

Reconciling the Tension Between Behavioral Change and Stability

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The ability of organisms to show highly flexible behaviors in response to life-stage transitions, seasonal cues, and environmental change often seems at odds with observations of consistent differences in behavior among individuals, populations, and species. I suggest that resolving this apparent contradiction requires understanding of the proximate mechanisms underlying both behavioral change and stability. A review of neuroendocrine mechanisms suggests that stable differences in behavior among individuals is underlain by structural variation in neuroendocrine components, and this relatively inflexible scaffold is needed to enable more flexible components to function. In particular, there is evidence that patterns of investment in distinct brain circuits produce tradeoffs in neural function that account for variation in personality traits among individuals. Thus, understanding where individuals fall on this spectrum of tradeoffs may help in constructing more individualized approaches to human behavioral change that take into account differences among individuals in how they perceive the world and make decisions.

What Is Behavioral Change?

Behavior is the activity of an individual and constitutes every action (or inaction) the individual engages in over the course of its life. Because organisms are constantly changing their activities on a daily, monthly, or annual cycle, it often seems that the default state of behavior is one of change; however, this change has consistent patterns. In particular, individuals often show consistent differences in

the level or intensity of expression of particular behaviors either across contexts (Sih, Bell, & Johnson, 2004) or over time within a context (Mischel & Shoda, 1995), reflecting a core stability in personality or temperament. In this chapter, I explore why such stability in expression of behavior occurs and how it might influence the ability of an individual to change its behavior over time. Answering these questions requires an understanding of the underlying physical basis for the expression of behavior. But before going into neuroendocrine mechanisms, it's important to delineate what I mean by behavioral change, since there are many different types of behavioral change and different mechanisms are linked to different types of change, including the inability to change.

In evolutionary biology, the 1980s brought a revival of interest in phenotypic plasticity (Pigliucci, 2005), yet most studies of plasticity focused on traits that were developmentally plastic, in which variable environmental conditions during ontogeny (i.e., from conception to reproductive maturity) produced drastically different adult phenotypes that were fixed for the life of the organism (Piersma & Van Gils, 2011). However, as the study of phenotypic plasticity matured, it became clear that the focus on developmental plasticity left out a number of plastic traits that changed in response to environmental variation throughout an organism's life. Filling in this gap, Piersma and Drent (2003) suggested the term "phenotypic flexibility" for types of plasticity that are reversible.

Yet even this expansion of the definition of plasticity to include more flexible traits that change within the lifetime of an organism does not fully capture the range of environmental influences on behavior. This is because flexibility is an inherent component of every behavior—all behaviors are reversible because they are only expressed in response to an internal or external stimulus; yet, at the same time, their *level* of expression may be developmentally plastic and highly consistent in adulthood, or it may be developmentally plastic and still retain some flexibility throughout life (Duckworth, 2009). Because developmental plasticity implies limits to postontogenetic change, it is often neglected as a cause of variation in behavioral traits. However, the processes that occur during ontogeny are fundamentally similar for all biological systems, including the neuroendocrine system, and thus, behaviors are no different from morphological traits in the importance of developmental plasticity to influence postontogenetic expression (Duckworth, 2015).

During development, tissues differentiate, grow, and mature, and this process requires a massive incorporation of resources to build an organism. Because of this, early ontogeny is a unique window when traits are particularly sensitive to environmental inputs, and once developmental processes come to an end, some components of traits are essentially fixed in expression for life. This process applies equally to the physical basis of behavioral traits—the nervous and endocrine

systems must also go through a process of cellular differentiation and growth in which they are particularly susceptible to environmental influences (Knudsen, 2004). Thus, similar to morphological traits, this finite period of growth and tissue organization is a sensitive period for behavioral development, when environmental information is incorporated on a large scale, shaping neuroendocrine structures and essentially limiting the range of variation that is possible later in life. While well established for the phenotype in general, the role of early development in producing behavioral variation has been controversial, particularly for complex human behavior. This stems in large part from a discomfort with the notion that complex behavior can be reduced to neural physiology (Bickle, 2006; Marshall, 2009). Moreover, there seems to be a general implicit assumption in psychology that complex human behavior requires the input of a complex social environment, and therefore any processes that occur after birth override prenatal influences on variation in behavior. This is evidenced by the fact that studies of human behavioral development tend to focus on the influence of the early social and cultural environment experienced by children, rather than the physiological processes that might influence behavioral development during the prenatal environment (Buss & Plomin, 2014). Yet the most massive and profound changes in the neuroendocrine system occur during the period from conception to birth. Elements of neuroendocrine structure and organization are entrenched during this time that cannot be changed later in life. This is evident in the severe effects of early exposure to diseases, drugs, and malnutrition on brain development and function (Kolb, 1995; Riley & McGee, 2005). However, what is less clear is whether more subtle environmental variation can influence brain development during this period in ways that permanently alter the normal range of variation in the behavior of adults. Given the ubiquity of such subtle, and often adaptive, environmental influences on other morphological traits, there is no logical reason to suppose that neuroendocrine systems would be immune to such influences, and recent studies of epigenetic effects, some of which are induced even before conception, support this idea. For example, in rats, housing fathers in a more complex environment before mating influenced both brain methylation patterns and behavior of their offspring (Mychasiuk et al., 2012). This particular finding mirrors a growing body of evidence in animals for early developmental effects on the expression of natural variation in behavior (Meaney & Szyf, 2005). Moreover, studies on temperament traits in humans show early developmental effects on behavior that are evident even in the fetus (Werner et al., 2007). Thus, permanent differences among individuals in temperament or personality traits may in part be due to environmental influences that act very early in development and organize structural components of the neuroendocrine system, since these are the

components that are most difficult to change postdevelopment (Duckworth, 2010, 2015).

Evidence Linking Personality Variation and Neuroendocrine Structure

Given the complexity of the neuroendocrine system, the idea that personality varies with the structure of neuroendocrine components, such as the size and composition of distinct brain regions, may seem overly simplistic; however, there is substantial evidence in both animal and human studies for a link between the two.

Variation in brain morphology is linked to affective and personality disorders in humans—for example, pituitary size has been linked to schizophrenia (Nordholm et al., 2013; Takahashi et al., 2011) and hippocampal, hypothalamic, and amygdala volumes have been linked to borderline personality disorder (Kuhlmann, Bertsch, Schmidinger, Thomann, & Herpertz, 2013; Schmahl, Vermetten, Elzinga, & Bremner, 2003). There is also evidence that structural variation in the brain is correlated with the normal range of variation in personality (DeYoung et al., 2010). For example, Bjornebekk and colleagues (2013), using the five-factor model of personality variation, found that neuroticism is negatively correlated with overall brain size, white matter microstructure, and frontotemporal surface area. Cremers and colleagues (2011) found that orbitofrontal and right amygdala volume were both positively related to extraversion, and Fuentes and colleagues (2012) showed that individual differences in anxiety-related personality traits were associated with reduced size of brain structures related to emotional control and self-consciousness. These are but a few of the now numerous studies that have found personality variation reflected in underlying structural variation in the brain (see Kennis, Rademaker, & Geuze, 2013, for review). Such correlations do not necessarily prove that structural variation in the brain is the cause of personality, but they are at least consistent with the idea.

Experimentally teasing apart cause and consequence of links between brain structural morphology and behavior is difficult in humans due to ethical considerations. However, evidence from animal studies supports a causal link between the two. For example, artificial selection on natural variation in guppy (*Poecilia reticulata*) brain size produced a correlated response in personality traits (Kotrschal et al., 2014), suggesting that changes in brain size across generations are causally linked to changes in personality traits. Another study used transgenic mice to attempt to understand the frequently observed correlation in humans between smaller hippocampal volume and anxiety-related personality disorders (Persson et

al., 2014). By creating mice that expressed the CYP2C19 gene, a gene that has an enzyme metabolic function in the human brain, they showed that mice with the gene developed a smaller hippocampus compared to mice without it and had impaired adaptation to stress as adults. Because the gene is expressed only in the fetal brain, it provides evidence that morphological changes in the brain precede behavioral changes observed in adults later, suggesting a causal role for reduced hippocampal volume during ontogeny and increased stress and anxiety in adulthood.

A causal connection between structural variation in the brain and personal variation may reflect tradeoffs between relative investment in different brain regions. Because structural components of the neuroendocrine system are the most stable across an organism's life and the least likely to change on short time scales (Duckworth, 2015), their potential influence on personality variation provides a mechanistic basis for consistency of behavior across an individual's life and also suggests that personality itself provides a stable framework for the expression of behavioral flexibility and change. Moreover, if subtle differences in structural variation of the brain do reflect tradeoffs in investment, it suggests that personality variation should be influenced by variation across all regions of the brain (i.e., there is no one region that can explain personality variation) and, in turn, personality variation should influence all aspects of behavior. In this sense, personality variation essentially lays the foundation on which behavioral responses are built. Thus, personality does not preclude behavioral flexibility and may even enable it, in the same way that the relatively inflexible structure of the skeletal system in vertebrates enables an animal to walk, run, and do other flexible activities.

Do Tradeoffs in Neural Processes Underlie Personality Variation?

Behavior is the final outcome of integration between many underlying neurobiological processes and information about current context and internal organismal state. Sensory information is processed in the brain by cognitive, motivation, and emotion circuits that, in turn, influence the decisions an individual makes and the transitory state of the individual's mood. The ultimate outcome of integration among all components of this dynamic system is behavior.

There is evidence that structural variation in the brain, rather than having isolated effects on distinct behaviors, influences how information is gathered, integrated, and processed via tradeoffs in function. An example of this is in decision-making processes. Recent studies have shown that personality not only

influences the process of decision making but also can influence decision-making competence (Bensi, Giusberti, Nori, & Gambetti, 2010; Dewberry, Juanchich, & Narendran, 2013; Maner et al., 2007). A potential basis for this link between personality and decision making is the speed-accuracy tradeoff, in which decisions can be made slowly with high accuracy or fast with high error rate (Chittka, Skorupski, & Raine, 2009). This tradeoff has a clear neurobiological basis (Bogacz, Wagenmakers, Forstmann, & Nieuwenhuis, 2009) and studies have shown distinct patterns of brain activity and connectivity among both individuals that preferentially prioritize speed versus accuracy and individuals that vary in their ability to flexibly adjust their level of caution (sometimes prioritizing speed, sometimes accuracy) (Forstmann et al., 2010; Perri, Berchicci, Spinelli, & Di Russo, 2014). Moreover, variation in how individuals deal with this tradeoff has been shown to relate to a variety of personality dimensions, such as risk sensitivity (Nagengast, Braun, & Wolpert, 2011), agreeableness (Bresin, Hilmert, Wilkowski, & Robinson, 2012), and neuroticism (Socan & Bucik, 1998).

Another potential neural tradeoff is between executive functions and the default mode network. Executive functions are cognitive processes that include control of attention, reasoning, problem solving, and planning, whereas the default mode network activates in the absence of external task demands and is associated with cognitive processes such as mind-wandering, future thinking, and perspective taking.

These two functions are associated with distinct regions of the brain and show an antagonistic pattern of activation—when attention to a task is required, the regions related to executive function are activated, and the default mode network is deactivated (Fox et al., 2005). Interestingly, individual variation in creative cognitive ability corresponds to structural variation in the brain regions associated with the default mode network (Jung, Mead, Carrasco, & Flores, 2013). Moreover, executive control and default mode networks are not always antagonistic in activation. Executive control prevails when study participants are required to have focused attention on an external task, and the default mode network prevails when there is no task. However, when study participants were asked to complete a task that required internal reflection, the two networks were activated simultaneously in a cooperative fashion (Beatty, Benedek, Kaufman, & Silvia, 2015). Importantly, both individual variation in executive function and structural variation in the brain underlying this network correlate with variation in personality; a strong executive function is associated with high conscientiousness, low neuroticism, and higher agreeableness (Williams, Suchy, & Rau, 2009). Moreover, individuals who showed higher impulsiveness had lower cortical thickness in areas associated with executive function (Schilling et al., 2012). Finally, there is evidence for competition between executive function, particularly in areas associated

with higher-level reasoning and future planning and emotion circuits of the limbic system that are associated with making decisions that give immediate rewards (McClure, Laibson, Loewenstein, & Cohen, 2004).

Taken together, these studies suggest that there is substantial variation among individuals in decision-making processes that is related to personality, and that this variation is underlain by variation in structural components of the brain. This suggests that personality variation among individuals may reflect where they fall along the spectrum of various neurological tradeoffs in the brain. Because there are multiple interacting tradeoffs (e.g., speed versus accuracy, attentional control versus mind-wandering, and immediate versus delayed gratification), this may explain why personality variation is a multidimensional complex trait that cannot easily be summarized on a single axis.

Studies on stress-induced phenotypes and coping styles in animals suggest that variation in personality traits may be due to the interaction between genetic variation and maternally induced stress during early development (Duckworth, 2015), and the phenotypes associated with stress are consistent with the tradeoffs outlined above. Many long-term consequences of early developmental stress are caused by a resetting of fetal hypothalamic–pituitary–adrenal (HPA) axis sensitivity, which is a major cause of variation in many behavioral traits, including personality (Koolhaas et al., 1999; Meaney & Szyf, 2005; Seckl & Meaney, 2004). The HPA axis comprises the hypothalamus, anterior pituitary, and adrenal gland, along with the hormones they secrete and to which they respond. In the brain, activity in the interconnected amygdala, hippocampus, and hypothalamus activates and regulates the HPA axis (Charmandari, Tsigos, & Chrousos, 2005). Interestingly, these are the parts of the brain that seem to be most intimately tied to the tradeoffs outlined above, since the amygdala mediates value judgments about external stimuli (Janak & Tye, 2015), the hypothalamus mediates reactions to stress and can impair performance in the prefrontal cortex specifically in relation to executive functions (Phelps, Lempert, & Sokol-Hessner, 2014), and the hippocampus is part of a functional loop designed to detect novelty and to transmit behaviorally significant information into the storage of long-term memory (Lisman & Grace, 2005), thus acting as a liaison between sensory systems, information acquiring and valuation systems, and higher cognitive processes. Finally, these systems are also the most highly influenced by developmental stresses experienced in the prenatal environment (Charil, Laplante, Vaillancourt, & King, 2010).

Stress-induced behavioral phenotypes are thought to be adaptive, preparing individuals for a harsh environment (Badyaev, 2005; Korte, Koolhaas, Wingfield, & McEwen, 2005; Wells, 2003). For example, in animals, aggression is related to stress coping style, with more aggressive individuals being bolder, less exploratory,

taking more risks in the face of potential dangers, and showing lower behavioral flexibility compared to less aggressive individuals. The aggressive strategy requires higher energy consumption and is thought to be advantageous in stable environments where food is abundant; whereas the nonaggressive, more behaviorally flexible type is thought to flourish in more stressful environments where resources are scarce. There is evidence from wild birds that such differences may be maintained by fluctuating selection, because food availability, which fluctuates across years, was a major determinant of survival of birds that differed in exploratory behavior (Dingemanse, Both, Drent, & Tinbergen, 2004).

Most importantly, the way that these distinct personality types deal with environmental challenges and stress is very different—proactive animals, because they rely on routines, are better at performing tasks despite minor distractions, but adapt slowly to changes in the environment; whereas reactive types are easily distracted but adapt to novel conditions faster (Coppens, de Boer, & Koolhaas, 2010). Such differences in adaptability between proactive and reactive types has been hypothesized to lead to divergent risks of disease and psychological problems in humans (Korte et al., 2005).

Implications for Human Behavioral Change

If a major cause of personality variation among individuals is stress-induced structural variation in the neuroendocrine system that cannot change substantially postdevelopment, then what are the implications of this for human behavioral change? First, it impacts our understanding of which aspects of behavior cannot be easily changed postdevelopment, and second, it implies that there may be substantial differences among individuals in how behavioral changes arise.

One of the main functions of the brain is to integrate novel information to allow the organism to respond flexibly to challenges. Yet, at the same time, the adult brain must preserve the circuitry and synaptic organization necessary to maintain continuity of behavior and long-term memories. Moreover, even though neural plasticity persists throughout the life span (Lledo, Alonso, & Grubb, 2006), it is highly constrained in the adult compared to the developing brain (Kolb, 1995). Large-scale reorganization of axons, dendrites, and myelination are limited in the adult brain because these structures provide a stable scaffold underlying neural circuits and, as a result, changes in structure are local and often short term (Bavelier, Levi, Li, Dan, & Hensch, 2010). Thus, the tension between behavioral stability and change is reflected in a similar tension between stability and change at the neural level. In general, neural rewiring is costly (Laughlin & Sejnowski,

2003), and this may lead to significant switching costs to changing behavior patterns (Wood & Runger, 2016).

If, as I suggest, personality variation reflects where individuals are on different ends of a continuum in neural tradeoffs, individuals should have different thresholds for responding to threat, engaging in social interaction, getting distracted, exploring their environment, and seeking out novelty. In animal studies, divergent ends along the personality spectrum are typically thought to reflect fitness tradeoffs, with some individuals being better adapted to more stressful or variable environments while others perform best in more benign or stable environments. However, in humans, some axes of personality variation are typically viewed as nearly universally positive or negative. For example, neuroticism is typically thought of as negative, and higher scores on this personality axis are associated with numerous psychological and health problems. Neurotic individuals are known to have a heightened sensitivity to threat (Perkins, Arnone, Smallwood, & Mobbs, 2015) and one relatively unexplored possibility is that high neuroticism is part of a stress-induced phenotype in humans that enables individuals to respond faster to potential threats. If so, then there may also be benefits to high neuroticism that perhaps are not evident in stable and benign environments, where thoughtful and reflective decision making is most highly valued. As evidence for this, individuals who were more neurotic did not experience the speed-accuracy tradeoff such that, under pressure, their accuracy increased with faster decision times (Bell, Mawn, & Poynor, 2013). Moreover, people high in neuroticism were less accurate if they slowed down on a task following error feedback (Robinson, Moeller, & Fetterman, 2010). These studies suggest that, in some contexts, there are benefits to high neuroticism, a point that has been made by others in the context of understanding the evolutionary maintenance of personality variation (Nettle, 2006) and attachment styles (Ein-Dor, Mikulincer, Doron, & Shaver, 2010). At the other end of the spectrum, extraversion is usually associated with positive health and psychological outcomes; yet at extreme levels, extraverts have a higher risk of bipolar disorder (Watson, Stasik, Ellickson-Larew, & Stanton, 2015). Thus, attributing strictly positive or negative attributes to personality dimensions irrespective of context is not warranted. Instead, problems are more apt to arise when individuals are at the extremes of any of the personality dimensions, and this raises the question of whether it is possible to moderate neural tradeoffs to allow individuals to become more centered in neural functions.

If personality variation is underlain by numerous tradeoffs in neural functioning that, in turn, are underlain by variable patterns of investment in distinct brain regions, then techniques that enable better integration across distinct cognitive, emotion, and sensory circuits may be the most powerful strategies for producing

long-term behavioral change. There is evidence that mindfulness-based meditation practices, which engage sensory, emotion, and cognitive functions (Brown, Ryan, & Creswell, 2007), can change the underlying structure of the brain in multiple areas that are known to affect personality, potentially moderating some of the tradeoffs in neural function discussed above (Holzel et al., 2011). There is also evidence that physical activity can impact brain structural properties, enhance cognition and aspects of executive function, and affect mood, emotion, and anxiety (Cotman, Berchtold, & Christie, 2007; Voelcker-Rehage & Niemann, 2013). Finally, neurobiological studies of cognitive behavioral therapies for anxiety and depression suggest that these strategies work by rebalancing activity in regions of the brain associated with emotion regulation and executive function (Clark & Beck, 2010). Thus, interventions can have powerful effects on human behavior by changing the underlying activity patterns and structural organization of the brain associated with functional tradeoffs. In particular, strategies of intervention that engage multiple attentional, physiological, cognitive, or emotional circuits in the brain, such as mindfulness, physical activity, or cognitive therapy programs, may be particularly effective in rebalancing tradeoffs among different components. Moreover, one unexplored possibility is that different personality types may respond differentially to different types of therapies that touch on distinct aspects of these tradeoffs. While recent assessments of various therapy techniques show that many are effective (Hayes, Villatte, Levin, & Hildebrandt, 2011), there is always a portion of the population that is not responsive to treatment. It would be informative to investigate whether personality variation explains some of the variance in treatment efficacy.

In conclusion, I suggest that a better understanding of both stability and flexibility of the physical basis of behavior is essential to understanding behavioral change. Therapies that take into account where individuals fall on the spectrum of various neurological tradeoffs that influence their attention, level of anxiety, and decision-making strategies may be most effective in producing long-lasting behavioral change. Thus, recognizing the limits of behavioral flexibility and patterns of behavioral stability across individuals may be the most important step in understanding how lasting behavioral change occurs.

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