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Theory and measurement of environmental unpredictability

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ABSTRACT

Over the past decade, there is increasing interest in the ways in which environmental unpredictability shapes human life history development. However, progress is hindered by two theoretical ambiguities. The first is that conceptual definitions of environmental unpredictability are not precise enough to be able to express them in statistical terms. The second is that there are different implicit hypotheses about the proximate mechanisms that detect unpredictability, which have not been explicitly described and compared. The first is the ancestral cue perspective, which proposes that humans evolved to detect cues (e.g., loss of a parent, residential changes) that indicated high environmental unpredictability across evolutionary history. The second is the statistical learning perspective, which proposes that organisms estimate the level of unpredictability from lived experiences across development (e.g., prediction errors encountered through time). In this paper, we address both sources of ambiguity. First, we describe the possible statistical properties of unpredictability. Second, we outline the ancestral cue and statistical learning perspectives and their implications for the measurement of environmental unpredictability. Our goal is to provide concrete steps toward better conceptualization and measurement of environmental unpredictability from both approaches. Doing so will refine our understanding of environmental unpredictability and its connection to life history development.

> I saw those Djakarta markets for what they were: fragile, precious things. The people who sold their goods there might have been poor, poorer even that the folks in Altgeld. They hauled 50 pounds of firewood on their back every day, they ate little, they died young. And yet for all that poverty, there remained in their lives a discernable order, a tapestry of trading routes and middle men, bribes to pay, and customs to observe, the habits of a generation played out every day. It was the absence of such coherence that made a place like Altgeld so desperate, I thought to myself; it was the loss of order.
>
> Barack Obama (1995). *Dreams from my Father.*

Barack Obama spent part of his childhood living in Jakarta, Indonesia, and his emerging adulthood working as a community organizer in Altgeld Gardens, a public housing project on Chicago's South Side. In his memoir, Obama described both Jakarta and Altgeld as tough environments in which people died young. Indeed, Jakarta and Altgeld seemed similar on a fundamental dimension of environmental risk—harshness—which Ellis, Figueredo, Brumbach, and Schlomer (2009) defined as age-specific rates of morbidity-mortality. At the same time, Jakarta and Altgeld appeared very different on a second key dimension of environmental risk: unpredictability. The challenges and struggles of life in Jakarta were tough but similar from day-to-day. In Altgeld, life was chaotic, haphazard, and disordered.

For decades, scholars have examined the link between environmental conditions, evolution, and the development of life-history strategies (Belsky, Steinberg, & Draper, 1991; Chisholm, 1993; Draper & Harpending, 1982). Recently, evolutionary-developmental theory and research have identified a unique role for environmental unpredictability in regulating human development (Ellis et al., 2009). For instance, studies have shown associations between environmental unpredictability and life history traits in humans, such as sexual behavior (Belsky, Schlomer, & Ellis, 2012; Simpson, Griskevicius, Kuo, Sung, & Collins, 2012), mating and relationship outcomes (Szepsenwol et al., 2017; Szepsenwol, Zamir, & Simpson, 2019), and parenting (Szepsenwol, Simpson, Griskevicius, & Raby, 2015). Studies have also linked environmental unpredictability to behavior and cognition, including risk-taking and temporal discounting (Griskevicius et al., 2013), executive functions and working memory (Mittal, Griskevicius, Simpson, Sung, & Young, 2015; Young, Griskevicius, Simpson, Waters, & Mittal, 2018), and decision-making (Griskevicius, Delton, Robertson, & Tybur, 2011; White, Li, Griskevicius, Neuberg, & Kenrick, 2013). Together, these findings appear to tell a convincing story: growing up in an unpredictable environment uniquely predicts human life history

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traits, even after controlling for other factors, such as poverty.

Although the empirical literature on environmental unpredictability has grown substantially in the past 10 years, this body of work faces theoretical and methodological challenges. The most visible challenge is the wide range of measures used to quantify unpredictability, which makes it difficult to compare findings and assess replicability. We believe this is a symptom of two major theoretical ambiguities. The first focuses on the definition of environmental unpredictability as a selection pressure across evolutionary time. Specifically, unpredictability has been defined as the level of spatial-temporal variation in environmental harshness (Ellis et al., 2009). However, current definitions do not specify the *pattern of variation* in statistical terms. In addition, current definitions do not address *stationarity* in environmental unpredictability. Stationarity refers to whether the statistical properties of an environment (e.g., mean, variance, autocorrelation etc.) remain constant across lifetimes. The statistical properties of a non-stationary environment change across the lifetime (e.g., changes in the mean, variance, or autocorrelation etc.). Whether environmental unpredictability is stationary or non-stationary affects environmental unpredictability as a selection pressure.

Even with precise concepts at the ultimate level, a second theoretical ambiguity concerns the proximate mechanisms—adaptations—that evolved to detect and respond to environmental unpredictability. Specifically, there are at least two conceptually distinct frameworks. The first is the *ancestral cue perspective,* which proposes that humans evolved to detect and respond to cues that reliably indicated high environmental unpredictability across evolutionary history. The second is the *statistical learning perspective*, which suggests that organisms estimate the level of unpredictability by integrating differences in lived experiences across development. Because these approaches imply different proximate mechanisms for detecting environmental unpredictability, drawing on one or the other has consequences for measurement.

Our goal is to highlight–and attempt to clarify–these theoretical ambiguities while also proposing some steps forward. We restrict our focus to two questions. First, what is environmental unpredictability and how can it be described in formal statistical terms? Second, how do organisms detect environmental unpredictability and what information triggers a response once detected? We do not address questions about the selection pressures posed by the developmental timing of exposures to environmental unpredictability (e.g., juvenile versus adult life stage), sensitive periods of development for responding to unpredictability, specific biological or cognitive mechanisms that mediate responses to unpredictability (e.g., stress physiology, mental representations, learning mechanisms), or adaptive responses to unpredictability (e.g., accelerating or decelerating life history development). In addition, we focus on how organisms estimate environmental unpredictability in a general sense and not on whether or how they estimate the environmental conditions in which an individual will reproduce (even if these variables may be related, for instance, when estimates of the former can inform estimates of the latter). With this narrow scope in mind, we proceed in four steps. First, we provide a brief overview of research on environmental unpredictability and illustrate the widespread inconsistency in its measurement. Second, we analyze environmental unpredictability at the ultimate level of explanation and identify possible statistical definitions, depending on whether the environment is stationary or non-stationary. Third, we outline the ancestral cue and statistical learning approaches that might characterize the proximate mechanisms for detecting environmental unpredictability and discuss their implications for the measurement of environmental unpredictability. Fourth, we propose ways in which the ancestral cue and statistical learning approaches could be integrated and outline future directions for research.

1. Environmental unpredictability: the past decade

In a foundational paper, Ellis et al. (2009) proposed a conceptual framework of unpredictability based on *life history theory* (Charnov, 1993; Roff, 1993; Stearns, 1992). Life history theory seeks to explain the way organisms allocate limited time and energy to the various activities during the life cycle. Natural selection favors organisms that optimize the timing of developmental activities based on the local ecology. Ellis et al. (2009) identified environmental unpredictability as a key influence on the evolution and development of life history strategies and defined it as variation in environmental harshness (age-specific rates of morbidity-mortality) over space and time. The central thesis is that, over evolutionary time, humans were exposed to environments that varied both in mean levels of harshness and in the degree of stochastic variation in harshness within and across generations. Variation in harshness affected fitness-relevant outcomes (e.g., survival and reproduction) of our ancestors over developmental time. In response, humans may have developed conditional adaptions that enabled accelerated life history development if exposed to environmental unpredictability.

The Ellis et al. (2009) analysis inspired empirical studies that, together, have generated a body of knowledge about the developmental effects of environmental unpredictability (Belsky et al., 2012; Brumbach, Figueredo, & Ellis, 2009; Doom, Vanzomeren-Dohm, & Simpson, 2016; Mittal et al., 2015; Simpson et al., 2012; Szepsenwol et al., 2015; Szepsenwol et al., 2017; Szepsenwol et al., 2019; Young et al., 2018). However, despite a common frame, empirical studies have measured environmental unpredictability in many different ways. For example, evolutionary-developmental psychologists tend to count the number of residential changes, family disruptions, or changes in parental financial status (Belsky et al., 2012; Brumbach et al., 2009; Ellis et al., 2009; Simpson et al., 2012). Evolutionary social psychologists tend to employ self-report questionnaires that quantify (retrospectively) individual differences in the *perception* of environmental unpredictability while growing up (Maner, Dittmann, Meltzer, & McNulty, 2017; Mittal et al., 2015; Young et al., 2018). Finally, other behavioral scientists typically measure household chaos, inconsistency in parental discipline/nurturance, and/or inconsistent routines (Evans, Gonnella, Marcynyszyn, Gentile, & Salpekar, 2005; Kolak, Van Wade, & Ross, 2018; Ross & Hill, 2002; Ross, Hood, & Short, 2016).

To illustrate the diversity in measures, we reviewed all studies citing Ellis et al. (2009) on Web of Science (search completed on February 8, 2020). Of the 422 studies citing Ellis et al. (2009), we identified 21 empirical studies that measured environmental unpredictability (see supplemental Table 1) but at least 15 different measures. Moreover, studies using the same measures do so because they report findings from the same dataset. Specifically, eight of the 21 studies come from either the Study of Early Childcare and Youth Development (NICHD Early Child Care Research Network, 2005) or the Minnesota Study of Risk and Adaptation (Sroufe, Egeland, Carlson, & Collins, 2005). This means almost half of the studies on environmental unpredictability have used just two data sources. In addition, the psychological literature also employs many different methods for capturing environmental unpredictability. For example, studies vary in report formats (e.g., self-reports, interviews), informants (e.g., target participant or caregiver), and report types (e.g., retrospective, prospective) to name only a few (see supplementary Table 1). As such, there is little overlap across studies in measures of environmental unpredictability. Moreover, to our knowledge, there are no studies that explore whether distinct measures are correlated with each other, indicate the same underlying construct, and predict the same outcomes in a dataset.

Diversity in measurement is not inherently bad but makes it difficult to compare findings and assess replicability. One solution would be to

conduct largescale psychometric analyses to evaluate the construct validity of measures. However, psychometric work only gets us so far; we also need to remove ambiguities in our conceptual definition of environmental unpredictability. At the ultimate level, we need to identify the potential statistical properties of environmental unpredictability that could impose a selection pressure. In addition, at the proximate level, we need clearer hypotheses about the design features of the mechanisms that may have evolved to detect and respond to environmental unpredictability. Are organisms detecting discrete events that indicated environmental unpredictability over evolutionary time, or are they integrating over differences in their lived experiences over the course of ontogeny, or both?

2. Statistical properties of unpredictable environments

Current definitions of environmental unpredictability focus on spatial and temporal variation in environmental harshness (Ellis et al., 2009). Although not always explicit, work in this area specifically focuses on *stochastic* (e.g., random) variation in harshness. We attempt to refine this definition in two ways. First, we identify the patterns of variation that make environments more or less predictable. For example, some patterns of variation are predictable, such as seasonal variation. After accounting for predictable variation (e.g., seasons or trends), any remaining variability (e.g., leftover noise) can be still be predictable if it is autocorrelated. The degree of autocorrelation in residual variation is sometimes referred to as the color of environmental noise, with white noise reflecting no autocorrelation and pink, red, and brown noise reflecting lower to higher degrees of autocorrelation (Burgess & Marshall, 2014; Frankenhuis, Nettle, & Dall, 2019; Marshall & Burgess, 2015; Vasseur & Yodzis, 2004; Wieczynski, Turner, & Vasseur, 2018). Second, we address *stationarity*, which refers to whether or not the statistical structure of an environment itself changes over a lifetime. For example, if environmental harshness is stationary in a lifetime, its mean, variance, and/or autocorrelation over the first 5 years of life (or any other arbitrary period of time) are equal to any other 5-year window across the life course. In contrast, non-stationary environments have a statistical structure that changes over time. If environmental harshness is non-stationary in a lifetime, its mean, variance, and/or autocorrelation over the first 5 years of life are different from other 5-year periods across the life course. Whether environmental unpredictability is stationary or non-stationary has implications for evolution and development, formal modeling, and measurement (Frankenhuis, Panchanathan, & Nettle, 2016).

In stationary environments, there are at least three relevant statistical properties for describing environmental unpredictability: variance, autocorrelation, and cue reliability (see Fig. 1a). Variance refers to average deviations from the mean. For example, high temporal variance in harshness means that the environment can vary widely from safe to dangerous (around a mean value) across time. However, whether or not high variance is unpredictable depends on whether it is autocorrelated. Autocorrelation refers to the degree to which current conditions are related to future conditions (e.g., are conditions today correlated with conditions tomorrow). Even when variance is high, such variation can be predictable if it is autocorrelated. Finally, cue reliability refers to the extent to which experiences or events provide information about current or future environmental conditions (Fawcett & Frankenhuis, 2015). For example, witnessing a fight could be a reliable cue to current or future levels of harshness, whereas seeing people lock their doors could be a less reliable cue to harshness (e.g., this happens in both safe environments and dangerous ones). Cues may provide information about current or future states of the environment, even if states of the environment are not autocorrelated. For instance, if a leader in your village, whom you trust, tells you that a gang, which you are a part of, will raid a neighboring village, it indicates a likely increase in the rates of morbidity and mortality in your environment, even if this increase could not be predicted based on past levels of animosity (i.e., autocorrelation), without the social cue.

In non-stationary environments, the underlying statistical structure of the environment changes over time. However, some types of non-stationary patterns are more predictable than others. For example, non-stationary environments could have a trend (e.g., slope), seasonal variation, and/or cyclic variation. A trend describes changes in the overall mean across time or space. Seasonal and cyclic variation refer to patterns of variation that repeat. Seasonal patterns repeat over regular intervals whereas cyclic variation repeat over irregular patterns (Jebb & Tay, 2017; Jebb, Tay, Wang, & Huang, 2015). Trend, seasonality, and cycles describe predictable patterns of change. For example, an upward trend in the mean level of harshness across time is predictable (e.g., tomorrow will be more dangerous than today). Likewise, a seasonal pattern is also predictable (e.g., winter is harsher than summer). However, non-stationary environments might be unpredictable if they contain random change points, or abrupt changes in one or more statistical properties of the environment (see Fig. 1b). For example, a change point could precede a sudden increase in mean levels of harshness (e.g., a natural disaster) or sudden increase in the variance of resource distribution (e.g., the stock market crashing).

If change points occur at irregular intervals (e.g., no seasonal or cyclic pattern), the environment is more unpredictable in at least two ways. First, the probability of another change point occurring at any given time might change, compared to what it was before the change point occurred. Second, experiences that happened prior to the change point are less informative about environmental conditions after the change point. Thus, after a change point occurs, organisms have a limited ability to predict future outcomes without gathering more information and experience in the new statistical structure of the environment. However, like unpredictable stationary environments, reliable cues could make the environment more predictable, even if random change points occur. For example, cues could indicate a change point has occurred or will occur, even if they do not indicate the type or direction of change. Similarly, if both the relevant cues and cue reliabilities do not shift as a function of a change point (e.g., cue reliability itself is unaffected and/or the same cues are still informative), cues can still provide reliable information about the state of the environment.

Our discussion highlights the need for formal models that explore the effects of stationary and non-stationary environmental unpredictability on evolution and development. For stationary unpredictability, models could compare the adaptive strategies for all combinations of variance (high, low) and autocorrelation (high, low). For non-stationary unpredictability, models could explore which strategies are adaptive when random change points occur in the mean, variance, or autocorrelation, or their combination. Models should also consider whether unpredictability has a different impact on different age classes (juveniles versus adults), affects all individuals in a population, or only a subset (Ellis et al., 2009). The statistical definition of unpredictability an empirical researcher adopts should inform the measures used to test hypotheses (e.g., measure mean levels, variance, and autocorrelation, or change points in these parameters). Finally, we have focused on environmental harshness (i.e., age-specific rates of mortality and morbidity) because this is a primary focus in evolutionary psychology. However, our discussion of concepts, measures, and proximate mechanisms could apply to any dimension of the environment. For example, social (e.g., rate of violence, parenting, etc.) and/or non-social (e.g., food availability) dimensions of the environment may vary across space and/or time in more or less predictable patterns (Frankenhuis et al., 2019). Quantifying patterns of unpredictability in these social and non-social variables in diverse human populations would be an interesting direction for future theoretical and empirical research.

3. Proximate mechanisms for detecting unpredictability

Clarifying and refining our conceptual definition of environmental unpredictability raises interesting questions about the types of

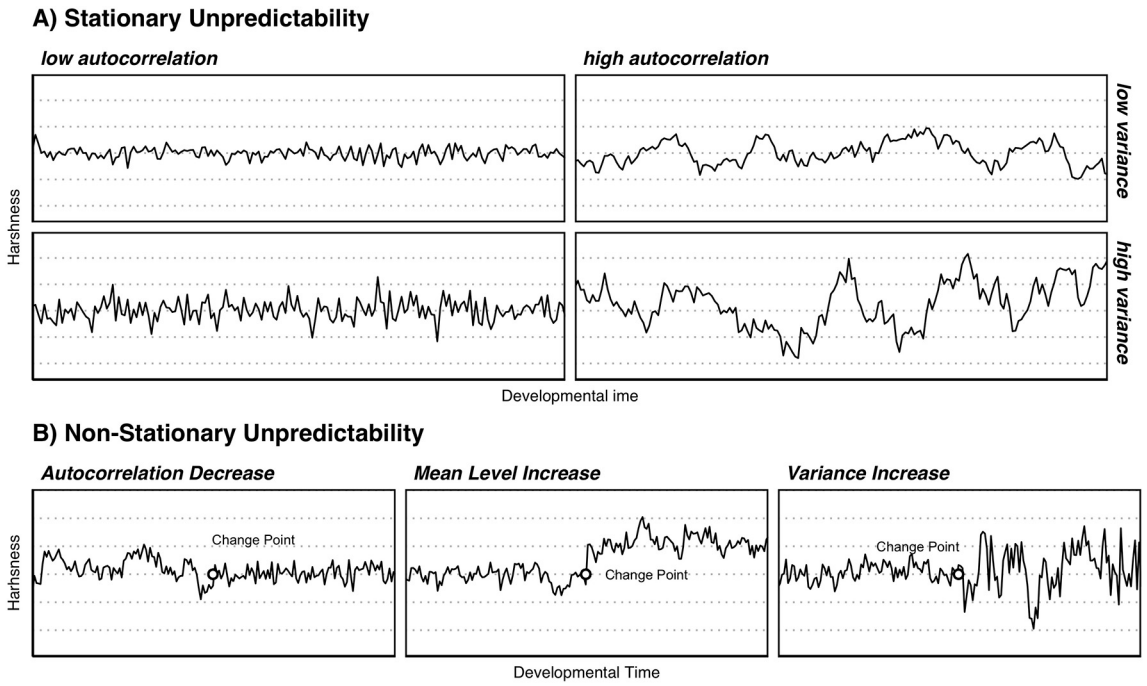

Fig. 1. Visual depiction of stationary and non-stationary environmental unpredictability. The x-axis depicts developmental time; the y-axis environmental harshness. A) Ignoring cue reliability, the predictability of a stationary distribution depends on its variance and autocorrelation. When variance is high, harshness fluctuates more than when variance is low. When autocorrelation is high, harshness in one time period is more related to harshness in future time periods. Even if variance is high, fluctuations might still be predictable, if autocorrelation is high. On the flip side, if autocorrelation is low, fluctuations might deviate only little from the mean, if the variance is low. An environment is the most unpredictable when autocorrelation is low and variance is high. B) Ignoring cue reliability, non-stationary environmental unpredictability may be characterized by random change points. Change points are abrupt shifts in the statistical distribution of the environment. Such shifts may occur in the mean, variance, or autocorrelation, or all of them. The timing of change points may itself be predictable or unpredictable (not depicted).

proximate mechanisms that may be favored under different types of unpredictability. For example, does natural selection favor the same proximate mechanisms for detecting and responding to stationary unpredictability as non-stationary unpredictability? The answer is unclear without future research and formal models that explicitly address this question. However, even before such models are developed, there are at least two distinct (but not mutually exclusive) hypotheses about the proximate mechanisms that may have evolved to detect environmental unpredictability.

The first is the *ancestral cue approach* to unpredictability (Ellis et al., 2009), which is anchored in the more general 'ancestral cue' perspective in evolutionary psychology (Buss, 1995; Tooby & Cosmides, 1990). The core assumption of this perspective is that our ancestral environments contained cues that were associated with fitness-relevant environmental conditions. As a consequence, natural selection may have shaped the brain to treat these cues as privileged sources of information. Thus, ancestral cues enable organisms to adjust development based on limited information; they do not need extended experience with these cues to interpret their meaning and respond to them quickly and effectively. For instance, female parasitic wasps start laying more eggs on low-quality hosts (i.e., increase their reproductive effort) in response to barometric pressure, which was (and is) associated with approaching and potentially fatal thunderstorms (Roitberg, Sircom, Roitberg, Vanalphen, & Mangel, 1993). Ancestral cues to environmental unpredictability could indicate either stationary or non-stationary environmental unpredictability. For example, cues to stationary environmental unpredictability may indicate environmental harshness is highly variable and shows no autocorrelation. Cues to non-stationary environmental unpredictability may indicate that change points occur randomly or that one has or will occur and, therefore, the statistical structure of the environment has or will change. In either case, a core (but untested) assumption of the ancestral cue approach is that, over our evolutionary history, cues were informative regarding the levels of environmental unpredictability within individual lifetimes.

The second perspective is the *statistical learning approach* (Frankenhuis et al., 2019; Frankenhuis, Gergely, & Watson, 2013). This approach suggests that natural selection shaped developmental mechanisms to track the statistical structure of the environment by integrating differences in lived experiences across development (Frankenhuis et al., 2013, 2019), without privileging particular sources of information per se. The organism uses its experience as raw data to build a model of the statistical structure of the environment. It then uses these models to 'estimate' (i.e., adapt to) the overall (e.g., mean) level, variance, and autocorrelation in harshness. For example, blue jays can weight recent versus past experiences differentially according to the rate of changing conditions in their environment, suggesting that they can detect and respond to patterns of change in the environment (Dunlap & Stephens, 2012). Organisms might also learn new cues (e.g., police sirens) or update estimates of the reliability of cues. For instance, people may learn to use police sirens as cues to danger, and experimental studies show that humans are good at learning about cue reliability through repeated exposures over short timescales (Behrens, Hunt, & Rushworth, 2009; Behrens, Woolrich, Walton, & Rushworth, 2007). Both of these abilities might involve, but do not require, high-level cognition. For example, rats are able to make causal inferences through experience and observations (Blaisdell, Sawa, Leising, & Waldmann, 2006). Importantly, the statistical learning approach assumes that individuals are able to track, store, and use experiences to build predictive models about the current and future state of the environment. The approach also assumes that past experience over developmental time – unlike the ancestral cue approach, not necessarily over evolutionary time – is informative about the current conditions, even if past experience has taught the individual that future conditions cannot be predicted with much accuracy.

The ancestral cue and statistical learning perspectives target the same process—estimating environmental unpredictability—but differ

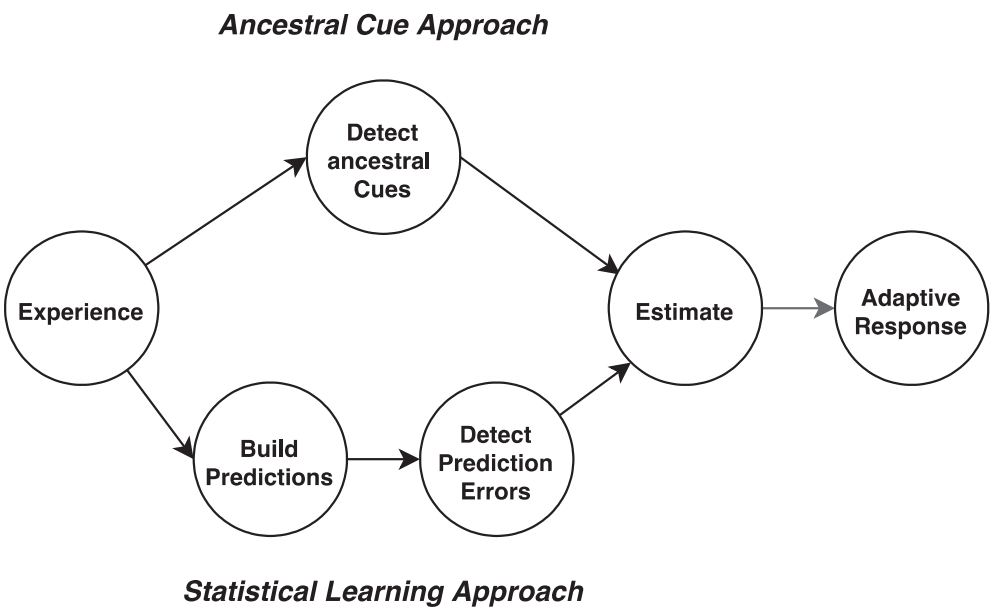

Fig. 2. The ancestral cue and statistical learning approaches. According to the ancestral cue approach, proximate mechanisms detect cues that carry ancestral information about environmental unpredictability. If an ancestral cue is detected, the organism 'estimates' environmental unpredictability is high and triggers an adaptive response. According to the statistical learning approach, proximate mechanisms use experience to develop predictions that guide behavior (not necessarily consciously or explicitly). Organisms compare their experience-based predictions to new experiences to evaluate 'model fit'. If model fit is poor, the organism detects a prediction error, 'estimates' environmental unpredictability is high, and triggers an adaptive response. Note that the two approaches are not mutually exclusive. We depict them separately to highlight their differences, however, it is possible that organisms integrate across both sources of information to estimate unpredictability (see Section 5).

in the types of information that trigger a response. Ancestral cues carry information about ancestral environments. If particular cues, for example geographic relocations (i.e., moving into a new territory), were reliably associated with environmental unpredictability, then natural selection may have equipped the mind to detect and respond directly to the cue (see Fig. 2). Thus, a developmental response may be triggered by only limited exposure to the cue. This type of proximate mechanism is efficient; organisms do not have to invest much time and energy in learning new cues and their reliability. However, it is also relatively inflexible because organisms are constrained in their abilities to learn new cues, extinguish associations with ancestral cues, or update their knowledge about cue reliability. If a geographic relocation happens to be unrelated to environmental unpredictability for a particular individual in their lifetime, that individual may develop a mismatched phenotype. In addition, relying solely on ancestral cues precludes the use of other sources of information for detecting environmental unpredictability. In this case, if an individual is never exposed to an ancestral cue (e.g., they never move), but there are other cues that are related to environmental unpredictability (e.g., stochastic fluctuations over time in police sirens), the individual may not detect environmental unpredictability.

In contrast, a statistical learning proximate mechanism responds directly to the statistical patterns of change in its environment. Specifically, the organism responds to environmental unpredictability when it detects a prediction error (see Fig. 2). For example, a geographic relocation will not trigger a response unless it renders past experience uninformative (e.g., the previous environment was safe and now it is dangerous). If the level of danger does not change after a relocation, the statistical learning mechanism will not make a prediction error, and therefore it will not trigger a response to unpredictability. This type of mechanism is less efficient than ancestral cues because it requires some amount of accumulated experience to first build a model and then produce predictions. In addition, it must compare its predictions to its current experience to evaluate 'model fit'. If the organism's model fit is continuously poor (e.g., prediction errors remain large throughout extended periods of time), the organism may then conclude the environment is highly unpredictable. However, this type of proximate mechanism is flexible. For example, it can use any source of information or experience that is associated with harshness and variability in harshness to fit any type of statistical model to predict future levels of harshness, but such models may be costly to build and fit. For example, an organism could use time series analysis to estimate autocorrelation or use a moving average to predict current or future harshness; it could also use contingency analysis or directly learn new (non-ancestral) cue reliabilities to learn about the causal relations in the environment (Frankenhuis et al., 2013).

In summary, the central difference between the ancestral cue and statistical learning perspectives lies in the type of information that triggers responses to environmental unpredictability. An ancestral cue mechanism is designed to look for and respond to cues (or categories of cues) that were reliably associated with environmental unpredictability in our evolutionary past. Statistical learning mechanisms need accumulated lived experience and triggers a response when it detects prediction errors. Importantly, our goal was to highlight possible ways organism might detect environmental unpredictability. Formal models will need to consider when organisms should implement one mechanism, the other, or both, depending on the statistical properties of environments over evolutionary and developmental timescales.

4. Implications for measurement

The ancestral cue and statistical learning perspectives have different implications for the measurement of environmental unpredictability. Studies drawing on the ancestral cue perspective need to select and measure the cues that are hypothesized to have indicated environmental unpredictability in our evolutionary past. However, identifying relevant cues is no easy task, especially because it is difficult (if not impossible) to empirically link a proposed ancestral cue or category of cues to (measured) spatial-temporal variation in harshness over evolutionary time. Although ancestral cues cannot be directly verified, the design of psychological mechanisms for responding to ancestral cues can be inferred by examining relations between exposures to hypothesized cues and relevant outcomes (i.e., life history-related traits and underlying biological systems), as per standard scientific methods (Ketelaar & Ellis, 2000).

One way to guide the selection of measures is to map potential cues on to the particular conceptual definition of environmental unpredictability at the ultimate level. For example, assuming environmental unpredictability was stationary, cues should map on to environments characterized by high variance and low autocorrelation in harshness. In this scenario, relevant cues could be related to the level of chaos or family conflict in the home environment. Likewise, there could also be ancestral cues to non-stationary unpredictability. For example, if unpredictability in our evolutionary past involved random change points

in the levels or degree of variation in harshness, relevant cues could be disruptive events that cause shifts in environmental conditions. For example, a parental transition could be a cue to unpredictability because a change in family composition is hypothesized to have been reliably associated with change points in harshness over evolutionary time. There are many potential ancestral cues that map on to stationary or non-stationary unpredictability. Examination of the ethnographic record would be an invaluable source of information about such cues, as it could shed light on potential ancestral cues that were present in hunter-gatherer societies.

In contrast to ancestral cues, studies drawing on the statistical learning perspective need to measure lived experiences across time and compile enough observations to model patterns of variation (e.g., variance, autocorrelation, change points etc.). To do so, researchers could use time series data and analytical techniques for characterizing patterns of change over time (Jebb et al., 2015; Jebb & Tay, 2017). For example, these techniques can decompose variation into predictable and more unpredictable components. Researchers could also calculate autocorrelation in time series data and/or detect change points. Similar to the ancestral cue approach, the key challenge for researchers is selecting the relevant variables to measure over time. Whatever the dimension, the selected variables should relate to environmental harshness. For example, some researchers have analyzed socioeconomic data over time to simultaneously measure harshness and unpredictability (Li, Liu, Hartman, & Belsky, 2018). Specifically, these researchers calculated an individual intercept and slope for each participants' income-to-needs ratio across six time-points. Then, they used individual-level intercepts to measure overall harshness and residual variance (e.g., variance around individual regression lines) to measure unpredictability. This approach is more closely aligned with the statistical learning perspective but residual variance could show different patterns of autocorrelation across individuals. Thus, from a statistical learning perspective, it would also be important to calculate autocorrelation in the data. However, using time series techniques is a double-edged sword—properly leveraging time series data requires many more observations per person than is typical of standard longitudinal designs, which can create practical limitations. Daily diary studies, experience sampling, or long-term longitudinal studies with relatively frequent measurements may be the best study designs to measure unpredictability from a statistical learning perspective.

5. Toward consilience and future directions

The ancestral cue and statistical learning perspectives are not mutually exclusive. In fact, they may operate in parallel. For example, organisms could leverage both sources of information (e.g., ancestral cues and statistical patterns of change) and use them to build a predictive model to estimate unpredictability. The organism could use lived experience as raw data where each experience is weighted equally and accumulates to reveal underlying patterns. If exposed to an ancestral cue, organisms could add them to their predictive models, using weights to account for the ancestral knowledge (i.e., information privileged by natural selection) associated with ancestral cues. Alternatively, individuals may track the statistical patterns of ancestral cues themselves. For example, an ancestral cue may itself be an important environmental dimension that can be tracked over time or space. Imagine that geographic relocations function as an ancestral cue. Organism could track the probability, the frequency, and/or the regularity of moving (e.g., moves occur regularly or irregularly). Thus, ancestral cues could both indicate environmental unpredictability and be integrated together with lived experience to estimate environmental unpredictability.

Another possibility is that ancestral cues indicate when the individual should recalibrate their model of the environment. For example, an organism's environment may be autocorrelated across many dimensions (e.g., level of danger, family conflict, economic conditions). Over the course of development, the organism integrates experiences to estimate the environmental unpredictability (e.g., conditions today will be similar tomorrow). However, upon detection of an ancestral cue, such as a geographic relocation, it may be adaptive to re-estimate these statistics because a move could mean that past conditions are no longer informative for predicting future conditions. As a result, the individual might throw out “old data” in favor of using “new data” (and potentially more representative of current conditions) after a transition occurs. In this scenario, ancestral cues more likely indicate non-stationary unpredictability; they were associated with change points that render older experiences less informative. However, the cue aids prediction by triggering statistical learning to pay attention to new environmental data.

The degree to which we should expect ancestral cues and statistical learning to operate together can be explored theoretically using formal models. For example, a formal model could examine the environmental and somatic conditions under which it is adaptive to use ancestral cues, integrate across current cues, or leverage some combination of both. Likewise, the degree to which ancestral cues and lived experiences are correlated can be tested empirically by measuring both. For example, future studies could measure to what extent geographic relocations across development correlate with stationary environmental unpredictability. If relocations are a reliable cue, they should be associated, on average, with high variance and low autocorrelation in measures of harshness across time. If relocations are a reliable cue to non-stationary unpredictability, researchers could measure harshness over time and track when ancestral cues appear. If ancestral cues indicate non-stationary unpredictability, the statistical properties of harshness should abruptly change after an ancestral cue is detected. For example, imagine that a researcher measures exposure to violence many times across development and calculates its mean, variance, and autocorrelation while also measuring residential moves. One prediction is that one or more statistical properties of violence exposure should abruptly change *after* the move occurs.

The above discussion highlights the need for studies that measure environmental unpredictability from both the ancestral cue and statistical learning perspectives. Ideally, future studies would include traditional measures of environmental unpredictability (e.g., residential changes, parental transitions, job changes, self-report questionnaires) alongside time series data of environmental variables from which the mean, variance, trend, seasonality, and autocorrelation can be estimated. This would allow researchers to explore how measures derived from both approaches operate, covary, and predict outcomes. To measure ancestral cues most appropriately, researchers will need to think carefully about which cues to measure and the type of unpredictability those cues are hypothesized to indicate. To measure unpredictability from a statistical learning perspective, researchers will also need to think carefully about which environmental dimensions to measure and acquire as many observations as possible over time, perhaps using daily diary or experience sampling techniques.

6. Conclusion

Research on environmental unpredictability has progressed rapidly over the past decade. We have argued that theoretical ambiguity at both the ultimate and proximate levels impedes progress. Our goal was to expose ambiguity at both levels and offer potential ways forward. At the ultimate level, we need to be explicit about how we describe the pattern of spatial-temporal variation that defines environmental unpredictability. This means precisely describing the patterns of variability in harshness and explicitly addressing stationarity (as well as what segments of a population environmental unpredictability primarily affects). At the proximate level, we need clear ideas about how organisms might detect environmental unpredictability. Organisms could use ancestral cues, statistical patterns of change, or both, and the specific measures of environmental unpredictability that we employ in

empirical studies should depend on the proximate mechanisms we hypothesize have evolved to detect it. Regardless of these challenges, we believe future research is well-situated to collect measures derived from both approaches and integrate insights. Doing so will refine our understanding of environmental unpredictability and its connection to life history development.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.evolhumbehav.2020.08.006.

References

Behrens, T. E. J., Hunt, L. T., & Rushworth, M. F. S. (2009). The computation of social behavior. *Science, 324*(5931), 1160–1164. https://doi.org/10.1126/science.1169694.

Behrens, T. E. J., Woolrich, M. W., Walton, M. E., & Rushworth, M. F. S. (2007). Learning the value of information in an uncertain world. *Nature Neuroscience, 10*(9), 1214–1221. https://doi.org/10.1038/nn1954.

Belsky, J., Schlomer, G. L., & Ellis, B. J. (2012). Beyond cumulative risk: Distinguishing harshness and unpredictability as determinants of parenting and early life history strategy. *Developmental Psychology, 48*(3), 662–673. https://doi.org/10.1037/a0024454.

Belsky, J., Steinberg, L., & Draper, P. (1991). Childhood experience, interpersonal development, and reproductive strategy: An evolutionary theory of socialization. *Child Development, 62*(4), 647. https://doi.org/10.2307/1131166.

Blaisdell, A. P., Sawa, K., Leising, K. J., & Waldmann, M. R. (2006). Causal reasoning in rats. *Science, 311*(5763), 1020–1022. https://doi.org/10.1126/science.1121872.

Brumbach, B. H., Figueredo, A. J., & Ellis, B. J. (2009). Effects of harsh and unpredictable environments in adolescence on development of life history strategies. *Human Nature, 20*(1), 25–51. https://doi.org/10.1007/s12110-009-9059-3.

Burgess, S. C., & Marshall, D. J. (2014). Adaptive parental effects: The importance of estimating environmental predictability and offspring fitness appropriately. *Oikos, 123*(7), 769–776. https://doi.org/10.1111/oik.01235.

Buss, D. M. (1995). Evolutionary psychology—A new paradigm for psychological science. *Psychological Inquiry, 6*(1), 1–30. https://doi.org/10.1207/s15327965pli0601_1.

Charnov, E. L. (1993). *Life history invariants. vol. 6*. USA: Oxford University Press.

Chisholm, J. (1993). Death, Hope, and sex—Life-history theory and the development of reproductive strategies. *Current Anthropology, 34*, 1), 1–24. https://doi.org/10.1086/204131.

Doom, J. R., Vanzomeren-Dohm, A. A., & Simpson, J. A. (2016). Early unpredictability predicts increased adolescent externalizing behaviors and substance use: A life history perspective. *Development and Psychopathology, 28*(4), 1505–1516. https://doi.org/10.1017/S0954579415001169.

Draper, P., & Harpending, H. (1982). Father absence and reproductive strategy: An evolutionary perspective. *Journal of Anthropological Research, 38*(3), 255–273.

Dunlap, A. S., & Stephens, D. W. (2012). Tracking a changing environment: Optimal sampling, adaptive memory and overnight effects. *Behavioural Processes, 89*(2), 86–94. https://doi.org/10.1016/j.beproc.2011.10.005.

Ellis, B. J., Figueredo, A. J., Brumbach, B. H., & Schlomer, G. L. (2009). Fundamental dimensions of environmental risk. *Human Nature, 20*(2), 204–268. https://doi.org/10.1007/s12110-009-9063-7.

Evans, G. W., Gonnella, C., Marcynyszyn, L. A., Gentile, L., & Salpekar, N. (2005). The role of chaos in poverty and children's socioemotional adjustment. *Psychological Science, 16*(7), 560–565. https://doi.org/10.1111/j.0956-7976.2005.01575.x.

Fawcett, T. W., & Frankenhuis, W. E. (2015). Adaptive explanations for sensitive windows in development. *Frontiers in Zoology, 12*, S3. https://doi.org/10.1186/1742-9994-12-S1-S3.

Frankenhuis, W. E., Gergely, G., & Watson, J. S. (2013). Infants may use contingency analysis to estimate environmental states: An evolutionary, life-history perspective. *Child Development Perspectives, 7*(2), 115–120. https://doi.org/10.1111/cdep.12024.

Frankenhuis, W. E., Nettle, D., & Dall, S. R. X. (2019). A case for environmental statistics of early-life effects. *Philosophical Transactions of the Royal Society, B: Biological Sciences, 374*(1770), Article 20180110. https://doi.org/10.1098/rstb.2018.0110.

Frankenhuis, W. E., Panchanathan, K., & Nettle, D. (2016). Cognition in harsh and unpredictable environments. *Current Opinion in Psychology, 7*, 76–80. https://doi.org/10.1016/j.copsyc.2015.08.011.

Griskevicius, V., Ackerman, J. M., Cantú, S. M., Delton, A. W., Robertson, T. E., Simpson, J. A., ... Tybur, J. M. (2013). When the economy falters, do people spend or save? Responses to resource scarcity depend on childhood environments. *Psychological Science, 24*(2), 197–205. https://doi.org/10.1177/0956797612451471.

Griskevicius, V., Delton, A. W., Robertson, T. E., & Tybur, J. M. (2011). Environmental contingency in life history strategies: The influence of mortality and socioeconomic status on reproductive timing. *Journal of Personality and Social Psychology, 100*(2), 241–254. https://doi.org/10.1037/a0021082.

Jebb, A. T., & Tay, L. (2017). Introduction to time series analysis for organizational research: Methods for longitudinal analyses. *Organizational Research Methods, 20*(1), 61–94. https://doi.org/10.1177/1094428116668035.

Jebb, A. T., Tay, L., Wang, W., & Huang, Q. (2015). Time series analysis for psychological research: Examining and forecasting change. *Frontiers in Psychology, 6*, 727. https://doi.org/10.3389/fpsyg.2015.00727.

Ketelaar, T., & Ellis, B. J. (2000). Are evolutionary explanations unfalsifiable? Evolutionary psychology and the Lakatosian philosophy of science. *Psychological Inquiry, 11*(1), 1–21. https://doi.org/10.1207/S15327965PLI1101_01.

Kolak, A. M., Van Wade, C. L., & Ross, L. T. (2018). Family unpredictability and psychological distress in early adulthood: The role of family closeness and coping mechanisms. *Journal of Child and Family Studies, 27*(12), 3842–3852. https://doi.org/10.1007/s10826-018-1211-4.

Li, Z., Liu, S., Hartman, S., & Belsky, J. (2018). Interactive effects of early-life income harshness and unpredictability on children's socioemotional and academic functioning in kindergarten and adolescence. *Developmental Psychology, 54*(11), 2101–2112. https://doi.org/10.1037/dev0000601.

Maner, J. K., Dittmann, A., Meltzer, A. L., & McNulty, J. K. (2017). Implications of life-history strategies for obesity. *Proceedings of the National Academy of Sciences, 114*(32), 8517–8522.

Marshall, D. J., & Burgess, S. C. (2015). Deconstructing environmental predictability: Seasonality, environmental colour and the biogeography of marine life histories. *Ecology Letters, 18*(2), 174–181. https://doi.org/10.1111/ele.12402.

Mittal, C., Griskevicius, V., Simpson, J. A., Sung, S., & Young, E. S. (2015). Cognitive adaptations to stressful environments: When childhood adversity enhances adult executive function. *Journal of Personality and Social Psychology, 109*(4), 604–621. https://doi.org/10.1037/pspi0000028.

NICHD Early Child Care Research Network (2005). *Child care and child development: Results from the NICHD study of early child care and youth development*. Guilford Press.

Obama, B. (1995). *Dreams from my father: A story of race and inheritance.* (reprinted by New York: Crown (2007) (1995)).

Roff, D. (1993). *Evolution of life histories: Theory and analysis*. Springer Science & Business Media.

Roitberg, B., Sircom, J., Roitberg, C., Vanalphen, J., & Mangel, M. (1993). Life expectancy and reproduction. *Nature, 364*(6433), https://doi.org/10.1038/364108a0 108.

Ross, L. T., & Hill, E. M. (2002). Childhood unpredictability, schemas for unpredictability, and risk taking. *Social Behavior and Personality, 30*(5), 453–473. https://doi.org/10.2224/sbp.2002.30.5.453.

Ross, L. T., Hood, C. O., & Short, S. D. (2016). Unpredictability and symptoms or depression and anxiety. *Journal of Social and Clinical Psychology, 35*(5), 371–385. https://doi.org/10.1521/jscp.2016.35.5.371.

Simpson, J. A., Griskevicius, V., Kuo, S. I.-C., Sung, S., & Collins, W. A. (2012). Evolution, stress, and sensitive periods: The influence of unpredictability in early versus late childhood on sex and risky behavior. *Developmental Psychology, 48*(3), 674–686. https://doi.org/10.1037/a0027293.

Sroufe, L. A., Egeland, B., Carlson, E. A., & Collins, W. A. (2005). *The development of the person: The Minnesota study of risk and adaptation from birth to adulthood*. Guilford Press.

Stearns, S. C. (1992). *The evolution of life histories*.

Szepsenwol, O., Griskevicius, V., Simpson, J. A., Young, E. S., Fleck, C., & Jones, R. E. (2017). The effect of predictable early childhood environments on sociosexuality in early adulthood. *Evolutionary Behavioral Sciences, 11*(2), 131.

Szepsenwol, O., Simpson, J. A., Griskevicius, V., & Raby, K. L. (2015). The effect of unpredictable early childhood environments on parenting in adulthood. *Journal of Personality and Social Psychology, 109*(6), 1045–1067. https://doi.org/10.1037/pspi0000032.

Szepsenwol, O., Zamir, O., & Simpson, J. A. (2019). The effect of early-life harshness and unpredictability on intimate partner violence in adulthood: A life history perspective. *Journal of Social and Personal Relationships, 36*(5), 1542–1556. https://doi.org/10.1177/0265407518806680.

Tooby, J., & Cosmides, L. (1990). The past explains the present—Emotional adaptations and the structure of ancestral environments. *Ethology and Sociobiology, 11*(4–5), 375–424. https://doi.org/10.1016/0162-3095(90)90017-Z.

Vasseur, D. A., & Yodzis, P. (2004). The color of environmental noise. *Ecology, 85*(4), 1146–1152. https://doi.org/10.1890/02-3122.

White, A. E., Li, Y. J., Griskevicius, V., Neuberg, S. L., & Kenrick, D. T. (2013). Putting all your eggs in one basket: Life-history strategies, bet hedging, and diversification. *Psychological Science, 24*(5), 715–722. https://doi.org/10.1177/0956797612461919.

Wieczynski, D. J., Turner, P. E., & Vasseur, D. A. (2018). Temporally autocorrelated environmental fluctuations inhibit the evolution of stress tolerance. *American Naturalist, 191*(6), E195–E207. https://doi.org/10.1086/697200.

Young, E. S., Griskevicius, V., Simpson, J. A., Waters, T. E. A., & Mittal, C. (2018). Can an unpredictable childhood environment enhance working memory? Testing the sensitized-specialization hypothesis. *Journal of Personality and Social Psychology, 114*(6), 891–908. https://doi.org/10.1037/pspi0000124.