Behavioral Heterochrony

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Abstract

Behavioral heterochrony is the study of the timing and speed of development of behavior from an evolutionary perspective. Key to studies of behavioral heterochrony is the comparison of development across different species. Such studies can illuminate whether a trait thought to be unique to a given species might in fact have its precursors in the early development of a closely related species. They can inform our understanding of how behavioral development is constrained by elements of somatic or reproductive maturation. Studies of behavioral heterochrony can also elucidate mechanisms by which behavior evolves, by targeting evolutionary shifts in developmental pathways. Finally, such studies can enrich our knowledge of human evolution, in contextualizing the vast shifts in human life history patterns relative to other primates in terms of corresponding changes in behavioral and cognitive development. On the whole then, research in behavioral heterochrony can advance our understanding of behavior through forging interdisciplinary links between anthropology, biology, and psychology.

INTRODUCTION

Social and life scientists have used a variety of methodologies to understand behavioral traits—whether investigating a behavior's ontogenetic origins, its proximate determinants, its phylogenetic distribution, or its potential adaptive value. The majority of these studies have focused on quantifying either a behavior's proximate determinants (*how* that behavior arises in the moment or across development), or the behavior's ultimate functions (*why* that behavior arises in certain species, and how it might function adaptively)—in line with the framework outlined by Niko Tinbergen nearly 50 years ago (Tinbergen, 1963). However, the adherence to this framework may have led studies of behavior to fall behind other areas of biology—where in fact, studies integrating *both* proximate and ultimate perspectives to investigate the evolution of development can provide the strongest means by which to understand a given trait. Here, therefore, we argue that studies of behavior should build on the insights gained from evolutionary developmental biology to investigate the evolution of behavioral development, or behavioral heterochrony.

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In essence, understanding changes in behavioral development across species may, in fact, facilitate conclusions that would be lost by comparing adults alone.

Studies of behavioral heterochrony are particularly relevant given the increasing evidence from the field of evolutionary developmental biology that evolutionary change frequently occurs via shifts in developmental trajectories. We argue, therefore, that studies of comparative behavioral and cognitive development can improve our understanding of how behavior and cognition evolve. Such studies can illuminate how aspects of behavioral development scale with (or shift independently of) somatic and reproductive maturation. These studies may also reveal that behaviors previously assumed to be novel in a given species or population, in fact, have roots in the early development of a closely related group. Finally, in the case of human origins, studies of comparative behavioral development will clarify the links between the well-known changes in human life history patterns and changes in our behavioral development.

We provide support for this argument by first discussing foundational research on the evolution of development. We then review recent studies in the area of behavioral heterochrony. We conclude by outlining key questions and debates that can be addressed by studies of behavioral heterochrony.

FOUNDATIONAL RESEARCH—SKELETAL HETEROCHRONY

The concept of heterochrony, or the evolution of development, has a long history in the study of skeletal morphology. Charles Darwin noted the importance of studying developmental pathways in The Descent of Man (Darwin, 1871), while Ernst Haeckel went so far as to assert that "ontogeny recapitulates phylogeny" in his study of embryology (Haeckel, 1866; ontongeny being the study of development). While Haeckel's argument may have been too simplistic, studies of biology and human evolution have continued to underscore the central role of development in generating variation between individuals and species (Carroll, 2003; Gould, 1977).

In the case of human evolution, in particular, studies of heterochrony have advanced our understanding of the changes occurring in the human skeleton throughout our recent evolutionary past. Comparisons of development between humans and other apes have revealed that humans are born with underdeveloped crania, yet develop more rapidly during infancy and juvenility to eventually exceed other apes in cranial capacity (Robson & Wood, 2008). Compounded with the evidence that humans also show a prolonged juvenile period relative to other primates, these findings suggest striking alterations in developmental trajectories in hominoid evolution

(Charnov & Berrigan, 1993). But how could such broad-scale changes in development have occurred?

Recent studies have identified a critical role of gene expression in mediating sweeping developmental change between individuals and species (Albert *et al.*, 2012; Atchley, 1987; King & Wilson, 1975). These studies have revealed that in addition to changes in genomic sequence, which can alter the specific proteins coded for by a given gene, changes in gene expression can influence the degree and timing of protein production, with significant effects on phenotype (Carroll, 2003). The field of evolutionary developmental biology has now extensively documented the ways in which developmental variation in gene expression can underlie evolutionary change in species ranging from plants to humans.

Findings from the field of "evo-devo" therefore suggest that minor alterations in development can lead to major differences in adult phenotype. We propose that, similarly, minor alterations in behavioral development can lead to significant differences in adult behavior, whether between individuals or species. Although this assertion is intuitive, that development should influence an adult state, the *role* of development in behavioral evolution is vastly understudied.

One example that illustrates this point comes from the study of helping behavior in communally breeding birds. In these communally breeding species, where juvenile individuals help to feed nestlings, it had been argued that this helping behavior arose *de novo* as an adaptive correlate of a species adapting a communal breeding strategy (Emlen, 1982). However, an alternative hypothesis proposes that this helping behavior arose as an unselected by-product of a shift in life history strategy. Specifically, with changes in ecology that made breeding dispersal less effective and heightened the tolerance of juvenile individuals by a breeding pair, juveniles were provided with an opportunity to exhibit helping behaviors that previously would only have been displayed in adulthood. Therefore, a shift in life history could have led to heightened helping by juveniles via "predisplacement" of helping behavior. Importantly then, a behavior argued to have evolved for its function in juveniles may instead have arisen as an unexpected by-product of larger selection pressures acting via shifts in life history (Hatchwell, 2009; Jamieson, 1989) This critical alternative could not have been revealed without the study of comparative development.

This example also illustrates one potential difficulty in studying behavioral heterochrony, in that developmental trajectories of behavior are not as predictable as those of morphological traits. Extensive work in the skeletal heterochrony literature has quantified the precise relationships in changes of the size and shape of a trait over time during growth, specifying precise terms for the varying combinations of shifts in these parameters (Gould, 1977; McKinney & McNamara, 1991). Skeletal traits typically begin at a smaller size, with an underdeveloped form, and eventually grow to reach the adult state, which is then fixed. For behavioral traits, however, development does not always happen steadily, nor is the adult state always fixed. In addition, there may be cases where a behavior is *absent* in adults, rather than fully grown—for example, in the case of play behaviors, which are typically prevalent among juveniles but minimal in adulthood. This means that studies of behavioral heterochrony may not fit the precise definitions set forth by studies of skeletal heterochrony, and that instead we must term such studies "comparative ontogenetic allometry" (Lieberman, 2012). Nonetheless, the critical advances that have been made in morphology and genetics by incorporating the study of development, particularly comparative development, are too notable for behavioral scientists to pass by. In the next section, we review some of the insights that have been gained from existing studies of behavioral heterochrony, before moving onto the key directions for future research.

CUTTING-EDGE RESEARCH—BEHAVIORAL HETEROCHRONY

There are a number of fields in which studies of behavioral heterochrony have enriched our understanding of behavioral traits. Here we discuss four main areas where behavioral heterochrony studies have made a significant contribution, reviewing studies that examine: (i) the genetic basis for changes in behavioral development; (ii) the correlation between behavioral development and the developmental trajectories of nonbehavioral traits; (iii) the effects of selection on developmental trajectories; and (iv) behavioral heterochrony during hominoid evolution.

GENETIC UNDERPINNINGS OF CHANGES IN BEHAVIORAL DEVELOPMENT

As mentioned, methodological advances allowing the study of gene expression have greatly expanded our understanding of how genetic changes can be expressed as changes in phenotypic development. For behavioral traits, connecting genotype to phenotype can often be extremely complex given that typically behavioral traits are polygenic and genetic changes are relayed through the brain in affecting behavioral outcomes. Nonetheless, studies of the mechanisms underlying behavioral development in model organisms have made significant gains in recent years.

One line of research where mechanisms have been particularly well elucidated comes from studies of social insects. Recent research has identified specific genes that can readily lead to the spread of ultra-sociality, also known as eusociality, through shifts in development (Linksvayer & Wade, 2005). Specifically, shifts in genes that regulate the expression of maternal care behaviors allowing them to be expressed earlier on in development would facilitate "maternal-care"-type behaviors between siblings, rather than only between mother and offspring (Toth *et al*., 2007). These findings provide a mechanism by which alterations in behavioral development, through changes in gene expression, might underlie the evolution of eusociality in promoting greater social behaviors throughout life (Linksvayer & Wade, 2005; Toth *et al*., 2007). These findings underscore the point that developmental changes can serve as a mechanism by which to produce species differences, with studies of model organisms allowing us to identify the specific genetic changes that accompany changes in phenotype.

These findings also align with a large body of literature in rodents cataloguing mechanisms by which early development can shape ultimate behavioral outcomes. This work has shown that early exposure to stress (particularly low levels of care by one's mother) can alter gene expression and ultimately constrain patterns of stress reactivity. In turn, these patterns of stress reactivity can constrain an individual's expression of appropriate maternal behaviors as an adult (Meaney, 2001). On the whole then, these studies highlight the importance of studying development to contextualize adult phenotypes, including a better understanding of the mechanisms that influence behavior and how they vary across individuals and species.

Correlations Between Behavioral Development and Other Aspects of Maturation

A second area in which studies of behavioral heterochrony have contributed valuable insight is in linking behavioral development with its broader maturational context. This perspective is increasingly important in our understanding of human health, given the recent argument that human developmental disorders can arise via a "mismatch" of psychological and physiological developmental trajectories (e.g., in the case of early sexual maturity precipitating precocious sexual behavior and greater risk-taking (Forbes & Dahl, 2010)).

Studies showing a strong correlation between behavioral development and somatic maturation have come from investigations of locomotor behavior, for example the ontogeny of flight behavior in birds. Researchers in this area have shown how changes in the ontogeny of feather microstructure directly influence birds' capacities to generate aerodynamic force during flight (Dial, Heers, & Tobalske, 2012). Moreover, the developmental trajectories of flight behavior have been found to differ between species in line with the varying uses of flight behavior among adults. In species where flight is used for predation avoidance and flight development is correspondingly fast or "precocial," individuals become competent in flight behavior early on in development but improve gradually toward adult levels of aerodynamic proficiency. In contrast, among species where flight is used for migration and its development is slow or "altricial," individuals only develop flight capacities upon reaching adult mass (Dial *et al.*, 2012; Jackson, Segre, & Dial, 2009). Future studies in this area can reveal the degree to which developmental trajectories of flight behavior shift in line with ecological pressures impacting the function of flight behavior among adults (even across populations within-species), providing new insight into the relationship between morphology and behavior through the study of their correlated development.

Morphological and behavioral traits are not always this tightly coupled, however. For example, certain species ranging from newts to orangutans show "facultative paedomorphosis," where individuals can "choose" to retain juvenile morphological characteristics into adulthood rather than fully develop into the adult form. Intriguingly, these subadult morphs have been shown to possess full reproductive capacity despite their skeletal juvenility (Denoel, 2002; Maggioncalda, Sapolsky, & Czekala, 1999). These results therefore indicate that there may be certain correlations in developmental trajectories across traits, for example, in the area of locomotor behavior, where the behavior itself is strongly constrained by morphology. However, in other areas, even those where physiological maturation plays a significant role, such as in reproductive behavior, these findings imply that we cannot assume that behavioral ontogeny will scale precisely with the concurrent maturational processes.

EFFECTS OF SELECTION ON DEVELOPMENTAL TRAJECTORIES

Recent studies using experimental selection in model organisms reveal that developmental shifts play a critical role in generating differences in phenotype between individuals and species. Some of the most notable research examining the effects of artificial selection on behavioral development comes from populations of mice selected differentially for their rates of aggression as adults. In two series of experiments (Cairns, MacComble, & Hood, 1983; Gariepy, Bauer, & Cairns, 2001), researchers found that in selecting for adult differences in aggressive behavior, the mechanism underlying these differences was a shift in behavioral development. While the unselected or high-aggression lines developed aggressive behaviors as they aged, the low-aggression line did not increase in aggressive behavior at maturity (Cairns *et al.*, 1983). Gariepy *et al.* (2001) illustrated this phenomenon particularly precisely by documenting the ontogenetic patterns of aggressive behavior across selected and unselected lines. This study revealed that while all of the mouse lines showed some increase in aggression from infancy to adulthood, the magnitude of increase at all ages was much less in the line selected for low aggression relative to either the control or high-aggression lines. Moreover, these differences in developmental trajectories became more extreme with more generations selected. These findings provide direct evidence that selective pressures can influence shifts in development, even in the case of a behavioral trait.

The findings from these mouse studies conform to other studies looking at the effects of selection against aggression, both within experimental populations (Belayev's foxes (Belyaev, 1979; Trut, 1999)) and studies comparing naturally domesticated species to their wild forebears (particularly work on guinea pigs, (Kunzl, Kaiser, Meier, & Sachser, 2003)). Across numerous taxa, selection against aggression has been found to produce individuals that retain juvenile characteristics into adulthood in features of their morphology, physiology, behavior, and cognition (Hare, Wobber, & Wrangham, 2012). These findings suggest the compelling possibility that common underlying mechanisms might govern the ontogeny of multiple traits, and that these mechanisms in turn may have been impacted by selection for any one of the traits—implying some genetic link, or pleiotropic effect, on the others. Continued studies in this area can therefore test the effects of selection on developmental trajectories, testing hypotheses about the origins of species differences through comparative study of the proximate mechanisms that facilitate these differences.

Using Behavioral Heterochrony to Understand Human Evolution

A final area where studies of behavioral heterochrony have contributed recent insight is in our understanding of human origins. For years researchers have extensively documented the differences in human life history relative to other primates—including our prolonged juvenile period, extended overall lifespan, and heightened reproductive rate relative to other primates. While patterns of somatic and reproductive maturation have been well studied in humans and comparative models, studies of behavioral and cognitive ontogeny in a comparative perspective have lagged behind in comparison.

Our recent work has therefore focused on behavioral and cognitive development in chimpanzees and bonobos, in using studies of heterochrony to understand the differences between these two apes but also to shed light on evolutionary mechanisms that may have been at play in recent human evolution. We first examined a behavior that is well known to differ between adult bonobos and chimpanzees—food sharing. Bonobos have been found to share food more readily than chimpanzees both in the wild and in experimental contexts (de Waal, 1989; Fruth & Hohmann, 2002; Hare, Melis, Woods, Hastings, & Wrangham, 2007), and their greater tolerance in food sharing allows them to cooperate in experimental situations where chimpanzee cooperation breaks down (Hare *et al.*, 2007). We examined whether the difference in sharing and tolerance between adults of the two species might be due to shifts in the development of these traits. We found that while the two species share food at similar, high rates as juveniles, chimpanzees develop intolerance in food sharing with age, while bonobos maintain these juvenile levels of tolerance in sharing into adulthood (Wobber, Wrangham, & Hare, 2010b). These results support the argument that shifts in behavioral development can underlie species differences in adult behavior (Wobber, Wrangham, & Hare, 2010a).

In addition, taken together with findings that bonobos also maintain several juvenile skeletal (Durrleman, Pennec, Trouve, Ayache, & Braga, 2012; Lieberman, Carlo, Ponce de Leon, & Zollikofer, 2007), endocrine (Wobber, Lipson, Hare, Wrangham, & Ellison, 2013), and cognitive (Wobber *et al.*, 2010a, 2010b) characteristics into adulthood, these findings suggest potential broad-scale shifts in development between bonobos and chimpanzees. In fact, these differences might be tied to selection against aggression in bonobos, given the strong evidence that this type of selection facilitates retention of juvenile characteristics into adulthood among domesticated and experimentally selected populations (Hare *et al.*, 2012). With the evidence that, in fact, bonobos are markedly less aggressive than chimpanzees (Kano, 1992; Muller, 2002), these findings begin to make testable a prediction from the ecology of the two species regarding their selection history and the mechanisms by which the differences between the two species arose. Further work in this area is needed to examine the degree to which patterns of human behavioral and cognitive ontogeny can be characterized as shifts in development, potentially owing to convergent selection pressures.

KEY ISSUES FOR FUTURE RESEARCH

Having reviewed recent findings in the area of behavioral heterochrony, we now turn to areas that can be addressed by future research. Given the broad spectrum of studies outlined, we believe that in fact there are a number of literatures and existing debates that can be enriched by greater study of behavioral heterochrony. We list just a few open questions, in the four areas that we have discussed:

Mechanisms of Development

To what degree are our adult behaviors shaped by early life or even prenatal factors? How can mechanisms of gene expression account for differing adult behavioral outcomes between individuals and species?

Are there behaviors that appear to be similar across species and therefore assumed to be shared via inheritance, but in fact develop via differing means, instead suggesting that they are independently derived?

Links Between Behavioral Development and Maturation

To what degree are aspects of behavioral development constrained or facilitated by aspects of somatic and reproductive maturation?

How can we recognize potential mismatches between developmental trajectories, including potentially treating these mismatches if they result in pathologies?

Effects of Selection on Development

How do differences in ecology shape behavioral development in closely related populations/species? Are there behaviors assumed to be novel responses to environmental circumstances that in fact have their roots in the early development of ancestral species?

If aspects of development across numerous traits (morphology, physiology, behavior) are linked, how can selective pressures lead to pleiotropic effects on multiple developmental trajectories with selection on only one target trait?

Development and Human Evolution

What selection pressures existed in human evolutionary history, and how might these have altered our patterns of development and adult phenotypes?

Does the prolonged juvenile period in humans correlate with prolonged behavioral and cognitive development, facilitating greater acquisition of skills in the domains of foraging and social interaction?

On the whole, it is an exciting time for studies of behavioral heterochrony. Novel methodologies, greater access to comparative models, and better cross-talk across disciplines can generate scientific advances that were unavailable to previous generations. Through studies of comparative behavioral development that target ontogenetic differences between individuals, populations, and species, we can grasp heretofore underappreciated insights into how behavior evolves and what it means to be human.

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