What Do Evolutionary Models Teach Us About Sensitive Periods in Psychological Development?

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Abstract: Sensitive periods in development are widespread in nature. Many psychologists and biologists regard sensitive periods as byproducts of developmental processes. Although this view may be correct in some cases, it is unlikely to be the whole story. There is large variation in sensitive periods (a) between species in the same trait (Beecher & Brenowitz, 2005), (b) between individuals of the same species (Frankenhuis, Panchanathan, & Belsky, 2015), and (c) between different traits within a single individual (Zeanah, Gunnar, McCall, Kreppner, & Fox, 2011). In this article, we discuss recent insights provided by formal models of the evolution of sensitive periods. These models help to identify the conditions in which sensitive periods are likely to evolve, and make predictions about the factors that affect their development. We conclude by discussing future directions for empirical research.

Keywords: evolution, natural selection, adaptation, development, sensitive periods, ontogeny, learning, cognition

In 1862, Charles Darwin predicted the existence of a moth species decades before its discovery (Kritsky, 2001). His prediction was based on his observations of an orchid species endemic to Madagascar, which had a nectary more than 10 inches long, with nectar only near the bottom. This moth was discovered in 1903, over 20 years after Darwin's death. It is now called *Xanthopan morganii praedicta* (the "predicted" moth). This story is compelling because it illustrates that a powerful theoretical framework can not only help explain observations about the natural world, but can lead to predictions about phenomena not yet observed. Moreover, it demonstrates the power of form-function thinking in biology – the notion that organisms are structured in ways that enable them to function well in specific environments.

The purpose of this article is to explore form-function thinking in psychological science. Specifically, we focus on sensitive periods in development, defined as periods or developmental stages in which experience shapes a given phenotype to a larger extent than it does in other periods or stages (Fawcett & Frankenhuis, 2015). Sensitive periods are widespread in nature (West-Eberhard, 2003) and are of interest for both scientific and applied reasons (e.g., timing of interventions). In human beings, sensitive periods are believed to exist for a variety of physical traits, such as metabolic physiology (Wells, 2014) and skeletal morphology (Lucas, 1998), as well as in psychological traits, such as visual and auditory perception (Takesian & Hensch, 2013), food preferences (Cashdan, 1994), attachment styles (Fraley & Heffernan, 2013), stress responses (Lupien, McEwen, Gunnar, & Heim, 2009), reproductive strategies (Del Giudice, 2014), and aspects of cultural learning (Cheung, Chudek, & Heine, 2011).

In a seminal paper, Tinbergen (1963) argued that a complete explanation of any given phenotype requires four different levels of explanation: causation, ontogeny, phylogeny, and function. Most studies of sensitive periods adopt a *proximate* perspective, focusing on causation (e.g., neural-physiological mechanisms) and ontogeny (e.g., the development of epigenetic markings). Fewer adopt an *ultimate* perspective, focusing on phylogeny (e.g., ancestral versions of traits) and function (e.g., the adaptive value of traits). Despite theoretical progress explaining the evolution of sensitive periods, until recently, there were few formal models examining the evolutionary selection pressures that produce sensitive periods. In this article, we discuss recent insights provided by the current crop of formal models of the evolution of sensitive periods.

Adaptation in Biology

In biology, the notion of adaptation refers to the fit between organisms and their environments (Barrett, 2015; Frankenhuis, Panchanathan, & Barrett, 2013). Individuals who reproduce more than their conspecifics in a given environment are more fit, if such differences result from variation in their traits, rather than chance events (e.g., a natural disaster killing individuals randomly). However, even within biology, "adaptation" has different meanings. It can refer to a trait that is the result of natural selection; to natural selection itself – a process that "adapts" populations to their ecologies across generations; or to development – a process that "adapts" organisms to their ecologies within generations. All of these meanings ultimately refer to reproductive success (fitness). We use "natural selection" to refer to the differential reproductive success of inherited variations (Buss, 2015). This definition includes sexual selection, competition for mates, as a special case.

Psychologists, in contrast, often use the term adaptation to refer to traits that increase health, wellbeing, and other desirable outcomes (Belsky, 2008; Ellis et al., 2012; Frankenhuis & Del Giudice, 2012). For example, psychologists may consider a person who is friendly and patient "well adapted," and a person who is mean and impulsive "maladapted." This notion of adaptation is conceptually orthogonal to the one in biology. For example, violent offenders may engage in more socially undesirable behaviors than nondelinquent peers, yet have more sexual partners (Palmer & Tilley, 1995; Yao, Långström, Temrin, & Walum, 2014) and even more children (Yao et al., 2014). In nonhuman animals, male elephant seals fight over beaches, which house hundreds of females. These fights may cause harm and even death. Nonetheless, fighting is an adaptive strategy, because males that succeed at procuring a beach (so-called "beach masters") attain very high reproductive success (Le Boeuf, 1974).

The adaptive (fitness) value of a strategy often depends on its ecological context (Geary, 2015). For example, in harsh and unpredictable environments people often discount the future more and act more impulsively (Frankenhuis & de Weerth, 2013; Frankenhuis, Panchanathan, & Nettle, 2016; Mittal, Griskevicius, Simpson, Sung, & Young, 2015). Such strategies could pay off in those environments because threats can appear without warning and opportunities to accrue resources can be fleeting. In contrast, in supportive environments, where there are few threats, social status depends on prestige (rather than dominance), and individuals look forward to stable prospects. In those conditions, steep future discounting and impulsivity may be maladaptive. The adaptive value of strategy may also depend on an individual's physical or psychological traits (Frankenhuis et al., 2013). For example, male elephant seals, who are physically small and whose chances to become "beach masters" are low, may adopt a so-called "sneaky fucker" strategy, stealing a mating from the dominant male while he is fighting with other ambitious males (Le Boeuf, 1974).

In summary, the term "adaptive" is often used in different ways in biology and psychology. It is important to appreciate the distinction because what psychologists might consider a "maladaptive" trait (e.g., aggression) has the potential to be adaptive in the context of natural selection. Similarly, traits that psychologists consider "adaptive" (e.g., unconditional altruism) may not be adaptive under certain selection pressures (e.g., in populations where defectors exploit unconditional cooperators). The adaptive value of a trait thus depends on ecological conditions (e.g., the social structure of the population) and an individual's state (e.g., physical size), both of which may change over time. In what follows, we use the term adaptation exclusively in the biological sense.

Evolution of Developmental Plasticity

A common belief in psychology is that evolution and development are in a zero-sum relationship: the more a trait develops (changes over time) depending on experience, the less it is a result of evolution, and vice versa. If this belief were true, it would imply that the more plastic a trait is – that is, the easier it is to change on the basis of experience and intervention – the less "useful" it is to seek functional explanations for it. We believe, however, that evolution and development are not opposing processes, but rather *nested processes*: development constructs phenotypes, which vary in their fitness, resulting in certain developmental mechanisms becoming more prevalent in future generations (Frankenhuis et al., 2013).

The implication of this perspective is that natural selection does not lead exclusively to the evolution of fixed or stable traits. Rather, it often results in *developmental plasticity* – the ability to adjust development on the basis of experience (Barrett, 2015; Bowlby, 1969; Frankenhuis et al., 2013; Geary, 2015; West-Eberhard, 2003). In some cases, the ecology creates selection pressures for mechanisms that produce a wide variety of phenotypes (plastic), and in others for a narrower range (fixed) (Frankenhuis et al., 2015; Nussey, Postma, Gienapp, & Visser, 2005; Stearns & Koella, 1986). Plastic traits are just as much products of evolutionary processes as are fixed traits, which develop similarly despite different experiences.

As an example, consider the developmental plasticity of soapberry bugs (*Jadera haematoloma*) (Carroll & Corneli,

1995). In Oklahoma, where climatic fluctuations cause unpredictable changes in the local sex ratio, males are plastic, adjusting their level of mate guarding to the local sex ratio. In contrast, the sex ratios are more stable in Florida where the males engage in a fixed amount of mate guarding. Moreover, if the Florida males are artificially introduced to variable sex ratios in the laboratory, they do not adjust their mate guarding behavior accordingly (Carroll & Corneli, 1995). It is unknown what specific experiences the Oklahoma males use to set their level of mate guarding (e.g., the number of males and females they have encountered), and whether the impact of these experiences is uniform or variable across the life span (e.g., sensitive periods). Nonetheless, this example helps to illustrate that developmental systems themselves are subject to natural selection and that plasticity in behavior can be more adaptive in some conditions than in others.

Evolution of Sensitive Periods in Development

Plasticity has the potential to be especially adaptive in environments that are variable across time and space (Dall, Giraldeau, Ollson, McNamara, & Stephens, 2005; DeWitt & Scheiner, 2004; Schlichting & Pigliucci, 1998). For example, if environmental states are weakly autocorrelated across time such that the availability of resources today indicates little about the availability of resources in the future, then organisms may benefit from maintaining some degree of plasticity across time. This plasticity can enable organisms to calibrate their behavior in a manner that is contingent on current cues in the local environment irrespective of the environmental cues received previously. In contrast, where there is a high degree of autocorrelation in environmental states, cues that occur early in development have the potential to be valid cues to ecological conditions later (Nettle, Frankenhuis, & Rickard, 2013; Rickard, Frankenhuis, & Nettle, 2014). In such circumstances, selection may favor organisms that sample environmental cues early in ontogeny and use that early information to lock-in to a specific developmental course.

Importantly, the potential costs and benefits of differentially weighting information from the past versus the present – create the opportunity for the emergence of sensitive periods in development (Fawcett & Frankenhuis, 2015; Geary, 2005; Geary & Huffman, 2002). In contexts in which the environmental conditions are variable, the organism may benefit by remaining plastic across ontogeny, using local cues about environmental conditions to calibrate its behavior – especially if the costs of maintaining plastic systems are low. In contrast, if the costs for remaining

Table 1. The strength of selection pressures favoring plasticity as a function of the stability of environmental conditions across ontogeny and the net benefit of plasticity – i.e., the benefit of phenotype-environment matching minus the maintenance costs of plasticity. If the net benefit is zero or less, natural selection does not favor plasticity.

Ontogenetic environment	Net benefit of plasticity	
	High	Low
Stable	Moderate selection	Weak selection
Variable	Strong selection	Moderate selection

plastic are high (e.g., resources used for this purpose are diverted from other necessary developmental systems), then there could be a net cost to plastic phenotypes. Of course, if the environmental conditions are stable across time, there may be little value in remaining highly plastic. Conclusions reached early in ontogeny will continue to be accurate grounds for governing future behavior.

By considering these issues in tandem, it is possible to articulate a basic set of postulates about when developmental systems will remain highly plastic and when they will not (see Table 1). If the environment is highly stable, for example, then there is little value added for the organism to continuously invest resources and energy in updating its assumptions about the world. For example, chronic exposure to violence (e.g., fighting with peers) in childhood indicates that the child may be developing in a dangerous world. And, if environmental states are autocorrelated across time, those early experiences can be informative about future environmental conditions as well (Nettle et al., 2013; Rickard et al., 2014). But if the environment is variable, then information acquired early in life is not necessarily useful later in ontogeny. In that case, natural selection may favor "adaptive forgetting" of outdated information (Dunlap, McLinn, MacCormick, Scott, & Kerr, 2009) and continual revising of an individual's information state, especially if the costs of maintaining plastic systems are low.

A Bayesian Perspective on Development

It is possible to examine some of these ideas formally by using a Bayesian model for how organisms update their beliefs about the world (see Fawcett & Frankenhuis, 2015). The model is designed to approximate the ways in which individuals update their beliefs; it is not designed to be a precise model for these processes (for work that does suppose this, see Gopnik & Wellman, 2012). Moreover, the model does not assume that individuals apply Bayesian rules consciously or that they are

consciously aware of the nature of the beliefs that they hold or are updating. The model does assume, however, that these beliefs have behavioral consequences.

Let us assume for the sake of discussion that the world can be dangerous or safe (i.e., two states), and that the organism can have varying degrees of belief in whether the world is a safe or dangerous place. If the organism believes the world to be safe, it may invest in specific phenotypic strategies (e.g., investing in embodied capital through an extended period of learning), whereas if it believes the world to be dangerous, it may invest in alternative phenotypic strategies (e.g., early maturation and reproduction).

Organisms may be born into the world with a 50-50 assumption about whether the world is a safe or dangerous place. But, as they develop, they have the opportunity to sample environmental cues (e.g., the behavior of their primary caregivers) and use that information to update their beliefs accordingly (see Figure 1A). If this Bayesian process is simulated in an iterative fashion, it reveals some important insights regarding sensitive periods. First, under some simplifying assumptions (e.g., cues are distributed evenly across time), the model predicts that plasticity typically declines with age (see Figure 1B). Thus, cognitive systems may exhibit sensitive periods: they are most plastic when they are maximally uncertain, which, in some cases, will be early in life. Early life uncertainty might explain the phenomenon of perceptual narrowing – in which individuals become better at discriminating common stimuli (e.g., phonemes in the native language, human faces), while becoming worse or even losing the ability to discriminate between uncommon stimuli – in infancy, in human beings (Kuhl et al., 2006; Scott, Pascalis, & Nelson, 2007), and in nonhuman primates (Cheney & Seyfarth, 1990; Sugita, 2008).

Second, the model predicts that the amount of updating that takes place varies as a function of the individual's uncertainty. When the individual is maximally uncertain about the state of the world (e.g., whether the world is safe or dangerous), cues are most likely to be informative and to maximally influence the phenotype. But not all uncertainty occurs early in life. As people transition from one context to the next (e.g., residential changes), they may require learning new information (e.g., about one's own social status in a new peer group). And although that information may be rooted in what they already know (e.g., "Peers often like me"), such transitions will typically increase an individual's uncertainty, and hence the value of information. Thus, understanding when individuals are uncertain, and what cues they use to reduce their uncertainty, is crucial for understanding the evolution of sensitive periods.

Third, individuals may reduce their uncertainty at different rates (Frankenhuis & Panchanathan, 2011a, 2011b; Panchanathan & Frankenhuis, in press). For example, some
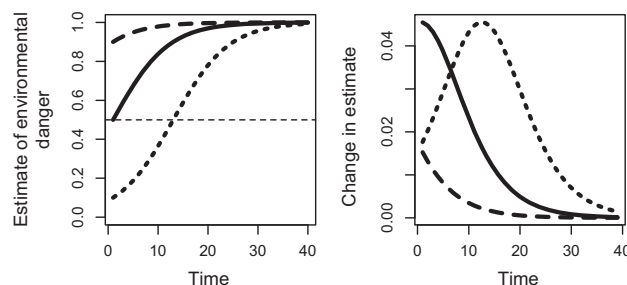

Figure 1. A Bayesian perspective on sensitive periods. (A) Individual's estimate of the probability that the environment is dangerous, conditional on receiving a series of cues indicating environmental danger. An estimate of 1.0 indicates the environmental state is certainly dangerous, and an estimate of 0.0 it is certainly safe. Three lines correspond to different starting values of this estimate (solid = .50, dashed = .90, dotted = .10). (B) The amount of change in estimates across time, as a function of the starting value. Notice that the amount of change is greatest when the individual is maximally uncertain about the environment (when the estimate of environmental danger is .50) (this figure is based on Fawcett & Frankenhuis', 2015, Figure 2).

may obtain highly consistent cues from their environment (e.g., a stream of danger cues), reducing their uncertainty, and hence their plasticity. Others may obtain more heterogeneous cues (e.g., some danger cues and some safe cues), remaining more uncertain, and hence retain their plasticity. As a result, individual differences in the retention and decline of plasticity – that is, in the duration of sensitive periods – may emerge over the course of development (Frankenhuis & Panchanathan, 2011a, 2011b; Panchanathan & Frankenhuis, in press). Individuals may sample different cue sets if they are in different environments, or even in the same environment, if cues are unreliable. Also, if individuals shape their own environments, those who create a more stable environment for themselves might sample more consistent cue sets, hence lose their plasticity at faster rates.

Factors that May Influence the Evolution of Sensitive Periods

To summarize, natural selection may result in developmental plasticity in variable environments, if experience provides information about the environmental state, and if the benefits of phenotype-environment matching outweigh the costs of being plastic (DeWitt & Scheiner, 2004; Schlichting & Pigliucci, 1998). In the sections that follow we use this framework to discuss more explicitly four ways in which sensitive periods may have evolved. The structure and content of the next section draws on a recent paper by Fawcett and Frankenhuis (2015), but is tailored for a psychological audience.

Variation in the Availability of Cues

One reason for the evolution of sensitive periods in development could be variation in the availability of cues (Fawcett & Frankenhuis, 2015). A given cue might only be available during particular times of life (e.g., in the womb), and not during others (e.g., after birth), or more available at some times than others. Organisms may evolve to be sensitive to a cue at times when they are likely to encounter this cue. In cases where a cue is only available in a specific time period, organisms may evolve sensitivity to the cue only during that time.

Variation in cue availability across ontogeny may be the same for all individuals, or different for different individuals. If the former (e.g., all nestling fledge on the same day and start encountering predators on that day), natural selection may result in a fixed timing of sensitivity (to predator cues). But if the latter (e.g., nestling fledge at different times, depending on their body weight), natural selection may result in a flexible timing of sensitivity, such that individual nestlings may become sensitive to the cue at the time of fledging, rather than after a fixed number of days.

Individuals may not only encounter new cues when they begin interacting with a new set of partners (e.g., after fledging), but also if the nature of the interactions with the same partners changes. For example, in childhood, interactions with opposite-sex peers offer cues mainly about friendship, but in adolescence these interactions begin to provide cues to reproductive opportunities as well (Del Giudice, 2014). Accordingly, in this life stage, people may develop sensitivity to social feedback about their mate value (Fawcett & Bleay, 2009; Kavanagh, Robins, & Ellis, 2010). In some species, the nature of social interactions and interaction partners might change simultaneously, when individuals make the transition from depending on their parents to interacting with peers – for example, in species that reach sexual maturity shortly after leaving the nest (e.g., rats).

However, even when interactions with others stay the same, because children's social attention changes as they mature, there might be changes in the availability of cues (Geary & Bjorklund, 2000). For instance, as the abilities of infants to detect and understand the emotional expressions of their parents improve, infants might be able to perceive threat cues that were present before but not available to them.

Variation in the Information Value of Cues

A second reason for the evolution of sensitive periods could be variation in the information value of cues (Fawcett & Frankenhuis, 2015). Even if the frequency of a given cue (e.g., violence) is constant over ontogeny, there may be variation in the extent to which this cue reduces a perceiver's uncertainty. For example, a younger and an older person may live in the same environment and use the same cue to estimate the level of environmental danger. However, as the older person has lived in this environment for longer, she/he may be less uncertain about the current environmental state. As a result, if given the same cue, the older person may update less than the younger one. Thus, the extent of updating will depend on one's prior information state, and this state may vary over the course of ontogeny. If we assume that the extent of updating is correlated with the extent of phenotypic change, the same cue may have variable impacts at different times of life. All else being equal, this idea predicts that if organisms are consecutively exposed to the same cue, the extent to which their phenotype changes (due to this cue) will decline over time (Fawcett & Frankenhuis, 2015; Stamps & Krishnan, 2014a, 2014b).

Irrespective of (endogenous) changes in the information state of the perceiver, the (exogenous) information value of cues could also change, that is, the extent to which the cue discriminates between different environmental states. For example, if the amount of information conveyed in social feedback about one's mate value at maturity increases with age, we may expect human beings to weight later experiences more heavily than earlier ones. This prediction can be tested by documenting the mate values of individuals at different times of their lives, plotting correlation coefficients between mate values at each of the earlier ages and at maturity, and studying whether this pattern predicts individuals' sensitivity to social feedback about their mate value.

It might be useful to examine some case examples of sensitive periods in psychological development. Caregiving experiences that take place early in life appear in some cases to be uniquely influential in shaping later outcomes (e.g., academic achievement, social competence) – outcomes that have the potential to be adaptive not only in the traditional psychological sense, but in the biological sense as well. For example, Fraley, Roisman, and Haltigan (2013) examined the predictive significance of variation in early caregiving experiences in the first three years of life and found that early maternal sensitivity was correlated with academic and social functioning in a relatively enduring way across ontogeny. But, importantly, they found that these correlations were relatively constant across time such that the association between maternal sensitivity in the first three years of life and social competence at age five was comparable to the same association over a 10-year period. These patterns held when examining a number of potential covariates and alternative explanations (e.g., maternal education, child gender, more recent or proximal measures of the caregiving environment). Taken together, these

findings suggest that caregiving experiences that take place early in life might be especially influential in shaping psychological phenotypes; human infants may have a sensitive period that makes them especially likely to weigh early information more strongly than information acquired later.[1]

In a related set of studies, Fraley and Heffernan (2013) examined the association between parental divorce and the security of parental relationships in adulthood. As might be expected, adults were more insecure in their relationships with their parents if their parents had divorced than if their parents had not divorced. However, adults were especially likely to have an insecure relationship with their parents if that divorce took place when individuals were under the age of four. One of the important features of this particular design is that Fraley and Heffernan were able to tease apart the relative contributions of early and later divorces by studying a large sample of individuals who varied in both the age at which their parents divorced and the amount of time that had passed since that event. They found that people were more likely to have an insecure relationship with their parents if the divorce happened recently. That is, divorces that took place in the distant past did not leave as strong a trace on attachment as divorces that happened more recently. But, after accounting for this effect, the timing of the divorce mattered. Namely, divorces that took place in early childhood were more strongly related to insecure attachment than divorces that took place later in childhood.

Taken together, these studies suggest an interesting and complex set of conclusions: Although recent experiences can be used to guide the development of psychological phenotypes, experiences that take place in early ontogeny have the potential to have enduring implications for psychological development. But how can these findings be explained? That is, why might people be shaped more by experiences that take place early in life relative to the same kinds of experiences when those take place later? In light of the considerations outlined previously, we would hypothesize that early experiences in important social relationships, such as those with primary caregivers, are used to configure the child's assumptions about the nature of the relationship and whether that person is likely to be available, responsive, and supportive in the future (see Bowlby, 1969). Although such updating has the potential to take place at any point in ontogeny, it might be especially pronounced when it takes place in early development because the child has yet to generate a rich knowledge base against which to check ongoing interactions. Stated differently, if a parent appears cool and distant, but the child recognizes that behavior as being atypical of the parent, the child may be more likely to discount it; the behavior is potentially an invalid cue to the parent's future behavior. But if the child does not yet have a strong belief regarding the availability and responsiveness of the parent, that information will be weighted more heavily than it normally would in the child's attempts to update his or her understanding of the world. In short, early experiences might contain more information value than the same kinds of experiences that take place later in development.

Variation in the Fitness Benefits of Information

A third reason for the evolution of sensitive periods could be variation in the fitness benefits of information (Fawcett & Frankenhuis, 2015). Even if the frequency and the information value of cues are constant, the fitness benefits of the same amount of information (i.e., the same reduction in uncertainty) may vary across the life span. For example, natural selection acts more strongly on traits that develop before maturity than on traits that develop after maturity, because fewer individuals survive to older ages (Charlesworth, 2000).

If the fitness value of the same amount of information varies with age, the fitness benefits of being sensitive to cues will vary also. For example, information about one's own mate value may enhance fitness more during those life stages in which individuals choose their mates (e.g., adolescence and adulthood), and less after closing of the reproductive window (e.g., after the onset of menopause). Hence, natural selection may result in psychological mechanisms that are more sensitive to cues to mate value in adolescence and adulthood compared with menopause. We may expect sensitivity to feedback to be greatest in those life stages in which the information that such feedback provides has the largest impact on fitness.

Why not always be maximally sensitive? Even though the fitness value of information is typically positive (McNamara & Dall, 2010), there may be fitness costs to developing and maintaining the neural-physiological systems that support the ability to perceive cues and use them to guide behavior (Auld, Agrawal, & Relyea, 2010; DeWitt, Sih, & Wilson, 1998; Frankenhuis et al., 2015; Relyea, 2002). Natural selection will only result in sensitivity to cues if the benefits of information outweigh the costs.

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[1] It is worth noting that these particular studies cannot rule out the possibility that genetic sources of variance – such as shared child-parent genes and genotype-environment correlations (Scarr & McCartney, 1983) – account for the observed patterns of association. However, analyses of twins drawn from the Early Childhood Longitudinal Study birth cohort indicate this kind of assessment of early maternal sensitivity reflects little, if any, genetic influence (Roisman & Fraley, 2006, 2008).

Variation in the Fitness Costs of Plasticity

A fourth reason for the evolution of sensitive periods could be variation in the fitness costs of plasticity across ontogeny (Fawcett & Frankenhuis, 2015). As noted, developing and maintaining the systems that support plasticity may be costly (Auld et al., 2010; DeWitt et al., 1998; Frankenhuis et al., 2015; Relyea, 2002). Other costs may include phenotype-environment mismatch resulting from prediction error due to imperfect cues (Donaldson-Matasci, Bergstrom, & Lachmann, 2013; Nettle et al., 2013; Rickard et al., 2014), costs to information search (e.g., time spent sampling cues), and lower phenotypic integration (e.g., phenotypic add-ons may be less effective than the same element integrated early in development). If such costs change (decrease or increase) across ontogeny, while the benefits of plasticity remain constant, there may be selection pressures for developmental variation in sensitivity to cues.

Future Directions

One of the purposes of this article was to summarize recent theory on the evolution of plasticity and sensitive periods in development. Most of this work is grounded in contemporary evolutionary biology, but we believe that there is a growing recognition that these perspectives may be valuable for understanding psychological phenotypes in human beings. With that as context, we close by outlining a few future directions for work in this area.

First, one of the central ideas in understanding developmental plasticity concerns the structure of the environment. It is of crucial importance to understand whether, in fact, certain developmentally informative cues (e.g., availability of resources, signs of danger) are typically stable across human development (Nettle et al., 2013; Rickard et al., 2014). For the most part, developmental psychologists have emphasized the study of continuity of individual differences – whether, for example, individuals who are secure as infants are also secure later in childhood (e.g., Fraley, Roisman, Booth-LaForce, Owen, & Holland, 2013). In contrast, little research has examined the stability of environmental cues that are fitness relevant. There is evidence that maternal sensitivity – an indicator of environmental stability and safety – is fairly stable from 1 month of age through age 16 (Fraley, Roisman, & Haltigan, 2013), suggesting that early experiences might, in fact, be valid indicators of future environments. Having said that, the field needs more systematic research on the stability of environmental cues. In this regard, the field could draw on methods and models used in vision science in order to quantify the statistics of natural scenes, which shape the design of our perceptual systems through evolution and experience (Geisler, 2008; Geisler & Diehl, 2002, 2003).

Second, we do not have a good understanding of the costs and benefits of maintaining plasticity across certain phases of development. Although many models assume a cost to maintaining plasticity (DeWitt et al., 1998), such costs have been difficult to demonstrate in nonhuman organisms (Auld et al., 2010; Relyea, 2002; for exceptions, see Mery & Kawecki, 2003, 2005); and in human beings, to our knowledge, no such attempts exist. One intriguing possibility is that plasticity is not so much constrained by costs – which "reduce the fitness of an individual, even when that trait matches the optimal phenotype across environments" (Scheiner & Holt, 2012, p. 751) – but rather by limitations, which "prevent an individual from developing a trait that matches the optimum, even when plasticity per se is cost-free" (idem). This would be consistent with our earlier suggestion that phenotypic add-ons may be less effective than the same element integrated early in development. Limitations on plasticity could be examined by testing whether individuals who start developing a trait earlier in life (e.g., an ability to detect threats in the environment) typically attain more adaptive versions of a trait than other individuals who start developing the same trait later in life (Frankenhuis & Panchanathan, 2011a, 2011b; Panchanathan & Frankenhuis, in press).

Finally, we need methods that enable us to understand when sensitive periods emerge in the life course and whether the timing of these periods varies as a function of the phenotype in question. Fraley and Roberts (2005) developed a mathematical model of the rank-order stability of psychological constructs that has the potential to be informative in this respect. Their model assumes that person-environment transactions take place such that people are not only shaped by their environments, but also, those environments are shaped by the people who inhabit them. This theme, which is common in developmental psychology (e.g., Sameroff & MacKenzie, 2003; Scarr & McCartney, 1983), is also discussed in evolutionary writings in the context of *niche construction* (Flynn, Laland, Kendal, & Kendal, 2013). The model also assumes the presence of developmentally stable factors (e.g., social-cognitive representations, genes, cultural norms) that can weakly or strongly influence the phenotype. The Fraley-Roberts model operationalizes developmental plasticity with respect to test-retest correlations. The assumption is that, to the extent to which people's phenotypes are being modified, the rank-order stability of individual differences should be lower than it would otherwise be.

One of the emergent predictions of the Fraley-Roberts model is that the test-retest stability of individual

differences increases from infancy to adulthood. Specifically, there is less continuity in psychological attributes early in life than there is later on, suggesting that early childhood functions as a period of plasticity in the development. Indeed, these predictions have been born out in meta-analytic data on personality traits (Roberts & DelVecchio, 2000) and attachment styles (Fraley & Brumbaugh, 2004). The reason sensitive periods emerge in this model is that, as person-environment interactions take place, people and their environments come to covary more strongly than they did initially. Thus, as individuals develop, they diverge less and less from the environments in which they find themselves. In addition, the effects of whatever stable components exist in the system tend to accumulate both via direct and indirect influences on the emerging phenotype. The natural result of such a dynamic system is that individuals are more plastic earlier in life than they are later in life. But, if the environment were to change in a dramatic way, the system would reorganize itself and, in the process of doing so, temporarily exhibit heightened plasticity (Fraley & Brumbaugh, 2004).

We opened this article with a reference to the power of form-function thinking in biology and how it can be used to generate predictions about species that, at the time of Darwin's original writings on evolution, had yet to be observed. Although current evolutionary models of sensitive periods in development are not currently sophisticated enough to predict something as exceptional as *Xanthopan morganii praedicta*, we believe they may be useful in guiding the search for developmental phenomena that have yet to be documented and explained. Using this perspective, for example, we should expect to find that developmental plasticity is greatest when individuals are maximally uncertain about the state of their environments. This uncertainty is most likely to be at a maximum in early childhood, but is also likely to peak during significant developmental transitions, such as the transition to adolescence (Fawcett & Frankenhuis, 2015). In addition, an evolutionary perspective suggests that continued plasticity should be most likely when environments are weakly autocorrelated across time. We have reviewed some data that align with these expectations, but the true test of the utility of this framework will come in what it reveals about developmental phenomenon not yet uncovered.

Acknowledgments

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