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Individual Differences in Developmental Plasticity May Result From Stochastic Sampling

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Abstract

The ability to adjust developmental trajectories based on experience is widespread in nature, including in humans. This plasticity is often adaptive, tailoring individuals to their local environment. However, it is less clear why some individuals are more sensitive to environmental influences than others. Explanations include differences in genes and differences in prior experiences. In this article, we present a novel hypothesis in the latter category. In some developmental domains, individuals must learn about the state of their environment before adapting accordingly. Because sampling environmental cues is a stochastic process, some individuals may receive a homogeneous sample, resulting in a confident estimate about the state of the world—these individuals specialize early. Other individuals may receive a heterogeneous, uninformative set of cues—those individuals will keep sampling. As a consequence, individual variation in plasticity may result from different degrees of confidence about the state of the environment. After developing the hypothesis, we conclude by discussing three empirical predictions.

Keywords

phenotypic plasticity, differential susceptibility, stochastic sampling, decision theory, fetal programming

Phenotypic Plasticity

Phenotypic plasticity—the ability to adjust developmental trajectories based on experience (West-Eberhard, 2003)—is present in nearly all life forms (Schlichting & Pigliucci, 1998), including humans (Belsky, 2010; Buss, 2009; Del Giudice, 2009). Phenotypic plasticity evolves because it allows organisms to match their phenotypes to spatially and temporally varying environments (Dall, Giraldeau, Ollson, McNamara, & Stephens, 2005; DeWitt, & Scheiner, 2004; Figueredo, Hammond, & McKiernan, 2006; Levins, 1963, 1968; Stephens, 1991; West-Eberhard, 2003; D. S. Wilson, 1994). Recent studies of human development show that phenotypic plasticity itself may vary across individuals; some individuals are more affected than others by the same experiences (Belsky, 1997; Boyce & Ellis, 2005). This finding has major implications—for instance, it suggests that individuals may benefit or suffer differentially from such experiences as nurturance or abuse (Boyce et al., 1995; see also Belsky et al., 2009; Belsky & Pluess, 2009a, 2009b; Pluess & Belsky, 2010, 2011), including clinical interventions (Rudolph, Troop-Gordon, & Granger, 2011). Though it is not well understood how interactions between endogenous and exogenous factors affect plasticity, progress has been made and a strong interest in the topic has emerged (Belsky et al., 2009; Ellis & Boyce, 2008).

Differential plasticity resulting from differences in genes

One line of research investigates the contribution of genotype-by-environment (G×E) interactions (Lewontin, 1974; Via, 1987; Via & Lande, 1985). Studies with humans (see the Fall 2007 special issue of *Development and Psychopathology*) and other animals, including rhesus macaques (Barr et al., 2004; Suomi, 2006), show that genotypic factors codetermine individuals' responsiveness to particular environmental influences. For instance, maternal insensitivity correlates with oppositional and aggressive behaviors in preschoolers carrying the DRD4 7-repeat allele, but not in children without this combined risk

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factor (Bakermans-Kranenburg & van IJzendoorn, 2006, 2007). Maltreatment in childhood strongly predicts antisocial behavior in adolescent males with the low-MAOA activity genotype, but it is not as strong a predictor in adolescent males with the high-MAOA activity genotype (Caspi et al., 2002; see also Kim-Cohen et al., 2006). It is possible that individual characteristics—genotypic, endophenotypic, and behavioral—enhance an individual's sensitivity to experience for better and for worse (Belsky, Bakermans-Kranenburg, & van IJzendoorn, 2007; Pluess & Belsky, 2010, 2011). That is, the same individuals who are less resilient against harmful or unsupportive environments may also benefit more from nurturance and other facilitative circumstances (Belsky et al., 2009). As a statistical pattern, G×E can also arise when experiences affect the gene expression of carriers of one version of an allele but do not affect another version (Belsky & Pluess, 2009a, 2009b).

Why does genetic variation in plasticity exist in the first place? Such variation could be due to natural selection, polygenic effects, pleiotropy, or genetic drift of selectively neutral alleles. If we focus on adaptive explanation, a question arises: If there were an optimal level of plasticity, should natural selection not have favored this level, eliminating genetic variation? One hypothesis states that it may be adaptive for parents to produce offspring with varying levels of plasticity:

> Because the future is and always has been inherently uncertain, ancestral parents, just like parents today, could not have known (consciously or unconsciously) what child-rearing practices would prove most effective in promoting the reproductive fitness of offspring—and thus their own inclusive fitness. As a result, and as a fitness-optimizing strategy involving the hedging of bets, natural selection would have shaped parents to bear children varying in developmental plasticity. (Belsky & Pluess, 2009a, p. 887; see also Belsky, 1997; Belsky et al., 2009; Belsky & Pluess, 2009b)

In a predictable world, parents do best by producing a single type of offspring that is well adapted to the predicted state of the environment. However, when the future is unpredictable, parents may benefit from hedging their bets by producing offspring that vary genetically in their sensitivity to particular experiences, including parenting (Belsky & Beaver, 2011; for accessible papers discussing various forms of bet hedging, see Bull, 1987; Childs, Metcalf, & Rees, 2010; Cooper & Kaplan, 1982; Donaldson-Matasci, Lachmann, & Bergstrom, 2008; Hopper, 1999; Meyers & Bull, 2002; Philippi & Seger, 1989).

A second hypothesis is that frequency-dependent selection maintains genetic variation in plasticity (Ellis, Boyce, Belsky, Bakermans-Kranenburg, & van IJzendoorn, 2011; Ellis, Jackson, & Boyce, 2006; Korte, Koolhaas, Wingfield, & McEwen, 2005; Wolf, van Doorn, & Weissing, 2008, 2011). Frequency-dependent selection refers to conditions in which the fitness of a phenotype is dependent on its frequency relative to other phenotypes in a population. *Negative frequency-dependence* occurs when the fitness of a phenotype increases as it becomes more rare (e.g., if predators prefer the more common type of a prey, then the rare type of prey will increase, until it becomes the more common type). Individual differences in plasticity may persist due to negative frequency-dependent selection when plastic phenotypes have higher fitness than resilient phenotypes in a population composed mostly of resilient individuals and vice versa. One recent proposal views resilient individuals as specialists who achieve higher fitness than plastic individuals when they are in the niche that fits their phenotype—for instance, a resilient extrovert may be more successful in social settings where this phenotype is rewarded than would a plastic individual who adopts the extrovert phenotype. However, plastic individuals may be more successful than resilient individuals at changing niches, which becomes beneficial when their preferred niche is overcrowded as it reduces competition costs. Combined, these two processes might enable resilient and plastic individuals to coexist in a stable equilibrium (Ellis et al., 2006; for formal models, see D. S. Wilson & Yoshimura, 1994; Wolf et al., 2008, 2011).

Differential plasticity resulting from differences in experiences

There may be mechanisms other than genetic variation that give rise to individual differences in plasticity. In particular, levels of plasticity may be affected by developmental experiences at earlier life stages (Boyce & Ellis, 2005; see also Del Giudice, Ellis, & Shirtcliff, 2011; Ellis et al., 2011; Pluess & Belsky, 2011). For example, when growing up under extreme environmental conditions, individuals may benefit from developing heightened reactivity in neurobiological stress systems (or heightened biological sensitivity to context). Such heightened reactivity may augment vigilance to threats and dangers in stressful environments and enhance the benefits derived from care and support in protective environments (Boyce & Ellis, 2005; Del Giudice et al., 2011; Ellis et al., 2006). Intermediately stressful environments may downregulate reactivity, thereby avoiding the physiological costs associated with persistently elevated levels of reactivity, when there are no large benefits to doing so (Ellis & Boyce, 2008). This biological sensitivity to context hypothesis has received support from data showing a curvilinear, or *U*-shaped, relation between early adversity and stress-reactive profiles (Ellis & Boyce, 2008; Ellis et al., 2011; Ellis, Essex, & Boyce, 2005).

In this article, we offer a novel hypothesis explaining individual differences in plasticity: Individual variation in plasticity may result from different degrees of confidence about the state of the environment. We first present the logic of the hypothesis, then an example by analogy, and conclude with three empirical predictions.

Phenotypic Specialization

Organisms often assess fitness-relevant dimensions of the physical and social environment and adjust their phenotypic development accordingly (Ellis & Boyce, 2008; Houston & McNamara, 1992). This assessment stage can be conceptualized

as a sampling process in which individuals receive cues to the current state of the environment (e.g., observations of violence indicate a dangerous world). Individuals develop sensitivities to these cues because these cues are informative about the state of the environment over evolutionary time. During their lifetime, individuals use these cues to make developmental "decisions," such as how to specialize their phenotype at different stages in the life span (Belsky, Steinberg, & Draper, 1991; DeWitt & Scheiner, 2004; Donaldson-Matasci, Bergstrom, & Lachmann, 2010; Mangel & Clark, 1988; McNamara, Green, & Olssen, 2006; Whitman & Agrawal, 2009). For instance, organisms may develop higher levels of vigilance in environments perceived to be dangerous. The developmental mechanisms underlying such decisions are the products of natural selection, tending to yield adaptive phenotypic outcomes through interactions with recurring features of ontogenetic environments (Barrett, 2007; Panchanathan, Frankenhuis, & Barrett, 2010). Phenotypically plastic systems may have constitutive costs, such as the energy required for developing and maintaining learning machinery (Auld, Agrawal, & Relyea, 2010; DeWitt, Sih, & Wilson, 1998; Relyea, 2002). Natural selection favors plasticity only when the benefits of adapting to variable environments outweigh the constitutive costs of plasticity.

Before proceeding, a note on terminology. We use the term *decisions* metaphorically: development results from mechanistic processes, not (usually) from conscious choices. Similarly, when we describe organisms as "drawing inferences" or having a "degree of confidence," we do not imply subjective experience (see, for example, Kepecs, Uchida, Zariwala, & Mainen, 2008). Instead, we mean that organisms adjust their development, based on environmental cues, in a way consistent with them drawing a particular inference (e.g., the world is dangerous) or assigning particular probabilities to particular states of the world (e.g., observing a violent episode increases confidence in the environmental state being dangerous).[1] We use the term *confidence* in a Bayesian sense to refer to an individual's degree of belief in his or her parametric estimate. This notion of confidence is distinct from the concept of *uncertainty*, which is often used (e.g., in economics) to denote randomness that cannot be expressed in terms of specific mathematical probabilities (Knight, 1921). This definition of uncertainty does not apply, in our case, because in our model organisms have specific probabilistic estimates.

Environmental stability within the lifespan

For our hypothesis to apply, individuals must generally spend their mature years in environments similar to the ones they grew up in. This assumption is common when modeling the evolution of phenotypic plasticity, unless the migration of individuals, genes, or groups is explicitly of theoretical interest (e.g., bird migration). It implies that, on average, individuals do not migrate to a vastly different environment (measured along some fitness-relevant dimension) and that the environmental state does not often change (e.g., from safe to dangerous). If the early environment does not correlate with the later one, there is little point to assessing the state of the environment early in life and adapting accordingly. If the correlation were weak (or nonexistent), natural selection would unlikely favor the kind of plasticity we are discussing—instead, it might favor either a (nonplastic), generalist type or a chameleon-like type, which adapts to a constantly shifting environment. Although we did not tailor our hypothesis to humans, evidence suggests that human ancestral environments did remain constant along certain ecological dimensions within a single generation (Potts, 1998; Richerson, Boyd, & Bettinger, 2001; see also Gluckman & Hanson, 2004; Kuzawa, 2005). Further, even in contemporary environments, children often do not migrate to a vastly different environment within their lifetime.

Benefits of specializing early

If, over evolutionary time, the environment remains stable within the lifespan of organisms, then natural selection might favor organisms that sample cues to the environmental state early in life and use this information to start constructing a phenotype that is adaptive later in life. Such anticipatory construction may be beneficial, even necessary, when the time invested in developing a trait correlates with the adaptive "fit" to the environment later in life. Such correlations are plausible for traits that depend on cumulative growth or extensive practice. This idea was already nicely stated by anthropologists in the early 1980s:

> We wish to call attention especially to the role of early, or sensitive-period, learning in development. If prolonged practice and attention is required for the successful function of some activity in adulthood, and if at the same time there is environmental variability changing through time, but changing slowly compared to the scale of an individual lifetime, then the optimum mode of adaptation may be to establish a learning track early in development. (Draper & Harpending, 1982, p. 268)

Proving that organisms benefit from earlier specialization is not easy. A demonstration requires evidence that individuals who begin tailoring their phenotype to local conditions earlier in life achieve higher fitness than those who do so later. Such evidence is difficult to obtain in humans because we cannot modify developmental trajectories (for ethical reasons). However, such evidence does exist in animals (Auld et al., 2010; DeWitt et al., 1998). For instance, water fleas that begin tailoring their phenotype prenatally towards a "predator-rich" environment develop more effective protective helmets than individuals who specialize after they are born (Agrawal, Laforsch, & Tollrian, 1999; for evidence in fish, see Dill, 1983; for evidence in social insects, see Chittka & Muller, 2009).

In many hunter–gatherer societies, men only begin to produce more calories than they consume in their early 20s, because "high levels of knowledge, skill, coordination, and strength are required to exploit the suite of high-quality, difficult-to-acquire resources that humans consume. The attainment of those abilities requires time and a significant

commitment to development'' (Kaplan, Hill, Lancaster, & Hurtado, 2000, p. 156). By hypothesis, incremental specialization may also characterize other domains of human development. For instance, children growing up in hostile environments may gradually tailor their perceptual abilities to recognizing dangers, perceiving angry (but not other) facial expressions more accurately than other children (Pollak, 2005, 2008; Pollak & Sinha, 2002; Shackman, Shackman, & Pollak, 2007) and developing better abilities for deception (Mealey, 1995). Children growing up in a safe environment may delay reproduction (Ellis, 2004; see also Belsky, Houts, & Fearon, 2010; Belsky et al., 1991; Chisholm, 1993, 1999; Draper & Belsky, 1990; Nettle, 2011; Quinlan, 2007) in order to invest in incremental growth and development (Helle, 2008), acquisition of skills and knowledge, and construction of long-term cooperative networks.

In nonhuman primates, males pursue status primarily through dominance. In humans, males pursue social status through two distinct pathways: by physically dominating other men or by attaining prestige based on high levels of skill or knowledge (Henrich & Gil-White, 2001). For each of these strategies, earlier specialization may provide advantages. For dominance-seeking men, the more time spent fighting, the better the fighter. For prestige-seeking men, the more time spent learning, the more refined knowledge. In choosing whether to pursue a strategy of dominance or prestige, men may benefit from assessing their own aptitudes (e.g., relative physical size), if these aptitudes affect the payoffs associated with following particular developmental trajectories. For instance, physically larger males may be more likely to succeed at dominance-based strategies than smaller males. If so, then men may benefit from spending some fraction of their ontogeny assessing their relative physical size and formidability (e.g., through play and sports) before committing to a life of prestige or dominance seeking.

Costs of specializing early

Despite its benefits, earlier specialization may also have associated costs (Boyce & Ellis, 2005, p. 290). Earlier specialization implies less time for learning about the state of the environment and, therefore, a higher risk of miscalibration (i.e., developing an inappropriate phenotype; Bateson, 2001; Nepomnaschy & Flinn, 2009). Miscalibration can be costly for a number of reasons. First, developmental specialization may be irreversible, in which case organisms are ''stuck'' their entire lifetime with a maladapted phenotype (e.g., Greene, 1989). Second, even if phenotypic development can be reversed in light of new experiences (e.g., if the world changes from safe to dangerous and the organism reorganizes its phenotype accordingly), there may be costs to shifting from one phenotype to another, such as the reworking of tissues that are committed to other functions (i.e., entrenchment; Wimsatt & Schank, 2004). Third, development is a path-dependent process, such that what happens at earlier stages might affect the cost and benefits of future options. For instance, having developed a large body, an organism may sacrifice agility in the future, because the costs of producing the morphology required to remain agile with a larger body are too great. Fourth, organisms are suites of correlated characters, and the development of one trait often influences the developmental possibilities of other traits, often narrowing them (Maynard Smith et al., 1985).

In humans, incorrect calibration may impose major physical health costs, including elevated risk of cardiovascular disease, obesity, and diabetes (Barker, 1994; Bateson et al., 2004; Gluckman, Hanson, Spencer, & Bateson, 2005; Kuzawa, 2004, 2008; Kuzawa & Quinn, 2009; Schooling et al., 2009). For instance, prenatal exposure to undernutrition may result in the development of metabolic processes designed to retain and store insulin and fatty acids (Barker, 1994). This response might be adaptive if the postnatal environment matches the prenatal environment. However, if resources are plentiful in the postnatal environment, individuals may be at increased risk for health problems. These detrimental effects appear absent when the postnatal environment continues to be lacking in resources (Stanner & Yudkin, 2001), suggesting that phenotype-environment mismatch (rather than undernutrition) may be the root cause.

Animal research suggests that incorrect calibration may also have psychological costs. For instance, when tested under adverse conditions, rat pups growing up in beneficial environments (with high levels of maternal care) show diminished memory performance in comparison with pups growing up in adverse environments (with low levels of maternal care); however, this pattern is reversed when pups are tested under beneficial conditions, suggesting it is the mismatch itself that imposes costs (Champagne et al., 2008; see also Oitzl, Champagne, van der Veen, & de Kloet, 2010; Oomen et al., 2010; Schmidt, 2011).

Trading off sampling and specialization

Our hypothesis (that individual variation in plasticity may result from different degrees of confidence about the state of the environment) assumes there is a trade-off between sampling the environment and constructing a well-adapted phenotype. Individuals may benefit from specializing earlier because it allows more time to achieve an adaptive fit with the state of the environment. However, earlier specialization may result in a worse estimate of the state of the world and thus a greater likelihood of developing an incorrect phenotype.

Linking Differential Plasticity to Inferential Processes

We define a *cue* as a feature of the environment, animate (e.g., father absence in early ontogeny) or inanimate (e.g., resource scarcity), that on average improves an individual's estimate about the state of the environment. An individual may therefore use a cue as a guide to action, such as making developmental decisions. In a world of perfect information, each cue exists only in the corresponding environmental state (e.g., violence

is seen only in a dangerous environment, social support only in a safe environment), and organisms need only to obtain a single cue to know the true state of the environment: The cue provides, as it were, a transparent window onto reality. However, cues often indicate the state of the environment probabilistically (e.g., violence can happen in a safe world, social support in a dangerous world), such that multiple states of the world remain possible having observed any particular cue. The *cue validity* specifies the probability of obtaining a cue, given some environmental state (e.g., how likely violence is in a dangerous world and in a safe world, and how likely social support is in a safe world and in a dangerous world). After having sampled a stochastic cue, the probabilities of being in different states of the world will change depending on the cue validities. Thus, *stochastic sampling* refers to the sampling of cues (e.g., violence or social support) that probabilistically indicate the state of the environment (e.g., dangerous or safe).

With continued sampling, certain states of the world become more likely than others. Consider the process of statistical inference: Even if the first few observations point in the same direction, we should not rush to judgment—the errors may be large. As more data trickles in, our confidence intervals shrink, depending on the consistency in our samples. If the data cluster closely, we develop a more confident estimate of the relevant parameters. However, if the data points in different directions, our error bars may remain large. In this case, we may choose to obtain more samples in an attempt to improve our estimate, depending on such factors as the costs of gathering more data.

Variability, predictability, and confidence

Focusing on the stochastic nature of information acquisition, we will see that identical organisms growing up in the same environment may arrive at different estimates about the state of the environment if they obtain different cue sets, and this may lead them to choose different developmental trajectories. To see why, it is useful to distinguish three concepts: variability, predictability, and confidence. We use the term *variability* to refer to the rate at which an environment varies across space and time along a particular dimension (e.g., Colwell, 1974, Stearns, 1981; see also Brumbach, Figueredo, & Ellis, 2009; Ellis, Figueredo, Brumbach, & Schlomer, 2009). We use the term *predictability* to refer to the extent to which individuals have access to cues that they can use to predict the state of the environment. For instance, environments with high rates of change may be perfectly predictable, if individuals have access to informative cues. Finally, the term *confidence* refers to the extent to which an individual can predict fitness-relevant properties of the environment (''a state of mind''). Despite growing up in the same environment and using the same decision rule, individuals may obtain different cue sets and thus develop different degrees of confidence in their estimate about the state of the world. They may draw different cue sets because sampling is a stochastic process.

Hypothesis: Differential plasticity results from stochastic sampling

Assuming a trade-off between sampling and specialization, when should an individual commit to a particular developmental pathway, contingent on the information so far obtained? To illustrate the inferential task faced by a developing organism, consider the following analogy.

Imagine a population of individuals whose ancestors faced two states of the world—safe or dangerous—each with 50% probability. The two different states require different phenotypes, such that incorrectly specializing yields much lower fitness than correctly specializing. Initially, individuals assume they are equally likely to be in either state. Then, at each stage of ontogeny, individuals face a choice: They can either specialize towards one state of the world, or they can sample a cue to the state of the world. We assume these two choices are mutually exclusive, such that each cue sampled implies one lost increment of specialization (the opportunity cost of information seeking). If individuals specialize early in life, they become well adapted to one particular state of the world. However, since they have not sampled much, there is a greater risk of miscalibration (i.e., developing a phenotype mismatched to the state of the environment). Alternatively, individuals may start out sampling many cues before specializing, in order to obtain a better estimate of the state of the world. These individuals reduce the risk of miscalibration. However, they end up with a less specialized phenotype. The optimal decision for each state of the developing organism depends on the expected values associated with choosing to sample and choosing to specialize.

The extent of reliance on sampling favored by natural selection depends on how informative cues[2] are (Frankenhuis & Panchanathan, in press; see also Ellis et al., 2011; Pigliucci, 2001). At one extreme, cues may be relatively uninformative, in which case natural selection may favor specialization with minimal sampling, or no sampling at all (Debat & David, 2001). Sampling is not favored when cues are relatively uninformative because many cues are needed to obtain a better estimate, and the time spent sampling diminishes investment in specialization. At the other extreme, cues may be very informative, in which case selection may also favor minimal sampling for a different reason. When cues are informative, small samples yield highly accurate estimates, and the opportunity cost of foregone expertise disfavors continued sampling. When cues are of intermediate value, organisms may sample relatively extensively until they have obtained sufficient confidence in their estimate of the environmental state. However, they should not sample so much that meaningful specialization is sacrificed.

A thought experiment

Let us suppose a population of individuals is descended from a lineage that faced two equally likely states of the world (50–50) and that they have access to cues of intermediate validity (75%)—meaning that 75% of the cues indicate ''safe'' and 25% of the cues indicate ''danger'' in a safe environment, and

that 75% of the cues indicate danger and 25% indicate safe in a dangerous environment. Let us also suppose that all individuals demand 90% confidence in their estimate about the state of the world before specializing. We pick this threshold value for illustrative purposes. In an evolutionary model, we analyze the evolution of developmental systems, including this threshold, across a range of cue validities, prior distributions, and mappings from specialization to fitness, deriving optimal developmental decision rules and distributions of mature phenotypes produced by these rules (Frankenhuis & Panchanathan, in press).

Now, suppose that the environmental state is, in fact, safe. Because the cue validity is 75%, three in four individuals drawing their first cue will draw the "safe" cue, and one in four will draw the "danger" cue. Using Bayes' theorem with a 50–50 prior distribution and a cue validity of 75%, three in four individuals will be 75% confident they are in a safe world, and one in four will be 75% confident they are in a dangerous world. That is, all individuals will have a posterior confidence[3] of 75%. Because cues are assumed to be independent, with two cues, 9 in 16 will sample two safe cues, 1 in 16 will sample two danger cues, and 6 in 16 will sample one of each cue. Individuals sampling one of each cue reset their posterior confidence level to 50%. These individuals continue sampling, as they have not reached their desired confidence level. Individuals that draw two consecutive safe or danger cues reach their desired confidence level of 90% and so transition from sampling to specialization. (This two-cue lead before reaching a decision corresponds to the actual Bayesian computation.) As a result, after two rounds of sampling, some individuals will have specialized, whereas others continue to sample. Iterated over time, this process can result in differential susceptibility to environmental information (i.e., differential plasticity), even when these individuals are genetically identical, follow the same developmental "program," and grow up in the same environment.

To summarize: Because sampling cues is a stochastic process, some individuals may receive a homogeneous sample, resulting in a confident estimate about the state of the world—these individuals specialize early. Other individuals may receive heterogeneous, uninformative set of cues—those individuals keep sampling. As a consequence, individual variation in plasticity may result from different degrees of confidence about the state of the environment.

Predictions and Empirical Tests

Models are by design simplified, idealized versions of reality. They may strive to capture some essential components of a process or system, while being aware that the "real" world is a mess of interconnected causalities that no model could ever capture. We view our model of differential plasticity primarily as headlights in dark unexplored territory (Epstein, 2008). Still, our hypothesis makes several novel and unique predictions that are testable if scientists succeed at measuring the relevant variables.

Our predictions apply only to developmental domains in which a trade-off exists between learning about the environmental state and phenotypic specialization. Demonstrating this trade-off requires proof that there is a premium on earlier specialization and that sampling environmental cues reduces the risk of costly miscalibration. We have previously discussed the benefits and costs of specializing early. Our assumption that sampling cues reduces the risk of miscalibration is general to models of phenotypic plasticity (Dall et al., 2005). Such learning has been demonstrated in animals as well as plants (Dall et al., 2005; DeWitt et al., 1998; Karban, Agrawal, Thaler, & Adler, 1999; Krebs, Kacelnik, & Taylor, 1978; Schlichting & Pigliucci, 1998; West-Eberhard, 2003). Once the trade-off has been established, we make the following predictions.[4]

Prediction 1: Variation in plasticity should be correlated with consistency in previous experience

One prediction of our hypothesis is that variation in the degree of confidence about the state of the environment should correlate with variation in plasticity. At a given age, individuals who are more confident about the state of the environment should devote less of their future to sampling the environment and more toward specializing. This degree of confidence may depend on the consistency of previous experiences. Individuals who repeatedly sampled the same cue may have a more confident estimate than individuals who sampled different cues. Hence, individuals with a more consistent cue set should specialize earlier toward the perceived environmental state. The rate at which plasticity diminishes across development should be a function of the degree of internal consistency in the sampled cue set—developmental plasticity should diminish faster in individuals that sample more consistent cues compared to individuals that sample less consistent cues.

In many inferential tasks, organisms may use different sources of information of varying validity. For example, to estimate whether the environment is safe or harsh, an individual might observe whether adults frequently engage in lethal aggression (presumably a highly informative cue) and whether adults frequently engage in yelling at one another (presumably a more weakly informative cue). Given the same environment, some individuals may experience the highly informative cue and thus be quite confident in the environmental state. By contrast, another individual may only have access to a weakly informative cue and thus be less confident. As a consequence, the first individual might begin specializing earlier on, while the second individual continues to sample. In this way, individual differences in plasticity could arise when there are multiple cues of varying validity.

In order to test the proposed predictions, researchers can measure three dimensions: the perceived (or subjective) confidence of individuals about the state of the environment (Hill, Ross, & Low, 1997; Ross & Hill, 2002), the actual (or objective) consistency in ontogenetic experiences of individuals, and between-subjects

variation in plasticity. We distinguish objective consistency in experiences from subjective confidence, because perception errors may result in some degree of discrepancy between the two dimensions (e.g., a safe cue being perceived as indicating danger). Our hypothesis predicts that these dimensions should be correlated with each other in the following ways: confidence should be positively correlated with consistency, confidence should be negatively correlated with plasticity, and consistency should be negatively correlated with plasticity. How these dimensions can best be measured remains an open question.[5]

We know of at least one study with results consistent with our hypothesis that children receiving consistent cues (e.g., abuse) may start specializing earlier and, as a result, lose their plasticity earlier than children receiving more heterogeneous cue sets. This study shows that behavioral strategies at age 2 predict levels of inhibition at age 7, but only in children exhibiting extreme levels of inhibition at 2 years—that is, highly timid, shy, and quiet kids *or* highly sociable, talkative, and spontaneous ones (Kagan, Reznick, & Snidman, 1988). Children at the extreme ends show less flexibility than children in the middle of the distribution (for similar results, see Kerr, Lambert, Stattin, & Klackenberg-Larsson, 1994; Sanson, Pedlow, Cann, Prior, & Oberklaid, 1996). The researchers mention that a combination of genetic predisposition and early environmental stress may account for these individual differences. Although possible, it is also conceivable that consistency in earlier experiences alone affects the rate at which plasticity diminishes. The 2-year-olds exhibiting extreme levels of inhibition might have previously experienced consistent cues pointing either to a world in which it pays to be extremely shy or extremely sociable. As a result, these kids continued along their extreme developmental pathways, giving rise to the intertemporal correlation. By contrast, those 2-year-olds exhibiting intermediate levels of inhibition might have previously experienced ambiguous cues. As a result, they continued sampling the state of the world. Because these 2-year-olds retained their plasticity, there was no correlation between their temperament at 2 and at 7. This account requires that children sample more consistent cue sets in extreme environments—a possibility that remains to be explored. Our hypothesis predicts that children specializing earlier in life toward extreme levels of inhibition (i.e., extremely high or extremely low) become better adapted to environments in which these levels are adaptive in comparison with children specializing later in life.

Prediction 2: Individual differences in plasticity should be greatest in mechanisms using intermediately informative cues

We argued previously that, given a trade-off between sampling and specialization, the greatest reliance on sampling evolves when cue validities are intermediate. When cues are highly informative, small samples yield accurate estimates and the opportunity cost of foregone expertise disfavors continued sampling. When cues are weakly informative, organisms would need many samples for an accurate estimate. But a heavy reliance on sampling means little opportunity for specialization and, thus, low expected fitness (therefore, organisms may not sample at all). With intermediate cue validities, there should be a heavier reliance on learning (for a related finding, see Todd & Miller, 1991). The more time that individuals spend sampling, the more potential variation there is in what they learn. The more variation there is in learning outcomes, the more variation there will be in plasticity. So, we can predict that individual differences in plasticity should be greatest, and also more common, when cues are intermediately informative. This prediction invites the methodological challenge of measuring the value of information—we need to quantify the probability of observing a particular cue, given different environmental states. In general, evolutionary developmental psychologists should accept this challenge because many current hypotheses make assumptions about cue validities. For instance, they assume that cues are reliable without providing evidence for this assumption or specifying what ''reliability'' entails.

So, we expect developmental mechanisms using intermediate cues to exhibit greater individual differences in plasticity than mechanisms using weakly or highly informative cues. This prediction can be tested comparatively (i.e., across species) or within a given species. Across species, all else being equal (e.g., the prior probability of different environmental states), those species having access to intermediate cues should exhibit greater individual differences in plasticity than species using weakly or highly informative cues. We might compare two closely related species facing identical patterns of variation across evolutionary time scales (i.e., resulting in similar priors) along some environmental dimension (e.g., predator density)—one of these species has access to highly (or weakly) informative cues, whereas the other is limited to using intermediate cues. In such a scenario, our hypothesis predicts that the species using highly (or weakly) informative cues will show less extensive individual differences in plasticity than the species relying on intermediate cues. This prediction could directly be borne out by subjecting populations of organisms to different experimental treatments (here, two different cue validities) and observing the evolutionary outcomes.

It is also possible to test the prediction—that individual differences in plasticity should be greatest when cues are intermediately informative—within a single species, such as humans. Developing organisms often calibrate their phenotype along a number of dimensions, using information relevant to each domain (Cosmides & Tooby, 1994; see also Frankenhuis & Ploeger, 2007). For instance, children may calibrate their stress responses based on cues of danger (Ellis et al., 2006), levels of risk-taking based on cues of extrinsic mortality rates (Brezina, Tekin, & Topalli, 2009; Fessler, 2010; M. Wilson & Daly, 1997), and food preferences based on cues of resource abundance (Fessler, 2003; Monaghan, 2008). Our hypothesis predicts that domains in which intermediate cues are used to calibrate development should have greater individual differences in plasticity than domains in which cues are either weakly or highly informative.

Prediction 3: Loss of plasticity in a population should exhibit a geometric decay distribution

So far, we have generated predictions about factors that may account for individual differences in plasticity (such as consistency in earlier experiences) and about factors that may predict variation in the extent of individual differences in plasticity across developmental domains (such as cue validities). We can also ask the following question: To the extent that stochastic sampling is responsible for individual differences in plasticity, what form would the decay of plasticity take at the population level?

As noted, individuals may transition from sampling to specialization at different points in ontogeny, depending on the confidence they have in their estimate about the state of the environment (which, in turn, may depend on the consistency in their cue set, or on the value of the cues sampled). Each time an individual "chooses" to specialize toward a particular environmental state, the fraction of plastic individuals reduces, until eventually all individuals are specializing. In our model, individuals never sample after having specialized (Frankenhuis & Panchanathan, in press). This irreversibility is not assumed; it emerges from a strict trade-off between sampling and specialization, when the environment does not change within an individual's life span. The prediction we describe below depends on this result: that whenever an organism switches from sampling to specialization, it loses its plasticity entirely (i.e., it stops gathering information).

Recall our fictitious population of individuals, descendants from a lineage that faced two equally likely states of the world (50–50) and had access to cues of intermediate validity (75%). Let us suppose, again, that all individuals demand 90% confidence in their estimate about the state of the world, before specializing. All individuals sample at least twice because, as noted before, Bayes' theorem dictates that, given the current parameters, it takes a two-cue lead to reach 90% confidence. On these first two draws, 10 in 16 (62.5%) individuals will draw a homogeneous set—two safe cues or two danger cues ($3/4 \times 3/4 + 1/4 \times 1/4 = 10/16$)—and then begin specializing. The remaining 6 in 16 (37.5%) will draw a heterogeneous set—one safe cue and one danger cue. Their prior belief remains unchanged, as the two opposite cues cancel each other out (assuming that cues are independent). They continue sampling. The process repeats itself, only with 37.5% of the original number continuing to learn. After four periods, 85.9% of the original number will be specializing, and 14.1% will continue to sample. Every two draws, 62.5% of the remaining plastic individuals will transition from sampling to specialization, until all individuals are specializing. Although the exact rate of decay will depend on specific parameters, such as the prior probability distribution and the cue validity, this process generally results in a geometric decay distribution.

Conclusion

We have offered a novel hypothesis to explain how individuals become differentially sensitive to experience. In some developmental domains, individuals must learn about the state of their environment before adapting accordingly. When the time allocated to developing a particular phenotype correlates with the adaptive fit to the environment, a trade-off results: More sampling results in a better estimate of the environmental state; however, earlier specialization results in a tighter fit between the phenotype and environment and a higher risk of incorrect calibration. Because sampling cues is a stochastic process, some individuals may receive a homogeneous sample, resulting in a confident estimate about the state of the world—these individuals specialize early. Other individuals may receive a heterogeneous, uninformative set of cues—those individuals will keep sampling. As a consequence, individual variation in plasticity may result from different degrees of confidence about the state of the environment. This hypothesis generates novel testable predictions. We have described three. We hope that developmental psychologists will consider these predictions in their analyses of current and future data. As Nobel Laureate Robert Millikan noted in 1924: "Science walks forward on two feet, namely theory and experiment. . . . Sometimes it is one foot that is put forward first, sometimes the other, but continuous progress is only made by the use of both."

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The authors declared that they had no conflicts of interest with respect to their authorship or the publication of this article.

Notes

1. In this article, we are not concerned with issues of instantiation: So long as developmental mechanisms approximate adaptive solutions, they may take many forms.
2. We assume that the developmental system of individuals "knows" the value of cues, in the same way that it "embodies" the prior distribution (50–50), due to a history of natural selection.
3. The posterior confidence describes an individual's estimate of being in a particular environmental state after having sampled a cue.
4. These predictions apply only to mechanisms that are currently developing in environments that have similar fitness-relevant properties as the ecologies in which they evolved (i.e., no evolutionary disequilibrium).
5. Of course, for our predictions to apply, all measures should be taken within the same developmental domain (e.g., calibration of vigilance levels).

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