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Sources of Behavioral Variability and the Etiology of Psychopathology

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All organisms, including humans, are products of natural selection. As a consequence, any comprehensive explanation of behavior requires at least some engagement with evolutionary theory. No other theoretical approach can so effectively and parsimoniously account for behavior across a wide range of biological taxa and in multiple domains. Life history theory is a similarly powerful metatheoretical framework firmly derived from evolutionary principles. It provides an understanding of how organisms allocate limited time and energetic resources to such essential biological functions as survival, growth, reproduction, and parental investment. Although life history theory is a relatively newer development in the biological sciences—and an even newer development in the human behavioral sciences—it, like evolutionary theory, enjoys substantial cross-taxa empirical support.

Both evolutionary theory and life history theory are particularly valuable for understanding the etiology of psychopathology in that they provide a blueprint of the Platonic ideal of how to "carve nature at its joints." For this reason, Del Giudice's (this issue) work provides a substantial and important contribution to the literature on the etiology of psychopathology. In this commentary, we expand on a key point that Del Giudice makes in his analysis: Psychopathology (and behavior more generally) is a product of the interaction of both stable individual differences (i.e., life history strategies) and situational and environmental factors (both persistent and acute; pp. 263, 265). We consider the case of risk-taking behavior—an area of our own expertise—as an example of the importance of examining acute environmental and situational inputs for behavior. We conclude with a brief discussion of some implications of an interactive approach for the prevention and treatment of psychopathology.

Behavioral Plasticity and the Influence of Acute Situational and Environmental Factors

Del Giudice (this issue) suggests that life history strategies must be functionally self-consistent to be maximally adaptive (p. 262). This characterization of life history strategies is most consistent with the idea that these strategies are analogues of stable individual differences in personality, where personality describes patterns of consistent behavior across situations and contexts. Someone with a "fast" life history strategy, for example, would exhibit behavior consistent with this strategy across multiple contexts. Others have made similar arguments suggesting that stable individual differences in multiple different domains, including personality traits, may be products of specific life history strategies (e.g., Buss, 2009; Mishra, in press; Simpson, Griskevicius, & Kim, 2011; Wolf, van Doorn, Leimar, & Weissing, 2007). In nonhuman animals, the term "behavioral syndrome" has been used to describe patterns of consistent behavior across contexts (effectively animal "personalities"; reviewed in Sih, Bell, & Johnson, 2004; Sih, Bell, Johnson, & Ziemba, 2004). Growing evidence suggests that behavioral syndromes are also in part products of life history trade-offs (e.g., Biro & Stamps, 2008).

Research evidence clearly suggests that individual differences in personality (in humans) and behavioral syndromes (in nonhuman animals) account for important variance in behavior. However, a substantial portion of behavioral variability appears to be a more plastic product of acute environmental and situational inputs. For example, in a meta-analysis, Bell, Hankison, and Laskowski (2009) showed that approximately 35% of the variance in nonhuman animals' behavior could be accounted for by stable individual differences. Of course, we do not mean to imply that behavior can be neatly separated into products of stable individual differences and acute environmental or situational factors (this approach recalls the flawed "person–situation" dichotomy in social psychology; Fleeson & Noftle, 2008; Roberts, Kuncel, Shiner, Caspi, & Goldberg, 2007). Behavior is necessarily the product of a complex interaction between nonindependent individual differences and environmental factors. However, we do seek to emphasize that any comprehensive understanding of a behavioral phenomenon (especially one as complex as psychopathology) requires explicit acknowledgment of the influence of more acute social and environmental inputs.

A perfectly adaptive organism would have infinite behavioral plasticity so as to respond optimally to any and all stochasticity in their environments. Of

course, infinite plasticity is not possible due to necessarily bounded physiological and cognitive limitations. In particular, life history trade-offs impose constraints on phenotypic flexibility due to the necessity of clusters of traits and behaviors co-occurring together (e.g., late growth is incompatible with early reproduction). However, behavioral plasticity is not lost as a product of stable life history strategies. Rather, life history strategies can be considered stable individual differences that predispose—but do not necessitate—certain patterns of behavior. We illustrate the importance of considering more acute environmental and situational influences on behavior by considering the etiology of risk-taking behavior, an area of our own expertise. Risk taking is a particularly useful behavior to examine because there is relatively extensive work demonstrating that it is both a product of stable individual differences (i.e., life history strategies) and acute environmental factors (reviewed in Mishra, in press).

The Case of Risk-Taking Behavior

In the context of life history theory, risk-taking behavior is typically considered to be part of a "fast" life history strategy associated with future discounting, impulsivity, and short subjective life expectancy (reviewed in Del Giudice, this issue; Mishra & Lalumière, 2008). However, risk taking has a complex etiology, and many forms of risk taking appear to be less a manifestation of a life history strategy and more a product of acute situational or environmental inputs. In fact, risk-taking behavior appears to be highly plastic, even within individuals (reviewed in Mishra, in press). Here, we describe some different pathways that have been proposed to lead to varied patterns of risk-taking behavior over the lifespan (Quinsey, Skilling, Lalumière, & Craig, 2004).

Adolescent-limited risk taking is a normative pattern of risky behavior in multiple domains (e.g., promiscuous sexuality, reckless driving, substance use and experimentation, interpersonal conflict, etc.) mostly confined to adolescence and early adulthood (Moffitt, 1993). Adolescent-limited risk taking is in large part a product of acute situational and environmental factors. The adolescent years are marked by particularly intense social competition (just ask anyone about their high school years!), and young people are at steep competitive disadvantage relative to older people who have had greater time to accumulate embodied capital, social status, and resources (Wilson & Daly, 1985; reviewed in Mishra, in press). As a consequence of these competitive pressures, younger individuals engage in greater risk taking in an attempt to obtain outcomes that may not be attainable through safer, low-risk means.

Most people desist from risk-taking behavior as they leave their teenage years behind (Moffitt, 1993). This reduction in risk-acceptance corresponds with acute changes in the costs and benefits of risk taking. Marriage, a stable job, and having children are reliably associated with reductions in risky behavior later in life (reviewed in Mishra & Lalumière, 2008). Notably, those who lose this stability later in life (e.g., by being widowed, or divorced) engage in subsequently greater risk taking (Daly & Wilson, 2001), suggesting relatively high plasticity in behavior. Of course, not everybody desists from risk taking after the teenage years; there are those who continue to engage in persistent risk-prone behavior, largely due to more stable individual differences linked with particular life history strategies (e.g., low embodied capital resulting in persistent competitive disadvantage; Mishra, in press; Mishra, Barclay, & Lalumière, 2014; Mishra & Lalumière, 2008).

Other evidence for the plasticity of risk-taking behavior comes from experimental studies demonstrating support for risk-sensitivity theory. Risk-sensitivity theory posits that decision makers engage in risk taking when low-risk options are unlikely to meet one's desired goals or outcomes (Mishra, in press; Mishra & Lalumière, 2010). In circumstances of need—great disparity between one's present and desired or goal states—risk taking allows for obtaining outcomes that might otherwise be unavailable or unattainable through safer, low-risk means. Several experimental studies have shown that acute manipulations of the perception of need lead to immediate changes in risk propensity, consistent with risk-sensitivity theory (reviewed in Mishra, 2014). These immediate changes in risk taking have also been shown to occur independent of stable individual differences in risk propensity (e.g., Mishra & Lalumière, 2010; Mishra, Daly, Lalumière, & Williams, 2012).

For example, Mishra et al. (2012) showed that people from disadvantaged socioeconomic backgrounds who had demonstrably engaged in persistent risky behavior (e.g., problem and pathological gamblers, ex-convicts, drug addicts) are actually risk-sensitive decision makers who modulate risk acceptance as a product of environmental cues. Risk-persistent participants in this study clearly exhibited a constellation of behaviors consistent with a stable "fast" life history strategy. In their everyday environments, they engaged in domain-general risk taking, including substance abuse, problem gambling, and property and violent crime. However, in laboratory tasks that manipulated the perception of need in domains they were unfamiliar with (i.e., in computer game–like tasks involving foraging for digital apples to "survive" and earn money), participants exhibited adaptive risk-sensitive behavior. That is, they were

risk accepting when far from a goal (i.e., in a situation of high need), but acutely shifted to risk avoidance when risk taking was unlikely to provide positive outcomes (i.e., when the costs of risk taking exceeded the benefits).

These results suggest that although those in impoverished environments appear to engage in stable, risk-persistent behavior in their everyday environments, they are also sensitive to acute environmental and situational cues regarding the costs and benefits of risk taking. Thus, what may appear to be a "fixed" fast, risk-prone life history strategy may instead be a plastic product of environmental inputs that consistently facilitate risk taking. Risk-persistent individuals may experience what has been termed *enduring situational evocation*, whereby certain consistent environmental features elicit persistent patterns of behavior (Buss & Greiling, 1999). Such persistent behavior may thus be a result of behavioral plasticity, not stable life history strategies or individual differences. Consistent with this hypothesis, some evidence suggests that people often make risk-sensitive decisions independent of stable individual differences in risk-propensity (Mishra et al., 2012; Mishra & Lalumière, 2010; reviewed in Mishra, in press).

Of course, at the other end of the spectrum, there are individuals who demonstrate very low levels of behavioral plasticity in the domain of risk taking. Those who fit the criteria for psychopathy (an extreme manifestation of antisocial personality disorder) show a pattern of persistent risk-taking behavior across the lifespan that appears to be largely a product of genetic influences (Lalumière, Mishra, & Harris, 2008; Mealy, 1995). Similarly, those who have been severely physiologically disadvantaged early in life by experiencing such neurodevelopmental insults as head trauma/brain injury, maternal substance abuse, or obstetrical complications also engage in persistent and relatively inflexible risk taking across the lifespan (reviewed in Mishra, in press; Mishra & Lalumière, 2008). This is especially true when these neurodevelopmental insults interact with impoverished social environments involving such negative experiences as parental divorce, sexual and physical abuse, and poor nutrition, among others (Moffitt & Caspi, 2001; Rutter, 1997). These more stable patterns of risk-taking behavior behavior—psychopathy and (what has been termed) *life-course-persistent offending*—likely correspond to more stable life history strategies that are a product of more persistent inputs (i.e., genes and early developmental environments).

A consideration of the etiology of risk taking is useful for more generally understanding the complexity of behavior of any kind, including psychopathology. Explaining behavior requires elucidation of multiple causes: genetic influences, early developmental environments, stable environmental cues, and more acute environmental or situational factors. Any comprehensive framework for understanding behavior must therefore explicitly acknowledge multiple sources of variation for behavior, and caution must be exercised when invoking any particular explanations (e.g., individual differences vs. situational factors; Fleeson & Noftle, 2008; Roberts et al., 2007).

Implications for Prevention and Treatment of Psychopathology

Del Giudice's life history analysis of psychopathology provides a naturalistic understanding of what factors predispose people to suffering from certain disorders. This approach focuses on explicating the sources of stable individual differences in life history strategies, which in turn are associated with certain clusters of psychopathology. Although the life history approach is certainly very useful in elucidating the etiology of psychopathology—"carving nature at its joints"—it has fewer direct implications for treatment. One of the virtues of a focus on identifying acute environmental and situational cues that facilitate psychopathology is that this approach offers a direct pathway for treatments and interventions. The life history strategy approach to psychopathology, by contrast, offers more by way of prevention strategies (similar to the ecologically relevant prescriptions provided by Ellis et al., 2012, for reductions in adolescent risk taking). Collectively, the two approaches provide a complementary, powerful, and comprehensive framework for treatment, intervention, and prevention of psychopathology.

The case of depression provides an excellent illustration of the importance of considering both acute situational/environmental cues and life history predispositions for the treatment and prevention of psychopathology. Growing evidence suggests that depression serves the adaptive function of focusing one's analytical attention on an instigative problem through substantially increased rumination (reviewed in Andrews & Thomson, 2009). Research suggesting that depressed people have enhanced ability to solve analytical problems is consistent with this hypothesis (e.g., Braverman, 2005; Storbeck & Clore, 2005; reviewed in Andrews & Thomson, 2009). This understanding of depression emphasizes the importance of targeting acute environmental and situational factors that facilitate depressive symptoms for treatment. The adaptive model of depression has other implications for treatment, including reduced use of antidepressant drugs (which interfere with people's ability to ruminate), and a focus on analytical thinking in cognitive behavioral therapy sessions (Andrew & Thomson, 2009; Andrews, Thomson, Amstadter, & Neale, 2012).

By contrast, a life history approach to the problem of depression would be most effective when guiding prevention strategies as opposed to treatment strategies. A fast–slow framework of understanding individual differences helps to identify those individuals who are most susceptible to psychopathology like depression. Prevention strategies could thus be designed and targeted to reduce the baseline risk of the development of psychopathology by highlighting conditions that facilitate susceptibility to mental disorder. It is clear that both life history–facilitated predispositions and acute environmental and situational factors must be considered to most effectively address both prevention of psychopathology (through addressing root causes of dysfunctional or maladaptive life history strategies) and treatment of psychopathology (after symptoms have already manifested) wherever possible.

Finally, one particularly important implication of Del Giudice's naturalistic, evolutionary-based framework of psychopathology (as well as other evolutionarily guided frameworks) is that there are normative, "natural" biological mechanisms that give rise to such dysfunctional or unwanted outcomes as mental disorder. In our view, communicating this reality to those suffering from mental disorder for psychopathology allows for a far more productive starting point for interventions and treatments. One can imagine that it would be much more affirming to those seeking treatment to start with an understanding of their experience as a product of natural processes (rather than as "disease" that can be cured in a biomedical sense). Of course, we must be careful to not to commit the naturalistic fallacy—the mistake of proclaiming that what is natural must necessarily be desirable, good, or excusable (especially in the case of more antisocial forms of psychopathology, e.g., psychopathy, that cause harm to others). Rather, we advocate facilitating understanding among sufferers of psychopathology that normally functioning mechanisms often give rise to dysfunctional, disordered, and/or unwanted behaviors. This approach is particularly valuable in our present sociocultural climate where those who suffer from psychopathology are stigmatized and marginalized because of their suffering from a "disease." Such a starting point would allow for more productive engagement with effective treatment strategies that reduce distressing outcomes for sufferers of mental disorder.

Del Giudice's evolutionary life history approach for understanding psychopathology is an important and substantial addition to the scientific literature. Del Giudice provides a compelling framework for understanding the sources of individual differences in susceptibility to psychopathology. In this commentary, we suggest that this laudable approach is effectively complemented with a consideration of more acute situational and environmental influences on the development and manifestation of psychopathology. Understanding psychopathology as a product of both stable individual differences in predispositions
(i.e., life history strategies) and more acute situational and environmental factors allows for a more comprehensive approach for prevention and treatment of mental disorder. Nature does not give up its secrets easily, and frameworks such as Del Giudice's are a needed step in the right direction.

Note

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