

CHAPTER 5

Personality Neuroscience

A Developmental Perspective

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From birth through old age, individual human beings are at least somewhat predictable. Some 5-year-olds are consistently more fearful or more talkative than others, and so are some 75-year-olds. People exhibit clear consistencies in their thoughts, emotions, motivations, and behaviors. Individual differences between people in these consistent patterns are sufficiently reliable that the concept of “personality” is self-evident to most people, and it has been well established scientifically, too. But where do differences in personality come from? This is one of the major questions that personality psychology aims to answer, and it is also one of the most difficult. Most research on this question has focused on what can be called the *distal causes* of personality, trying to determine to what extent differences in personality traits are caused by genetic versus environmental forces, then trying to understand how specific genes and specific environmental forces shape personality. In contrast, in this chapter, we focus on the *proximal causes* of personality in the brain.

Researchers have begun to make substantial progress toward understanding the neurobiological systems underlying personality only in the last two decades. Nonetheless, the field of personality neuroscience is growing quickly, and its findings are beginning to have important implications for understanding personality development over the life course. Such

research is crucial for a full understanding of where personality comes from because all behavior and experience, aside from the simplest spinal reflexes, is generated by the brain. Thus, even environmental influences on personality are “biological,” in the sense that the environment must have a lasting effect on the brain in order to influence personality. When personality changes, whether at age 5, 35, or 75, the brain necessarily changes, too. In this chapter, we go beyond previous summaries of personality neuroscience research by attempting to link what is known about the neural correlates of personality to what is known about brain development.

Before attempting to understand the sources of personality from a developmental perspective, one needs to have a reasonably robust picture of the structure of personality across the life course and how it changes over time. By “structure,” we mean the patterns of traits that tend to appear together in individuals; this is interpersonal structure, in contrast to the intrapersonal structure of one individual’s personality. By early childhood, personality appears to have roughly the same interpersonal structure that it does in adulthood, with most individual differences well captured by one of five broad trait dimensions known as the “Big Five”: extraversion, neuroticism, conscientiousness, agreeableness, and openness/intellect (Caspi &

Shiner, 2006; Mervielde, De Clercq, De Fruyt, & Van Leeuwen, 2005). The Big Five show increasing rank-order stability from childhood to old age, when they finally begin to become less stable again, but even in adulthood they are not immune to change or disruption (Roberts & DelVecchio, 2000; Roberts, Walton, & Viechtbauer, 2006; Soto, John, Gosling, & Potter, 2011; Specht et al., 2014). In addition to increasing rank-order stability, they show normative patterns of mean-level change, with particularly large changes in adolescence and young adulthood followed by more gradual changes over the rest of the lifespan. These patterns of stability and change can be meaningfully linked to brain development.

Personality neuroscience has two main goals: (1) to identify stable patterns of brain functioning that are proximally responsible for personality and (2) to understand how those patterns are shaped by more distal causal factors in the genome and the environment. Both goals have important connections to development. By understanding the maturation of biological systems, personality researchers will be better equipped to explain the patterns of continuity and change in personality that occur over the course of development. Additionally, the reverse may be true as well: Understanding how personality changes may help guide hypotheses about neural processes. Research on personality development has already provided a wealth of data showing how developmental factors (e.g., stress and adversity, life transitions) are related to personality functioning (e.g., Shiner, Allen, & Masten, 2017; Specht, Egloff, & Schmukle, 2011). Adding a neuroscience perspective allows us to better understand the mechanisms involved in these transactions.

As with all scientific endeavors, personality neuroscience is likely to be most effective in pursuing its goals when guided by sound theory. A number of theories have attempted to identify the psychological mechanisms underlying each of the Big Five (Denissen & Penke, 2008; DeYoung, 2015; Nettle, 2006, 2007; Van Egeren, 2009), and they are sufficiently similar to suggest that we can identify the general type of mechanism involved in each trait dimension. This perspective has two implications that are particularly useful for a developmental approach to personality neuroscience. First, once the psychological functions underlying traits are made explicit, existing knowledge about how those functions are carried out by the brain,

and how the relevant brain systems develop, can be used to form neuroscientific hypotheses. Importantly, any given psychological function is likely to be affected by many different neural parameters. Further, a given neural parameter, such as the density of a particular neurotransmitter receptor, may influence multiple psychological functions. Hence, the mapping of traits to their neurobiological sources is likely to be many-to-many, not one-to-one (Allen & DeYoung, 2017; Yarkoni, 2015).

Second, identifying the psychological functions underlying traits helps to account for *heterotypic continuity*, in which the same traits have different manifestations at different times during development. Many of the patterns of behavior and experience that the Big Five describe in adulthood may not be applicable in childhood; nonetheless, the same underlying psychological functions may be at work across the lifespan. For example, the interest in poetry or philosophy that is characteristic of adults high in openness/intellect is unlikely to be apparent in childhood, but the underlying mechanisms of this trait are nonetheless likely to be apparent in the child's curiosity and imaginative play. Thus, theories that identify the mechanisms underlying traits are crucial for a lifespan developmental perspective on personality. Additionally, heterotypic continuity may be a useful guide to personality neuroscientists, as traits reflecting the same psychological mechanism are likely to have considerable continuity in their biological mechanisms as well.

Developmental Origins of Personality

Personality can be considered to encompass all reasonably persistent psychological individual differences, incorporating not just broad traits such as the Big Five but also specific goals, beliefs, skills, and roles that people acquire through experience, and even conscious identity or life narrative (DeYoung, 2015; McAdams & Pals, 2006). Because most of these latter constructs have received little attention from a neurobiological perspective, we focus exclusively on traits. Research on psychological traits has historically been conducted under two distinct headings, temperament and personality, depending on the age of the individuals under study. "Temperament" has typically been used by developmental psychologists to refer to early-emerging, genetically influenced indi-

vidual differences in emotional reactivity and self-regulation (Rothbart & Derryberry, 1981), whereas research on “personality” has more often focused on adolescent and adult populations. Despite emerging from different research traditions, however, constructs described as temperament or personality traits appear to describe the same phenomena. Behavioral genetics studies indicate that traits are subject to substantial genetic influences, regardless of whether they were initially labeled “temperament” or “personality” (Krueger & Johnson, 2008; Saudino & Wang, 2012). Trait measures from both traditions show both stability and change over the life course. Contrary to some early perspectives, neither temperament nor personality is immune to environmental influence during development, though both become more consistent over time (Roberts & DelVecchio, 2000; Specht et al., 2014). Perhaps most convincingly, conceptual and empirical investigations show that temperament and personality trait models exhibit a high degree of structural similarity, despite being developed independently (Caspi & Shiner, 2006; De Pauw & Mervielde, 2010; De Pauw, Mervielde, & Van Leeuwen, 2009; Shiner & DeYoung, 2013; Soto & Tackett, 2015).

Our perspective is that temperament traits are personality traits, and that we can reconcile traditional usages in developmental and personality psychology by considering the usual conception of childhood temperament to describe the early basis of personality, which becomes broader and more differentiated as the developing child acquires new tendencies and competencies through both genetically programmed maturation and environmentally mediated learning (Shiner & DeYoung, 2013). We organize our review from the perspective of the Big Five personality model because the five factors appear able to capture the most important individual differences in both children and adults. (Activity level often appears as a separate, sixth dimension in childhood, but it is clearly incorporated within extraversion during adolescence; Soto & Tackett, 2015.)

Nonetheless, we recognize that the Big Five are not the only trait dimensions of interest. For one thing, personality is structured hierarchically. Traits at higher levels of the hierarchy describe real patterns of covariation among traits at lower levels of the hierarchy, but, at every level of the hierarchy, traits also have their own unique, valid variance. In other words, for each

trait, some variance is shared with others at its own level, giving rise to the traits at the next higher level of the hierarchy, but some variance is unique. Thus, traits at any level of the hierarchy may be important for understanding a given phenomenon. The bottom level of the hierarchy contains relatively narrow traits traditionally described as “facets.” Between the Big Five and their facets, an intermediate level of traits has been described as “aspects” (DeYoung, Quilty, & Peterson, 2007). Each of the Big Five contains two aspects that represent the major empirical subdimensions of each Big Five domain, often demonstrating discriminant validity (DeYoung, 2015). The discovery of the aspects may be useful in unifying child and adult personality research, as many of the aspect-level traits map onto distinctions that have been made in childhood personality research as well (Shiner & DeYoung, 2013).

One additional level of the trait hierarchy exists above the Big Five. Though they were originally thought to be orthogonal, the Big Five in fact covary in a consistent pattern that indicates the existence of two overarching metatraits, stability and plasticity, which have been demonstrated in children as well as adults (DeYoung, 2006; Digman, 1997; Slobodskaya, 2011; Wang, Chen, Petrill, & Deater-Deckard, 2013). *Stability* comprises the shared variance of neuroticism (reversed), agreeableness, and conscientiousness and appears to reflect the tendency to maintain stable, goal-directed functioning without disruption by emotions, impulses, doubts, and distractions. *Plasticity* comprises the shared variance of extraversion and openness/intellect, and appears to capture variation in a broad tendency toward exploration, through which people generate new interpretations of the world, and new goals and strategies for acting in it (DeYoung, 2015).

The importance of the metatraits can potentially be seen very early in life. Abe and Izard (1999) found that 18-month-olds’ facial expressions of emotion in the Strange Situation Paradigm predicted parent ratings of Big Five traits at 3.5 years, with the following pattern: Negative emotional expression predicted neuroticism, agreeableness, and conscientiousness, whereas strong positive emotional expression predicted extraversion and openness/intellect. It seems that even the earliest emotional regularities are related to the basic functions of maintaining stability and engaging flexibly with the world.

The metatraits allow a reasonably succinct summary of many of the normative changes observed in the Big Five over the course of the lifespan. Neuroticism, agreeableness, and conscientiousness tend to change at the same time within individuals, as do extraversion and openness/intellect, a phenomenon known as *correlated change* (Klimstra, Bleidorn, Asendorpf, van Aken, & Denissen, 2013). On average, people decrease in the stability traits during early adolescence, and then increase at the end of adolescence and into early adulthood (Soto et al., 2011; Van den Akker, Deković, Ascher, & Prinzie, 2014). Further increases in stability are gradual throughout adulthood, and some evidence suggests a decline begins in old age (Möttus, Johnson, & Deary, 2012; Roberts et al., 2006; Wagner, Ram, Smith, & Gerstorf, 2016). In contrast, plasticity tends to decrease from middle age through old age (Specht et al., 2011; Srivastava, John, Gosling, & Potter, 2003).

We do not focus on the metatraits in our review of personality neuroscience because most research that is potentially relevant to their biological substrates has been carried out at the Big Five level. However, it is worth noting that our theory identifies general levels of serotonin and dopamine in the brain as likely substrates of stability and plasticity, respectively (Allen & DeYoung, 2017; DeYoung, 2006). A recent study provided the first direct test of the stability hypothesis, showing that people high in stability have greater serotonergic function than those moderate or low in stability (Wright, Cresswell, Flory, Muldoon, & Manuck, 2018). The decline in plasticity in adulthood is consistent with known declines in dopaminergic function during adulthood, but direct evidence of a causal relation is lacking (Bäckman, Lindenberger, Li, & Nyberg, 2010; Erixon-Lindroth et al., 2005). Indeed, most inferences regarding links between personality development and brain development are still indirect at this point. Before moving to a review of direct evidence in personality neuroscience, therefore, we discuss some additional core findings from personality development and their parallels in brain development.

Remarkably, individual differences in behavior are apparent even prior to birth (e.g., DiPietro, Hodgson, Costigan, & Johnson, 1996; Eaton & Saudino, 1992), and many more emerge rapidly postnatally. Within the first year of life, infants begin to show reliable differences in their

tendencies toward positive and negative affect, interest, and attention (Gartstein & Rothbart, 2003; Rothbart & Bates, 2006). As infants gain new capabilities, personality becomes more expansive, and new traits begin to emerge. During this early period, spanning the first 3 years of life, personality is at its most changeable (Roberts & DelVecchio, 2000).

This early flexibility reflects rapid brain development, mediated by *experience-expectant* and *experience-dependent* processes involved in *synaptogenesis*, or synapse formation (Greenough, Black, & Wallace, 1987). *Synapses* are the tiny gaps between neurons, where the axon of one neuron meets the dendrite of another. Neurotransmitters are released across this gap to transform electrical signaling within neurons into chemical signaling between neurons. During prenatal development and infancy, synaptogenesis occurs rapidly, as new dendrites and axons sprout and the brain's wiring becomes more and more intricate. Interestingly, the brain becomes more highly wired than it ultimately needs to be, with more synapses being made than will survive. In experience-expectant development, environmental inputs dictate which synapses are necessary for maximizing the brain's efficiency, and these synapses are retained and strengthened. Conversely, unnecessary synapses are destroyed in a process called *synaptic pruning*, which continues well into adolescence. Though much of the brain is wired in an experience-expectant manner, experience-dependent processes are important as well. In this type of development, new synapses are created in response to specific environmental inputs, allowing the brain to respond flexibly to the unique input of each developing person's context. Thus, both experience-dependent development (via synaptogenesis) and experience-expectant development (via pruning) are important mechanisms by which environmental factors shape long-term individual differences in human behavior.

Another important mechanism of brain development is *myelination*, in which glial cells wrap neuronal axons in a sheath of fatty tissue (called *myelin*) that serves to insulate the electrical impulses transmitted down the axon, greatly increasing the speed of neural transmission. Myelination typically begins in the third trimester and continues through adolescence, proceeding from the brainstem toward the cortex and from the rear of the brain (primarily responsible for processing sensory information)

to the front (primarily responsible for organizing thought and action around complex goals) (Inder & Huppi, 2000; Webb, Monk, & Nelson, 2001). This trajectory of myelination has potentially important implications for personality. Because neurons in the prefrontal cortex (PFC) are typically last to be myelinated, traits most influenced by this region are likely to be slower to develop and subject to greater developmental change when myelination does occur. This may be one reason why extraversion and neuroticism—traits that reflect differences in positive and negative emotional systems based primarily in subcortical regions—are typically identified earlier than traits such as conscientiousness or openness/intellect, which rely more heavily on prefrontal regions.

The PFC undergoes extensive and rapid maturation in the period from 2 to 5 years of age, but there is another very important period of prefrontal maturation in adolescence and young adulthood (Bunge & Zelazo, 2006; Somerville, Jones, & Casey, 2010). Studies of normative mean-level trait change show more pronounced shifts during adolescence and young adulthood than at any other time during the lifespan (De Fruyt et al., 2006; Roberts et al., 2006; Soto et al., 2011; Van den Akker et al., 2014), and these changes are likely to reflect the underlying dynamics of brain maturation. Studies of brain structure in adolescents show an initial increase in gray matter (which is correlated with the number of synapses) early in puberty, followed by a subsequent decline thought to be mediated by additional synaptic pruning (Giedd et al., 1999). At the same time, myelination continues throughout the brain, leading to linear increases in white matter (bundles of axons) and advances in network efficiency (Lenroot & Giedd, 2006). The PFC matures at a slower rate than the subcortical structures that drive motivation, leading adolescents to become more impulsive and prone to externalizing problems such as antisocial behavior and drug abuse, as their reactions to potential rewards and punishments reach adult levels of sensitivity before the full maturation of the cortical systems that will constrain and regulate those reactions in adulthood (Casey, 2015). The stability traits—conscientiousness, agreeableness, and (low) neuroticism—which dip sharply in adolescence, are the major correlates of impulsivity and externalizing behavior in the Big Five (DeYoung, Peterson, Séguin, & Tremblay, 2008; DeYoung & Rueter, 2016).

Neural Correlates of the Big Five

In the rest of this chapter, we provide an overview of the biological systems that are most central to personality differences, focusing on the neural correlates of the Big Five. We rely on methodologically rigorous research as much as possible, typically avoiding, or at least offering caveats when citing, studies conducted in small samples. We are somewhat limited by the paucity of personality neuroscience studies conducted in child samples. Nonetheless, as much as possible, we discuss neural mechanisms in a developmental context.

Extraversion

Most theories of the Big Five posit that extraversion reflects variation in the biological systems governing sensitivity to reward, which causes characteristics as diverse as being talkative, sociable, physically active, joyful, and assertive to covary within a single broad trait dimension. Reward systems can be divided into those governing *incentive rewards*, which are cues that a reward may be obtained in the future and which involve desire, and those governing *consummatory or hedonic rewards*, which occur when a reward is achieved in the present and involve pleasure.

Individual differences in these systems are present within the first few months of life, evidenced by variation in the degree to which babies smile, laugh, or otherwise express positive affect (Gartstein & Rothbart, 2003). Early positive emotionality can be considered both a sign of infants' hedonic enjoyment and an incentive-motivated attempt to prolong an interaction with rewarding stimuli. The behaviors infants use to pursue rewards become more complex and refined over the course of development, as they attain new competencies—for example, the emergence of motor skills in the first year of life that allows for increased exploration of the environment and more vigorous pursuit of potential rewards (Rothbart, 2007). The emergence of language abilities in toddlerhood allows for even further expansion of extraversion, as children become more talkative and expressive. During the school years, children's sociability takes on growing import, as children gain greater exposure to peers. Thus, extraversion expands and grows more differentiated throughout the childhood years.

The heterotypic continuity of extraversion during this developmental period has been demonstrated empirically. Infant activity level, sociability, and positive emotionality all predict individual differences in facets of extraversion later in childhood (Caspi & Shiner, 2006; Hagekull & Bohlin, 2003; Rothbart, Derryberry, & Hershey, 2000), and early facets of the trait often predict *other* facets later on (e.g., Durbin, Hayden, Klein, & Olino, 2007; Dyson et al., 2015). Studies by Fox and colleagues have found that both motor activity and positive emotionality at 4 months of age predict increased approach behavior and higher levels of sociability throughout the first 4 years of life (Calkins, Fox, & Marshall, 1996; Fox, Henderson, Rubin, Calkins, & Schmidt, 2001; Hane, Fox, Henderson, & Marshall, 2008).

Personality neuroscience sheds light on the mechanisms likely to underlie and unify these changing manifestations of extraversion. One of the most robust findings in personality neuroscience to date is that extraversion is associated with the neurotransmitter dopamine, which is the core of the brain's incentive reward system (Depue & Collins, 1999; DeYoung, 2013; Wacker & Smillie, 2015). The most direct evidence comes from studies indicating that extraversion moderates the effect of pharmacological manipulations of the dopaminergic system. In these studies, researchers administer a drug known to modulate the dopaminergic system, and effects of the drug are then assessed via behavioral measures or a neurobiological assay. If a personality trait moderates the drug's effect on the outcome of interest, one can be reasonably sure that the trait is linked to the system targeted by the drug. For example, Depue and Fu (2013) found that those high in extraversion were more sensitive to the rewarding properties of a *dopamine agonist* (a drug that increases dopaminergic function), leading them to develop preferences for the context in which the drug was administered that introverts did not develop.

Additional evidence linking the incentive reward system to extraversion comes from studies using electroencephalography (EEG), which is a noninvasive method of monitoring the brain's electrical activity using electrodes placed along the scalp. EEG has excellent temporal resolution, at the level of milliseconds; it is highly effective at tracking *when* things happen in the brain. One important EEG finding involves a waveform known as the *reward positivity*

(confusingly, this waveform is more commonly known as the "feedback-related negativity," Proudfit [2015] has convincingly demonstrated that it is best viewed as a positivity related reward, occurring 200–350 milliseconds after receiving feedback about an outcome). A recent meta-analysis examining studies of the reward positivity found that it is best considered a prediction error signal; it spikes in response to better-than-expected outcomes and declines below baseline in response to worse-than-expected outcomes (Sambrook & Goslin, 2015). Importantly, dopaminergic neurons projecting from the midbrain to the anterior cingulate cortex (ACC) show this same pattern of firing (Bromberg-Martin, Matsumoto, & Hikosaka, 2010), supporting the theory that the reward positivity is dopaminergically mediated. Adult studies have indicated repeatedly that extraversion is associated with reward positivity amplitudes following feedback about reward (Bress & Hajcak, 2013; Cooper, Duke, Pickering, & Smillie, 2014; Lange, Leue, & Beauducel, 2012; Smillie, Cooper, & Pickering, 2011).

The relation between extraversion and the reward positivity in EEG is one of the few findings in personality neuroscience that has been replicated in a study of child development. Kujawa and colleagues (2015) examined the association in 381 children assessed at ages 3 and 9 years. Positive emotionality measured through behavioral observation at age 3 and self-reported positive emotionality at age 9 were both significantly related to reward positivity amplitudes following monetary gains and losses at age 9. Considered with adult research on the reward positivity, these findings indicate that dopaminergically mediated responses to reward are likely to play an important role in the neurobiological basis of extraversion throughout the lifespan.

As noted earlier, dopamine is the main neurotransmitter in the incentive reward system. An *incentive reward* is a cue that one is moving toward a valued goal, whereas a *hedonic reward* involves the actual attainment of a goal. Both types of reward are present throughout the lifespan; the child who earns a star on a "star chart" at school has earned an incentive reward, a sign that progress toward a larger goal is underway. The child who completes the star chart and cashes in on the reward of an ice-cream sundae revels in the enjoyment of a hedonic reward. The distinction between *incentive* and *hedonic* has been described as the difference between

“wanting” and “liking” (Berridge, Robinson, & Aldridge, 2009), and the two processes are governed by different neurotransmitter systems. Whereas dopamine produces desire and approach behavior, it is the opioid system that produces pleasure.

The distinction between these two neurotransmitter systems has been linked to the difference between extraversion’s two aspects, assertiveness and enthusiasm (Allen & DeYoung, 2017; DeYoung, 2013). Assertiveness, sometimes referred to as *agentive extraversion*, reflects individual differences in traits such as drive, activity, and decisiveness. It is also closely related to dominance and leadership, traits that become more salient as children are increasingly integrated into peer environments. Assertiveness seems likely to be driven primarily by desire and, hence, dopamine. Indeed, studies employing pharmacological manipulations typically find that measures of assertiveness are more strongly related to dopaminergic functioning than are measures of enthusiasm (Mueller et al., 2014; Wacker, Mueller, Hennig, & Stemmler, 2012). Enthusiasm, in contrast, includes lower-order traits related to positive emotionality and sociability, and appears to reflect not only incentive motivation but also the hedonic enjoyment of reward. At this point, very limited evidence links enthusiasm to the opioid system. In one study, social closeness, a good marker of the enthusiasm aspect, moderated the effects of an opiate manipulation (Depue & Morrone-Strupinsky, 2005; DeYoung, 2013).

Our hypothesis that enthusiasm reflects variation in both dopaminergic and opioid function has to do with the fact that rewards are often simultaneously incentive and hedonic, due to the nested nature of goals. To achieve complex goals, we must break them down into various subgoals. Achieving one of those subgoals thus represents simultaneously the pleasurable summation of one goal and a cue of progress toward a larger goal. Using our classroom example, one can easily imagine that completing the star chart and receiving the ice-cream sundae is experienced by the child as not only a hedonic reward, pleasing to the taste buds, but also a sign of progress toward even larger goals, such as earning the esteem of peers, finishing at the head of the class, or making his or her parents proud. Similarly, it is likely that receiving each individual star, before the chart is complete, causes the child to experience momentary pleasure (opiate-mediated), as well as increased

desire to earn more stars and progress toward receiving the sundae (dopaminergically mediated). It seems likely, therefore, that individual differences in dopaminergic function and incentive reward sensitivity are the dominant force underlying extraversion in general, whereas individual differences in opioid function and hedonic reward sensitivity make a more specific contribution to its enthusiasm aspect.

The importance of the distinction between assertiveness and enthusiasm is highlighted by developmental research finding that mean-level changes in extraversion during late adolescence and young adulthood vary according to the facet of extraversion being investigated (Roberts et al., 2006). A look at the facets discussed in Roberts and colleagues’ meta-analysis reveals that they largely resemble the two aspects; what they called “social vitality” (sociability, gregariousness, and positive emotionality) aligns with enthusiasm, whereas what they called “social dominance” (assertiveness and independence) aligns with assertiveness. Dominance increases more during adolescence and young adulthood than does vitality, which increases briefly in adolescence before declining in young adulthood (Roberts et al., 2006; Urošević, Collins, Muetzel, Lim, & Luciana, 2012).

Whereas the neurobiological research we have so far examined for extraversion has been based in EEG and pharmacological manipulation, a number of neuroimaging studies have also provided evidence that extraversion reflects variation in the brain’s reward system. The most common neuroimaging technique, magnetic resonance imaging (MRI), allows noninvasive scanning of both the structure and functioning of the brain. Dopaminergic neurons in the mid-brain send axons to both cortical and subcortical regions involved in response to reward, including the medial orbitofrontal cortex (mOFC), ventral and dorsal striatum (including the nucleus accumbens and caudate, respectively), the ACC, and the amygdala. Studies have indicated that individual differences in extraversion are related to either the structure or function of nearly all of these regions in adults (Cremers et al., 2011; DeYoung et al., 2010; Grodin & White, 2015; Lewis et al., 2014; Passamonti et al., 2015; Wu, Samanez-Larkin, Katovich, & Knutson, 2014).

Urošević and colleagues (2012) extended these findings in a developmental context, using MRI to investigate longitudinal changes in reward sensitivity and related neural parameters among 149 9- to 23-year-olds assessed at two

time points, 2 years apart. To measure reward sensitivity, they used a behavioral approach system (BAS) sensitivity questionnaire that is a reasonably good proxy for extraversion (Quilty, DeYoung, Oakman, & Bagby, 2014). Developmental changes in reward sensitivity were mirrored by structural findings in the reward system. Increases in a Drive subscale (which is a marker of assertiveness; Quilty et al., 2014) during adolescence and young adulthood were positively associated with increases in the volume of the left nucleus accumbens during the same period. Thus, structural changes to the ventral striatum may help explain why many youth become increasingly motivated to attain rewards during the adolescent and young adult years. Interestingly, the study also found that baseline volumes of the nucleus accumbens and mOFC were positively correlated with increases in reward sensitivity during adolescence, suggesting that a higher density of synapses within these regions may be associated with increased susceptibility to the environmental rewards that become available in adolescence.

Neuroticism

Neuroticism, or negative emotionality, reflects individual differences in the biological systems governing defensive responses to threat, punishment, and uncertainty (Allen & DeYoung, 2017; Shackman et al., 2016). Individuals high in neuroticism experience more negative affect of all sorts, such as sadness, anxiety, fear, anger, irritability, and insecurity. These emotions emerge very early in life. Anger, frustration, and distress are present within the first 2–4 months of life, and anxiety, sadness, and fear emerge later in the first year, as the infant undergoes further maturation and socialization (Lewis, 2000). Variation in these early negative emotions serves as an important developmental precursor to later neuroticism. For instance, infant expressions of negative emotion observed at 18 months predicted individual differences in neuroticism during early childhood (Abe & Izard, 1999). Over time, neuroticism is differentiated and refined, spurred along by cognitive development that enables the developing child to represent both the self and the external world. For children high in neuroticism, their early representations are likely to be colored by negative affect, leading to low self-worth and more pessimistic views about the future.

Neural correlates of neuroticism can be divided into three major groupings: (1) medial temporal lobe structures, including the amygdala and hippocampus; (2) the hypothalamic–pituitary–adrenal (HPA) axis; and (3) frontal lobe structures, including the ACC, insula, and medial PFC. The structure most frequently linked to neuroticism is the amygdala, which is centrally involved in the coordination of response to threat (Shackman et al., 2016). Functional MRI (fMRI) studies in adults have indicated that neuroticism is positively associated with amygdala activation during tasks involving threatening or ambiguous stimuli (Everaerd, Klumpers, van Wingen, Tendolkar, & Fernández, 2015; Schuyler et al., 2014). In one developmental study of 165 adults, males (but not females) who had been classified as highly reactive infants (defined as high levels of motor activity accompanied by crying and fretting during a laboratory task) at age 4 months displayed heightened amygdala activation in response to neutral faces as adults (Schwartz et al., 2012).

In a structural MRI study of over 1,000 adults, neuroticism was positively correlated with the volume of both the amygdala and the hippocampus (Holmes et al., 2012). The hippocampus is particularly implicated in anxiety and, in one meta-analysis (Gray & McNaughton, 2000), neuroticism was positively associated with hippocampal activation during fear learning, the process by which an individual learns to predict threats from environmental cues (Servaes, Riese, et al., 2013). Very little research on children has examined the link between neuroticism and the amygdala or hippocampus. In one study of 89 adolescents, neuroticism was *negatively* correlated with amygdalar volumes (Dennison et al., 2015).

One of the main targets of amygdalar outputs is the hypothalamus, which forms the top of the HPA axis that controls the body's response to stress. The HPA cascade begins with the release of corticotropin-releasing hormone (CRH) and vasopressin from the paraventricular nucleus of the hypothalamus. A number of studies have linked variation in the CRH receptor 1 gene to neuroticism in individuals with a history of childhood maltreatment, though the effects sometimes vary by race or type of maltreatment (Bradley et al., 2008; DeYoung, Cicchetti, & Rogosch, 2011; Grabe et al., 2010; Kranzler et al., 2011; Polanczyk et al., 2009). Neuroticism has been more convincingly associated with the

terminal result of HPA activation, release of the stress hormone cortisol. In adults, Neuroticism is positively associated with baseline cortisol levels (Garcia-Banda et al., 2014; Gerritsen et al., 2009; Miller, Cohen, Rabin, Skoner, & Doyle, 1999; Nater, Hoppman, & Klumb, 2010; Folk, Cohen, Doyle, Skoner, & Kirschbaum, 2005). Studies of children also seem to support a positive association between cortisol levels and early neuroticism. Behaviorally inhibited and highly emotional children have higher levels of baseline cortisol (Kagan, Reznick, & Goldsmith, 1987; Schmidt et al., 1997; Tyrka et al., 2010). Remarkably, it may even be the case that exposure to cortisol in breast milk leads to increased neuroticism, as level of cortisol in breast milk has been shown to predict infant negative emotionality, and maternal cortisol levels predicted negative emotion in breast- but not formula-fed infants (Glynn et al., 2007; Grey, Davis, Sandman, & Glynn, 2013). Longitudinal studies provide evidence for prospective links between these two constructs as well, as neuroticism measured in the preschool years predicts cortisol levels later in childhood (Hugherty et al., 2013; Mackrell et al., 2014). Somewhat surprisingly, however, this association does not appear to be present in adolescence. Two longitudinal studies of adolescents found no prospective associations between cortisol levels and neuroticism (Evans et al., 2009; Shoal, Giancola, & Kirillova, 2003). If it indeed the case that the association between neuroticism and cortisol temporarily vanishes in adolescence, this could be related to the very large shifts in personality traits, including neuroticism, that occur in adolescence (Evans et al., 2011; Van den Akker et al., 2014). On the other hand, even the adult literature is not entirely consistent here: In a study of 490 adolescents, Miller and colleagues (2016) found no association between cortisol and neuroticism, but did find an association between cortisol function and extraversion. More large studies are needed in adolescence.

Individuals high on neuroticism are prone to experience negative affect in part because they have difficulty regulating emotions. While variation in brain structures such as the amygdala and hypothalamus is likely to explain neuroticism's relation to emotion generation, cortical structures are more likely to be involved in problems of emotion regulation. In the frontal lobe, the rostral/subgenual ACC and adjacent medial PFC have

been heavily implicated in emotion regulation (Etkin, Egner, & Kalisch, 2011), and several lines of evidence link neuroticism to this region and its connections to the threat system. For instance, in the study of over 1,000 adults mentioned earlier, neuroticism was negatively correlated with cortical thickness in a region of the medial PFC that encompassed the rostral/subgenual ACC (Holmes et al., 2012).

More direct studies of connectivity, both structural and functional, also support this idea. The brain's white matter consists of bundles of axons that connect regions of gray matter to each other, and the coherence or integrity of these white-matter tracts can be measured through diffusion tensor imaging (DTI), an MRI technique that detects the diffusion of water molecules along axons. Several DTI studies have shown that neuroticism is negatively associated with white-matter integrity in axons connecting cortical and subcortical regions (Bjørnebekk et al., 2013; Taddei, Tettamanti, Zanoni, Cappa, & Battaglia, 2012; Westlye, Bjørnebekk, Grydeland, Fjell, & Walhovd, 2011; Xu & Potenza, 2012). This pattern is consistent with results from two fMRI studies examining functional connectivity in adults. (*Functional connectivity* refers to synchrony between the activity of brain regions over time, which implies that they are causally linked in their operations—though it cannot indicate direct cause or causal direction.) Both studies found that neuroticism was associated with reduced connectivity between the amygdala and prefrontal regions, including the dorsomedial and dorsolateral PFC (Mujica-Parodi et al., 2009; Servaas, van der Velde, et al., 2013). Similarly, in a study of adolescents, Davey and colleagues (2015) found that functional connectivity between the amygdala and subgenual ACC was positively correlated with neuroticism at baseline and 2 years later. Further, change in the amygdala-ACC connectivity over this 2-year period was positively correlated with change in neuroticism.

Shifting from our discussion of global neuroticism to traits beneath it in the hierarchy, we note that two forms of neuroticism, dubbed *anxious distress* and *irritable distress*, have received special attention during early development (Caspi & Shiner, 2006; John, Caspi, Robins, Moffitt, & Stouthamer-Loeber, 1994; Rothbart & Bates, 1998). Whereas anxious distress involves inwardly directed forms of negative affect, including anxiety, sadness, guilt,

and insecurity, irritable distress encompasses tendencies toward more externalized negative affect, including anger, frustration, and labile mood. Evidence from studies of youth suggests these two subdimensions of neuroticism may have different developmental correlates, leading some theorists to recommend measuring them separately in research on child personality (Caspi & Shiner, 2006; Shiner & Caspi, 2003).

Anxious distress and irritable distress appear to be developmental antecedents to neuroticism's two aspects in adults, withdrawal and volatility (DeYoung, 2015; DeYoung et al., 2007). *Withdrawal* reflects anxiety, depression, and insecurity, whereas *volatility* reflects irritability, anger, labile mood, and the tendency to get upset easily. In parsing the distinction between withdrawal and volatility, we refer to Gray and McNaughton's (2000) theory that neuroticism reflects the joint sensitivity of two underlying brain systems, the behavioral inhibition system (BIS) and the fight-flight-freeze system (FFFS). The BIS, centered around the amygdala and hippocampus, governs response to threats in the form of conflicts between goals, most often approach-avoidance conflicts (e.g., wanting to impress one's peers in a class presentation, but dreading the embarrassment that might accompany a mistake). In situations in which conflict or uncertainty is detected, the BIS increases passive avoidance, leading to heightened anxiety, increased vigilance and rumination, and inhibition of approach behavior; all of these effects are characteristic of both anxious distress and withdrawal. The label "Withdrawal" does not refer specifically to being socially withdrawn (which could be a function of low extraversion), but rather to the partial or complete withdrawal of effort from a goal, which is the core of all forms of passive avoidance.

Whereas the BIS responds to situations involving conflict between goals, in which one is uncertain about whether to continue to approach, the FFFS, centered around the hypothalamus and periaqueductal gray (a region of midbrain below the hypothalamus), is sensitive to situations in which one's only motivation is to escape or eliminate a threat. In these instances, the FFFS triggers active defensive responses, such as panicked flight or defensive anger. The anger component, at least, is clearly reflected in volatility. Many general neuroticism scales are weighted toward withdrawal rather than volatility, and the biological correlates of irritable dis-

tress and volatility are much less well studied than those of anxious distress and withdrawal. One area in which the distinction between withdrawal and volatility is important is in EEG research, which has consistently found that neuroticism predicts a pattern of increased activity in right, relative to the left, prefrontal regions both when viewing stimuli and while at rest (for meta-analyses, see Thibodeau, Jorgensen, & Kim, 2006; Wacker, Chavanon, & Stemmler, 2010). Developmental research examining this rightward pattern of EEG asymmetry has shown that the effect is present as early as 6 months of age (Buss et al., 2003). Other methods also seem to point to increased activity of the right frontal lobe as a potential substrate of neuroticism. In adults, blood flow to this region is positively associated with neuroticism during anticipation of an aversive stimulus (Morinaga et al., 2007). Focal damage to the left frontal lobe (leaving function biased toward the right hemisphere) is also associated with higher neuroticism scores (and specifically the anxiety facet; Forbes et al., 2014).

Importantly, the relation between rightward EEG asymmetry and neuroticism appears to be confined specifically to the withdrawal aspect (which, as noted, tends to be emphasized in global assessments of neuroticism). Traits related to volatility, especially anger, are associated with a pattern of leftward frontal EEG asymmetry instead (Everhart, Demaree, & Harrison, 2008; Harmon-Jones, 2004; Harmon-Jones & Allen, 1998). This differential asymmetry appears to stem from the fact that avoidance and approach behavior are differentially related to the right and left hemispheres, respectively (Davidson, 1992; Fox, 1991). Anger is an approach-oriented negative emotion that facilitates approach to threats when aggression is used as an active defense or when effort is needed to overcome frustration. (Consistent with the link between the left hemisphere and approach, there is also some evidence of a relation between leftward frontal EEG asymmetry and extraversion as well; Wacker et al., 2010; Wacker, Mueller, Pizzagalli, Hennig, & Stemmler, 2013).

The link between withdrawal and rightward asymmetry is consistent with research on a related early childhood trait known as *behavioral inhibition*. The origin of this label comes from descriptions of childhood temperament, not from Gray's theory of the BIS, but the evidence is consistent with the hypothesis

that the BIS is an important contributor to this form of behavioral inhibition. "Behavioral inhibition" was originally used by Kagan and colleagues to describe a group of shy toddlers who became withdrawn and inhibited when confronted with novel or unfamiliar situations (Garcia-Coll, Kagan, & Reznick, 1984; Kagan, Reznick, Snidman, Gibbons, & Johnson, 1988). Since then, considerable research has examined the biological basis of behavioral inhibition, its continuity over time, and its relation to important developmental outcomes, including psychopathology (Fox, Henderson, Marshall, Nichols, & Ghera, 2005). Investigations of its relations to other personality traits in youth suggest it is a blend of neuroticism and extraversion. Despite being most similar in theory to the withdrawal aspect of neuroticism, some studies suggest that it predicts low extraversion even more strongly than neuroticism (Muris et al., 2009; Vreeke & Muris, 2012). In general, withdrawal and related problems such as anxiety and depression are negatively correlated with extraversion, which is not surprising given that a primary function of the BIS is to inhibit approach behavior (DeYoung, 2015; DeYoung et al., 2007; Naragon-Gainey, Watson, & Markon, 2009).

Research on the the neurobiological correlates of behavioral inhibition shows considerable overlap with the literature on neuroticism and withdrawal, including the links to rightward frontal EEG asymmetry (Fox, Calkins, & Bell, 1994; Fox et al., 2001) and increased cortisol (Kagan et al., 1987; Schmidt et al., 1997). Behavioral inhibition in childhood has been linked to amygdala activation and connectivity in both adolescents and adults, although mostly in studies with small samples (Blackford, Allen, Cowan, & Avery, 2013; Pérez-Edgar et al., 2007; Roy et al., 2014). Some studies on behavioral inhibition seem to be more reflective of its relation to extraversion. In particular, several fMRI studies have found that a history of behavioral inhibition in childhood is associated with alterations in the structure and function of both the nucleus accumbens and striatum, regions strongly involved in reward (Bar-Haim et al., 2009; Clauss et al., 2014; Guyer et al., 2006; Lahat, Benson, Pine, Fox, & Ernst, 2016). The neural evidence on behavioral inhibition is consistent with its ties to both neuroticism and low extraversion, and future research would benefit from examining these two components of behavioral inhibition separately.

Conscientiousness

As any parent knows, the gradual (and sometimes downright plodding) emergence of self-regulatory capacities is a defining feature of development. The behavior and emotions of young children are often chaotically buffeted by the impulses to approach or avoid that are associated with extraversion and neuroticism. Nonetheless, from early childhood onward, humans show reliable individual differences in their persistence, planfulness, distractibility, and orderliness. Within the Big Five, variation in these regulatory characteristics is reflected primarily in conscientiousness. The mechanisms associated with conscientiousness function to facilitate nonimmediate goal pursuit and promote rule-based behavior, which requires avoiding distractions and suppressing disruptive impulses (DeYoung, 2015). Conscientiousness is closely aligned with the temperament trait *effortful control*, which Rothbart and colleagues (Rothbart, Ellis, Rueda, & Posner, 2003; Rothbart & Rueda, 2005) have defined as the ability to inhibit or suppress a dominant response in favor of a subdominant response. Although very little research has examined the developmental origins of conscientiousness specifically, much research has examined the foundations of effortful control.

Whereas variation in positive and negative emotionality is present within the first few months of life, regulatory capacities related to effortful control appear slightly later, typically emerging only toward the end of the first year (Posner & Rothbart, 1998). Differences in attentional processes during infancy predict the development of effortful control in toddlerhood (Bridgett et al., 2011; Gartstein, Slobodskaya, Putnam, & Kinsht, 2009; Kochanska, Murray, & Harlan, 2000; Putnam, Rothbart, & Gartstein, 2008). Additionally, high early emotionality is associated with lower effortful control in childhood, which is consistent with the adult correlation between neuroticism and conscientiousness, and also suggests that the intensity and frequency of early emotions may complicate the normative development of regulatory systems (Caspi & Shiner, 2006; Kochanska & Knaack, 2003; Putnam et al., 2008). Though effortful control may be measured during the toddler years, it remains very much a developing construct during this period. Indeed, children show considerable mean-level increases in effortful control in early childhood (Carlson,

2005). Despite these normative mean-level increases, however, the rank-order stability and internal consistency of effortful control are similar to those of most other trait constructs from the age of 3 years onward (Kochanska & Knaack, 2003).

Neurobiological research on effortful control and conscientiousness suggests that these traits are strongly linked to the frontal lobes. In particular, Posner and colleagues have posited that effortful control is associated with the development of brain regions known to be involved in the control of attention, including the ACC and a number of lateral prefrontal regions (Posner & Fan, 2008; Posner & Rothbart, 2007; Rothbart & Posner, 2006). Indeed, the dorsolateral prefrontal cortex (DLPFC), which is crucial for the ability to maintain nonimmediate goals, flexibly modulate attention, and follow complex rule systems (Bunge, 2004; Bunge & Zelazo, 2006), has repeatedly been linked to conscientiousness. In adults, several structural imaging studies have revealed that conscientiousness is positively associated with volume of regions in DLPFC (DeYoung et al., 2010; Jackson, Balota, & Head, 2011; Kapogiannis, Sutin, Davatzikos, Costa, & Resnick, 2013). Another study found that, in a large sample of patients with brain damage ($N = 199$), focal damage to the left DLPFC was associated with lower scores on conscientiousness (Forbes et al., 2014). However, some structural studies have failed to replicate the link between the DLPFC and conscientiousness (Bjørnebekk et al., 2013; Liu et al., 2013).

In adults, functional connectivity studies indicate that the lateral prefrontal regions involved in controlling attention encompass nodes of two broad networks that are extensively intertwined—these are the frontoparietal or cognitive control network and what we have called the *goal priority network* (Rueter, Abram, MacDonald, Rustichini, & DeYoung, 2018; Yeo et al., 2011). (Yeo and colleagues referred to the latter network as the “ventral attention network,” but the network they identified in a sample of 1,000 subjects is larger than the standard ventral attention network and comprises an amalgamation of networks traditionally labeled “ventral attention” and “salience.”) Functionally, the frontoparietal network is strongly linked to working memory and intelligence, abilities that are primarily related to the openness/intellect domain within the Big Five (DeYoung, Peterson, & Higgins, 2005; DeYoung et al., 2009;

Taki et al., 2013). In contrast, the goal priority network, which includes regions of the middle frontal gyrus, ACC, right inferior frontal gyrus, temporoparietal junction, and anterior insula, is specifically associated with conscientiousness (Allen & DeYoung, 2017; Rueter et al., 2018). Broadly, the function of this network seems to be to prioritize goals based on motivationally salient stimuli and maintain focus on the selected goal. The prefrontal components of this network appear especially responsible for directing attention away from distracting stimuli and back to the task at hand (Fox, Corbetta, Snyder, Vincent, & Raichle, 2006).

One study of 200 healthy adults applied graph theory analysis to resting functional connectivity data (Davis et al., 2013). In highly impulsive individuals, medial and lateral regions of the PFC broke off into a distinct module from subcortical regions, including the amygdala, hippocampus, thalamus, and brainstem, suggesting that high impulsivity reflects a breakdown between top-down control structures and those governing more immediate emotional responses. A conceptually related study found that effortful control in 3- to 5-year-olds was positively associated with integration, differentiation, and efficiency of functional networks in lateral PFC (Fekete, Beacher, Cha, Rubin, & Mujica-Parodi, 2014). Finally, Rueter and colleagues (2018) found that conscientiousness predicted both increased functional connectivity within the frontal portion of the goal priority network, encompassing DLPFC, anterior insula, and dorsal ACC, as well as increased connectivity of these regions with other more posterior parts of the network. Thus, it seems plausible that an important basis of conscientiousness is the ability of the goal priority network to control the brain's lower-level emotional and motivational systems.

Beyond the DLPFC, other regions of the ventral attention network also seem to be associated with conscientiousness, although the literature is still relatively sparse and conflicted (Allen & DeYoung, 2017). Multiple studies have found measures of conscientiousness or effortful control (or impulsivity, which often reflects the low pole of conscientiousness and effortful control) to be associated with structural variation in the ACC and adjacent medial cortex (mainly the supplementary motor area), insula and adjacent ventrolateral PFC, and putamen (Liu et al., 2013; Nouchi et al., 2016; Sakai et al., 2012). One study exploring the relation

between the insula and conscientiousness in a sample spanning ages 10–22 years, found that planning (vs. impulsivity) was negatively correlated with cortical thickness in the anterior insula, and that age was associated with higher levels of planning and lower cortical thickness (Churchwell & Yurgelun-Todd, 2013). Functional studies have also reported associations in these regions, typically between conscientiousness and activation during response inhibition tasks (Brown, Manuck, Flory, & Hariri, 2006; Farr, Hu, Zhang, & Li, 2012).

Some developmental evidence exists for a link between the ACC and conscientiousness. A study following participants over the course of adolescence found that greater thinning of the ACC was associated with smaller reductions in effortful control between ages 12 and 16 (Vijayakumar et al., 2014). This finding may be relevant to studies showing mean-level decreases in conscientiousness during adolescence (Soto et al., 2011; Van den Akker et al., 2014), and to the pattern of brain development in which prefrontal development catches up to subcortical development only toward the end of adolescence (Casey, 2015; Somerville, Jones, & Casey, 2010). Cortical thinning of the ACC during this period may reflect synaptic pruning of overabundant synapses, with greater pruning leading to more efficient cognitive control. If this is the case, one might expect that structural changes to the ACC would be associated with greater regulation of impulses later in development. Indeed, Vijayakumar and colleagues (2014) found that cortical thinning of the ACC was associated with reductions in both internalizing and externalizing psychopathology, and this relation was mediated by changes in effortful control.

An additional region that has repeatedly been associated with conscientiousness and effortful control is the orbitofrontal cortex (OFC), especially lateral areas of the orbital surface (Jackson et al., 2011; Matsuo et al., 2009; Nouchi et al., 2016). One longitudinal study of 107 adolescents assessed effortful control and OFC volume at 12 years, then assessed substance use and abuse at 15, 16, and 18 years (Cheetham et al., 2017). Effortful control at age 12 predicted both OFC volume and the severity of substance problems over the three later assessments. Further, OFC volume could account statistically for the covariance between effortful control and substance problems.

Agreeableness

As a social species, human beings must navigate the needs and goals of others in order to achieve their own goals. This requires willingness to accommodate and even work for the needs and goals of others. Variation in traits involved in cooperation and altruism is reflected in the personality trait of agreeableness (DeYoung, 2015; Graziano & Tobin, 2013). Less is known about the developmental origins of agreeableness than some of the other Big Five traits, in part because most measures of temperament have not included a trait comparable to agreeableness, although *affiliativeness* has been suggested as a component of temperament and included in some more recently developed instruments (Rothbart & Bates, 2006). Nonetheless, developmental antecedents of agreeableness, including individual differences in aggression, empathy, and prosocial behavior, are evident quite early in life.

Aggression, falling at the low pole of agreeableness, emerges during the first year of life and increases into toddlerhood, peaking sometime between 24 and 42 months after birth, before decreasing steadily throughout the rest of childhood (Côté, Vaillancourt, LeBlanc, Nagin, & Tremblay, 2006; Tremblay et al., 2004). The emerging ability to restrain aggressive impulses can be considered a key component of agreeableness from then on. Empathy and concern for others likewise emerge in the first year, increasing in frequency over the course of infancy and early childhood (for a review, see Davidov, Zahn-Waxler, Roth-Hanania, & Knafo, 2013). The capacities associated with agreeableness gradually come online over the course of infancy, leading to decreases in aggression and increases in empathy, prosociality, and compliance as children age. By early childhood, most temperament and personality models yield an agreeableness factor similar to the one found in the Big Five (De Pauw et al., 2009).

Nonetheless, there are some subtle differences between childhood and adulthood agreeableness. In youth, compared to adulthood, agreeableness is even more closely tied to the two other traits, neuroticism and conscientiousness, that constitute the broader metatrait stability (Tackett et al., 2012). Both low agreeableness and high neuroticism are consistently associated with elevated levels of physical aggression, relational aggression, and rule-breaking behavior throughout childhood and adolescence

(Becht, Prinzie, Deković, Van Den Akker, & Shiner, 2016; Tackett, Daoud, De Bolle, & Burt, 2013). These types of antagonistic behaviors are more central to the childhood variant of agreeableness than to its adult counterpart (De Pauw et al., 2009; Digman & Shmelyov, 1996; Tackett et al., 2012). Adult studies of the Big Five indicate that, although aggression remains an important component of low agreeableness, traits reflecting politeness and compassion are emphasized more. Additionally, in adults, the facet-level traits of irritability and anger have their primary loading on neuroticism (though they also show a strong secondary loading on agreeableness), but in childhood some ambiguity remains regarding whether they are more closely aligned with neuroticism or agreeableness (De Pauw et al., 2009). Brain development may offer one explanation for the age-related shift in agreeableness content away from anger and aggression. In childhood, the presence or absence of cooperative and altruistic behavior is likely to be more strongly determined by angry and aggressive impulses because the prefrontal brain systems that come to inhibit those impulses (and to promote emotion regulation, empathy, and concern for others) are still maturing.

The closer link between agreeableness and conscientiousness in childhood is consistent with Ahadi and Rothbart's (1994) proposal that early individual differences in effortful control may underlie the development of both agreeableness and conscientiousness. Effortful control is positively associated with agreeableness in both childhood and adulthood (Cumberland-Li, Eisenberg, & Reiser, 2004; Jensen-Campbell et al., 2002), but it nonetheless appears to become more differentiated over time, leading to increasingly distinct agreeableness and conscientiousness factors in later childhood and adolescence (Soto, John, Gosling, & Potter, 2008; Tackett et al., 2012). Again, we may trace this differentiation back to the relatively late development of the PFC.

The two aspects of agreeableness are compassion and politeness (DeYoung et al., 2007). Compassion encompasses empathic concern about others, whereas politeness reflects tendencies to conform to social norms and avoid belligerent and exploitative behavior. Both compassion and politeness can be identified in childhood, and longitudinal studies show that the two traits differentially predict adult outcomes (Kern et al., 2013). Compassion, in particular,

is likely to be strongly related to the development of theory of mind or "mentalizing" abilities, which reflect one's capacity to understand the mental states of others (Premack & Woodruff, 1978). Meta-analysis of theory-of-mind tests showed that mentalizing ability is positively associated with prosocial behaviors such as helping, cooperation, and comforting others (Imuta, Henry, Slaughter, Selcuk, & Ruffman, 2016). This is not surprising given the difficulty of coordinating one's goals with those of others if one cannot understand others' intentions and desires. Research on the development of theory of mind suggests that it follows a similar trajectory to agreeableness, increasing during late adolescence and adulthood (Dumontheil, Apperly, & Blakemore, 2010). Performance on theory of mind tasks has been positively related to agreeableness and to compassion more specifically (Allen, Rueter, Abram, Brown, & DeYoung, 2017; Nettle & Liddle, 2008). This link between theory of mind and compassion is consistent with studies showing high correlations between theory of mind and questionnaire measures of empathy (Baron-Cohen & Wheelwright, 2004) given that empathy falls within compassion rather than politeness. Indeed, a recent structural study found that compassion was positively correlated with gray matter volume in the bilateral ACC and anterior insula, and meta-analyses have linked both of these regions to empathy as well (Hou et al., 2017).

To the extent that agreeableness is associated with mentalizing capabilities, it is likely to be associated with regions of the so-called "default network" that are involved in decoding the mental states of others (Andrews-Hanna, Smallwood, & Spreng, 2014). (The "default network" got its name because it tends to be active when people are engaged in self-directed thought, such as daydreaming, but it appears to be crucial for any simulation of experience, including imagining the experience of others.) Though relatively little research has examined the neurobiological correlates of agreeableness specifically, several studies have examined the neural substrate of individual differences in empathy using questionnaire measures that are good indicators of compassion. A structural MRI study of 567 adults indicated that empathy was negatively correlated with gray-matter volume in various regions of the default network, including the medial PFC, precuneus, temporal pole, and superior temporal sulcus (STS) (Takeuchi

et al., 2014). Two other studies have reported negative correlations between agreeableness and volume in the posterior STS, a region that is important for interpreting the actions and intentions of others by decoding biological motion (DeYoung et al., 2010; Kapogiannis et al., 2013). A recent resting functional connectivity study found that empathy was associated with greater connectivity between medial PFC, precuneus, and left STS (Takeuchi et al., 2014).

A longitudinal neuroimaging study relevant to the neural substrates of agreeableness examined the structural development of brain regions implicated in social cognition, beginning in late childhood and extending into young adulthood. Gray-matter volume and cortical thickness of regions including the medial PFC and posterior STS peaked in late childhood or early adolescence, before declining over the course of adolescence (Mills, Lalonde, Clasen, Giedd, & Blakemore, 2014). These findings are consistent with studies of personality suggesting that agreeableness falls in early adolescence and then rises again in late adolescence and early adulthood (Soto et al., 2011; Van den Akker et al., 2014).

Finally, the hormone testosterone appears to be negatively associated with agreeableness, and its politeness aspect specifically, based on research relating it to interpersonal behavior and aggression (DeYoung, Weisberg, Quilty, & Peterson, 2013; Montoya, Terburg, Box, & Van Honk, 2012; Turan, Guo, Boggiano, & Bedgood, 2014). More complexly, two studies found that agreeableness moderated the association between testosterone and externalizing behavior problems, such that high testosterone was associated with externalizing only when agreeableness was low (Reardon, Herzhoff, Tackett, 2015; Tackett, Herzhoff, Harden, Page-Gould, & Josephs, 2014). Finally, in a longitudinal study of 216 individuals between ages 6 and 22 years, Nguyen and colleagues (2016) found that, independent of age and sex, testosterone levels, aggression, and the covariance of amygdala volume and cortical thickness in the medial PFC were all mutually interrelated. Such a complex finding needs replication, of course, but the overlap with the substrates of neuroticism in the amygdala and medial PFC is notable and may speak to the connection between aggression and failure to suppress angry or hostile impulses. Testosterone may suppress that inhibitory control.

Openness/Intellect

The last Big Five trait, openness/intellect, reflects individual differences in imagination, creativity, innovation, curiosity, and aesthetic and intellectual interests and abilities. The tendency toward cognitive exploration appears to be what unifies these traits (DeYoung, 2014, 2015). Of all the Big Five, openness/intellect has been the least studied in a developmental context, largely due to the fact that most models of child temperament have not included a dimension similar to openness/intellect (Caspi & Shiner, 2006; De Pauw et al., 2009; Shiner & DeYoung, 2013). Direct research on the developmental precursors of openness/intellect is scarce, although conceptually it is clearly linked to early behaviors such as imaginative play and curious exploration. In adults, openness/intellect incorporates perceived intelligence and is the one Big Five trait to be substantially associated with IQ (DeYoung, 2014). The fact that curiosity, stimulation seeking, and exploration of new situations in early childhood have been found to predict IQ later in life (Caspi & Shiner, 2006; Raine, Reynolds, Venables, & Mednick, 2002) therefore suggests patterns of heterotypic continuity for openness/intellect.

One adult temperament model includes a factor of orienting sensitivity that corresponds well empirically to openness/intellect (Evans & Rothbart, 2007), and a similar factor has been found in a large study of 5-year-old children, marked by scales measuring *low-intensity pleasure* and *perceptual sensitivity*, which include items such as “Enjoys looking at picture books” and “Notices the smoothness or roughness of objects he or she touches” (De Pauw et al., 2009). By the preschool years, researchers have been able to measure openness/intellect directly, but the reliability of these measures has not always been very high (Abe, 2005; Gjerde & Cardilla, 2009; Halverson et al., 2003). Beginning around age 6 or 7 years, however, studies consistently recover a robust openness/intellect factor that is reliable and structurally stable over time (Herzhoff & Tackett, 2012; Soto & John, 2014).

The two aspects of openness/intellect are readily apparent in its compound label: *openness to experience* and *intellect* (DeYoung, 2014; DeYoung et al., 2007). Whereas openness to experience encompasses tendencies to engage with sensory and perceptual information—through art or fantasy, for example—intellect

primarily reflects engagement with abstract or intellectual material through reasoning. Broadly, both of these tendencies serve to generate new interpretations of experience, but openness more in terms of sensory patterns and intellect more in terms of causal or logical patterns (DeYoung, 2014, 2015). We use the compound label "openness/intellect" to refer to the Big Five domain and "openness" or "intellect" to refer to one aspect specifically.

Very little personality neuroscience research has examined correlates of openness/intellect in childhood or adolescence, presumably due to its exclusion from most temperament models. Nonetheless, existing adult research may inform future developmental work. One promising hypothesis is that dopamine is involved, which may help to explain why openness/intellect shows a regular correlation with extraversion. Given dopamine's role in positive affect and approach, the fact that high-intensity pleasure in childhood predicts later openness/intellect as well as extraversion is suggestive (Abe & Izard, 1999). Whereas global levels of dopamine may influence both extraversion and openness/intellect, we have argued that the distinction between two different types of dopaminergic neuron is relevant to differentiating the two traits (Allen & DeYoung, 2017; DeYoung, 2013). As noted earlier, the type of neuron linked to extraversion encodes the value of stimuli, increasing its firing rate to positive stimuli and decreasing to negative. In contrast, the type proposed to be linked to openness/intellect encodes salience, becoming more active in response to both better- and worse-than-expected outcomes and triggering cognitive processing to explore these potentially meaningful events (Bromberg-Martin et al., 2010). Thus, differences in dopaminergic function may explain why those high in openness/intellect are curious and find information rewarding.

Most evidence supporting this hypothesis is indirect and stems from correlations between openness/intellect and variables known to be influenced by dopamine (e.g., working memory capacity; DeYoung, 2013). More direct evidence comes from a recent fMRI study that examined functional connectivity between the small area of the midbrain where dopaminergic neurons originate and other parts of the brain to which they send axons and hence dopamine. While viewing images of food, smelling pleasant odors, or even just at rest, individuals high in openness/intellect showed more synchrony between the

dopaminergic region and areas of the DLPFC involved in attention (Passamonti et al., 2015). This finding suggests greater dopaminergic influence on information processing in those high in openness/intellect and is consistent with the fact that salience-coding dopamine neurons preferentially project to the DLPFC (Bromberg-Martin et al., 2010).

The association of openness/intellect and functioning of the DLPFC is consistent with findings to which we alluded while discussing conscientiousness—namely, that openness/intellect is associated with intelligence and working memory (which is the ability to manipulate and rapidly update information in short-term memory). Both working memory and intelligence appear to rely heavily on the DLPFC and the broader frontoparietal network (Jung & Haier, 2007). Studies in children, adolescents, and adults have shown that variation in the functioning of this network is consistently associated with individual differences in working memory (Darki & Klingberg, 2015; Klingberg, 2006). Working memory is the cognitive function that appears to contribute most to intelligence (Conway, Kane, & Engle, 2003). It is intellect specifically, not openness, that is related to working memory and intelligence (DeYoung, Quilty, Peterson, & Gray, 2014; DeYoung, Shamosh, Green, Braver, & Gray, 2009). One study of the neural basis of this association found that intellect, but not openness, predicted neural activity in regions of the DLPFC and medial PFC that supported accurate performance on a difficult working memory task performed during fMRI (DeYoung et al., 2009). Thus, one's tendency toward intellectual confidence and engagement is, not surprisingly, linked to one's actual cognitive abilities. (Openness may nonetheless be related to DLPFC function, but presumably more in the context of directing attention toward sensory stimuli of interest.)

Although little developmental research has been done on openness/intellect, an expanding body of literature examines the neural development of working memory and intelligence, and this is informative regarding the trait of intellect. Working memory capacity increases during childhood and adolescence, a developmental trend consistent with the late cortical maturation of the frontal lobes, involving synaptic pruning and cortical thinning (Conklin, Luciana, Hooper, & Yarger, 2007; Finn, Sheridan, Kam, Hinshaw, & D'Esposito, 2010). In one longitudinal study, Tamnes and colleagues (2013)

found that improvement in working memory in children and adolescents over a span of 2.5 years was related to reduction of cortical volume in PFC and parietal cortex. Similarly, multiple studies have found that intelligence is associated with greater rates of cortical thinning, especially in PFC during late childhood and adolescence, once again suggesting the importance of relatively late pruning processes for cognitive abilities (Schnack et al., 2015; Shaw et al., 2006; Tamnes et al., 2011).

As mentioned earlier, the frontoparietal network is extensively intertwined with the ventral attention network that has been linked to conscientiousness, and the close proximity of these two networks, in conjunction with the late development of the PFC, may help to explain developmental changes in the covariance structure of personality traits. Measures of intellect (but not openness) are more strongly correlated with conscientiousness in childhood than they are later in life (Mervielde, Buyst, & De Fruyt, 1995; Mervielde & De Fruyt, 2000). Furthermore, childhood measures of openness/intellect tend to emphasize intellect content (Gjerde & Cardilla, 2009; Herzhoff & Tackett, 2012), which may account for the occasional difficulty of identifying an openness/intellect factor in childhood. In the study of 5-year-olds mentioned earlier, measures of intellect loaded on the conscientiousness factor rather than on the factor resembling openness that included measures of perceptual and sensory engagement (De Pauw et al., 2009).

Functional connectivity research shows that, over the course of development, the correlations between regions of the brain that are anatomically close lessens, whereas the correlations between more distal regions within networks increases (Fair et al., 2009). It may be that during childhood, individual differences in overall development of the PFC are more important in determining which traits appear together in an individual than are individual differences in the more specific networks that underlie each trait. Later in development, the different networks in PFC that are associated with conscientiousness and intellect presumably become more functionally differentiated, and intellect becomes more closely aligned with the other forms of cognitive exploration reflected in openness.

One neural substrate common to both intellect and openness may be found in parameters of the default network, which we have already discussed in relation to agreeableness. The

default network is extensive, contains at least three subnetworks, and is likely to be involved in multiple important personality traits. Areas of this network, especially in the left temporal lobe, are linked to intelligence, probably because of their involvement in language (Choi et al., 2008; Jung & Haier, 2007). However, the default network is better known for its role in imagination, which is so central to openness/intellect that "imagination" was proposed as an alternative label for the domain (Saucier, 1992). In keeping with this fact, a resting-state fMRI study using two independent samples found that openness/intellect was positively associated with information-processing efficiency in the default network (Beatty et al., 2016). The default network seems to be a particularly promising target for research on the development of openness/intellect in children given that imagination is one component of the trait that is evident at an age long before appreciation of art or philosophy might be relevant.

Conclusion

Having reviewed neurobiological research pertaining to each of the Big Five and their development, it should be obvious that, whereas personality neuroscience is a still young field, *developmental* personality neuroscience is still in its infancy. Nonetheless, we hope that our endeavor has provided some insight into the underlying biological systems that shape the patterns of behavior and experience described by the major dimensions of personality. For each of the Big Five, and often at the level of narrower traits below them, we can point to evidence consistent with the idea that numerous biological parameters contribute to trait variation, but that these parameters are reasonably coherent in being linked to a particular function that seems to unify the trait in question. For example, extraversion appears to be associated with a number of neural parameters involved in processing information about rewards and motivating approach toward them.

It is one thing to identify the neural systems involved in a personality trait and another to understand how those systems develop and how their development is linked to changes in the content and level of that trait. Neuroscience is beginning to reveal a great deal about the way that the brain develops across the lifespan, but we still know very little about how individual

differences fit into this story. We can be reasonably confident that the child who is energetic and expressive and then becomes an adolescent who loves parties and excitement has a dopaminergic system that is more sensitive to cues of reward than the child (and adolescent) who is reserved and introverted. We can even say that the proneness of extraversion to be expressed in riskier behavior during adolescence than at other ages is due, at least in part, to the relatively late development of the PFC. However, we have no direct evidence regarding how changes in dopaminergic function might be linked to changes in personality in an extraverted child versus an introverted child. Providing this evidence, for extraversion and also for other traits, will require extensive additional research, and developmental personality neuroscience is the field that will carry it out.

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