation at the level of individual ontogeny, only at the level of the population in evolutionary time. Rather, it is ahistorical laws of self-organization that characterize what is possible in the dynamics of relation among developmental resources – that account for which combinations of developmental resources are viable and stable in
relation to one another and for how those resources interrelate as systems. Thus, the statistical regularities that reflect an increased representation of phenotypic form in a population should not be reified into antecedent forces of guidance in the construction of individual ontogenies.

Proponents of EDP fall victim to precisely this error of reification. By viewing natural selection as (a) constructing and preserving across evolutionary time the very existence of phenotypic form, in the abstract, and as (b) helping to shape the ontogenetic realization of such form in the individual, proponents of EDP attach the antecedent process dynamics of natural selection – appropriate only for population-level change – to their conceptualization of individual, ontogenetic dynamics via the explanatory construct of evolved probabilistic cognitive mechanisms and thereby conflate population- and individual-level dynamics in the process.

EDP and DS proponents thus hold ontologically incompatible views both of developmental processes and of evolutionary processes (e.g., natural selection) as they pertain to developmental processes. EDP proponents view development in terms of transmission and expression; DS proponents view development in terms of construction and emergence. EDP proponents see population-level, evolutionary changes via natural selection as shaping individual ontogeny via inherited mechanisms; DS proponents see evolutionary changes as an outgrowth of individual ontogeny and its developmental processes, with natural selection acting as an antecedent process for population-level changes but not for individual ontogenies. Far from integrating selectional and developmental explanatory perspectives, EDP proponents wed themselves to a selectional vantage point, assimilate DS principles to this vantage point, and in the process profoundly misrepresent what it means to adopt a developmental perspective. DS proponents, in contrast, wed themselves to a developmental perspective but acknowledge the value of a selectional approach in the context of population-level change. Where does this leave the question of synthesis between selectional and developmental explanatory perspectives? If, as we have argued, EDP fails to take development seriously, does the DS approach take evolutionary processes seriously enough to advance a legitimate synthesis of evolutionary and developmental perspectives?

Integrating Development and Evolution: DS and Explanatory Pluralism

For DS proponents, “evolutionary changes are the result of developmental changes” [Lickliter & Honeycutt, 2013, p. 186, italics added], “modifications to development create evolutionary change (rather than the other way around)” [Lickliter & Berry, 1990, p. 357], and “selection … is a consequence, not a cause of phenotypic change” [Johnston & Gottlieb, 1990, p. 484]. Inverting Haeckel’s [1874] famous dictum that “phylogenesis is the mechanical cause of ontogenesis” (p. 5) – as Løvtrup [1984] did over 30 years ago – DS proponents revive Garstang’s [1922] argument that “Ontogeny does not recapitulate Phylogeny: it creates it” (p. 98). Given its particular explanatory aims within developmental science, the DS approach’s framing of evolutionary change as an outcome relative to developmental processes makes perfect sense, although it can easily be misconstrued as treating evolutionary change in essentially epiphenomenal terms [Johnston & Gottlieb, 1990; Oyama, 1992]. Hochman [2013], in fact, has argued that DS proponents explanatorily reduce evolutionary
changes to a historical series of developmental-level changes and commit what he has termed an *ontogeny fallacy* in the process. Hochman’s critique, however, fails to acknowledge DS’s active endorsement of selectional explanation at the level of evolutionary change. Despite arguing that individual-level phenotypic traits – their construction, their maintenance, their transformation – remain a product of developmental rather than evolutionary processes, DS proponents fully appreciate that understanding the workings of phylogeny – the historical record of evolutionary change – requires population-level phenomena like natural selection, not just developmental dynamics, to explain changes in the distribution of phenotypes within populations. DS proponents simply reserve the selective pressures of natural selection for population-level changes in phenotypic distribution and insist on conceptually distinguishing what happens to the phenotypic characteristics of a population qua population from what happens to the phenotype of an individual organism.

Nonetheless, Hochman’s [2013] critique does raise important concerns when applied specifically to the question of how evolutionary change might be related to developmental change, for this direction of interrelation suffers from routine neglect in DS writings and can indeed promote a unidirectional treatment of relations between development and evolution. EDP proponents have leveled precisely this criticism against the DS approach in accusing DS proponents of dramatically undervaluing the role that evolutionary processes play in the organization of ontogeny [Bjorklund et al., 2007; Frankenhuis et al., 2013]. And as long as debate over the role of evolutionary processes in ontogeny presupposes an orthodox Darwinian framing of natural selection as a mechanical, antecedent force, the only real alternative to EDP’s reification of population-level dynamics as evolved ontogenetic mechanisms is an epiphenomenal framing of evolutionary change relative to developmental change. However, DS proponents explicitly endorse interdependent relations between evolutionary and developmental processes [e.g., Lickliter, 2008]. To capture true interdependence between developmental and evolutionary processes, DS proponents need to formally advance an alternative conceptualization for how the population-level dynamics of evolutionary processes might relate to the individual-level dynamics of development, one that explanatorily transcends the “shaping force” discourse around which discussions of development-evolution relations have routinely revolved (and to which EDP proponents remain wedded).

The building blocks for one such alternative, we argue, are already available in negative, pre-Darwinian readings of natural selection as eliminator of the unfit rather than generator of the fit [Gould, 2002]. DS proponents endorse a negative role for natural selection vis-à-vis the construction of phenotypes themselves and the relation of evolutionary processes to developmental processes [Ho, 2010; Johnston & Gottlieb, 1990; Lickliter & Honeycutt, 2003a]. What does it mean exactly for natural selection to assume a negative, rather than a positive, role in phenotypic construction? In general terms, natural selection *as eliminator of the unfit* can help to explain the absence of certain phenotypic forms/traits – why certain variants are not available – in a current population of developmental variants. With respect to developmental re-

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1 It is important to note that arguments about natural selection as eliminator of the unfit have been historically subject to devastating misapplication and distortion when aligned with ideas of genetic reductionism, to which the racial hygiene and eugenics movements of the early 20th century convincingly attest [see Lerner, 1992, 2002, for an extended analysis of such flawed applications].
sources available across generations, natural selection could explain why certain resources (e.g., certain alleles) are no longer available in a population of resources.

But explaining absence in a population is, of course, far removed from explaining presence, either in a population or in an individual. With respect to phenotypic presence in ontogeny, relations among available developmental resources do all of the positive, bottom-up, shaping force work of constructing phenotypic development – both before and after a population has been subject to the pressures of natural selection (e.g., the tissue formation processes that first produced long necks in a minority of individuals must still occur in newly developing individuals after long necks come to represent the prototypical morphology of a population). These ontogenetic processes set the formative stage for population-level change in the first place, given that “reliable developmental courses are the prerequisites for such population patterns” [Oyama, 1992, p. 224]. Natural selection, operating as an antecedent process in population-level change, can then alter a population’s distribution of phenotypes and usher in a new characteristic look to the population as a whole (e.g., now everyone has a long neck). The phenotypes that comprise this new, characteristic look to the population, however, are still products of ontogenetic dynamics and therefore explainable in terms of those dynamics, without any need for appeal to natural selection and its consequences. The fact that particular phenotypes are now reflected in the look of the population as a whole does not add anything (like a regulatory mechanism) to the activity of ontogenetic processes in development (e.g., tissue formation processes still do all of the work). Instead, it is what gets left out of the population – elimination of the unfit via natural selection – that can, in seemingly paradoxical fashion, exert some form of influence on postselection ontogenetic developments. What is the nature of this influence by absence? How does an understanding of absent forms or resources in a population – population-level changes born of natural selection – significantly contribute to our understanding of what actually emerges during development as a function of relations among extant developmental resources?

Perhaps population-level change via elimination of the unfit can be usefully framed in terms of a constraining influence on the construction of future, individual ontogenies. In other words, perhaps evolutionary changes set limits (through, for example, the variety of developmental resources no longer available in a population) on the very ontogenetic processes that help give rise to these changes. The notion of constraining influences – or simply “constraints” – is potentially problematic, however, because it can easily connote an antecedent process conceptualization of influence [see Deacon, 2012, however, for a critical exception]. As routinely employed in both evolutionary and developmental literatures, for example, constraints basically function as secondary causes [Oyama, 1993; Stearns, 1986]. Relative to the primary forces spurring developmental or evolutionary change, constraints reflect modulatory or regulatory processes, but they are still conceptualized in functional terms, as antecedent processes that place regulatory limits on a developmental or evolutionary outcome. A negative, “absence” reading of evolution’s relation to development, we argue, sharply diverges from such antecedent process dynamics – regulatory or otherwise – and requires, instead, a fundamentally different kind of explanatory framework. It requires a structural explanatory framework [Saunders, 1989; Webster & Goodwin, 1982], one that frames the relation of population-level dynamics to individual-level dynamics not in terms of temporally based, material exchanges of energy but in atemporal, whole-to-parts terms [Winther, 2011].
From Functional to Structural Explanation: Evolutionary Change as Organizational Constraint

What Overton [1975] has termed holistic structuralism provides the kind of structural explanatory framework necessary to capture how evolutionary change relates to an understanding of developmental change. Holistic structuralism figures prominently in Overton and Lerner’s extension of the DS approach, relational-developmental systems [Overton, 2010, 2015; Overton & Lerner, 2014], and to understand what it entails, one must first understand the antireductionist, pluralistic stance that it brings to bear on the nature of explanation itself. Proponents of holistic structuralism reject the idea of an absolute, foundational base for reality; ontologically and epistemologically, there is no fixed, ground-level set of elements upon which universal complexity is built and to which it reduces [Overton, 1975]. This means that the lower-order parts and processes of any higher-order system are no more foundational than the system as a whole and, in fact, cannot be understood independently of the system as a whole. As a result, the system as a whole – its organization, structure, form – is not merely something to be explained by its parts and processes but constitutes a necessary mode of explanation in its own right, lending irreducible meaning to the very parts and processes that give rise to it [Overton, 1975, 1991]. Sperry [1980] illustrated this concept with the example of a wheel. He noted that the atoms and molecules that make up the substance of a wheel are not changed individually by being in a wheel, but because of the constraints on their relative mobility with one another, they collectively have the property of being able to move across the ground in a different pattern than could be exhibited in any other configuration. Sperry pointed out that being a part of a whole indirectly changes some of the properties of the parts by affording some possibilities while restricting others. In other words, being part of a particular kind of whole (a wheel) alters possible movement options available to its parts [see also Deacon, 2012]. Critically, this mode of explanation that wholes provide relative to their parts and processes – the explanatory significance of holistic structure – differs fundamentally from the more scientifically orthodox, “functional” mode of explanation that parts and their processes provide relative to the whole [Witherington & Heying, 2013]. What distinguishes a structural, whole-to-parts mode of explanation from its functional, parts-to-whole explanatory counterpart?

Couched in terms of Aristotle’s fourfold explanatory framework, functional (parts-to-whole) modes of explanation invoke material and efficient causes to capture the changing dynamics of part-to-part coactions constitutive of new, higher-order levels of system organization, all in the service of explaining how new levels of system organization arise in development. Both material and efficient causes are spatiotemporally concrete in their grounding. With respect to explaining the behavior of organisms, material causes appeal to the material substance or substrate underlying an organism’s activity in order to explain that activity, as when psychologists invoke parts of the brain to explain a person’s behavior. Efficient causes appeal to the events and conditions – either intra- or extraorganismic – that temporally and regularly precede an organism’s activity in order to explain the activity, as when psychologists explain a person’s behavior by means of neurological processes, information-processing mechanisms, particular stimulus events or environmental factors, or combinations thereof. As the centerpiece of scientific inquiry since the 17th century, efficient causes represent the classic propelling, initiating, or shaping force explanations of a phe-
nomenon [Bates, 1979]. Efficient causes are necessarily instantiated in temporal terms, but so too are material causes, given that material causes explain by means of identifying a phenomenon’s material grounding, the substances out of which a phenomenon arises. Both of these functional modes of explanation, therefore, frame understanding in terms of an antecedent-consequent framework, identifying the temporally precedent conditions – which include material grounding – that give rise to whatever phenomenon is under investigation [Overton, 1991]. Functional modes of explanation, in other words, target classic questions of mechanism and process, capturing what it means to explain a system and its functioning in terms of the bottom-up dynamics involved when parts of a system interrelate to generate the system as a whole.

Structural (whole-to-parts) modes of explanation, in contrast, invoke what in Aristotelean terminology are called formal and final causes, which explain any given phenomenon by means of abstracting pattern and organizational regularities from the spatiotemporal particularities of that phenomenon’s activity in context. Unlike functional modes of explanation, structural explanations do not offer traditional “causal” accounts in the sense of identifying temporal antecedents – whether in the form of processes or material groundings – relative to a consequent. Rather, formal and final causes are atemporal, organizational levels of explanation that meaningfully frame the temporal, cause-effect sequences of functional explanation [Juarrero, 1999; Rychlak, 1988]. These structural modes of understanding explain without recourse to the flow of time or the particularities of context by invoking higher levels of abstraction themselves as means of explanation [Overton, 2002; Rychlak, 1988]. With respect to explaining the behavior of organisms, for example, formal causes abstract patterning (a form, structure, organization) from an organism’s activity and employ this patterning to explain the activity, as when psychologists invoke the construct of personality or appeal to a stage of development to explain a person’s behavior. Final causes abstract a goal, future end, or functional significance from an organism’s activity to explain that activity, as when psychologists invoke the functional consequences of an activity to explain it or when they look to later periods of development toward which a person would typically develop in order to make sense of that person’s current level of activity and functioning. Both of these structural modes of explanation have explanatory value vis-à-vis the formal and directional patterning they abstract because the patterning itself serves to organize the particularities of that activity’s real-time content in terms of general, invariant structure and function, across time and context. The patterning, in other words, renders the domain under investigation intelligible and provides a meaningful, holistic framework – the structural and functional organization of the system as a whole – within which to investigate the temporally unfolding dynamics of a process via part-to-part coactions.

Both functional and structural modes of explanation represent unique, equally legitimate, and simultaneously applicable perspectives from which to understand change in natural phenomena, such that complete understanding of a phenomenon emerges only through the pluralism that both explanatory perspectives in conjunction confer [Rieppel, 1990; Walsh, 2013; Winther, 2011]. Critically, this means that structural explanation is not intended to explain what functional explanation targets, namely the content of an organism’s activity in context, or to identify the antecedent and material circumstances for such a content. Instead, structural explanation targets an understanding of an organisms’ specific activities in terms of the general organiza-
tion and directional goals those activities evince, as a whole [Overton, 1991]. The organization of organisms, as systems, provides a structural, topological precondition for understanding the very processes that give rise to this organization. A key point in this conceptual framework is that the organization of a system is not something that is added to the system or something that constitutes a property of the system [Deacon, 2012]. Rather, a system’s organization is the system, considered in its simultaneous totality, providing a critical explanatory backdrop or framework – a ground – against which the temporally unfolding part-to-part relations of the system – the figure – must be understood. Though coactions among parts of a system yield new levels of organization in the system via developmental dynamics, these parts and processes always operate within the context of an existing level of organization, an organization that necessarily informs the very nature of the parts and processes themselves.

In this way, systems constrain, in whole-to-parts fashion, the very nature of their component parts and the relations that can occur among those components, with the caveat that constraint should not be conceptualized in functional terms, like a regulatory mechanism, but in organizational terms [Deacon, 2012; Juarrero, 1999]. Constraint signifies a lessening of variability, a narrowing of degrees of freedom, and as such plays a critical role in explanation by virtue of delineating limitations for what kinds of bottom-up processes are available to a given system [Deacon, 2012; Juarrero, 1999; Thompson, 2007]. Again, it is important to note that constraint refers to absence rather than presence. As Deacon [2012] has articulated:

The concept of constraint does not treat organization as though it is something added to a process or to an ensemble of elements. It is not something over and above these constituents and their relationships [sic] to one another. And yet it neither demotes organization to mere descriptive status nor does it confuse organization with the specifics of the components and their particular singular relationships [sic] to one another. Constraints are what is not there but could have been, irrespective of whether this is registered by any act of observation. (p. 192)

Looking at a system exclusively in terms of its temporally sequenced part-to-part relations loses sight of the broader organizational ground on which the system operates. This broader context of understanding – one that looks across the particularities of specific time and context to abstract organization and directional ordering – arrives through structural explanation and serves as a complement to the scientific orthodoxy of functional explanation, as an indispensable mode of understanding the world in its own right [Witherington, 2011].

Structural explanation involves a hierarchy of different organizational frames of meaning for the explanatory significance of system wholes relative to their parts. Couching an organism’s specific action in context in terms of the form of the organism’s activity – its invariant, context-general organization, exemplified in appeals to cognitive structure or a stage of development – offers a first level of structural explanation for characterizing the organism as an organizational whole at any given point in developmental time, one step removed from the particularities of activity in context. Any given form characterizing a particular point in developmental time, however, is itself situated within a higher-order frame of meaning two steps removed from the particularities of activity in context. This next level of structural explanation couches the current form of an organism itself in terms of a directional flow of forms: the developmental sequence of prior and subsequent forms across developmental time.
within which any given developmental form is ontogenetically embedded. Such a sequential framing embodies what it means to study a phenomenon developmentally from the standpoint of structural explanation, as when developmental scientists characterize development as proceeding from sensorimotor to preoperational to increasingly complex operational forms of cognitive functioning, or from global, undifferentiated, homogenous structures to increasingly differentiated, heterogeneous structures [Mascolo, Pollack, & Fischer, 1997; Overton, 1991, 2010; Werner, 1957]. Each nested level of structural explanation in the hierarchy assumes the explanatory significance of a whole relative to the levels of organization that it structurally frames.

Changes in the distribution of phenotypes across evolutionary time, occurring at the population-level of species, constitute a whole relative to the developmental sequence of forms that characterizes organismic ontogeny, just as any given species constitutes a whole relative to the individual organisms – the parts – that comprise it. In other words, the whole that is evolutionary change organizationally frames the sequence of forms that characterizes individual ontogeny, establishing an evolutionary history of past ontogenetic sequences relative to a current ontogenetic sequence, a phylogenetic tree of descent that yields a directional sequence of ancestral ontogenetic organizations as well as potential future ones, given certain ecological conditions [see Frankenhuis et al., 2013, for ways in which the "design stance" of an evolutionary framework might afford insight into which DSs are likely to survive the filter of natural selection]. As a species-typical developmental sequence frames any given level of developmental organization (which, in turn, frames specific activity in context), so an evolutionary sequence – the phylogenetic history for a species, with ancestral and potential future species’ ontogenies representing different levels of organization in an evolutionary sequence – frames the species-typical developmental sequence, establishing a higher-order structural context even further removed from the particularities of any given organism’s activity in context.

Thus, the explanatory significance of evolutionary change for development arrives not through postulation of information-processing mechanisms that control organismic activity but through the structural framing it provides for the current ontogenetic sequence of form relative to an evolutionary sequence of ancestral ontogenetic organizations. The beginnings of such a structural framing have long been evident in developmental science. Developmental stages, after all, routinely reflect what is characteristic of the population as a whole, representing, in other words, species-typical formal characterizations of human functioning. The structural explanations of pioneers in developmental science like Baldwin [1902], Piaget [1971], and Werner [1948], among others, all grew out of a decidedly comparative understanding of human development [Valsiner, 2006]. Refinements and, at times, revisions of these classic structural frameworks have certainly taken place [e.g., Fischer, 1980], but such revisions have not lost sight of the significant framing of phylogeny. To stake a claim within the formal and final spheres of explanatory efforts in developmental science, EDP’s proponents must first articulate how their evolutionary framework substantively refines or revises those structural frameworks already available to developmental science.

Because both form and adaptive function have informed past structural characterizations of development, what new ground does EDP provide for understanding the organizational characteristics of developmental sequence? It is unclear whether proponents of EDP are even equipped to answer such a question, given their explicit repudiation of holism and its ontological category of necessary organization [see Del
Giudice & Ellis, 2016]. By mechanistically treating natural selection and the population-level changes to which it can give rise as antecedent, shaping forces or factors of influence in individual ontogeny, EDP’s ontological framework adopts a thoroughly monistic stance toward the nature of explanation. Of course, proponents of EDP are far from alone in their reductionist focus on functional explanation via material and efficient causes. Orthodox modern science still embraces a monistic – rather than pluralistic – view of explanation, one that stems from its commitment to prediction as the hallmark of scientific knowing, its explicit rejection of directional explanation as valid explanation, and its continued devotion to Newtonian style, mechanistic thought (Howard, 1990; Overton, 2015; Saunders, 1989).

Explanatory monism in science privileges functional levels of explanation and discounts structural levels of explanation as, at best, temporary heuristics devoid of any true explanatory power (Overton, 1991). As a consequence, the patterns and organization that structural explanation identifies count as legitimate explanations only when filtered through the narrow lens of functional explanation, meaning that the invariant forms and functions of structural explanation must be reframed in terms of antecedent-consequent causality for them to serve as explanations at all. Such explanatory monism unnecessarily narrows the nature of scientific explanation. It also unwittingly encourages a pernicious and conceptually misguided tendency to reify the structural and functional patterning to which structural explanation appeals, wherein abstractions that characterize organisms as wholes – such as intentions, personality structures, developmental levels of cognitive organization – become conceptualized as concrete parts of the organism, parts that temporally precede and initiate, in bottom-up, efficient causal fashion, the organism’s consequent behavior. Reification of structural explanation represents an ontological confusion of wholes for parts, conflating two fundamentally different modes of explanation, and in a world where only functional explanation is considered legitimate, such reification – and the mereological fallacy that it represents – is likely to run rampant (Bennett & Hacker, 2003; Kenny, 1971; Wittgenstein, 1958).

In the field of developmental psychology, for example, Piaget’s holistic structur- alist orientation has been commonly and wrongly framed in terms of functional explanation ever since its extensive introduction to the USA in the middle of the last century. What existed for Piaget as structural explanation (e.g., identification of forms and stages of cognitive development) transmogrified, in the hands of many US developmental psychologists, into “competencies” inside the child that, alongside performance factors, served to determine children’s behavior, as antecedents to a consequent (Chapman, 1988; Lourenco & Machado, 1996). In Chapman’s (1988) words:

Inevitably, perhaps, developmental psychologists assimilated Piaget’s structural-stage theory to their own functionalist approach. Thus, Piaget’s observation of rough developmental synchrony at the population level was interpreted as implying synchrony at the individual level, and his ‘structures’ were understood as functional constructs intended to explain this synchrony. Instead of being seen as morphological criteria for classifying forms of knowing and reasoning, structures were viewed as the functional antecedents of age-related behaviors. (p. 363)

As we have argued, proponents of EDP fall victim to precisely this conflation of structural and functional explanation, reifying their adaptationist levels of explanation in terms of concrete mechanisms for generating developmental change. Treating the
population-level dynamics of natural selection as a mechanistic force of influence on
ontogenetic development (via probabilistic evolved psychological mechanisms) mis-
takenly conceptualizes the relation between a whole (population-level changes in the
distribution of phenotypes) and its parts (the individual-level phenotypes themselves,
which make up the population) in antecedent-consequent terms; such treatment re-
frames what should be a structural level of explanation in decidedly functional terms.

For more than 30 years, proponents of the DS approach have been at the fore-
front of arguments against structural reification in developmental science [e.g., John-
ston & Gottlieb, 1990; Lickliter & Berry, 1990; Oyama, 1985; Thelen & Smith, 1994].
However, DS proponents have not explicitly couched the problem of reification in
terms of a conflation between structural and functional levels of explanation. Gener-
ally speaking, the question of different levels of explanation for capturing parts-to-
whole and whole-to-parts relations has not really surfaced as a topic of conceptual
regard in DS accounts [Witherington & Heying, 2013; see Ford & Lerner, 1992, for
an exception]. This lack of focused regard for the explanatory significance of orga-
nization poses less of a problem when efforts center on explaining developmental or-
ganization from the bottom up (via the self-organizing dynamics of developmental
construction) but emerges as a serious neglect when the question arises of how evo-
olutionary change might be related to developmental change.

For the DS approach to adequately capture the interdependence of developmen-
tal and evolutionary change, its explanatory framework will need to explicitly broaden
to consider both structural and functional explanation in the approach to develop-
ment-evolution interrelation. This is precisely what relational-developmental systems
establish as an extension of the DS approach, and in so doing, fully realize the expan-
antory pluralism of a process-relational paradigm for developmental science [Lerner,
Agans, DeSouza, & Hershberg, 2014; Overton & Lerner, 2014]. An outgrowth of Over-
ton’s [e.g., 2010, 2015] extensive articulations of relational metatheory, the pro cess-
relational paradigm ushers in an ontological and epistemological framework within
which classic polarities such as structure and function, process and organization, parts
and wholes, constitute a synthetic unity as “differentiated polarities (i.e., coequals) of
a unified (i.e., indissociable) inclusive matrix” [Overton, 2010, p. 14]. Each member of
a polarity analytically offers a distinct, alternative, yet equally legitimate explanatory
perspective or point of view taken toward a phenomenon under investigation [Over-
ton, 2015], fostering an inclusive metatheoretical space “where foundations are
groundings, not bedrocks of certainty, and analysis is about creating categories, not
about cutting nature at its joints” [Overton, 2010, p. 13]. Assigning explanatory sig-
nificance to both the structural explanation of wholes and the functional explanation
of the part-to-part nonlinear relations that comprise them, the process-relational par-
adigm promotes a perspectivist framework within which “synthesis and analysis, to-
gether with reason and observation, operate in an interpenetrating reciprocal fash-
ion … in which each individual approach is valued not as a potentially privileged van-
tage point, but as a necessary line of sight on the whole” [Overton, 2010, p. 18].

Following Rieppel [1990], we argue that the search for overarching synthesis in
understanding development-evolution interrelations requires explanatory modes
other than the routine antecedent-consequent, force conceptualization of causality
that graces typical discussions of how processes like natural selection and self-orga-
nization complement one another in generating phenotypic form across develop-
mental and evolutionary time [e.g., Badcock, 2012; Hoelzer, Smith, & Pepper, 2006;
Pigliucci, 2007]. Organizational patterns that characterize species as a whole, sequentially embedded in terms of a phylogenetic history of previous species patterns, meaningfully frame current ontogeny and its sequence of forms in the context of prior ontogenies and potential future ontogenies. To capture the interdependence of evolutionary and developmental change requires such a framing of interrelations in part-to-whole and whole-to-part terms and an explanatory pluralism in which both the antecedent-consequent, functional level of explanation and the atemporal, structural level of explanation effectively complement one another.

Conclusion

The challenge facing current models of the interrelation between ontogenesis and phylogenesis is a conceptual one: to forge an overarching synthesis that transcends the ontological division of selectional and developmental explanatory perspectives. In its integration of principles from evolutionary psychology and from DS approaches to development, the field of EDP has emerged within psychological and developmental science as a potential solution to this challenge, but despite its efforts to take developmental processes seriously, EDP remains firmly entrenched in a selectional perspective on the organization of phenotypic form and consequently fails to conceptually represent the DS approach and its principles of development. DS approaches to development, in contrast, offer a levels-of-organization model of development-evolution interrelations that both embeds itself in the explanatory significance of developmental processes for phenotypic formation and change in individual ontogeny and in the explanatory significance of a selectional process for formation and change in the distribution of phenotypes in populations. With respect to the critical question of how evolutionary change is related to developmental change, DS approaches recognize the conceptual mistake of treating natural selection as an antecedent, shaping force in individual ontogeny.

However, DS proponents have yet to propose an alternative conceptualization for the nature of interdependence between population- and individual-level dynamics. We have argued that understanding the role of population-level evolutionary change in individual-level developmental change requires a structural, whole-to-parts – rather than a functional, parts-to-whole – mode of explanation, in which the phenotypic distributional consequences of population-level change organizationally frame the succession of forms that characterize individual development and provide an important context of meaning within which to understand the very nature of developmental forms themselves. This, in turn, requires a pluralistic approach to scientific explanation, one that moves beyond traditional antecedent/consequent, mechanistic views of causality to embrace both structural and functional modes of explanation as distinct, equally legitimate, and irreducible perspectives taken toward the understanding of any given biological or psychological phenomenon.

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