Evolution and development of handedness: An Evo–Devo approach

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Abstract

Hand preference is a sensorimotor skill whose development both reflects and promotes the development of hemispheric lateralization for manual and cognitive functions. Extensive comparative, crosscultural, and paleoanthropological evidence demonstrates the prevalence of limb lateralized preferences across vertebrate species and the prevalence of right-handedness within hominid evolution. Many reviews of the evolution and development of human handedness have proposed adaptive explanations for its evolution. However, during the last 3 decades a new approach to understanding evolution (the Extended Evolutionary Synthesis—EES) provided a persuasive alternative to the conventional (Neo-Darwinian Synthetic Theory—ST) evolutionary and developmental accounts. EES combines modern evolutionary and developmental research (Evo–Devo) in ways that alter understanding of natural selection, adaptation, and the role of genes in development and evolution. These changes make obsolete all past accounts of the evolution and development of lateralization and handedness because EES/Evo–Devo requires new study designs. The developmental trajectories of any structural or functional trait must be specified so that it may be related to variations in the developmental trajectories of other traits. First, we describe how the EES/Evo–Devo differs from the conventional ST, particularly for understanding of how traits develop. Then, we apply Evo–Devo to the study of handedness development in infancy and its relation to the development of other cognitive functions. Finally, we argue that identifying the development of atypical traits would benefit from knowledge of the range of individual differences in typical developmental trajectories of hand-use preference and their relation to variations in the developmental trajectories of cognitive functions.

Keywords

Handedness, Evo–Devo, Evolution, Development, Human, Cognition, Lateralization

1 INTRODUCTION

Our intent in this chapter is to place investigations of human handedness development within a modern Extended Evolutionary Synthesis/Evolutionary–Developmental (EES/Evo–Devo) conceptual framework (cf., Hall, 1999, 2012; Maienschein and Laubichler, 2014; Morange, 2011; Müller, 2017). Recent extensive reviews of the research literature examining the evolution and development of handedness (e.g., Cochet, 2016; Cochet and Byrne, 2013; Ocklenburg et al., 2014a, b; Rogers, 2014; Vallortigara et al., 2011) reduce our need to reiterate the empirical literature. However, previous reviews have used the conventional (Neo-Darwinian Synthetic Theory—ST) account of evolution and development. EES/Evo–Devo requires a reconceptualization of evolution and development and the employment of different research designs. To understand the Evo–Devo approach requires that we first describe how the modern EES differs from the prevalent ST notions of evolution but still retains Darwin's conceptual insights.

2 EVOLUTIONARY THEORY: HOW THE EES DIFFERS FROM THE CONVENTIONAL SYNTHETIC THEORY

Darwin's theory (1859/1968) challenged the notion of species as natural types. By eliminating the need for species members to share common morphological features or physiological processes and traits, Darwin resolved the individual variability problem in species taxonomy. There can be extensive variability of traits among species members because they are united only by common ancestry (homology). To account for the similarities and differences among species members, Darwin appealed to developmental processes (cf., Huxley, 1880). Unfortunately, Darwin's notion of species violates our intuitive expectation that members of any category should be united by some essential features (homoplasy). The rise of population genetics in the early 20th century seemed to account for the inheritance of traits and their resemblance across individuals (common genes) while genetic variance seemed to account for individual diversity (Sarkar, 2017). Thus, our intuitive expectation that species share essential features was satisfied by the notion of species-common genes.

About 8 decades ago, the Neo-Darwinian Modern Synthesis or Synthetic Theory (ST) of evolution integrated concepts about evolution from multiple fields of biology by describing speciation as the operation of natural selection on the distribution of genotypes in populations (cf., Huxley et al., 2010). The ST combined Darwinian principles of individual variation, inheritance of traits, differential reproductive

success (natural selection) with Mendelian experimental breeding techniques, the notion that genes are independent units, and the mathematics of population genetics. In the ST, trait variation within a population and across species is explained by adaptation to specific fitness landscapes (ecological conditions) and derives from differences in gene (allelic) frequencies "chosen" by natural selection.

ST required (cf., Laland et al., 2000; Walsh, 2015) that:

1. populations contain genetic variation that arises randomly via mutation and recombination among genes and that populations evolve via changes in gene frequency that reflects primarily the effects of natural selection;
2. genes produce phenotypic traits that enable survival and reproductive success;
3. genetic inheritance alone accounts for the intergenerational transmission of those traits that are naturally selected to "fit" the phenotype to the ecological circumstance;
4. new species (with new traits) arise when gene flow is prevented within a population and these reproductively separated populations exist in ecological circumstances sufficiently different to permit the operation of natural selection;
5. the phenotypic differences among broad taxonomic groups (e.g., hominins vs great apes, or Old-World monkeys, or New World monkeys, etc.) result from the gradual accumulation of large amounts of genetic variation; and
6. natural selection is the only factor that can direct evolution; therefore, each species-typical trait must be an adaptation to a specific identifiable ecological circumstance (this is known as the adaptationist program, Gould and Lewontin, 1979).

Thus, ST proposes that the gene, rather than the organism, is the causal unit for the processes of development, inheritance of traits, adaptive change in population traits, and the origin of novel traits during evolution. Random mutation of genes is the ultimate source of evolutionary novelties. ST minimizes developmental explanations of evolutionary novelties by assuming that development is determined by inheritance: organisms develop what they inherit and individually specific developmental events cannot be inherited. In ST, genes are the privileged and primary explanatory units of development—they are a "code," "script," "program," or "blueprint" that specifies a determinate phenotype (within a delimited range of variability, cf., Goldman and Landweber, 2016). In ST, development is just the process of translation of genetic instructions into biological forms that determine functions; an individual organism's genotype determines that individual's morphological and behavioral traits. Therefore, ST implies that it is possible to know the organism's features and behavioral traits just by knowing its DNA sequence (cf., Sarkar, 2006).

Although the expression of genes is known to vary among individuals and during development, ST assumes that this developmental variability of gene expression is also under genetic control (Müller, 2017). ST accepts that many nongenetic factors can distort development, but those nongenetic factors interfere with the development of adapted traits and cannot contribute to evolution by natural selection. Since differences in gene frequencies among and within populations are sufficient to

account for evolution, developmental biology contributes to evolution only by: (1) describing how certain genes regulate the expression of other genes and (2) speculating about how these regulatory genes may have been chosen by natural selection.

New methodologies and modern evidence from molecular genomics, developmental biology, epigenetics (how factors other than DNA control protein production and cellular biochemistry), physiological plasticity, systems biology, network analyses, ecology, and the behavioral, cultural, and social sciences have challenged both the conceptual frame of, and predictions from, the ST models (cf., Annila and Baverstock, 2014; Bateson, 2014; Gilbert et al., 2015; Gilbert and Epel, 2015; Jablonka and Lamb, 2005; Latham, 2017; Müller, 2017; Sultan, 2017). An organism's actions such as niche selection, niche construction activities, physiological adjustment to conditions, and mobility to seek other conditions have all played formative roles in evolution (see Bateson, 2015; Lickliter and Harshaw, 2010 for reviews). Therefore, many have called for EES to unite the new properties of evolutionary change with aspects of ST (e.g., Laland et al., 2000; Pigliucci and Muller, 2010), or even to serve as a new theory of evolution (e.g., Müller, 2017). EES changes our understanding of natural selection, adaptation, and the role of genes in development and evolution.

2.1 EVOLUTIONARY THEORY: NATURAL SELECTION

Oddly, the most distinctive weakness of ST is that it misconstrues Darwin's concept of natural selection (Walsh, 2015). ST proposes that natural selection is a causal process responsible for the adaptiveness of traits. That is, natural selection causes changes in gene frequencies (and hence phenotypes) via differential reproduction. Those individuals with genes that produce phenotypes that better "fit" the environment leave more offspring than those with genes that do not. Natural selection (differential reproduction) ensures that structures and functions are adapted to the environmental circumstances.

For Darwin (1859/1968, p. 114), natural selection is not a force or causal process; rather, the cause of biological fitness and diversity derives from each organism's developmental "struggle" to live and reproduce—nothing more is needed to "guide" evolution. Darwin's "natural selection" is an effect on a population of the variety of causes (physiological and ecological) involved in each individual's developmental adjustments to live and reproduce. When individuals vary in their heritable capacity to survive and reproduce, a population will change the characteristics of its lineage. This change means that a population appears to better match the ecological conditions of its existence not because the circumstances selected particular genes but rather because the individual has adjusted (physiologically and developmentally) to its circumstances.

Treating natural selection as an effect rather than a cause, greatly changes notions about the adaptation of traits. Consider two individuals: one may not "fit" some facet

of their common ecological circumstance as well as the other. Nevertheless, the first produces more offspring than the second. If the production of more offspring is passed on to the offspring (via many mechanisms other than gene transfer; cf., Jablonka and Lamb, 2005; West-Eberhardt, 2003), the descendants of that first individual eventually will come to predominate in that population. Natural selection did not cause that change in the population; that change is natural selection. To consider the offspring of the first individual more "fit" to the environment than offspring of the second individual is to miss that the second individual's traits "fit" the environment better than the first individual and that difference continues for their descendants.

For a concrete example, consider the blackcap, a European passerine bird (Bearhop et al., 2005). Typically, these birds are seasonal migrants with spring migration affecting the start of breeding. Until 50 years ago, all European blackcaps migrated back and forth together, spending summers in northern Europe and the British Isles and winters in Portugal, Spain, and North Africa before migrating in spring to breed in southern Germany and Austria. However, some blackcaps began wintering in Britain and Ireland because of increased availability of winter provisioning provided by bird feeders and other human activities. Thus, northern-wintering blackcaps are exposed to the photoperiods that contribute to the initiation of migration and the onset of gonadal development 10 days earlier than their southern-wintering species–mates.

Although all blackcaps continue to gather each year at the same mating sites in Germany and Austria, the northern blackcaps arrive earlier, establish territories and mate with other earlier arriving birds. Southern-wintering blackcaps arrive later and mate with each other, serving to reproductively separate northern-wintering birds from the later-arriving southern-wintering population. This shift in migratory patterns results in the northern-wintering pairs producing one more egg per season than the southern-wintering pairs (Bearhop et al., 2005).

Note that both groups appear to be adapted to their ecological circumstances. Only empirical investigation conducted over many generations would determine the relative fitness between these two groups within this species. The northern blackcap gets to the breeding site earlier and has an advance in breeding but must endure the harsh winter. The additional egg may (or may not) compensate for the losses suffered in winter. In contrast, the southern blackcaps must endure a longer migration. Of course, there are many more differences in the circumstances of these two groups that affect their survival and reproductive success. Natural selection is not guiding their evolutionary changes (if any); rather, developmental processes of plasticity and social influence on migratory activities and overwintering are producing differential reproduction that we note as natural selection. If speciation occurs, we would conclude that the two species are adapted to different ecological circumstances but that would conceal the developmental patterns involved in the establishment of the northern and southern groups. This applies equally well to the evolution of human handedness.

2.2 EVOLUTIONARY THEORY: ADAPTATION

It is misleading to assume that the predominance of a trait in a population automatically means that those individuals with the predominant traits are better fit to the environment than those with traits that do not predominate. As Gould and Lewontin (1979) demonstrated decades ago, not all traits affect reproductive success and not all traits have evolutionarily relevant functions. Many traits derive from developmental events and function within development but may have little consequence on reproductive success (Gould and Vrba, 1982). Acceptance of this view of adaptation, forces the undertaking of empirical investigations to determine whether a trait contributes to reproductive success or simply enables an individual to develop reproductive capacity.

Consider again the Blackcap example: The northern and southern groups may function equally as well in their respective responses to winter. Running computational models with cost–benefit analyses will not answer the question of whether the northern-wintering is an adaptation because we do not have the information about all the causes and consequences of the differences in migratory patterns. The northern-wintering may result in an increase in eggs and chicks but overwintering may result also in a greater loss of juvenile or adult birds. Only systematic assessment of the role of northern-wintering in the survival of the birds can shed light on adaptiveness of the trait.

The ST distortion of Darwinian natural selection and adaptation had profound consequences on accounts of the evolution of adaptive traits, including the evolution of lateral asymmetries (cf., Rogers, 2014). Computational modeling (Ghirlanda and Vallortigara, 2004) revealed that a population bias in the domestic chicken's hemispheric asymmetry emerged when lateralized individuals had to interact with one another. However, the model assumed that only lateralization affected the social interaction. Many factors affect social interaction and each is likely to be related to reproductive success because social interaction is necessary for reproduction. The ST notion that each trait should fulfill a specific requirement of some feature of the environment (or it would have been eliminated by natural selection) is not required by EES. Traits only need to not disrupt survival to remain in the repertoire of the species. It is even possible for some traits to reduce reproductive success but enhance survival because of their crucial functions during development. These traits may be part of a developmental "package" that may work well enough for individuals to leave offspring and hence these traits will continue to be present across generations (cf., Oppenheim, 1984). Therefore, engaging in simulations of the adaptiveness of traits using computational models is unlikely to capture the causes of population change. Nor do these models reveal what makes adaptive evolution "adaptive" (Walsh, 2015).

Just as establishment of dorsal/ventral and anterior/posterior asymmetric dimensions are developmental events that do not contribute directly to reproductive success (rather, they ensure that an organism can function in its environment); so, too, lateralized asymmetry (left/right) may simply derive from the three-dimensionality

of an animal and need not represent any specific adaptive function (Cartwright et al., 2004). These 3D bodily asymmetric distinctions permit an animal to orient effectively within its environment. Layering additional specific adaptive functions is not necessary, as they could all derive from effective orientation. Currently, it is unknown whether handedness or its variations are adaptive (i.e., contribute to reproductive success) for humans. Handedness may play a role in development of specific abilities (e.g., tool use and manufacture, gestural communication, and spatial comprehension) without affecting reproductive success. Such developmental functions for handedness can contribute to its continued expression in a population without the need to invoke natural selection.

2.3 EVOLUTIONARY THEORY: THE ROLE OF GENES IN EVOLUTION AND DEVELOPMENT

Whereas ST focuses on genetic and adaptive variation in populations when proposing accounts of the evolution of organismic complexity, EES emphasized constructive processes in development, ecological influences (including social and cultural conditions), and system dynamics (Hall, 2012; Laubichler, 2010; Maienschein and Laubichler, 2014; Müller, 2017). EES dispenses with the privileged role of genes in phenotypic development by adopting multilevel, reciprocal, and coaction causation in the development of traits (Annila and Baverstock, 2014). In EES, the pressures of living to reproduce operate on the development of each of the individual's component systems. As Gould (2002) argued, the developmental processes that produce the phenotypic characteristics of an organism may constrain the course of subsequent evolution or they may facilitate a particular form of evolutionary change. Developmental processes, not genetic mutation and natural selection, help guide evolutionary lineage.

Consistent with EES, Jablonka and Lamb (2005) demonstrated that inheritance of both trait resemblance and difference can be achieved without the process of gene transmission. They argued that control over the pattern of inheritance is distributed throughout the organism–environment system. Although transgenerational transfer of DNA plays a role in some aspects of inheritance (particularly in providing an "alphabet" for protein construction), other aspects of inheritance derived from: epigenetic processes (changes in protein production by modifying gene expression via environmental and other influences on cellular processes), behavioral processes (such as developmental plasticity and learning), and niche construction and selection by parents (Gilbert and Epel, 2015). For humans, social processes of enculturation, education, written records, stories, etc., also are involved in inheritance (Latham, 2017; Michel, 2010).

Unlike ST, EES proposes that the activities of genes in a network are neither independent nor additive (Goldman and Landweber, 2016; Sarkar, 2017), and they are context sensitive (Sultan, 2017). Genes become a resource (like an alphabet) rather than a program governing development. Molecular biology has shown that the

architecture of genetic regulatory networks during development and function exhibits feedback loops, cyclical causation, and coaction among multiple regulatory pathways (Annila and Baverstock, 2014; Latham, 2017). The activity of a "gene" in such a network is part of the context of its own activity (Goldman and Landweber, 2016); not the expression of a program or code. This means that even the "alphabet," and certainly the way it is used, is plastic in its character. Consequently, inheritance is not "genetic" or "epigenetic," or "environmental," or "cultural"; it is holistic (Walsh, 2015).

2.4 EVOLUTIONARY THEORY: INHERITANCE HOLISM

Inheritance holism implies that every phenotypic trait is a result of the complex, causal coaction among genomes/epigenomes, organisms, and their environments during development (Annila and Baverstock, 2014; Latham, 2017). All organisms are somewhat modular in that they are composed of relatively independent components or subsystems. Consider the mammalian nervous, endocrine, immune, circulatory, digestive system, skeletal–muscle systems. These systems are integrated in a manner that partially couples them to one another (Michel and Moore, 1995). Partial coupling permits the components to operate somewhat independently from the others, which facilitates compensation for perturbations to the component or for disruptions of other components. However, partial coupling also allows the components to contribute to the regulation of the activities of other components in ways that ensure the robust maintenance of the whole organism's general state and its ability to adjust to changing circumstances (Annila and Baverstock, 2014). The regulatory activities of any individual component of an organism ramify throughout the other components and ultimately reverberate back to the originating component. In complex systems, the activities of a component are among the causes of that component's own activities, via direct and indirect "feedback" loops. All component parts are involved and none is causally privileged or primary. Organisms remain stable because the relations among their components permit compensation for changes around them.

The properties of such partially coupled modular architecture operate throughout development and include the components that compose the cellular biology of the zygote, the tissue differentiation and morphogenesis of the embryo, and development throughout the life span to produce reliably a viable individual typical of its kind despite genetic mutations, epigenetic alterations, or environmental perturbations (cf., Annila and Baverstock, 2014; Latham, 2017). Simultaneously, these properties also allow "exploration" of ecologically neutral traits that could permit "rapid" generation of phenotypic novelties in the event of the emergence of new ecological opportunities (Pigliucci, 2010; remember the northern-wintering blackcaps). The processes of development involve not just the establishment and refinement of these component systems but also the architecture of their coupling. Thus, the individual's "adaptive" resources continue to change and emerge during the life span (Bateson, 2014; Michel, 2013, 2018a). Adaptability of organisms, particularly behavioral

adaptability, helps buffer them against extinction in changing conditions. Thus, in EES, the conditions of the environment do not simply set problems to which organisms must evolve solutions; rather, the organism is capable of modulating, and/or creating, or even seeking out an environment in which it can live and reproduce (Lewontin, 1982; Lickliter and Harshaw, 2010; Michel, 2010).

Through its capacity to adjust to conditions, an organism's developmental resources are capable of producing novel, stable, and viable forms (e.g., the northern-wintering blackcaps), without the need for genetic changes (Sultan, 2017; West-Eberhardt, 2003). The evolution of complex forms and functions requires the coordination of an organism's partially coupled developmental systems. What was once considered evidence against the possibility of rapid evolutionary change, because of all the adjustments that would be needed by a major change in one trait now can be accommodated by recognizing the partial coupling of components of a system which makes traits mutually dependent. As organisms continue to occupy new ecological niches, this would inevitably lead to the subsequent emergence of more efficient morphological, physiological, and biochemical adjustments to those niches and the likelihood of speciation (e.g., Pfennig et al., 2010; Pfennig and McGee, 2010). Thus, the individual organism plays an important role in the evolution of its descendants through its actions, its control of the environment, and its phenotypic adjustment to its circumstances (Bateson, 2014).

3 Evo–Devo: CONTRASTS BETWEEN ST AND EES IN DEVELOPMENTAL THEORY

The mid-20th century discovery of a biochemical "code" of nucleotides in the DNA molecule that identified the specific amino acids that comprise peptides, polypeptides, and proteins gave credence to the ST notion that genes (the DNA) sequestered information. This information was assumed to have been established by natural selection and represented the instructions for ensuring the organism's adaptation to its environment. Moreover, since much of the DNA has been conserved across broad phyletic groups, DNA appeared to represent the evolutionary history of the necessary biochemical instructions for life and the development of phenotypes. This fit well with ST notions about development being irrelevant to evolution.

However, observations that the same phenotype may be obtained from different combinations of informational sources in the genotype (cf., Alberch, 1991) and different phenotypes may be obtained from the same genotype (cf., Pigliucci, 2010), challenge the notion that genes specify the development of organismal forms. Rather, the genotype is only one of the several factors operating during development that jointly determine the phenotype, with developmental events both being affected by, and in their turn, affecting genetic expression and protein production (Annila and Baverstock, 2014; Goldman and Landweber, 2016; Latham, 2017; Sultan, 2017). Each specific genotype can play a role in the expression of different phenotypes

but this relation depends on the environmental context. The variety of these pheno-typic differences is unpredictable from knowledge of the genotype.

Although certain base sequences of DNA relate directly to amino acids and these "chained" arrangements of amino acids in mRNA are translated into specific peptide, polypeptide, and protein products, the arrangement of amino acids is controlled by biochemical processes (the epigenome) that permit (or not) parts of DNA to be transcribed into mRNA. Moreover, various DNA parts are combined in unexpected ways before mRNA is created. Since any sequence of DNA could be combined with numerous other sequences for eventual translation into an indefinite number of products (proteins, polypeptides, etc.)—a way of creating "new genes" from "old genes"—research has focused on this regulation of transcription and translation (Sarkar, 2006).

Cells are organized by an intricate and dynamic set of chemical messengers that travel within and between cells to permit the transcription of specific parts of the DNA into mRNA. This layer of biochemical reactions is the epigenome, which affects the pattern and timing of mRNA transcription and translation during devel-opmental transformations as well as the biochemical "signaling" pathways operative at any time in the cell's life. Molecular genetics traces the biochemical networks and signaling pathways that connect the use of various sequences of DNA to the devel-opmental appearance of phenotypic traits. Cellular and nuclear networks and path-ways (phenotypes) emerge during development via complex, epigenomically influenced, regulatory processes. These molecular phenotypes, in turn, influence the development of the dynamic traits of physiology and behavior that enable an organism to adjust to and modify its environment.

Epigenomic processes are open to many environmental influences, which can be-gin before conception during the formation of parental germ cells (eggs and sperm) and continue throughout the life span. Such developmental "plasticity" enables organisms to meet the requirements of their habitat (niche selection) or adjust their habitat to their requirements (niche construction). Such developmental plasticity not only alters "external conditions for the individual… [but also] … for co-occurring plants, animals and microbes in its habitat" (Sultan, 2017, p. 3). Examination of these ecological influences on heredity and individual development became the focus of ecological developmental biology (Eco–Devo, Gilbert and Epel, 2009, 2015).

What appeared from the perspective of heredity across populations as a blueprint-like relation between genes and phenotypic traits became an illusion when an indi-vidual's networks of cellular processes were examined. As the concept of heredity expanded to include the epigenetic consequences of environmental events, research revealed that a variety of environmental conditions, inherited from parents, can affect offspring development. These may include: viruses, microbiota (e.g., bacteria, fungi, and various parasites), habitats and shelters, relatives and neighbors, food (prey types and edible vegetation), etc. Incorporation of Evo–Devo and Eco–Devo into the EES is the reason why some have argued that the EES is a distinctly different evolutionary theory from the ST. Evo–Devo and Eco–Devo consider development to be the product of ongoing, bidirectional interactions among DNA, proteins, cells,

physiological processes, behavior, and the environment that simultaneously contributes to both the stability and the variability of traits (Gilbert and Epel, 2009; Keller, 2002; Sansom and Brandon, 2007; West-Eberhardt, 2003). Thus, cerebral asymmetries and handedness would be shaped (maintained, transformed, promoted, inhibited, or eliminated) by extensive interactions between the developing individual and diverse environmental influences throughout the life span.

3.1 Evo–Devo: A ST ACCOUNT OF PRIMATE HANDEDNESS

To date, only one theory (the postural origins theory—POT) has been proposed to account for the evolution of primate handedness (MacNeilage, 1987), and this theory illustrates the differences between the ST and the ESS theories. POT includes the ecological context (i.e., where the species lived, what its members ate) to argue that this context shaped a division of labor between the hands. POT proposes that the earliest arboreal primates exhibited left-hand specialization for ballistic smash-and-grab acquisition of insect prey because the right hand was used for postural support that required more feedback control. As later evolving primates shifted to a terrestrial ecology, this ecological change produced a concomitant change in hand use for eating. The feedback mechanisms controlling the right hand became specialized for skilled sensory-controlled hand movements. The presumed shift from the left-hand preference observed in many modern day prosimian species to the right-hand preference seen in great apes, including the right-hand predominance in humans, was considered reconciled by POT.

POT inspired many new studies of primate handedness which provided only mixed support (MacNeilage, 2007; Papademetriou et al., 2005). POT continues to guide investigations, but no studies have been designed to refine the theory or devise an alternative theory. POT accounts for ecology, but in keeping with ST, it invokes a past environment to explain hand-use preferences observed in the present. Little attention has been paid to the function of lateralized hand use within a species' current ecological conditions and life span. Also, by focusing at the population bias level of handedness, there have been few studies of the development of individual handedness or of parsing individual variability into different developmental patterns. Thus, POT does not account for why there is a preference or how it got there.

In EES, parents provide an ecological niche for offspring, which ensures a delimited range of environmental events and potential experiences (West et al., 1988). If organisms, including humans, develop within a niche inherited from parents, then whatever constitutes the environment for an individual cannot be presumed a priori, but must be specified in detail. For example, consider the well-known association of maternal handedness with offspring handedness (Annett, 2002; McKeever, 2000). Parental hand preferences can affect the development of their infant's hand preferences via interactive social factors during dyadic play with objects (Michel, 1992). This is a complicated interaction because whereas right-handed mothers can be strikingly dominant in the use of their right hand during dyadic play, left-handed mothers show only moderate bias toward left-hand use. As a result, infants

developing a right-hand preference might have their manual asymmetry strengthened by their strongly right-handed mothers, or only mildly disrupted by their moderately left-handed mothers. In contrast, infants who are developing a left-hand preference could have their manual asymmetry strikingly disrupted by their strongly right-handed mothers, or have a chance to develop their left-hand preference under the influence of a moderately left-handed mother. In the latter case, however, infants' left-hand preference will not be as strong as the preference of infants who are developing a right preference with their right-handed mothers (Michel, 2002). The continuation of such influences beyond the child's first year remains unstudied.

The measurement of any potential environmental influence on development must be defined, in part, by reference to the individual's sensory, biomechanical, and motoric character at that point in development. von Uexküll (1957) labeled this personal quality of environments the Umwelt. The individual engages with its environment via the sensory/perceptual processes and biomechanical/physiological actions possible for that individual at that point in its life span. Both the individual and its Umwelt can change throughout development as a consequence of their continuous coactive engagement. Such change forces developmental investigations to focus on characterizing trajectories in development and the discovery of those factors that maintain consistency in any trajectory, as well as those that foster changes in trajectory vectors. Relations among the developmental trajectories of different phenotypic traits create individual differences, and these trajectories are created by individual–Umwelt coaction (Michel, 2010).

This makes untenable any notion of development as an interaction of two separate/separable influences such as gene–environment, biology–culture, nature–nurture, not because these do not interact, but because they are conceptually and empirically fused in development. Whereas some Umwelt features can be consistent across a wide range of individuals/species (e.g., gravity, atmospheric pressure, oxygen content of the medium, heat from Sun or Earth's core, and social engagement with more developed companions), others are delimited to an ecological niche (e.g., atmospheric pressure in deep seas vs mountain tops, deliberate education of young by more developed companions). The construct of Umwelt ensures that developmental investigations of any human trait must include how human culture can be transduced into epigenomic factors.

3.2 Evo–Devo: THE Evo–Devo APPROACH TO DEVELOPMENT

An Evo–Devo approach to psychological development requires identifying similarities and differences among individuals not according to their expressed traits at any point during development (e.g., handedness or working memory) but rather according to the pattern of their developmental trajectories. Although alterations in trajectories that occur earlier in development have a more noticeable consequence than those that occur later, development continues throughout the life span. Even biological structures, organs, and systems continue their development until death, despite being described as "mature." For psychological traits, describing trajectories

requires large sample sizes with carefully defined traits, measured longitudinally more than a few times (Kagan, 2016).

Once trajectory details are the focus of development, Evo–Devo identifies four main developmental processes generating the phenotypic diversity upon which evolution can occur. All four involve changes in a developing trait's relation to other developing traits; hence, trajectory details about trait development are essential for understanding both evolution and development.

1. *Heterochrony* involves changes of the timing or duration of expression of developmental events. It involves two differences in developmental trajectories: (1) the beginning and/or end of one trait's most distinctive trajectory vector relative to those of other traits and (2) the rate (faster or slower) of development of one trait relative to trajectories of other traits. For example, infants who develop a hand preference before their first year exhibit more advanced language and visuospatial skills than those who develop a hand preference in their second year (Michel et al., 2013b).
2. *Heterotopy* involves changes in the organization of developmental traits so that an individual's repertoire exhibits atypical patterns. For example, the newborn's attraction to moderate intensities of stimulation contributes toward establishing familiarity with circumstances, companions, and events. This exposure creates "neural circuits" that permit detection of stimuli that vary from the "familiar" and increases the probability of withdrawal, wariness, or cautious behaviors. We expect that similar early establishment of neural circuits controlling one hand for acquiring objects would increase likelihood that those circuits would be expanded as that hand becomes more employed for tool use and object construction actions (Michel et al., 2013b). Moreover, these circuits may be shared with those involved in developing the understanding of spatial relations among objects.
3. *Heterometry* involves changes in the intensity of expressions of a trait. Thus, individual differences in the strength of handedness would likely have consequences on the development of other differences in sensorimotor, language, and cognitive traits (Michel et al., 2013b).
4. *Heterotypy* involves rearranging a developing trait's relation to other developing traits. For example, the prenatal influence on postnatal postural asymmetry (bias for supine rightward head orientation) combined with the emergence of hominin bipedal locomotion created a right-hand biasing factor in the distribution of human handedness (Michel et al., 2013a) that is not present in most primate species. The prolonged postnatal period of ineffective sensorimotor control in human infants resulted in more frequent supine conditions during early infancy which permitted the rightward bias in head orientation to affect the development of eye hand and proprioceptive arm neural control. This, in turn, led to the distinctive right bias in human handedness.

Incorporating these four developmental processes into the development of hemispheric specialization and handedness alters the interpretation of research designs.

Comparing individual differences in handedness to individual differences in any cognitive, social, or emotional trait (cf., Cochet et al., 2014) or even to differences in neural processes (Joliot et al., 2016) reveals nothing about the developmental relation of that trait/process to handedness. Even our own work on examining the relation of different trajectories in hand preference development during infancy with the language skills of older children only hints at a developmental relation (Michel et al., 2016). We need to adopt new research designs in order to examine the relation of handedness development to the development of any other trait or neural process (Michel, 2018b).

4 RELATIONS OF EES AND Evo–Devo TO HANDEDNESS

Before examining how the modern conceptions of evolutionary and developmental biology affect accounts of the evolution and development of handedness, let us emphasize some important notions:

1. A general overriding notion is that genes are not privileged, nor are they primary explanations of either development or evolution. This has profound consequences on how we approach the study of familial resemblance in handedness and the cross-species comparison of handedness (Michel, 2013). Many genetic models of human handedness postulate a single gene as the responsible agent (e.g., Annett, 2002; McManus, 2002). According to Annett (2002), a biasing (rs+) allele would shift a random distribution of hemispheric specialization toward a left-hemisphere control of language and consequently a shift to a right-handed bias in a continuous distribution of handedness because of the left-hemisphere's control of the right hand. Inheritance of this gene would result in greater resemblance among parents and offspring. Those lacking the left-hemisphere biasing allele are presumed to have their handedness determined by relatively contingent events of culture and development.

These single gene models are good predictors of handedness distribution in offspring populations given knowledge of handedness in the parental populations. However, no single gene responsible for lateralization has been identified. The evidence is inconsistent even for the notion that several genes are involved in the control of hemispheric specialization (Ocklenburg et al., 2014a, b; Van Agtmael et al., 2002; Warren et al., 2006). Since EES proposes that phenotypes are not controlled by DNA "codes," it should not be surprising that genome-wide association studies fail to provide convincing evidence of a genetic control of handedness or hemispheric specialization of function (cf., McManus et al., 2013). An Evo–Devo approach expands the realm of factors that should be examined when seeking the causes for familial resemblance and individual diversity for handedness to include subtle epigenomic, familial, and sociocultural influences (cf., Ocklenburg et al., 2014a, b; Vuoksimaa et al., 2009).

2. Populations contain much phenotypic variation that arises from developmental processes in coaction with the ecological circumstances of the individual members of the population and those that affected their ancestors. Populations evolve via changes in how well individuals can survive to reproduce. Natural selection is not causing change, it is not a pressure or a guide; it is an effect of individual developmental success in surviving and reproducing. This new notion should alter the way we examine the evolution of handedness in primates and its relation to nonprimate limb asymmetries (cf., Michel, 2013). Although handedness among primates involves the use of the homologous forelimbs, there is no other evidence that handedness is homologous. Nor is there evidence that the different manifestations of handedness throughout development are homologous. Thus, primate handedness may be a developmental phenomenon that enables orientation toward environmental events (e.g., anterior/posterior and dorsal/ventral asymmetries affect orientation) and each manifestation of it during development is not the manifestation of the same underlying characteristic, but rather a cascading concatenation in which later handedness builds on early handedness.

3. Since natural selection is not the cause of changes in lineage traits and characteristics, organisms do not contain bundles of traits, each specifically adapted to particular ecological features. Rather, they develop general "tools" for adjusting to their environments and for adjusting their environments to them so that they can survive to reproduce. This refocuses attention on the functions of a hand preference during the life span and away from trying to identify some important adaptive significance to its occurrence. We must determine empirically how a hand preference contributes to survival and eventual reproduction (however indirectly) during the life span and whether a population bias in handedness affects survival and reproduction. Since natural selection is not a causal agent, we cannot assume that natural selection would have eliminated any polymorphism unless it had important adaptive consequences.

4. Holistic inheritance accounts for the transmission of traits across generations. The individual's developmental processes "carve" the phenotype and the ecological circumstances so that they appear to "fit." The development of handedness must be characterized by trajectory analyses that specify both the factors that maintain a vector as well as those that alter a vector. Then, we can compare handedness trajectories to the developmental trajectories of other traits according to the four developmental processes (heterochrony, heterotopy, heterometry, and heterotypy) that generate both handedness resemblance and diversity in a population. Such comparison with development of gesture, tool use and manufacture, problem-solving abilities, language abilities, and spatial representation should enrich our understanding of both development (and what disrupts typical development) and evolution (and what can lead to novelties for speciation).

5. The phenotypic differences among broad taxonomic groups result from distinct differences in their ecological and developmental histories and not differences in

their genetic information. This new notion should change our investigation of the handedness of other species to determine what ecological niches foster handedness or permit variability in handedness. It should affect also the investigation of those factors that contribute to the appearance of lateralized asymmetries throughout the vertebrate and perhaps invertebrate species. Are there ubiquitous conditions (e.g., the 3D of bodies) shaping such asymmetries of development?

6. Developmental processes involve coaction of epigenomic/physiological plasticity with ecological (physical, biological, and social) contexts. There is no gene-by-environment interaction for the development of phenotypic traits because the action of DNA cannot be separated from the action of ecological contexts. This notion alters current behavior-genetic approaches that try to partition population variance in handedness characteristics (left-, right-, or ambilateral) into estimates of genetic, environmental, and gene-by-environment influences. These are not substitutes for developmental studies that specify how handedness develops from its precursors, what factors maintain or alter its trajectory throughout the life span, and how its vector relates to the developmental vectors of other traits.

5 AN Evo–Devo APPROACH TO THE STUDY OF HUMAN HANDEDNESS

Both the EES and Evo–Devo approaches require that human handedness be carefully defined and studied longitudinally, so that its developmental trajectory can be compared with the trajectories of other traits, which also must be carefully defined and studied longitudinally. Both also require that comparative studies search for evidence of homology in human handedness. Finding evidence for determining handedness homologies, either phylogenetically across species or even serially within individual development, has been difficult to accomplish (Michel, 2013). Homology requires extensive comparative work on both morphology of structures and the structure–function relation in neural processes underlying handedness across a wide range of species. Finally, identification of homology in handedness requires detailed descriptions of its developmental trajectory, especially in closely related species (Atz, 1970; Michel, 2013). Elsewhere, Michel (2013, 2018b) argued that we lack the type of research that would permit examination of phylogenetic homology for human handedness and the comparison of handedness development with the development of other traits.

Nevertheless, there are two characteristics of the human hand preference that might distinguish it from the forelimb preferences of other vertebrates and even other hominids: (1) the preference is consistent across a variety of manual tasks, even when the "demands" of each task elicit few or no motor skills in common for their execution (McGrath and Kantak, 2016) and (2) the handedness consistency is

unevenly distributed in the population toward a distinct right-hand skew. These two characteristics would fit the criterion of special or unusual quality needed for identifying a phylogenetic homology (Michel, 2013). Archeological evidence seems to support the idea that the right bias in human handedness is an evolutionary extension of a right bias in hominin handedness (cf., Uomini, 2009a, b, 2014). Whereas there is some evidence for a right-hand bias in great ape handedness (Hopkins et al., 2011), this bias does not exhibit the same kind of consistency across tasks. Moreover, there are groups of apes with a left-hand bias and some groups for which there is no evidence of a population bias (Uomini, 2009a). By contrast, cross-cultural research does not find any human group with more than 30% left-handers (Raymond and Pontier, 2004).

The Apprenticeship Complexity Theory (Högberg et al., 2015; Uomini, 2009b; Uomini and Lawson, 2017) proposes that as hominins began to manifest complex skills of tool use and manufacture, social learning became important for the transmission of these skills. A group-shared handedness biases would facilitate faster learning of such manual skills through imitation. From an ST perspective, the pressure to quickly and accurately learn tool use and manufacture early in development would likely favor those whose hand preference matched that of their "tutors." Unfortunately, the evidence for the importance of concordance in handedness for the acquisition of manual skills via observation is weak (Michel and Harkins, 1985; Uomini and Lawson, 2017). Moreover, this account provides no explanation for why left-handedness remains in all human groups.

It is unlikely that children are motivated to develop handedness but they do have immediate needs to manually engage with social companions and physical objects. Such interactions have functional demands that require reducing competition between hands in initiating action, reducing the decision time for hand selection for unimanual actions and for distribution of hand actions in complementary bimanual manipulation. These identify a function for handedness, but not for the population-level right bias. The right population bias may be an incidental consequence of a typical developmental "package" and there may be little or no "cost" for left- or ambihandedness. What may be a unique character for humans is how handedness is assembled during development. It is possible that hominins did not "need" to manifest a particular pattern (right handedness) for handedness.

5.1 DEVELOPMENT OF HUMAN HANDEDNESS DURING INFANCY

Early cellular events may have important effects on the development of asymmetries in the embryo. Before the revolution in examining the epigenome, Morgan (1977) argued that the spatial information in the oocyte may affect gene expression that can contribute to subsequent development of structural asymmetries as the asymmetries of the oocyte translate into the morphological asymmetries of the developing organism via differential growth. This could be the early developmental origin of all vertebrate lateral asymmetries of structure and function (Vallortigara et al., 2011). However, despite well-developed theories of oocytic asymmetries, there is

no conclusive evidence to support the notion that early neural growth is a necessary condition for establishing the asymmetrical differences in neural processing involved in human hemispheric specialization of function and handedness.

For humans, it is likely that oocytic asymmetries coalesce with other fetal asymmetries and the asymmetrical prenatal environment to create prenatal asymmetries of structural development (Previc, 1991). The asymmetry of the uterus and the specific gravity of the fetus contribute to the fetus' predominant head-down position with the fetus typically facing mother's right side. Mother's bipedal locomotion produces asymmetrical vestibular stimulation of the otolith organs of the fetus to create different patterns of activation in the two hemispheres (Previc, 1991). This asymmetrical development of the otoliths means that unless the head is oriented to the right postnatally, the otoliths will be generating asymmetrical stimulation. Michel and Goodwin (1979) observed that position in utero (the typical "facing mother's right side" vs the much less frequent "facing mother's left side," as estimated during birth) predicted the direction (right and left, respectively) of the neonate's head orientation preference (HOP). The direction of the neonatal HOP predicts the infant's hand preference for acquiring objects up to 18 months of age (Michel and Harkins, 1986). Thus, there may be a prenatal influence on the early organization of postural asymmetries (perhaps, involving spinal lateral asymmetries of development, Ocklenburg et al., 2017) that affect infant hand use.

The differential sensitivity of the left and right otoliths activates the infant's neck muscles producing a neonatal supine HOP during the first 2–3 months of life (Gesell and Ames, 1947; Michel, 2002). This HOP places one hand in the infant's visual field more than the other, and it results in asymmetric activity of the hands and the consequent asymmetric proprioceptive feedback (Michel and Harkins, 1986). It is the hand on the infant's face side during HOP that becomes the preferred hand for initial reaching and object manipulation (Michel, 2002). Indeed, the direction of the infant's HOP was found to be predictive of right- and left-hand preferences at 10 years (Gesell and Ames, 1947). This early HOP induces differences in visual, haptic, and proprioceptive experiences which contribute to differences in the neuromotor control mechanisms, which, in turn, cascade (through continued use of the preferred hand) into distinct differences in neural circuitry between the left and right hemispheres of the brain (Pool et al., 2014; Serrien et al., 2006; Volkmann et al., 1997). As sensorimotor skills get continuously refined by proprioceptive, somatosensory, and other sensory experiences and feedback during early development, the neural control shifts from spinal circuits to brainstem to cortical circuits (Hopkins and Rönnqvist, 1998; Michel et al., 2013a).

The pelvic changes associated with hominin bipedal locomotion and upright posture likely made a shortened gestation period more prevalent. This, in turn, resulted in infants with less developed sensorimotor abilities that required maternal carrying and occasional resting on the ground. This early postural asymmetry, combined with increased time in supine positions as a neonate, may be the unique manner by which human handedness is assembled during development. Other primates do not exhibit such extensive bipedal locomotion during pregnancy, and the newborn

is behaviorally much more precocial and is seldom supine. Thus, human-typical prenatal vestibular experience might play a key role in the formation of neonatal postural asymmetries, which are accentuated by the relative behavioral/postural incompetency of the young infant, resulting in more supine experience which, in turn, helps shape hand-use preferences and, perhaps, hemispheric asymmetries for cognitive processing (Michel et al., 2013a). Elevated visual and kinesthetic sensory feedback from the movement of the face–side hand likely establishes sensorimotor circuits in the nervous system that ensures more precise sensory control of face–side hand movements. Such circuits could also serve as the foundation for the develop-ment of other sensorimotor neural circuits that would contribute to the embodiment of various cognitive functions (Michel et al., 2016).

The early development of infant hand-use preferences suggests a progressive expansion from an initial preference to a wider range of increasingly complex man-ual skills (Michel, 2002; Michel et al., 2013b). Handedness for object manipulation is initially observed in a preference for reaching and subsequently for acquiring objects (Michel, 1983). These preferences then concatenate into the preferences for unim-anual object manipulation (Campbell et al., 2015; Hinojosa et al., 2003) which, in their turn, influence hand preference for the later-developing role-differentiated bimanual manipulation (RDBM) skill (i.e., the two hands performing different but complementary manipulative movements on one or several objects). RDBM requires sophisticated bimanual coordination and considerable interhemispheric transfer of information (Babik and Michel, 2016a; Michel et al., 1985; Nelson et al., 2013). Eventually, manual preferences for RDBM form the foundation of handedness in artifact construction and tool use skills (Marcinowski et al., 2016; Vauclair, 1984), which involve higher-level cognitive skills such as imitation of complex actions, planning, decision making, and the ability to comprehend the spatial char-acter of objects and situations.

Importantly, hand preference for later-emerging skills might also influence hand use for already established skills. Thus, an apparent decline in the hand-use prefer-ence for acquisition observed after 12 months (Ferre et al., 2010) coincides with the development of hand preference for later-developing RDBM skills. Perhaps, as the sensorimotor circuits for acquiring objects become more efficient, they get associ-ated with circuits for RDBM (Michel et al., 1985). Thus, the nonpreferred hand could be employed to obtain the object so that the preferred hand could immediately initiate RDBM without the need to transfer the object between the hands (Michel, 2018b). Such bidirectional developmental transformations in how handedness are assembled during infancy likely produce the occasionally reported variability in longitudinal studies of handedness development.

Oddly (from an Evo–Devo perspective), the developmental trajectory of early handedness for acquiring objects appears to be unrelated to the trajectory for development of early postural control for sitting, crawling, and walking (Babik et al., 2014). Also, the trajectory for the development of general neuromotor control is unrelated to the development of infant hand preference for object acquisition (Campbell et al., 2018). Developmental trajectories of infant hand preferences for

acquiring objects, for engaging in unimanual manipulation of objects, and for RDBM seem to relate to one another in a developmental cascade-like pattern (Babik and Michel, 2016a, b, c; Campbell et al., 2015). More research is needed to determine how the developmental trajectories of these different forms of infant hand preferences relate to handedness development and other forms of neuromotor development during childhood.

6 HANDEDNESS AND COGNITION

Hand preferences for manual actions reflect underlying lateralized difference in neural control (Pool et al., 2014), some of which may be shared with manual actions involved in gestural communication, which could link the development of handedness to the development of speech–sound gestures (cf., Arbib, 2006; Greenfield, 2006). Although there is some evidence of an association between handedness for object manipulation and that for gesture (e.g., Cochet, 2016), it is not reliably obtained and may depend on age, research design, and type of skills assessed (e.g., Cochet and Vauclair, 2010; Esseily et al., 2011). Indeed, Ocklenburg et al. (2014a, b) found evidence of some genetic and neural circuit associations between adult handedness and hemispheric lateralization for language, but these associations were weak, at best. Nevertheless, production of manual actions and production of speech both depend upon finely timed and appropriately ordered sequences of acts and the development of each could be facilitated by some shared neural circuits (Abbs and Grecco, 1983; Corballis, 2003).

Embodied cognition theory proposes that symbolic cognitive processes, such as abstract reasoning, concept formation, and language, derive from sensorimotor experiences during infancy that are mediated through alterations in brain structure/functioning (Anderson, 2003; Aziz-Zadeh et al., 2006; Barsalou, 2008; Boulenger et al., 2009). The differential proficiency of their preferred hand means that right- and left-handers receive different sensorimotor experiences, and ought to engage in correspondingly different neurocognitive processing (Michel et al., 2013a). Therefore, the development of handedness and its relation to the development of language and other cognitive abilities should be a good test of embodiment theory.

The early development of hand-use preference is associated with the more effective bimanual control while manipulating objects and the early development of the artifact construction skills (i.e., stacking blocks), both of which reflect and contribute to the development of knowledge of spatial relations (Marcinowski et al., 2016). Hand preference for object acquisition also facilitates the development of object storage skills (Kotwica et al., 2008), an ability considered to reflect the cognitive capabilities of "planning" and early symbolic knowledge (Bruner, 1973). Perhaps, more efficient performance of these manual skills would facilitate the development of higher-level cognitive abilities, such as understanding of spatial and temporal characteristics of objects and situations, comprehending relations between objects,

imitation of complex actions, planning, decision making, and language development (Michel et al., 2013a). All these hypotheses need further investigation.

Early development of hand-use preferences seems to predict advances in toddler language skills (Nelson et al., 2014) and consistency of a hand preference across infancy (6–14 months) and toddlerhood (18–24 months) also predicts advances in language skills at the age of 3 years (Nelson et al., 2017). Previous research has shown that preschool design-copying skills are excellent predictors of middle school math, science, and reading achievement test scores (Cameron et al., 2012; Grissmer et al., 2010). Since design-copying skills represent visual-motor manual skills, Michel et al. (2013b) proposed that individuals with early hand-use preferences are likely to excel in copying designs compared to their peers without early hand-use preferences. If early hand-use preference is related to better design-copying skills, then different trajectories of hand-use preferences might represent different trajectories of neurobehavioral development highly relevant for the development of mathematical, scientific, and reading abilities.

Although atypical lateralization is not a sign of pathology, right hemisphere dominance, and more bilateral specialization for fine motor movements and language have been associated with different neurobehavioral dysfunctions (e.g., Illingworth and Bishop, 2009; Ribolsi et al., 2009; Whitehouse and Bishop, 2008). An Evo–Devo approach emphasizes that exploration of the origins of hemispheric specialization of function in human ontogeny is imperative for both understanding typical development and identifying factors that might shift hemispheric specialization and contribute to dysfunctional behavior. Therefore, understanding how handedness is acquired and maintained during the life span can provide insight into why it is often associated with neurobehavioral dysfunctions.

7 CONCLUSIONS

If EES and Evo–Devo are taken seriously when examining studies of handedness, then it is clear that too few studies have been designed to examine the homology of handedness, and the processes of its development or its relation to the developmental trajectories of cognitive functions. The underlying phylogenetic relation among current primates is too small a base upon which to propose notions about the evolution of handedness in primates. It is uncertain whether nonhuman primate handedness is homologous with human handedness (Michel, 2013). Primates homologously share two forelimbs; therefore, any population could show: no population bias, a left bias, or a right bias—there are no other options. Although the limbs are homologous (as demonstrated by careful analysis; see Shubin, 2008), it would be misleading to assume that primate handedness is homologous. It may be that primate handedness is not related by evolution, but rather has been constrained by developmental processes that are common among primates. However, the upright posture of hominins initiated the development of a population-level right-hand bias. Thus, natural selection may play little role in the origin and maintenance of the asymmetry.

Lateral asymmetries seem to be a deep homology throughout animals (vertebrate and invertebrate) that may have something to do with the evolution of multicellular organisms (which created the anterior–posterior and dorsal–ventral asymmetrical organizations; see Cartwright et al., 2004). Although most population biases in the lateral asymmetries of traits might depend in their initial developmental stages on some underlying lateralizing factors that would not address issues about the evolution of human handedness. Too often, it is assumed that the presence of handedness was guided by natural selection (which, according to EES, natural selection does not do) and therefore handedness must be adaptive to a specific environmental circumstance and its development must be genetically controlled. Because of the problems with these assumptions, we tried to set the record straight on what constitutes the study of evolution. We do need to have details about the developmental trajectories for handedness and for other abilities so that we can examine issues of heterochrony, heterotopy, heterometry, and heterotypy. This knowledge would add to our understanding of what is different across primates, mammals, etc., and provide insight into possible evolutionary scenarios. Moreover, understanding of these four issues would provide more insight into how those trait differences, which we identify as atypical, develop. More of this research needs to be done.

REFERENCES

Abbs, J.H., Grecco, V.L., 1983. Sensorimotor actions in the control of multi-movement speech gestures. Trends Neurosci. 6, 391–396.

Alberch, P., 1991. From genes to phenotype: dynamical systems and evolvability. Genetica 84, 5–11.

Anderson, M.L., 2003. Embodied cognition: a field guide. Artif. Intell. 149, 91–130.

Annett, M., 2002. Handedness and Brain Asymmetry: The Right Shift Theory. Psychology Press, Hove, UK.

Annila, A., Baverstock, K., 2014. Genes without prominence: a reappraisal of the foundations of biology. J. R. Soc. Interface 11, 1–8.

Arbib, M.A., 2006. The mirror system hypothesis on the linkage of action and languages. In: Arbib, M.A. (Ed.), Action to Language via the Mirror Neuron System. Cambridge University Press, New York, NY, pp. 3–47.

Atz, J.W., 1970. The application of the idea of homology to behavior. In: Aronson, L.R., Toback, E., Lehrman, D.S., Rosenblatt, J.S. (Eds.), Development and Evolution of Behavior. Freeman, San Francisco, CA, pp. 53–74.

Aziz-Zadeh, L., Wilson, S.M., Rizzolatti, G., Iacoboni, M., 2006. Congruent embodied representations for visually presented actions and linguistic phrases describing actions. Curr. Biol. 16, 1818–1823.

Babik, I., Michel, G.F., 2016a. Development of role-differentiated bimanual manipulation in infancy: part 1. The influence of hand-use preferences for the acquisition of objects. Dev. Psychobiol. 58 (2), 243–256.

Babik, I., Michel, G.F., 2016b. Development of role-differentiated bimanual manipulation in infancy: part 2. Hand preferences for object acquisition and RDBM—continuity or discontinuity? Dev. Psychobiol. 58 (2), 257–267.

Babik, I., Michel, G.F., 2016c. Development of role-differentiated bimanual manipulation in infancy: part 3. Its relation to the development of bimanual object acquisition and bimanual non-differentiated manipulation. Dev. Psychobiol. 58 (2), 268–277.

Babik, I., Campbell, J.M., Michel, G.F., 2014. Postural influences on the development of infant lateralized and symmetrical hand-use. Child Dev. 85 (1), 294–307.

Barsalou, L.W., 2008. Grounded cognition. Annu. Rev. Psychol. 59, 617–645.

Bateson, P., 2014. New thinking about biological evolution. Biol. J. Linn. Soc. 112, 268–275.

Bateson, P., 2015. Ethology and human development. In: Overton, W.F., Molenaar, P.C.M. (Eds.), Handbook of Child Psychology and Developmental Science, seventh ed. Theory and Method, vol. 1. Wiley, Hoboken, NJ, pp. 208–243.

Bearhop, S., Fiedler, W., Furness, R.W., Votier, S.C., Waldron, S., Newton, J., et al., 2005. Assortative mating as a mechanism for rapid evolution of a migratory divide. Science 310, 502–504.

Boulenger, V., Hauk, O., Pulvermüller, F., 2009. Grasping ideas with the motor system: semantic somatotopy in idiom comprehension. Cereb. Cortex 19, 1905–1914.

Bruner, J.S., 1973. Organization of early skilled action. Child Dev. 44 (1), 11.

Cameron, C.E., Brock, L.L., Murrah, W.M., Bell, L.H., Worzalla, S.L., Grissmer, D., Morrison, F.J., 2012. Fine motor skills and executive function both contribute to kindergarten achievement. Child Dev. 83 (4), 1229–1244.

Campbell, J.M., Marcinowski, E.C., Babik, I., Michel, G.F., 2015. The influence of a hand-use preference for acquiring objects on the development of a hand-use preference for unimanual manipulation from 6 to 14 months. Infant Behav. Dev. 39, 107–117.

Campbell, J.M., Marcinowski, E.C., Michel, G.F., 2018. The development of neuromotor skills and hand preference during infancy. Dev. Psychobiol. 60, 165–175.

Cartwright, J., Piro, O., Tuval, I., 2004. Fluid-dynamical basis of the embryonic development of left-right asymmetry in vertebrates. Proc. Natl. Acad. Sci. U. S. A. 101 (19), 7234–7239.

Cochet, H., 2016. Manual asymmetries and hemispheric specialization: insight from developmental studies. Neuropsychologia 93, 335–341.

Cochet, H., Byrne, R.W., 2013. Evolutionary origins of human handedness: evaluating contrasting hypotheses. Anim. Cogn. 16, 531–542.

Cochet, H., Vauclair, J., 2010. Pointing gestures produced by toddlers from 15 to 30 months: different functions, hand shapes and laterality patterns. Infant Behav. Dev. 33, 432–442.

Cochet, H., Jover, M., Oger, L., Vauclair, J., 2014. Morphological differences between imperative and declarative pointing: hand shape, arm extension, and body posture. J. Mot. Behav. 46 (4), 223–232.

Corballis, M.C., 2003. From mouth to hand: gesture, speech, and the evolution of right-handedness. Behav. Brain Sci. 26, 198–208.

Darwin, C., 1859. The Origin of Species by Means of Natural Selection. [reprinted 1968]. Penguin, London, UK.

Esseily, R., Jacquet, A.-Y., Fagard, J., 2011. Handedness for grasping objects and pointing and the development of language in 14-month-old infants. Laterality 16 (5), 565–585.

Ferre, C.L., Babik, I., Michel, G.F., 2010. Development of infant prehension handedness: a longitudinal analysis during the 6-to 14-month age period. Infant Behav. Dev. 33 (4), 492–502.

Gesell, A., Ames, L.B., 1947. The development of handedness. Pedagog. Sem. J. Genet. Psychol. 70 (2), 155–175.

Ghirlanda, S., Vallortigara, G., 2004. The evolution of brain lateralization: a game theoretical analysis of population structure. Proc. R. Soc. B 271, 853–857.

Gilbert, S.F., Epel, D., 2009. Ecological Developmental Biology: Integrating Epigenetics, Medicine, and Evolution. Sinauer Associates, Incorporated Publishers, Medford, MA.

Gilbert, S.F., Epel, D., 2015. Ecological Developmental Biology: The Environmental Regulation of Development, Health, and Evolution. Sinauer Associates, Incorporated Publishers, Medford, MA.

Gilbert, S.F., Bosch, T.C., Ledón-Rettig, C., 2015. Eco–Evo–Devo: developmental symbiosis and developmental plasticity as evolutionary agents. Nat. Rev. Genet. 16 (10), 611.

Goldman, A.D., Landweber, L.F., 2016. What is a genome? PLoS Genet. 12 (7), e1006181.

Gould, S.J., 2002. The Structure of Evolutionary Theory. The Belknap Press of Harvard University, Cambridge, MA.

Gould, S.J., Lewontin, R.C., 1979. The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme. Proc. R. Soc. Lond. Ser. B Biol. Sci. 205, 581–598.

Gould, S.J., Vrba, E.S., 1982. Exaptation: a missing term in the science of form. Paleobiology 8, 4–15.

Greenfield, P., 2006. Implications of mirror neurons for the ontogeny and phylogeny of cultural processes: the examples of tools and language. In: Arbib, M.A. (Ed.), Action to Language via the Mirror Neuron System. Cambridge University Press, Cambridge, UK, pp. 501–533.

Grissmer, D., Grimm, K.J., Aiyer, S.M., Murrah, W.M., Steele, J.S., 2010. Fine motor skills and early comprehension of the world: two new school readiness indicators. Dev. Psychol. 46 (5), 1008.

Hall, B.K., 1999. The Neural Crest in Development and Evolution. Springer Science & Business Media, New York, NY.

Hall, B.K., 2012. Evolutionary Developmental Biology. Springer Science & Business Media, New York, NY.

Hinojosa, T., Sheu, C.F., Michel, G.F., 2003. Infant hand-use preferences for grasping objects contributes to the development of a hand-use preference for manipulating objects. Dev. Psychobiol. 43 (4), 328–334.

Högberg, A., Gärdenfors, P., Larsson, L., 2015. Knowing, learning and teaching—how Homo became Docens. Camb. Archaeol. J. 25, 847–858.

Hopkins, B., Rönnqvist, L., 1998. Human handedness: developmental and evolutionary perspectives. In: Simion, F., Butterworth, G.E. (Eds.), The Development of Sensory, Motor and Cognitive Capacities in Early Infancy: From Sensation to Cognition. Psychology Press, Hove, pp. 191–236.

Hopkins, W.D., Phillips, K.A., Bania, A., Calcutt, S.E., Gardner, M., Russell, J., Schaeffer, J., Lonsdorf, E.V., Ross, S.R., Schapiro, S.J., 2011. Hand preferences for coordinated bimanual actions in 777 great apes: implications for the evolution of handedness in hominins. J. Hum. Evol. 60, 605–611.

Huxley, T., 1880. The coming of age of the origin of species. Nature 22, 1–4.

Huxley, J., Pigliucci, M., Müller, G.B., 2010. Evolution: The Modern Synthesis: The Definitive Edition. MIT Press, Cambridge, MA.

Illingworth, S., Bishop, D.V., 2009. Atypical cerebral lateralisation in adults with compensated developmental dyslexia demonstrated using functional transcranial Doppler ultrasound. Brain Lang. 111 (1), 61–65.

Jablonka, E., Lamb, M.J., 2005. Evolution in Four Dimensions: Genetic, Epigenetic, Behavioral, and Symbolic Variation in the History of Life. The MIT Press, Cambridge, MA.

Joliot, M., Tzourio-Mazoyer, N., Mazoyer, B., 2016. Intra-hemispheric intrinsic connectivity asymmetry and its relationships with handedness and language lateralization. Neuropsychologia 93, 437–447.

Kagan, J., 2016. An overly permissive extension. Perspect. Psychol. Sci. 11 (4), 442–450.

Keller, E.F., 2002. Developmental robustness. Ann. N. Y. Acad. Sci. 981 (1), 189–201.

Kotwica, K.A., Ferre, C.L., Michel, G.F., 2008. Relation of stable hand-use preferences to the development of skill for managing multiple objects from 7 to 13 months of age. Dev. Psychobiol. 50 (5), 519–529.

Laland, K.N., Odling-Smee, J., Feldman, M.W., 2000. Niche construction, biological evolution, and cultural change. Behav. Brain Sci. 23 (1), 131–146.

Latham, J., 2017. Genetics is giving way to a new science of life. Independent Science News. February 6, https://www.independentsciencenews.org/.

Laubichler, M.D., 2010. Evolutionary developmental biology offers a significant challenge to the neo-Darwinian paradigm. In: Ayala, F.J., Arp, R. (Eds.), Contemporary Debates in Philosophical Biology. Wiley-Blackwell, Malden, MA, pp. 199–212.

Lewontin, R.R., 1982. Organism and environment. In: Plotkin, H.C. (Ed.), Learning, Development, and Culture: Essays in Evolutionary Epistemology. Wiley, New York, NY, pp. 151–172.

Lickliter, R., Harshaw, C., 2010. Canalization and malleability reconsidered: the developmental basis of phenotypic stability and variability. In: Hood, K., Halpern, C., Greenberg, G., Lerner, R.D. (Eds.), Handbook of Developmental Science, Behavior and Genetics. Wiley, Malden, MA, pp. 491–525.

MacNeilage, P.F., 1987. The evolution of handedness in primates. In: Ottoson, D. (Ed.), Duality and Unity of the Brain. Wenner-Gren Center International Symposium Series, Palgrave, Macmillan, London, UK, pp. 100–113.

MacNeilage, P.F., 2007. Present status of the postural origins theory. Spec. Top. Primat. 5, 58–91.

Maienschein, J., Laubichler, M.D., 2014. Exploring development and evolution on the tangled bank. In: Thompson, P., Walsh, D. (Eds.), Evolutionary Biology: Conceptual, Ethical, and Religious Issues. Cambridge University Press, Cambridge, UK, pp. 151–171.

Marcinowski, E.C., Campbell, J.M., Faldowski, R.A., Michel, G.F., 2016. Do hand preferences predict stacking skill during infancy? Dev. Psychobiol. 58 (8), 958–967.

McGrath, R.L., Kantak, S.S., 2016. Reduced asymmetry in motor skill learning in left-handed compared to right-handed individuals. Hum. Mov. Sci. 45, 130–141.

McKeever, W.F., 2000. A new family handedness sample with findings consistent with X-linked transmission. Br. J. Psychol. 91 (1), 21–39.

McManus, C., 2002. Right Hand, Left Hand: The Origins of Asymmetry in Brains, Bodies, Atoms, and Cultures. Harvard University Press, Cambridge, MA.

McManus, I.C., Davison, A., Armour, J.A.L., 2013. Multilocus genetic models of handedness closely resemble single-locus models in explaining family data and are compatible with genome-wide association studies. Ann. N. Y. Acad. Sci. 1288, 48–58.

Michel, G.F., 1983. Development of hand-use preference during infancy. In: Young, G., Segalowitz, S., Corter, C., Trehub, S. (Eds.), Manual Specialization and the Developing Brain. Academic Press, New York, NY, pp. 33–70.

Michel, G.F., 1992. Maternal influences on infant hand-use during play with toys. Behav. Genet. 22 (2), 163–176.

Michel, G.F., 2002. Development of infant handedness. In: Lewkowicz, D., Lickliter, R. (Eds.), Conceptions of Development: Lessons from the Laboratory. Psychology Press, Philadelphia, PA, pp. 165–186.

Michel, G.F., 2010. The roles of environment, experience, and learning in behavioral development. In: Hood, K., Halpern, C., Greenberg, G., Lerner, R. (Eds.), Handbook of Developmental Science, Behavior and Genetics. Wiley, Malden, MA, pp. 123–165.

Michel, G.F., 2013. The concept of homology in the development of handedness. Dev. Psychobiol. 55 (1), 84–91.

Michel, G.F., 2018a. Evolutionary developmental biology. In: Hopkins, B., Geangu, E., Linkenauger, S. (Eds.), The Cambridge Encyclopedia of Child Development, second ed. Cambridge University Press, New York, NY, pp. 43–49.

Michel, G.F., 2018b. How might the relation of the development of hand preference to the development of cognitive functions be examined during infancy: a sketch? Front. Neurosci. 11, 739.

Michel, G.F., Goodwin, R., 1979. Intrauterine birth position predicts newborn supine head position preference. Infant Behav. Dev. 2, 29–38.

Michel, G.F., Harkins, D.A., 1985. Concordance of handedness between teacher and student facilitates learning manual skills. J. Hum. Evol. 14, 597–601.

Michel, G.F., Harkins, D.A., 1986. Postural and lateral asymmetries in the ontogeny of handedness during infancy. Dev. Psychobiol. 19, 247–258.

Michel, G.F., Moore, C.L., 1995. Developmental Psychobiology: An Interdisciplinary Science. MIT Press, Cambridge, MA.

Michel, G.F., Ovrut, M.R., Harkins, D.A., 1985. Hand-use preference for reaching and object manipulation in 6- through 13-month-old infants. Genet. Soc. Gen. Psychol. Monogr. 111, 407–428.

Michel, G.F., Babik, I., Nelson, E.L., Campbell, J.M., Marcinowski, E.C., 2013a. How the development of handedness could contribute to the development of language. Dev. Psychobiol. 55 (6), 608–620.

Michel, G.F., Nelson, E.L., Babik, I., Campbell, J.M., Marcinowski, E.C., 2013b. Multiple trajectories in the developmental psychobiology of human handedness. In: Lerner, R.M., Benson, J.B. (Eds.), Embodiment and Epigenesis: Theoretical and Methodological Issues in Understanding the Role of Biology within the Relational Developmental System Part B: Ontogenetic Dimensions. Elsevier Inc., Academic Press, New York, NY, pp. 227–260.

Michel, G.F., Campbell, J.M., Marcinowski, E.C., Nelson, E.L., Babik, I., 2016. Infant hand preference and the development of cognitive abilities. Front. Psychol. 7, 410.

Morange, M., 2011. What will result from the interaction between functional and evolutionary biology? Stud. Hist. Philos. Biol. Biomed. Sci. 42 (1), 69–74.

Morgan, M., 1977. Embryology and inheritance of asymmetry. In: Harnad, S. et al., (Ed.), Lateralization in the Nervous System. Academic Press, New York, NY, pp. 173–194.

Müller, G.B., 2017. Why an extended evolutionary synthesis is necessary. Interface Focus 7, 20170015. https://doi.org/10.1098/rsfs.2017.0015.

Nelson, E.L., Campbell, J.M., Michel, G.F., 2013. Unimanual to bimanual: tracking the development of handedness from 6 to 24 months. Infant Behav. Dev. 36, 181–188.

Nelson, E.L., Campbell, J.M., Michel, G.F., 2014. Early handedness in infancy predicts language ability in toddlers. Dev. Psychol. 50, 809–814.

Nelson, E.L., Gonzalez, S.L., Coxe, S., Campbell, J.M., Marcinowski, E.C., Michel, G.F., 2017. Toddler hand preference trajectories predict 3-year language outcome. Dev. Psychobiol. 59, 876–887.

Ocklenburg, S., Beste, C., Arning, L., 2014a. Handedness genetics: considering the phenotype. Front. Psychol. 5, 1300.

Ocklenburg, S., Beste, C., Arning, L., Peterburs, J., Güntürkün, O., 2014b. The ontogenesis of language lateralization and its relation to handedness. Neurosci. Biobehav. Rev. 43, 191–198.

Ocklenburg, S., et al., 2017. Epigenetic regulation of lateralized fetal spinal gene expression underlies hemispheric asymmetries. eLife 6, e22784.

Oppenheim, R.W, 1984. Ontogenetic adaptations in neural and behavioral development: toward a more "ecological" developmental psychobiology. In: Prechtle, H.F.R. (Ed.), Continuity of Neural Functions From Prenatal to Postnatal Life. Lippincott, Philadelphia, PA, pp. 16–29.

Papademetriou, E., Sheu, C.-F., Michel, G.F., 2005. A meta-analysis of primate hand preference for reaching and other hand-use preferences. J. Comp. Psychol. 119 (1), 33–48.

Pfennig, D.W., McGee, M., 2010. Resource polyphenism increases species richness: a test of the hypothesis. Philos. Trans. R. Soc. Lond. B Biol. Sci. 365, 577–591.

Pfennig, D.W., Wund, M.A., Snell-Rood, E.C., Cruickshank, T., Schlichting, C.D., Moczek, A.P., 2010. Phenotypic plasticity's impacts on diversification and speciation. Trends Ecol. Evol. 25 (8), 459–467.

Pigliucci, M., 2010. Genotype $\Rightarrow$ phenotype mapping and the end of the 'genes as blueprint' metaphor. Philos. Trans. R. Soc. Lond. B Biol. Sci. 365, 557–566.

Pigliucci, M., Muller, G.B., 2010. Evolution—The Extended Synthesis. MIT Press, Cambridge, MA.

Pool, E.-M., Rehme, A.K., Fink, G.R., Eickhoff, S.B., Grefkes, C., 2014. Handedness and effective connectivity of the motor system. Neuroimage 99, 451–460.

Previc, F.H., 1991. A general theory concerning the prenatal origins of cerebral lateralization in humans. Psychol. Rev. 98, 299–334.

Raymond, M., Pontier, D., 2004. Is there geographical variation in human handedness? Laterality 9, 35–51.

Ribolsi, M., Koch, G., Magni, V., Di Lorenzo, G., Rubino, I.A., Siracusano, A., Centonze, D., 2009. Abnormal brain lateralization and connectivity in schizophrenia. Rev. Neurosci. 20 (1), 61–70.

Rogers, L.J., 2014. Asymmetry of brain and behavior in animals: its development, function, and human relevance. Genesis 52, 555–571.

Sansom, R., Brandon, R.N. (Eds.), 2007. Integrating Evolution and Development: From Theory to Practice. MIT Press, Cambridge, MA.

Sarkar, S., 2006. From genes as determinants to DNA as resource. In: Neumann-Held, E.M., Rehmann-Sutter, C. (Eds.), Genes in Development: Re-Reading the Molecular Paradigm. Duke University Press, Durham, NC, pp. 77–95.

Sarkar, S., 2017. Haldane's the causes of evolution and the modern synthesis in evolutionary biology. J. Genet. 96 (5), 753–763.

Serrien, D.J., Ivry, R.B., Swinnen, S.P., 2006. Dynamics of hemispheric specialization and integration in the context of motor control. Nat. Rev. Neurosci. 7, 160–166.

Shubin, N., 2008. Your Inner Fish: A Journey into the 3.5-Billion-Year History of the Human Body. Pantheon, New York, NY.

Sultan, S.E., 2017. Developmental plasticity: re-conceiving the genotype. Interface Focus 7, 20170009. https://doi.org/10.1098/rsfs.2017.0009.

Uomini, N.T., 2009a. The prehistory of handedness: archaeological data and comparative ethology. J. Hum. Evol. 57, 411–419.

Uomini, N.T., 2009b. Prehistoric left-handers and prehistoric language. In: de Beaune, S.A., Coolidge, F.L. (Eds.), The Emergence of Cognitive Abilities: The Contribution of Neuropsychology to Archaeology. Cambridge University Press, Cambridge, UK, pp. 37–55.

Uomini, N.T., 2014. Paleoneurology and behaviour. In: Bruner, E. (Ed.), Human Paleoneurology. Springer, Berlin, Germany, pp. 121–144.

Uomini, N., Lawson, R., 2017. Effects of handedness and viewpoint on the imitation of origami-making. Symmetry 9, 182–194.

Vallortigara, G., Chiandetti, C., Sovrano, V.A., 2011. Brain asymmetry (animal). Wiley Interdiscip. Rev. Cogn. Sci. 2, 146–157.

Van Agtmael, T., Forrest, S.M., Williamson, R., 2002. Parametric and nonparametric linkage studies of several candidate regions for genes for human handedness. Eur. J. Hum. Genet. 10, 623–630.

Vauclair, J., 1984. Phylogenetic approach to object manipulation in human and ape infants. Hum. Dev. 27, 321–328.

Volkmann, J., Schnitzler, A., Witte, O.W., Freund, H.-J., 1997. Handedness and asymmetry of hand representation in human motor cortex. J. Neurophysiol. 79 (4), 2149–2154.

von Uexküll, J., 1957. A stroll through the world of animals and men. In: Schiller, C.H. (Ed.), Instinctive Behavior. International Universities Press, New York, NY, pp. 5–80.

Vuoksimaa, E., Koskenvuo, M., Rose, R.J., Kaprio, J., 2009. Origins of handedness: a nationwide study of 30161 adults. Neuropsychologia 47, 1294–1301.

Walsh, D.M., 2015. Challenges to evolutionary theory. In: Humphreys, P. (Ed.), The Oxford Handbook of Philosophy of Science. Oxford University, Oxford, UK, pp. 1–29.

Warren, J.D., Scott, S.K., Price, C.J., Griffiths, T.D., 2006. Human brain mechanisms for the early analysis of voices. Neuroimage 31 (3), 1389–1397.

West, M.J., King, A.P., Arberg, A.A., 1988. The inheritance of niches. In: Developmental Psychobiology and Behavioral Ecology. Springer, Boston, MA, pp. 41–62.

West-Eberhardt, M.J., 2003. Developmental Plasticity and Evolution. Oxford University Press, New York, NY.

Whitehouse, A.J.O., Bishop, D.V.M., 2008. Hemispheric division of function is the result of independent probabilistic biases. Neuropsychologia 47, 1938–1943.