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Personality Neuroscience and the Biology of Traits

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Abstract

Personality neuroscience involves the use of neuroscience methods to study individual differences in behavior, motivation, emotion, and cognition. Personality psychology has contributed much to identifying the important dimensions of personality, but relatively little to understanding the biological sources of those dimensions. However, the rapidly expanding field of personality neuroscience is increasingly shedding light on this topic. This article provides a survey of progress in the use of neuroscience to study personality traits, organized using a hierarchical model of traits based on the Big Five dimensions: Extraversion, Neuroticism, Agreeableness, Conscientiousness, and Openness/Intellect. Evidence is reviewed for hypotheses about the biological systems involved in each trait.

The mission of personality psychology is ''to provide an integrative framework for understanding the whole person'' (McAdams & Pals, 2006; p. 204), and many different methods must be brought to bear to accomplish such an ambitious goal. The field of *personality neuroscience* rests on the premise that the whole person cannot be understood without understanding the brain. In this article, I discuss the role that neuroscience can play in personality research and review the progress of this rapidly expanding field. (For more in depth review of the field and its influential theories see DeYoung & Gray, 2009; and Zuckerman, 2005.)

Personality psychology's attempt to understand the whole person calls for a broad conception of personality itself, such as the one provided by McAdams and Pals (2006, p. 212):

> Personality is an individual's unique variation on the general evolutionary design for human nature, expressed as a developing pattern of dispositional traits, characteristic adaptations, and integrative life stories, complexly and differentially situated in culture.

This definition describes three levels at which personality can be analyzed: traits, characteristic adaptations, and life stories. Personality neuroscience has focused primarily on traits, which are relatively stable patterns of behavior, motivation, emotion, and cognition (Pytlik Zillig, Hemenover, & Dienstbier, 2002; Wilt & Revelle, 2009) that are not specific to a particular social milieu or culture. This is not to say that traits are evident to the same extent or with identical manifestations in all cultures, but rather that any trait can be observed in a subset of situations in any culture. In contrast to traits, characteristic adaptations and life stories describe the individual's specific responses to his or her particular life circumstances. Obviously, the latter two levels of analysis are crucial for understanding any individual, but their complexity renders them less amenable to study by neuroscience, and this article focuses on the biology of traits.

Traits can be considered probabilistic descriptions of the frequency and intensity with which individuals exhibit various behavioral, motivational, emotional, and cognitive states

(Fleeson, 2001; Fleeson & Gallagher, 2009). Individuals who are high in some trait will experience the states associated with that trait more often and more intensely than individuals low in that trait. For example, someone high in Extraversion will be talkative, outgoing, and excited more often than someone low in Extraversion, but even the person low in Extraversion may experience those states occasionally. The aim of personality neuroscience is to understand both the biological systems that are responsible for the states associated with traits and the parameters of those systems that cause them to function differently in different individuals. The systems themselves are presumed to be present in every intact human brain – hence McAdams and Pals' (2006) reference to ''the general evolutionary design for human nature'' – but their parameters will vary from person to person. (For example, all people have brain systems that respond to rewards, but in different individuals these systems will respond with different degrees of vigor to a particular reward, and the systems' average level of response may be associated with some personality trait.)

When considering the biological sources of personality, one must distinguish between proximal and distal sources. The proximal sources, just described, consist of stable differences in the functioning of the neural systems that produce the states associated with traits. The distal sources are both genetic and environmental, as indicated by the fact that heritability estimates for personality traits are in the range of 40% to 80%, depending on trait and method (Bouchard & McGue, 2003; Riemann, Angleitner, & Strelau, 1997). (The heritability of a trait indicates the amount of its variation in a population due to genetic, rather than environmental, variation.) It is important to remember that when either genes or situations have lasting effects on traits, they must do so by changing the brain; thus, personality differences are 'biological' regardless of their heritability, in the sense that they must be proximally generated by the brain no matter whether they originated in genes or environment.

Methods in Personality Neuroscience

Scientific investigation of the biological basis of personality has been limited, until relatively recently, by a lack of technology to examine brain structure and function in living human beings. Prior to the development of neuroimaging, the sole means for assessing brain activity was the electroencephalogram (EEG), which measures the brain's electrical activity at the scalp. Today a number of methods are available for personality neuroscience. Five important categories of neuroscientific methods are (1) neuroimaging (e.g., magnetic resonance imaging [MRI] or positron emission tomography [PET]), which allows assessment of brain structure and function with a relatively high spatial resolution; (2) molecular genetics, which allows assessment of variation in specific genes that are expressed in the brain; (3) EEG, which provides the highest temporal resolution of neural activity of any available method; (4) assays of endogenous psychoactive substances or their byproducts (e.g., hormone levels in saliva or neurotransmitter metabolites in cerebrospinal fluid); and (5) psychopharmocological manipulation (e.g., tryptophan depletion or augmentation to alter levels of the neurotransmitter serotonin).

Personality neuroscience employs these methods in conjunction with the methods of personality psychology, attempting to link biological variables to traits. Measurement of traits is typically accomplished by questionnaire, through self-report and/or ratings by peers or other knowledgeable informants. Questionnaires provide a convenient and reliable method for assessing a broad range of stable individual differences, drawing on raters' experiences over a far greater span of time than is available in the laboratory. However,

traits can also be assessed in other ways, such as through laboratory tasks, behavioral observation, or experience sampling, and personality should not be identified exclusively with the variables provided by personality questionnaires. What we want to explain in personality neuroscience is not how people answer questionnaires, but rather why they exhibit stable patterns of behavior, motivation, emotion, and cognition.

Most studies discussed in this review begin with some psychological trait and attempt to discover its biological basis. Another valid and useful approach is to begin with stable individual differences in some biological parameter (such as asymmetry in the level of left versus right cortical hemisphere activity, measured at rest by EEG) and then to attempt to discover what psychological trait or traits are associated with that biological trait.

An important caveat for anyone exploring the literature on personality neuroscience or contemplating entering the field as an investigator is that much inconsistency exists in the findings to date. In neuroimaging research, inconsistency is probably due in large part to the use very small samples, due to cost. Unfortunately, small samples often lack statistical power to detect true effects (Yarkoni, 2009). Worse still, low power has the unfortunate additional consequence of increasing the proportion of false positives among significant findings (Green et al., 2008). In genetic studies, though larger samples are typically used, power may still be an issue, and inconsistency may arise, because each trait is influenced by many genes, each accounting for only a very small amount of the variance of the trait (Green et al., 2008). These difficulties highlight the importance of testing reasonably focused hypotheses, rather than simply exploring associations with biological variables in the absence of any theory of the causal mechanisms that might underlie a given trait.

The Structure of Personality Traits

Personality neuroscience can usefully be guided by existing knowledge about the structure of personality – that is, knowledge about how various traits relate to one another and to the major dimensions of personality. In order to produce a coherent overview of the progress of personality neuroscience, one needs to relate findings to a reasonably comprehensive taxonomy of traits, such as that provided by the Five Factor Model or *Big Five*, which categorizes the majority of traits within five broad domains, typically labeled Extraversion, Neuroticism, Agreeableness, Conscientiousness, and Openness/Intellect (Digman, 1990; John, Naumann, & Soto, 2008).

The Big Five model is the result of decades of work using factor analysis to map the patterns of covariation among traits. In order to be accurate, such factor analyses require a reasonably comprehensive and unbiased pool of traits to analyze. The *lexical hypothesis* states that natural language (as represented in dictionaries) provides just such a pool of trait descriptors (John et al., 2008; Saucier, 2009). Existing personality questionnaires constitute another source of a large and broad pool of traits in which to locate general factors. Lexical and questionnaire research have both provided evidence for the Big Five (Digman, 1990; John et al., 2008; Markon, Krueger, & Watson, 2005).

The suitability of the Big Five model for personality neuroscience may not be immediately obvious because it was developed as a purely descriptive model, remaining silent on why those particular five dimensions describe the major axes of covariation among personality traits. However, explanatory models for the Big Five should be possible because a key premise of the factor-analytic approach is that multiple traits covary, indicating a factor, due to some shared underlying cause (Haig, 2005). This cause need not be exclusively biological (an alternative cause, for example, might be a frequently occurring class of situations that evokes behaviors related to multiple traits with distinct biological

causes), but shared biological causation is at least a reasonable hypothesis. Individual differences in the Big Five are strongly genetically influenced (Bouchard & McGue, 2003; Riemann et al., 1997), and the genetic factor structure of the Big Five appears to be invariant across European, North American, and East Asian samples (Yamagata et al., 2006). We have good reason, therefore, to look for biological systems underlying the Big Five.

However, the Big Five do not constitute the only level of personality traits of interest. Traits can be arranged hierarchically, with correlated groups of more specific traits categorized together in broader traits (Markon, 2009). The existence of traits both narrower and broader than the Big Five may indicate additional biological causes both more and less specific than those that influence the Big Five.

At least one level of structure exists above the Big Five. Although the Big Five were originally conceived as independent traits and the most general level of personality description, research has shown that they are regularly intercorrelated and possess a higher-order factor structure (DeYoung, 2006; Digman, 1997; McCrae et al., 2008). The shared variance of Neuroticism (reversed), Agreeableness, and Conscientiousness constitutes one higher-order factor or metatrait, labeled α or *Stability*, and the shared variance of Extraversion and Openness/Intellect constitutes another, labeled β or *Plasticity*.

Additionally, multiple levels of the trait hierarchy exist below the Big Five. Each Big Five domain comprises the shared variance of a large number of lower-level traits, often called *facets*, with no consensus as to how many facets exist for each domain. Each facet has been shown to have a unique genetic contribution, suggesting the existence of specific biological parameters that differentiate facets within a single domain (Jang, McCrae, Angleitner, Riemann, & Livesley, 1998).

Finally, another level of personality structure appears to exist between the Big Five and their facets. Jang et al. (2002) found that two genetic factors were necessary to account for the shared genetic variance among facets within each of the Big Five. If the Big Five were the next level above the facets, only one genetic factor should have been necessary for each domain. These mid-level factors were characterized in more detail through factor analysis of many facets for each domain, followed by examination of how the resulting factors were correlated with over two thousand personality items (DeYoung, Quilty, & Peterson, 2007). This analysis indicated that each of the Big Five comprises two separable but correlated aspects, which constitute a level of personality structure between the facets and the Big Five.

The four levels of the personality hierarchy just described are depicted in Figure 1. (Remember that labels for personality traits are always imperfect attempts to capture what is shared among the various characteristics encompassed by each trait.) Each level can be considered to reflect causal influences of differing breadth. The existence of the bottom level indicates that some causes are unique to each facet. At the second level, causes are shared between facets within each aspect but are not shared with facets in the complementary aspect in each pair. At the third level, all traits within each of the Big Five share causes that are not shared with traits in other Big Five domains. Finally, the existence of the metatraits implies that traits share causal influences even across some of the Big Five domains.

At least one caveat must be made regarding the model in Figure 1. It is necessarily an oversimplification because personality does not have simple structure, which means that some facets and aspects show correlations, not modeled by the hierarchy in Figure 1, with facets and aspects in other Big Five domains. As one biologically pertinent example, Assertiveness is negatively correlated with Politeness (which has belligerence at its low pole), despite the fact that these traits are subsumed by two Big Five traits that are unre-

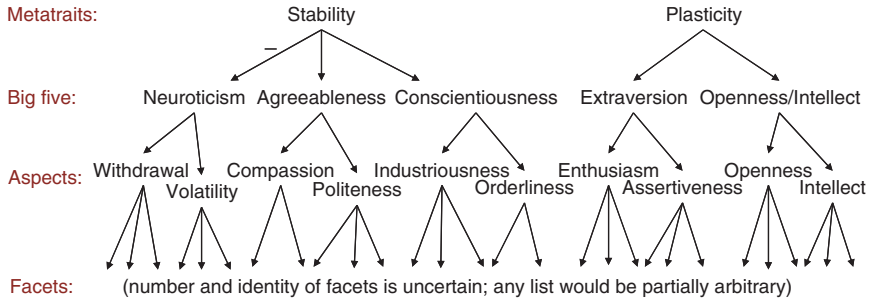

Figure 1 A hierarchical model of personality traits based on the Big Five, depicting four levels of organization. Each level is hypothesized to represent a different set of biological factors that cause personality traits to covary. (The negative sign by the path from Stability to Neuroticism indicates that Neuroticism is negatively associated with Stability.).

lated (DeYoung et al., 2007). This association is likely to be of interest for personality neuroscience because these two traits appear to be influenced in opposite directions by testosterone (Luxen & Buunk, 2005; McIntyre et al., 2007; Netter, 2004), which may account for their covariation. To include a trait reflecting this putative causal influence of testosterone in Figure 1, we would need to add an additional variable outside of the existing hierarchy (perhaps labeled 'Competitiveness' or 'Dominance'), with arrows directed at Assertiveness and Politeness. To account for the full complexity of personality structure, many such additional variables are likely to be necessary. Nonetheless, the model in Figure 1 can effectively be used to organize most of what is currently known about the neurobiology of traits.

Neurobiology of the Trait Hierarchy

A crucial step in the investigation of the biology of personality traits is identification of the psychological functions shared by all of the lower-level traits within each trait of interest. Because much is known about how the brain enacts a wide variety of psychological functions, development of a hypothesis about the psychological functions responsible for a personality trait provides the necessary stepping stone to a hypothesis about the brain systems involved in that trait. Personality psychologists have produced many theories about the psychological functions underlying various traits, but only a few have attempted to identify the psychological functions underlying all of the Big Five (Denissen & Penke, 2008; DeYoung, 2010; DeYoung & Gray, 2009; Nettle, 2006, 2007; Van Egeren, 2009). Such theories offer psychological explanations for the Big Five that go beyond mere description.

Considerable agreement is evident among these theories about the functions associated with the Big Five. Extraversion and Neuroticism are thought to be the primary manifestations in personality of sensitivity to reward and positive affect (Extraversion) and sensitivity to punishment and negative affect (Neuroticism). Agreeableness reflects the tendency toward altruism as opposed to exploitation of others. Conscientiousness reflects top-down control of behavior and impulses in order to follow rules and pursue non-immediate goals. And Openness/Intellect reflects the tendency to detect, explore, appreciate, and utilize patterns of abstract and sensory information. Armed with these hypotheses, one can begin to develop and evaluate a model specifying which brain systems are likely to be involved in which traits.

Rather than beginning a review of personality neuroscience research with the Big Five, however, I begin with the metatraits, Stability and Plasticity, because they are likely to reflect biological systems with very broad impact on both brain function and personality. Stability appears to represent a general tendency to regulate or restrain potentially disruptive emotion and behavior, whereas Plasticity appears to represent a general tendency to explore and engage with possibilities (DeYoung, 2006, 2010; DeYoung, Peterson, & Higgins, 2002; Hirsh, DeYoung, & Peterson, 2009). Evidence is accumulating to suggest that Stability is related to serotonin, whereas Plasticity may be related to dopamine (DeYoung & Gray, 2009; Yamagata et al., 2006).

Serotonin and dopamine are very broadly acting neuromodulators that affect an extremely wide array of brain systems. One useful feature of the theory that serotonin and dopamine are important influences on Stability and Plasticity is that it helps to reconcile the many different roles that have been proposed for serotonin in personality. Serotonin typically has regulatory or inhibiting effects on mood, behavior, and cognition (Spoont, 1992) and has been associated with a variety of traits, both empirically and theoretically. However, almost all of those traits are associated positively or negatively with Stability and can be classified within Neuroticism, Agreeableness, or Conscientiousness. Low levels of serotonin are associated with aggression, poor impulse control, and depression, and drugs that boost serotonergic function are used successfully to mitigate these problems (Carver & Miller, 2006; Spoont, 1992). As more direct evidence for the role of serotonin in the Big Five, studies of variation in genes from the serotonin system, as well as studies using pharmacological manipulation of the serotonin system, have found associations of serotonergic function with Neuroticism, Agreeableness, and Conscientiousness (Cools et al., 2005; Greenberg et al., 2000; Jang et al., 2001; Lesch et al., 1996; Manuck et al., 1998).

Plasticity appears to reflect a general exploratory tendency, with Extraversion representing a more behavioral mode of exploration and Openness/Intellect a more cognitive mode. The role of dopamine in exploratory behavior and cognitive function is well-established (Ashby, Isen, & Turken, 1999; Braver & Barch, 2002; Depue & Collins, 1999; Panksepp, 1998), and a growing body of evidence directly implicates dopaminergic function in Extraversion (Depue & Collins, 1999; Wacker, Chavanon, & Stemmler, 2006; Wacker & Stemmler, 2006). Some evidence suggests that Openness/Intellect might also be influenced by dopamine (DeYoung & Gray, 2009; DeYoung, Peterson, & Higgins, 2005). The dopaminergic system has two branches that may reflect the difference between Extraversion and Openness/Intellect. One branch innervates brain structures, like the nucleus accumbens and amygdala, that are crucially involved in motivation, emotion, and reward (Extraversion), and another branch innervates the prefrontal cortex, the key brain region for higher cognition (Openness/Intellect).

Based on the evidence just reviewed, some parameters of the serotonergic and dopaminergic systems (such as those affecting rates of neurotransmitter synthesis) seem likely to account for shared variance among the Big Five. The rest of this review will shift to focus on biological systems that appear to be specific to each of the Big Five (and occasionally to their distinct aspects). A great deal is known about the neurobiology of responses to reward and punishment. As a consequence, more data is available on the neurobiology of Extraversion and Neuroticism than of Agreeableness, Conscientiousness, or Openness/Intellect. Virtually every personality taxonomy has included traits similar to Extraversion and Neuroticism. Current biological theories of Extraversion and Neuroticism are heavily influenced by the work of Jeffrey Gray (1982); Gray & McNaughton, 2000; Pickering & Gray, 1999), who developed a personality theory

based on a 'conceptual nervous system' that included a Behavioral Approach System (BAS) to respond to cues of reward and a Behavioral Inhibition System (BIS) and Fight-Flight-Freeze System (FFFS) to respond to threats. Although Gray (1982) originally considered traits of BAS and BIS sensitivity as somewhat different from Extraversion and Neuroticism, more recent research suggests that measures of BAS and BIS assess the same latent traits as measures of Extraversion and Neuroticism, respectively (Elliot & Thrash, 2002; Gray & McNaughton, 2000; Smillie, Pickering, & Jackson, 2006; Zelenski & Larsen, 1999).

Extraversion

Dopamine, an important component of the BAS, plays a key role in sensitivity to reward, driving behavior that involves approaching potential rewards (Depue & Collins, 1999). Many of the traits encompassed by Extraversion, such as assertiveness and talkativeness, appear to reflect this approach behavior. Speech, for example, is often used to attain social reward, and Extraversion is often manifested socially because many human rewards involve social affiliation or status. Dopamine is most responsible for the drive to achieve reward, rather than for the enjoyment of reward once it is achieved – for 'wanting' rather than 'liking,' in other words (Berridge, Robinson, & Aldridge, 2009). In addition to traits related to wanting, Extraversion encompasses traits that reflect liking, such as positive emotionality and enjoyment of social interactions. The two aspects of Extraversion in Figure 1 appear to represent this distinction between liking (Enthusiasm, which encompasses sociability and positive emotionality) and wanting (Assertiveness). Traits within Enthusiasm are likely to reflect the action of endogenous opioid systems, which are involved in the positive emotions that follow attainment or consumption of reward and which are particularly important in social affiliation. Pharmacological manipulation has demonstrated that opiate response to cues of affiliation is a function of Social Closeness, a trait measure that is an excellent marker of Extraversion and is more related to Enthusiasm than Assertiveness (Depue & Morrone-Strupinsky, 2005; Markon et al., 2005).

Neurotransmitters like dopamine and the endogenous opiates modulate specific neural networks that constitute the brain's reward and approach systems, and multiple neuroimaging studies have linked Extraversion to various structures within these systems. Functional MRI studies demonstrate that Extraversion is positively associated with brain activity at rest or in response to positive or rewarding stimuli, in the medial orbitofrontal cortex, nucleus accumbens, amygdala, and striatum (Canli, Sivers, Whitfield, Gotlib, & Gabrieli, 2002; Canli et al., 2001; Cohen, Young, Baek, Kessler, & Ranganath, 2005; Deckersbach et al., 2006; Mobbs, Hagan, Azim, Menon, & Reiss, 2005). Additionally, several structural MRI studies have found that Extraversion is associated with greater volume of medial orbitofrontal cortex, a region involved in coding the value of rewards (DeYoung et al., 2010; Omura, Constable, & Canli, 2005; Rauch et al., 2005).

A considerable amount of EEG research has been carried out on Extraversion because Eysenck (1967) hypothesized that Extraversion was a function of levels of cortical arousal (which EEG is well-suited to measure). Tests of this hypothesis have been rather inconclusive, as both EEG and fMRI studies have found that the association between Extraversion and cortical arousal is sometimes positive and sometimes negative (Matthews & Gilliland, 1999; Zuckerman, 2005). Although Eysenck's theory seems unlikely to be sufficiently fine-grained at the neural level (as the cortex is large and carries out many different functions), some aspects of it may be compatible with the reward sensitivity model.

Associations of Extraversion with cortical arousal are moderated by the type of situation in which arousal is measured, and the reward properties of the situation may be crucial in this moderation (Matthews & Gilliland, 1999). Pharmacological manipulation has shown that dopamine affects the association of Extraversion with patterns of cortical arousal (Wacker et al., 2006).

Neuroticism

Neuroticism describes the tendency to experience the negative emotions and cognitions that accompany experiences of threat and punishment, including anxiety, depression, anger, irritation, self-consciousness, rumination, and vulnerability. Various brain systems associated with these reactions to threat and punishment have been linked to Neuroticism. For example, neuroimaging has demonstrated that Neuroticism is associated with brain activity at rest or in response to aversive or novel stimuli, in the amygdala, insula, and anterior cingulate (Deckersbach et al., 2006; Eisenberger, Lieberman, & Satpute, 2005; Etkin et al., 2004; Cools et al., 2005; Haas, Omura, Constable, & Canli, 2007a; Keightley et al., 2003; Reuter et al., 2004). Neuroticism has also been associated with neural activity in medial prefrontal cortex that is suggestive of poor emotion regulation (Haas, Constable, & Canli, 2008; Williams et al., 2006) and with reduced volume in that region (DeYoung et al., 2010).

Gray and McNaughton (2000) suggested that Neuroticism is jointly determined by sensitivities of the BIS and FFFS, with the BIS responsible for passive avoidance in situations where goals are in conflict (e.g., an approach-avoidance conflict, such as wanting to initiate social contact but fearing rejection), and the FFFS responsible for response to proximal threat or punishment, in which the only motivation is to avoid or eliminate the threat. Important brain structures in the BIS are the hippocampus and amygdala, whereas important structures in the FFFS are the amygdala, hypothalamus, and periaqueductal gray. The FFFS overlaps with the hypothalamic-pituitary-adrenal (HPA) axis that is central to hormonal stress responses. Neuroticism has been associated with higher baseline levels of the stress hormone cortisol, but with reduced phasic increases of cortisol in response to specific stressors (Netter, 2004). This pattern suggests that those high in Neuroticism tend to be not only chronically stressed but also less able to mobilize resources to deal with particularly stressful situations.

The neurotransmitters serotonin and norepinephrine both modulate the BIS and FFFS (Gray & McNaughton, 2000), and Neuroticism has been associated with lower levels of serotonergic function through various methods, including molecular genetics, PET, psychopharmacological manipulation, and assays of cerebrospinal fluid (Cools et al., 2005; Hennig, 2004; Lesch et al., 1996; Manuck et al., 1998; Schinka, Busch, & Robichaux-Keene, 2004; Sen, Burmeister, & Ghosh, 2004; Tauscher et al., 2001). Some evidence also links Neuroticism to higher levels of norepinephrine (Hennig, 2004; White & Depue, 1999; Zuckerman, 2005).

Finally, EEG research has found that traits related to the Withdrawal aspect of Neuroticism are associated with greater activation of the right frontal lobe relative to the left (Shackman, McMenamin, Maxwell, Greischar, & Davidson, 2009; Zuckerman, 2005). The brain's right hemisphere appears to be preferentially involved in emotions and motivational states associated with withdrawal, whereas the left hemisphere is preferentially involved in approach (Davidson, 2002). To associate all aspects of Neuroticism with the right hemisphere would be oversimplistic, however. Anger-proneness is an important component of the Volatility aspect of Neuroticism, and EEG studies have shown anger

to be associated with greater relative left frontal lobe activation, presumably because anger involves approach (Harmon-Jones, 2004; Harmon-Jones & Allen, 1998).

Agreeableness

All of the traits encompassed by Agreeableness appear to reflect a tendency toward altruism and cooperation as opposed to antisocial and exploitative behavior. Agreeable people are interested in and considerate of others' needs, desires, and feelings, and they avoid aggressing or imposing their will on others. Such behavior requires the ability to understand others' emotions, intentions, and mental states, and Agreeableness has been found to predict tests of empathy, theory of mind, and other forms of social information processing (Graziano, Habashi, Sheese, & Tobin, 2007; Nettle & Liddle, 2008; Wilkowski, Robinson, & Meier, 2006). One MRI study found that Agreeableness is associated with volume in brain regions associated with social information processing, including superior temporal sulcus, posterior cingulate cortex, and fusiform gyrus (DeYoung et al., 2010).

Agreeableness also appears to be associated with the ability to suppress aggressive impulses and other socially disruptive emotions (Meier, Robinson, & Wilkowski, 2006), and an fMRI study found that Agreeableness predicted activity in left dorsolateral prefrontal cortex associated with emotion regulation (Haas, Omura, Constable, & Canli, 2007b). Presumably because aggression is often driven by anger, trait anger is correlated with Agreeableness as well as with Neuroticism, and anger has sometimes been treated as a component of low Agreeableness (Saucier, 2009). Its primary location within Neuroticism, however, is consistent with the tendency of all negative emotions to covary. Reactive aggression might be considered as the joint consequence of high Neuroticism and low Agreeableness, whereas more instrumental forms of aggression may be more exclusively associated with Agreeableness.

Although Agreeableness has not often been targeted explicitly by neuroscience, a number of fMRI studies have used self-report measures of empathy, which is a facet of Agreeableness. Individual differences in empathy have been associated with neural activity during observation and imitation of others' actions (Gazzola, Aziz-Zadeh, & Keysers, 2006; Kaplan & Iacoboni, 2006) and during perception of others' emotional expressions (Chakrabarti, Bullmore, & Baron-Cohen, 2007; Schulte-Rüther, Markowitsch, Fink, & Piefke, 2007). In these studies, empathy was found to be positively associated with activity in the medial prefrontal cortex, superior temporal sulcus, and mirror neuron system (regions of frontal and parietal cortex that are similarly active when performing or observing the same action). Another study (Tankersley, Stowe, & Huettel, 2007) found that a self-report measure of altruism was positively associated with activity in posterior superior temporal sulcus, while observing performance of a task, in contrast to performing the task oneself.

Conscientiousness

Human beings are unique as a species in their ability to govern their behavior by explicit systems of rules and to constrain their behavior in order to pursue goals that may be achieved only in the distant future. Conscientiousness appears to reflect variation in the capacity for self-discipline and organization that is necessary for this form of top-down control. Conscientiousness predicts academic and occupational success, as well as behavior that promote health and longevity (Ozer & Benet-Martinez, 2006). It is likely to be associated with functions of the prefrontal cortex, the brain region responsible for much of

the human ability to plan and follow complex rules (Bunge & Zelazo, 2006; Miller & Cohen, 2001). A structural MRI study found that Conscientiousness was associated with greater volume of the middle frontal gyrus in lateral prefrontal cortex (DeYoung et al., 2010), a region involved in maintaining goal-relevant information in working memory and in the execution of planned action based on abstract rules (Bunge & Zelazo, 2006).

As with Agreeableness, few neuroscience studies have targeted Conscientiousness explicitly. However, many studies have targeted related constructs (reflecting low Conscientiousness), such as impulsivity, novelty seeking, and sensation seeking. Functional neuroimaging studies have found that individual differences in self-reported impulsivity are associated with neural activity in both dorsal and ventral regions of lateral prefrontal cortex (Asahi, Okamato, Akado, Yamawaki, & Yokota, 2004; Brown, Manuck, Flory, & Hariri, 2006).

Caution is required in interpreting studies of impulsivity, novelty seeking, and sensation seeking because these traits are heterogeneous in their associations with the Big Five, usually associated with Extraversion and sometimes with Neuroticism, as well as with Conscientiousness (Depue & Collins, 1999; Markon et al., 2005; Whiteside & Lynam, 2001). They seem to be compound traits, influenced by multiple more basic traits. Their compound nature appears to reflect the fact that problems of impulse control may be exacerbated both by weakness of the top-down control systems that override impulses (the presumed substrate of Conscientiousness) or by potentiation of the impulses themselves, which may be responses to cues of reward (Extraversion) or punishment (Neuroticism). For example, Zuckerman (2005) noted that many studies have found traits in this group to be associated with high levels of dopaminergic function and low levels of serotonergic function. However, he argued that dopamine is associated with impulses to approach reward, whereas low serotonin is associated with the absence of control or restraint of those impulses. The serotonergic component is the one that appears to be related to Conscientiousness (Manuck et al., 1998), though recall that it is also associated with Neuroticism and Agreeableness.

Openness/Intellect

The two aspects of Openness/Intellect, not surprisingly, can be described as Intellect and Openness to Experience, which appear to reflect engagement with abstract or intellectual information (Intellect) and engagement with aesthetic or sensory information (Openness). These two traits are equally central to the larger Big Five domain (DeYoung et al., 2007; Johnson, 1994; Saucier, 1992), and both are likely to be associated with the functioning of attention and the ability to process complex information. In keeping with this hypothesis, Openness/Intellect is the only Big Five dimension consistently positively associated with cognitive abilities such as intelligence and working memory capacity (DeYoung, Shamosh, Green, Braver, & Gray, 2009; DeYoung et al., 2005).

Intellect is more strongly linked to intelligence and working memory than is Openness (DeYoung et al., 2005, 2009). An fMRI study demonstrated that Intellect, but not Openness, was associated with brain activity during a difficult working memory task, in two regions of the prefrontal cortex, the left frontal pole and the posterior medial frontal cortex (DeYoung et al., 2009). The frontal pole is involved in abstract integration of multiple cognitive operations and in drawing abstract analogies (Gilbert et al., 2006; Green, Fugelsang, Kraemer, Shamosh, & Dunbar, 2006; Ramnani & Owen, 2004). The posterior medial frontal cortex is involved in monitoring goal-directed performance and detecting the likelihood of error during cognitive tasks (Brown & Braver, 2005;

Ridderinkhof, Ullsperger, Crone, & Nieuwenhuis, 2004). Neural activity in the frontal pole was associated with self-ratings of Intellect because of variance shared between Intellect and performance on intelligence tests, suggesting that this region is involved in the ability component of Intellect. In posterior medial frontal cortex, however, Intellect remained significantly related to neural activity even after controlling for intelligence, suggesting that this region and its functions may be involved in intellectual engagement, independently of ability. In addition to intelligence, intellectual engagement entails a motivation to succeed at cognitive tasks, which is presumably associated with increased monitoring of cognitive performance.

Dopamine's involvement in Openness/Intellect is likely to be a function of dopamine's influence on the prefrontal cortex. One study (Harris et al., 2005) reports an association of variation in the catechol-*O*-methyltransferase (*COMT*) gene with Openness/Intellect, and *COMT* provides the enzyme that is the primary mechanism for clearing dopamine from the synapse in prefrontal cortex and thus regulates levels of dopaminergic activity in that brain region (Meyer-Lindenberg et al., 2006).

A Two-Way Street between Personality Psychology and Neuroscience

The review of research presented above was not intended to be fully comprehensive, either in its coverage of personality neuroscience studies or in its listing of biological systems that are likely to be related to personality traits. Rather, it was meant to illustrate the breadth of neuroscience research on personality traits and the possibility of integrating this research using theories of the psychological mechanisms underlying the most widely used taxonomy of traits, the Big Five.

Of course, the Big Five model is not the only personality taxonomy in existence, and some personality taxonomies were developed specifically to reflect biological hypotheses (e.g., Cloninger, 1987; Zuckerman, Kuhlman, Joireman, Teta, & Kraft, 1993). However, research has shown that the factor structure of these alternative models tends to be more accurately described by the Big Five than by their originally hypothesized structures (e.g., Angleitner, Riemann, & Spinath, 2004; Markon et al., 2005; Ramanaiah, Rielage, & Cheng, 2002). The Big Five is preferable to these models because it is empirically based, organizing traits according to the manner in which they vary together.

The other major contender for an empirically based personality taxonomy is a six factor model, which appears to be more replicable than the Big Five across languages (Ashton & Lee, 2007; Saucier, 2009). However, the Big Five appears likely to be a better choice of taxonomy for personality neuroscience because of the way in which the six factor model spreads traits related to altruism and negative affect across multiple factors, blending them with other traits (Ashton & Lee, 2007, footnote 4). In contrast, the Big Five model groups all traits related to negative emotion within one dimension (Neuroticism) and all traits related to altruism within another (Agreeableness). Obviously the biological systems involved in negative emotion and altruism are complex; nonetheless, traits related to each of these processes are likely to share many important biological influences, and grouping them together is a parsimonious approach to investigating their underlying causes.

The need to weigh the Big Five against a six factor model illustrates Eysenck's (1997) assertion that, although factor analysis is a useful tool for identifying plausible taxonomic systems for personality, it cannot, by itself, identify the best taxonomic system for a particular purpose. Theoretical considerations must come into play, both because personality does not have simple structure and because factor analyses are never completely unbiased.

Unfortunately, some biases will be present even in the pool of personality descriptors drawn from natural languages. Socially salient traits are likely to be over-represented, for example (because language is used primarily for social purposes), leading to the possibility of over-representation of factors related to socially oriented behavior. Thus, the mere fact that a six factor model is more replicable than the Big Five in various languages is not an inherently sufficient reason to prefer it to the Big Five. Additional theoretical considerations, such as patterns of association with biological mechanisms, are necessary, which highlights the role that neuroscience can play in theory construction in personality psychology.

The relationship between personality psychology and neuroscience should be viewed as a two-way street. Personality psychology can help to guide neuroscience hypotheses and to organize and synthesize neuroscience findings. Additionally, however, neuroscience data may influence personality psychologists in their development of trait models, as Eysenck (1997) suggested. Using neuroscience methods to study personality has the potential to produce explanatory biological models for trait taxonomies that were at first purely descriptive, and these models may help to realize the goal of a theory of personality as a system of dynamic, interacting elements that generates the ongoing flux of behavior and experience (DeYoung, 2010). Neuroscience is well suited to such a theory because each brain system interacts with many other brain systems, and neuroscience models typically attempt to consider these interactions. A causal theory of personality could be based on psychological constructs alone, but this would ignore the fact that the brain is the proximal cause of behavior and experience. Neuroscience can therefore usefully constrain psychological theorizing. Anyone interested in the psychological functions that underlie personality traits should be interested in the results of personality neuroscience, as neuroscience can be used to test and refine our understanding of the mechanisms involved in personality.

Short Biography

Colin DeYoung is Assistant Professor in Psychology at the University of Minnesota, in the Personality, Individual Differences, and Behavior Genetics area. He received an A.B. from Harvard University, completed his doctorate at the University of Toronto, and worked as a postdoctoral fellow at Yale University before moving to the University of Minnesota. In 2007, he won the J.S. Tanaka Dissertation Award for methodological and substantive contributions to the field of personality psychology. His research focuses on the structure and sources of personality, using neuroscience methods to investigate the biological substrates of personality traits.

Endnote

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