

Running Head: PERSONALITY NEUROSCIENCE

Personality Neuroscience: Explaining Individual Differences in Affect, Behavior, and Cognition

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To be published in the Cambridge University Press *Handbook of Personality*

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Human behaviors and experiences are generated by biological processes, primarily within the brain. On this basis, we may assume that the regularities in these behaviors and experiences that constitute personality are associated with regularities in the biological functions of the brain, making *personality neuroscience* possible. It is increasingly easy to study psychologically relevant individual differences using neuroscientific methods. Personality neuroscience endeavors to understand the proximal sources of personality in the brain and to trace those brain processes back to their distal sources in complex interactions between genes and environment. Heritability estimates for personality traits are typically around 50% or higher, indicating that the distal sources of personality lie in both the genome and the environment (Bouchard, 1994; Loehlin, 1992; Reimann, Angleitner, & Strelau, 1997). Both genes and environment must make their mark on the brain, however, if they are to have a lasting influence on personality.

Personality psychology attempts to answer some of the most fundamental questions about people: Why are individuals the way they are? How and why do people differ from each other? For much of the past century, personality psychology has been concerned more with describing personality than with explaining it – that is, with *how* people differ from each other rather than with *why* they differ from each other. One reason for this emphasis on description rather than explanation was the immaturity of human neuroscience. Tools for investigating the neurobiological underpinnings of individual differences have greatly increased in power with the rise of neuroimaging and molecular genetics.

Another reason that personality psychology tended to focus on description rather than explanation was the necessity of developing an adequate categorization system for personality

traits. Traits are relatively stable patterns of affect, behavior, and cognition (Fleeson, 2001; Pytlik Zillig, Hemenover, & Dienstbier, 2002). The existence of a multitude of such patterns raises the question of whether some relatively small number of broad trait categories can be used to classify and organize the majority of traits. Over the past 25 years, this question has been largely resolved by the emergence of the Five Factor Model or Big Five, which postulates that almost all trait descriptors can be categorized within five broad domains (or as blends of two or more of those domains): Extraversion, Neuroticism, Agreeableness, Conscientiousness, and Openness/Intellect (Costa & McCrae, 1992; Digman, 1990; Hofstee, de Raad, Goldberg, 1992; John & Srivastava, 1999; chapter 10, this volume). Our emphasis on the Big Five should not be misconstrued as a suggestion that the trait level of analysis alone can capture everything about personality—it cannot. Characteristic adaptations to particular situations and self-defining life narratives constitute two additional major levels of analysis that are more specific and better able to capture the rich detail and uniqueness of individual personalities (McAdams & Pals, 2006; Mischel & Shoda, 1998; Wood & Roberts, 2006). Incorporating these levels can complement and enrich the trait approach. At this early stage in personality neuroscience, however, linking traits to neurobiological substrates is a promising start.

The Big Five model offers a useful categorization scheme for personality neuroscience and can usefully organize a review of this young field. Despite some debate in lexical research on personality about whether a six- or seven-factor model might be more robust across languages (Ashton et al., 2004; Saucier & Goldberg, 2001), the Big Five is the most widely used taxonomy of personality and provides a useful common language for personality research, helping to ensure that results are comparable across different studies. Behavior genetic research shows that the Big Five are substantially heritable, with estimates ranging from 40% or 50% up to 80%, depending

on trait and method (Reimann et al., 1997). Recently, the genetic factor structure of the Big Five, as measured by the Revised NEO Personality Inventory, was shown to be invariant across European, North American, and East Asian samples, suggesting the biological universality of these traits (Yamagata et al., 2006). When measures of abnormal and normal personality traits are factor analyzed together, the standard Big Five solution appears (Markon, Krueger, and Watson, 2005), suggesting the utility of the Big Five for studying psychopathology. Finally, the Big Five appears to be an effective taxonomy of descriptors of individual differences in other species (Gosling & John, 1999), and cross-species comparisons are often important in neuroscience. All of these considerations suggest the potential utility of the Big Five for personality neuroscience, *as long as models can be developed that identify possible biological substrates of the Big Five and lead to testable hypotheses*. Fortunately, the field has now developed to the point where a synthesis of the literature may contribute to this sort of model.

Our aims in this chapter are first to review the methods and history of personality neuroscience and then to attempt a synthesis of findings across the range of personality traits, as represented primarily by the Big Five. The goal here is not to summarize every result for any particular method, but to determine how the array of findings to date contributes to a larger picture of the relation between variation in the brain and variation in personality. This strategy will highlight a point that we consider to be of major conceptual importance, namely that theories of personality must not be limited to a particular domain of information processing, but must consider individual differences in affect, behavior, and cognition, as well as how these different domains are integrated and interact (Gray, 2004; Gray, Braver, & Raichle, 2002). Only by taking a broad view will the field be able to fulfill the promise of personality psychology to understand the individual as he or she actually functions as a whole.

Methods in Personality Neuroscience

Personality neuroscience reflects the conjunction of personality psychology with methods for discovering the biological sources of individual differences. The measurement of personality is typically accomplished by questionnaire, through self-report and/or through ratings by peers or other knowledgeable informants. “Personality” is sometimes taken to mean the set of variables that result from questionnaire measures, but this confuses the instruments with the constructs. Questionnaires are simply a convenient and reliable method for assessing a broad range of stable individual differences, drawing on subjects’ experiences over a far greater span of time than is available in the laboratory. Other methods can be used to measure personality, if they can be validated psychometrically (i.e., as measuring stable patterns of affect, behavior, and cognition). Measures of intelligence and of the ability to delay gratification (Ohmura, Takahashi, Kitamura, & Wehr, 2006) are good examples. The challenge with such behavioral measures, because models of personality structure like the Big Five are typically operationalized with questionnaires, is to relate them back to those models so that they may be incorporated into the larger nomological network of personality psychology.

The general categories of neuroscientific methods that we see as currently most relevant to personality are (1) neuroimaging (e.g., magnetic resonance imaging (MRI) or proton emission tomography (PET)), (2) molecular genetics (a.k.a. genomics), (3) electrophysiological techniques (e.g., electroencephalography (EEG) or measurement of electrodermal activity (EDA)), (4) assays of endogenous psychoactive substances or their byproducts (e.g., hormone levels in saliva or neurotransmitter metabolites in cerebrospinal fluid), and (5) psychopharmacological manipulation (e.g., tryptophan depletion or augmentation to alter levels of serotonin).

Studies of personality using structural and functional MRI and PET are appearing at a rapid rate; over 50 have been published since 2003, almost tripling the existing number (see chapter 16, this volume). Molecular genetics has seen a similar explosion of personality research since the first studies of the effects of genetic variation on normal personality traits appeared in 1996 (see chapter 13, this volume). Electrophysiological research was the primary tool for investigating the biology of personality, prior to the advent of neuroimaging and molecular genetics; with a few exceptions, however, associations of electrophysiological variables with personality have been inconsistent (Zuckerman, 2005). Excellent reviews of research on the influence of neurotransmitters and hormones on personality have been written by Netter (2004), Hennig (2004), and Zuckerman (2005). Many inferences about personality can be drawn from the study of nonhuman animals (see chapter 14, this volume), and consistency with nonhuman analogs is a hallmark of good theory in personality neuroscience, but we limit our review to human methods.

Influential Theories in Personality Neuroscience

We briefly describe the influential models of Eysenck, Gray, Zuckerman, Cloninger, Depue, and Panksepp and relate each model to the Big Five, with the aim of translating results from different systems into a single common language. This approach is readily justified by the fact that these models have been demonstrated to fall within the same factor structure as the Big Five (e.g., Markon et al., 2005; Angleitner, Riemann, & Spinath, 2004). Most of the theorists have revised their models substantially over time; in the interest of space we discuss only the latest version of each.

Eysenck assigned traits to three “superfactors,” Extraversion, Neuroticism, and Psychoticism (Eysenck & Eysenck, 1985). Extraversion and Neuroticism are nearly identical in

Eysenck's system and the Big Five, whereas the unfortunately-labeled Psychoticism reflects a roughly equal blend of low Conscientiousness and low Agreeableness (Goldberg & Rosolack, 1994). In his biological theorizing, Eysenck (1967; Eysenck & Eysenck, 1985) relied heavily on the functions of the brain's ascending reticular activating system, associating Extraversion with the reticulo-cortical circuit and Neuroticism with the reticulo-limbic circuit. Eysenck hypothesized (a) that extraverts have lower baseline levels of cortical arousal than introverts and therefore choose more arousing activities in order to achieve their preferred level of arousal, and (b) that extraverts may have higher preferred or optimal levels of arousal. He hypothesized that neurotics are more easily aroused by emotion-inducing stimuli than are emotionally stable people. Eysenck did not develop as well-specified a biological model of Psychoticism, but at different times he hypothesized that Psychoticism was negatively associated with serotonergic function (Eysenck, 1992) and positively associated with dopaminergic function (Eysenck, 1997).

Jeffrey Gray, who was Eysenck's student, focused more heavily on neurobiology than on personality, with an emphasis on the development of a "conceptual nervous system" describing functional systems that could be mapped onto brain systems. The main components of this conceptual nervous system are the Behavioral Approach System (BAS), which responds to cues for reward, and the Fight-Flight-Freezing System (FFFS) and Behavioral Inhibition System (BIS), which respond to two distinct classes of threatening stimuli (Gray & McNaughton, 2000; Pickering & Gray, 1999). Immediately threatening, punishing, or frustrating stimuli activate the FFFS, which produces active avoidance (panic and flight) or attempted elimination (anger and attack). Stimuli that one needs or desires to approach but that also contain potential threat (thus creating an approach-avoidance conflict) activate the BIS, which produces vigilance, rumination, and passive avoidance, as well as anxiety and even potentially depression (Gray & McNaughton,

2000). (Approach-approach or avoidance-avoidance conflicts are less common but can also activate the BIS, which responds specifically to any conflict between goals.) Biologically, Gray linked the BAS to the dopaminergic system, the BIS primarily to the septo-hippocampal system but also to the amygdala, and the FFFS to the amygdala, hypothalamus, and periaqueductal gray.

Gray's model of personality, Reinforcement Sensitivity Theory (RST; see Chapter 18, this volume), describes personality traits as a function of individual differences in the sensitivities of BIS, BAS, and FFFS. Gray (1982) originally described two dimensions of personality associated with BIS sensitivity and BAS sensitivity, which he labeled Anxiety and Impulsivity respectively. Gray viewed Anxiety and Impulsivity as 30° rotations from Neuroticism and Extraversion, respectively. Gray and McNaughton (2000) noted, however, that questionnaire measures of Anxiety or BIS sensitivity are, in practice, difficult to distinguish from Neuroticism. Further, they described Neuroticism as a general sensitivity to threat produced jointly by FFFS and BIS. Additionally, several of Gray's colleagues have recently suggested that measures of Extraversion (not Impulsivity) may be the best measures of BAS sensitivity (Pickering, 2004; Smillie, Pickering & Jackson, 2006). These parallels are consistent with research showing that measures of BIS and BAS sensitivity tap the same latent constructs as measures of Neuroticism and Extraversion (Elliot & Thrash, 2002; Zelenski & Larsen 1999).

Zuckerman (2005) has provided the most extensive review of personality neuroscience to date, in the second edition of his book, *Psychobiology of Personality*. This book is organized around a hybrid of the Big Five and Zuckerman's own model of personality, the Alternative Five, which are Sociability, Neuroticism-Anxiety, Aggression-Hostility, Impulsive Sensation Seeking, and Activity. Zuckerman identified the first four of these with Extraversion, Neuroticism, Agreeableness (reversed), and Conscientiousness (reversed), respectively, in the

Big Five. Factor analyses largely bear out these associations (Aluja, Garcia, & Garcia, 2002, 2004; Angleitner et al., 2004; Zuckerman, Kuhlman, Joireman, Teta, & Kraft, 1993), though the situation is somewhat complicated for Impulsive Sensation Seeking, which is sometimes as strongly associated with Extraversion and Openness/Intellect as with Conscientiousness and also tends to show a moderate negative association with Agreeableness. Additionally, these factor analyses show that Zuckerman's Activity scale serves as a marker of Extraversion, Conscientiousness, or both.

We can not hope to summarize all of the biological research relevant to the Alternative Five that is synthesized in Zuckerman's (2005) *Psychobiology of Personality* (some of it will be discussed below). In brief, Zuckerman linked personality traits to underlying behavioral mechanisms, which he in turn linked to the brain functions of various neurotransmitters, hormones, and enzymes. One notable feature of his theorizing is that he described behavioral mechanisms (including approach, inhibition, and arousal) as determined by multiple biological systems and as contributing to multiple traits. In his model, for example, approach is influenced by both dopamine and testosterone and contributes to both Sociability and Impulsive Sensation Seeking.

In contrast, Cloninger (1987) developed a model of personality traits based on the premise that individual neurotransmitter systems might be related uniquely to specific traits. Cloninger hypothesized that the dopaminergic system was linked to a trait of Novelty Seeking, the serotonergic system to Harm Avoidance, and the norepinephrine system to Reward Dependence. Cloninger's latest model includes these three traits plus four others: Persistence, Self-Directedness, Cooperativeness, and Self-Transcendence (Cloninger, Svrakic, & Przybeck, 1993). He hypothesized that the original three traits and Persistence reflect dimensions of

temperament, meaning that they should be evident early in ontogeny and strongly genetically determined. In contrast, he hypothesized that Self-Directedness, Cooperativeness, and Self-Transcendence reflect dimensions of *character*, meaning that they should develop later, being determined by experience during development rather than primarily by genes.

Research has demonstrated several problems with Cloninger's model. First, a simple distinction between temperament and character appears untenable. The character traits show much the same levels of heritability as the temperament traits (Ando et al., 2004; Gillespie, Cloninger, Heath, & Martin, 2003). Second, evidence has accumulated to contradict the idea that single neurotransmitter systems are responsible for Novelty Seeking, Harm Avoidance, and Reward Dependence (Paris, 2005). Finally, Cloninger's seven-factor structure has not proven consistently replicable. Factor analyses have demonstrated (a) that the scales Cloninger developed do not group together in the manner that he assigned them to his seven traits (Ando et al., 2004; Ball, Tennen, & Kranzler, 1999; Herbst, Zonderman, McCrae, & Costa, 2000), and (b) that his instrument is best described by the five factor structure of the Big Five (Markon et al., 2005; Ramaniah, Rielage, & Cheng, 2002). Harm Avoidance and Self-Determination (reversed) are both markers of Neuroticism. Cooperativeness, Persistence, and Self-Transcendence are markers of Agreeableness, Conscientiousness, and Openness/Intellect, respectively. Reward Dependence combines Agreeableness and Extraversion. Finally, Novelty Seeking shows a pattern similar to Zuckerman's Impulsive Sensation Seeking: it is most strongly associated with Conscientiousness (reversed), but also consistently loads positively on Extraversion as well as sometimes negatively on Agreeableness and positively on Openness.

Depue describes five trait dimensions: Agentic Extraversion, Affiliation, Anxiety, Fear, and Nonaffective Constraint (Depue & Lenzenweger, 2005). Depue and Collins (1999) proposed

a theory of Extraversion linking it to the network of brain systems controlling sensitivity to cues of reward and generating approach behavior in response. They focused primarily on what they called “Agentic Extraversion,” encompassing assertiveness, dominance, and ambition, and distinguished this from “Affiliative Extraversion,” which is related to sociability and affiliative social bonding. “Extraversion” was eventually dropped from the label for the latter trait, and Depue and Morrone-Strupinsky (2005) proposed a theory of Affiliation, linking it to the brain systems controlling sensitivity to affiliative bonding and consummatory reward, focusing particularly on the endogenous opioids and sociosexual peptides like oxytocin. White and Depue (1999) distinguished Anxiety, which they associated with Neuroticism, from Fear, citing evidence that the amygdala responds to specific localized threat (producing fear), whereas the bed nucleus of the stria terminalis (BNST), which is often considered part of the “extended amygdala,” responds to indications of nonlocalized or potential threat (producing anxiety). Finally, Depue and Lenzenweger (2005) associated Nonaffective Constraint with Conscientiousness and with the broad inhibitory functions of the serotonergic system.

Depue has typically operationalized his constructs with the Multidimensional Personality Questionnaire (MPQ; Tellegen, 1982). The MPQ scales of Social Potency and Social Closeness, used to represent Agentic Extraversion and Affiliation respectively, both load primarily on Extraversion (Markon et al., 2005). Depue associates Anxiety most strongly with the MPQ Stress Reaction scale, which is a clear marker of Neuroticism. Fear he associates with MPQ Harm Avoidance, which, unlike Cloninger’s Harm Avoidance, specifically assesses aversion to physical danger and is not well described by the Big Five (Markon et al., 2005) (potentially because many of its items are forced choices between danger and boredom). MPQ

Control vs. Impulsivity, which Depue identifies as the best marker of Nonaffective Constraint, loads strongly on Conscientiousness (Markon et al., 2005).

Panksepp has focused primarily on animal research, but his name should be mentioned here because of his importance in the development of affective neuroscience and his advocacy of the idea that research in other mammals is strongly relevant to theories of human emotional functioning (Panksepp, 1998). He has recently developed a personality model for human research, hypothesizing the existence of six traits reflecting distinct emotional systems: Playfulness, Seeking, Caring, Fear, Anger, and Sadness. Playfulness correlates most strongly with Extraversion, Seeking with Openness/Intellect, and Caring with Agreeableness; Fear, Anger, and Sadness all correlate strongly with Neuroticism, (Davis, Panksepp, & Normansell, 2003).

Neurobiological Substrates of the Personality Hierarchy

Personality traits are arranged hierarchically, with correlated groups of more specific traits categorized together in broader traits. For example, the lower-level traits of talkativeness, assertiveness, enthusiasm, and sociability are all grouped within the trait of Extraversion. A key premise of the factor-analytic approach is that specific traits fall within the same larger factor because of some shared underlying cause (Haig, 2005). Though this cause need not be exclusively biological, the correlational structure of traits provides a useful clue for personality neuroscience. The Big Five were originally conceived as independent traits at the highest level of the personality hierarchy, but research has shown that they are regularly intercorrelated and possess a higher-order factor structure (DeYoung, 2006; DeYoung, Peterson, & Higgins, 2002; Digman, 1997; Jang et al., 2006; Markon et al., 2005). Neuroticism (reversed), Agreeableness, and Conscientiousness form one higher-order factor or metatrait, labeled α or *Stability*, and

Extraversion and Openness/Intellect form another, labeled β or *Plasticity*. Behavior genetic analysis has shown that the two metatraits have genetic origins (Jang et al., 2006), and evidence is accumulating that Stability is related to serotonin, whereas Plasticity may be related to dopamine (DeYoung, 2006; DeYoung et al., 2002; Yamagata et al., 2006). Serotonin and dopamine act as diffuse neuromodulators affecting a wide array of brain systems, and their broad influence is consistent with a role in the broadest level of personality structure.

The history of research on serotonin's role in psychopathology provides good reason to expect that increased serotonergic function should be associated positively with Agreeableness and Conscientiousness and negatively with Neuroticism. Low levels of serotonin are associated with aggression, poor impulse control, depression, and anxiety, and drugs that boost serotonergic function are used successfully to treat all of these problems (Spoont, 1992). More direct evidence exists as well. A combined behavior genetic and genomic study demonstrated that the correlation between Neuroticism and Agreeableness has a genetic basis and that variation in the serotonin transporter gene accounted for 10% of that correlation (Jang et al., 2001). A pharmacological manipulation that promotes serotonin release and inhibits reuptake has demonstrated that both low Neuroticism and high Conscientiousness are associated with increased serotonergic responsiveness (Manuck et al., 1998). And variation in the monoamine oxidase-A gene, which affects levels of serotonin, is associated with differences in Agreeableness and Conscientiousness (Rosenberg et al., 2006). The discovery of Stability as a metatrait encompassing the shared variance of Neuroticism, Agreeableness, and Conscientiousness may allow a parsimonious description of the broad effects of serotonin on personality, which largely reconciles the various hypotheses regarding serotonin proposed by the theorists described above.

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 flexibility is well-established, making it a plausible biological substrate for Plasticity (Ashby, Isen, & Turken, 1999; Braver & Barch, 2002; Depue & Collins, 1999; Panksepp, 1998). A growing body of evidence indicates that Extraversion is partly a function of dopaminergic activity (Depue & Collins, 1999; Wacker, Chavanon, & Stemmler, 2006; Wacker & Stemmler, 2006). Some evidence suggests that Openness/Intellect might also be modulated by dopamine. Both Openness/Intellect and Extraversion are associated with decreased latent inhibition, a low-level cognitive phenomenon that is known to be mediated by dopamine, and Plasticity predicts low latent inhibition better than either Extraversion or Openness/Intellect alone (Peterson & Carson, 2000; Peterson, Smith, & Carson, 2002). Additionally, variation in the catechol-*O*-methyltransferase gene (*COMT*), which regulates levels of dopamine in the prefrontal cortex, has been associated with Openness/Intellect in a sample of older adults (Harris et al., 2005).

Identifying serotonin and dopamine as likely biological substrates for the metatraits begins to develop a psychobiological model of the personality hierarchy based on the Big Five. However, the correlations among the Big Five that reveal the metatraits are not very strong, and each trait describes a clearly distinct domain of personality. Biological substrates must exist that are unique to each trait, in addition to the shared substrates that produce the metatraits. The following literature review allows the generation of hypotheses about what these unique substrates might be. We begin with Extraversion and Neuroticism, which appear to represent the primary manifestations in personality of sensitivity to reward and sensitivity to threat or punishment.

Extraversion

Depue's model of Extraversion is the most thorough and promising to date, linking it to the brain systems that govern sensitivity to reward and related positive emotions (Depue & Collins, 1999; Depue & Lenzenweger, 2005; Depue & Morrone-Strupinsky, 2005). This model is largely congruent with Gray's theory of the BAS, which has been increasingly linked to Extraversion (Smillie et al., 2006). The dopaminergic component of this reward circuitry may be particularly influential on the "agentic" aspect of Extraversion associated with drive and assertiveness (Depue & Collins, 1999), whereas the affiliative aspect of Extraversion may be associated more strongly with the endogenous opioid systems involved in the positive emotions that follow attainment or consumption of reward and that are particularly important in social bonding (Depue & Morrone-Strupinsky, 2005).

Multiple neuroimaging studies have found that brain activity at rest or in response to positive or rewarding stimuli is positively associated with Extraversion (or questionnaire measures of BAS sensitivity; Beaver et al., 2006) in the brain regions that both Depue and Gray identify as particularly important in the circuitry of reward and approach behavior. These include the medial orbitofrontal cortex, nucleus accumbens, amygdala, and striatum (Canli et al., 2001; Canli, Sivers, Whitfield, Gotlib, & Gabrieli, 2002; Cohen, Young, Baek, Kessler, & Ranganath, 2005; Deckersbach et al., 2006; Mobbs, Hagan, Azim, Menon, & Reiss, 2005). Additionally, genetic studies have found associations between Extraversion and several genes involved in the dopaminergic system (Benjamin et al., 1996; Bookman, Taylor, Adams-Campbell, & Kittles, 2002; Eichhammer et al., 2005; Ozkaragoz & Noble, 2000; Reuter & Hennig, 2005; Reuter, Schmitz, Corr, & Hennig, 2005; Tochigi et al., 2006), though these associations are not yet well established (see Chapter 13, this volume).

Some aspects of Eysenck's theory that Extraversion is associated with cortical arousal may be compatible with the reward sensitivity model. Evidence for the cortical arousal theory is complicated by the fact that EEG and fMRI studies have found that the association between Extraversion and arousal is sometimes positive and sometimes negative (Matthews & Gilliland, 1999; Zuckerman, 2005). These seemingly contradictory effects may be moderated by the type of situation in which arousal is measured and by the pattern of cortical arousal in question (Matthews & Gilliland, 1999; Wacker et al., 2006). The effect of a given situation on cortical arousal may depend in part on the situation's reward properties and may be mediated by dopamine. For example, pharmacological manipulation of dopamine D2 receptors has been shown to modulate frontal (relative to parietal) brain activity in EEG, but in opposite directions for groups high versus low in Extraversion (Wacker et al., 2006).

Several brain imaging studies have demonstrated that Extraversion is predictive of brain activity in cortical areas influenced by dopamine (such as the anterior cingulate), during working memory tasks that have no apparent affective content (Gray & Braver, 2002; Gray et al., 2005; Kumari, ffytche, Williams, & Gray, 2004). Interestingly, however, Extraversion is not typically predictive of working memory performance. These findings suggest the degree to which affective and cognitive processes are inter-related. Extraversion may be related to the ways in which individuals are motivated to perform difficult cognitive tasks and even to the manner in which those tasks are processed in the brain, whereas other traits, like Openness/Intellect (see below), may be more directly related to performance on those tasks.

Finally, testosterone levels have been positively associated with Extraversion, especially with assertiveness and dominance, in a number of studies (Netter, 2005; Zuckerman, 2005).

Zuckerman (2005) has suggested that the effects of testosterone on Extraversion may be due to interaction between testosterone and reward circuitry, particularly in the nucleus accumbens.

Neuroticism

Neuroticism appears to reflect sensitivity to threat and the whole range of negative emotions and cognitions that accompany experiences of threat and punishment, including anxiety, depression, anger, irritation, self-consciousness, and vulnerability. Because Neuroticism and sensitivity to threat are so strongly implicated in psychopathology, research on their likely biological substrates has been extensive. Gray and McNaughton's (2000) model of the BIS and FFFS, which jointly determine Neuroticism, is very thoroughly elaborated. This model is reasonably compatible with Depue's model of Anxiety and Fear, although Depue believes that Fear is not well represented within Neuroticism.¹ (Depue's use of the term "Fear" is complicated by the fact that colloquial usage often treats "fear" and "anxiety" as nearly equivalent, with the result that, in the Big Five, both fall within Neuroticism.) Gray and McNaughton associated the FFFS not only with fear but also with panic and anger, and these emotions are also associated with Neuroticism (Costa & McCrae, 1992; DeYoung, Quilty, & Peterson, 2007; Saucier & Goldberg, 2001).

Various brain systems associated with reactions to threat and punishment have been linked to Neuroticism. Neuroimaging studies have found that Neuroticism is associated with brain activity at rest or in response to aversive or novel stimuli, in brain regions associated with negative affect, including the amygdala, insula, and anterior cingulate (Deckersbach et al., 2006; Eisenberger, Lieberman, & Satpute, 2005; Etkin et al., 2004; Cools et al., 2005; Haas, Omura,

¹ Depue and Lenzenweger (2005) criticized Gray's theory of the BIS because they consider "behavioral inhibition" to be a marker of fear rather than anxiety; however, Gray and McNaughton (2000) clearly differentiated the general behavioral inhibition associated with anxiety and passive avoidance from the more immediate and stereotyped behavioral inhibition (which they labeled "freezing") associated with fear.

Constable, & Canli, 2007; Keightly et al., 2003; Reuter et al., 2004). Gray and McNaughton (2000) describe both serotonin and norepinephrine as modulators of the BIS and FFFS. Neuroticism has been associated with lower levels of serotonergic function through various methods, including genomics, 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). A smaller body of evidence links Neuroticism to higher levels of norepinephrine (Depue & White, 1999; Hennig, 2004; Zuckerman, 2005). Neuroticism has been associated also with higher baseline levels of the stress hormone cortisol, but with lower levels of cortisol in response to specific stressors (Netter, 2004). The association of Neuroticism with cortisol function is consistent with the importance of the hypothalamic-pituitary-adrenal (HPA) axis in responding to threat and other stressors (McEwan, 1998).

Finally, a number of EEG studies have demonstrated that Neuroticism (including various trait measures of negative emotionality) is associated with greater activation of the right frontal lobe relative to the left (Davidson, 2002; Zuckerman, 2005). Davidson (2002) has argued that the right hemisphere is preferentially involved in emotions and motivational states associated with withdrawal, whereas the left hemisphere is preferentially involved in approach. The one complication in linking the right hemisphere to Neuroticism is that anger is associated with approach motivation, and EEG studies have shown anger to be associated with greater relative left frontal lobe activation (Harmon-Jones, 2004; Harmon-Jones & Allen, 1998). Perhaps, therefore, hemispheric asymmetries may aid in differentiating the sources of two classes of negative emotions that have been identified within Neuroticism: those associated with withdrawal and those associated with volatility and anger (DeYoung et al., 2007).

Agreeableness

Because of the relation of Extraversion and Neuroticism to emotion and to reward and punishment, and because of the long history of biological theorizing about them, there is more evidence regarding their biological substrates than there is for Agreeableness, Conscientiousness, and Openness/Intellect. Additionally, few theories have been put forth to explain the nature of the latter three trait domains from biological or evolutionary perspectives (but see MacDonald, 1998; Nettle, 2006). Consideration of their grouping within the metatraits of Stability and Plasticity presents a useful starting point in this endeavor. Agreeableness, for example, appears to reflect a tendency toward the maintenance of social stability, encompassing traits reflecting prosociality vs antisociality: compassion, empathy, cooperation, politeness – a general tendency to be interested in and considerate of others' needs, desires, and feelings and to refrain from aggressing or imposing one's will on others. Such altruistic tendencies are of particular importance for social species, and traits resembling Agreeableness are found consistently in social mammals (Gosling & John, 1999).

Agreeableness seems likely to be supported by brain systems that are involved in social information processing. The growing body of neuroscience research on empathy, theory of mind, and perception of biological motion and intention is thus likely to be relevant to understanding the neurobiological substrates of Agreeableness. Brain regions associated with these forms of social information processing include the medial prefrontal cortex (Seitz, Nickel, Azari, 2006), superior temporal sulcus (Allison, Puce, & McCarthy, 2000), temporal-parietal junction (Saxe & Powell, 2006), and the mirror neuron system that includes inferior frontal gyrus and rostral posterior parietal cortex (Iacobono, 2007; Rizzolatti & Craighero, 2004). (Mirror neurons respond similarly when watching another agent perform a task and when performing it oneself.)

Several fMRI studies using trait measures of empathy have reported findings that are directly relevant to the link between Agreeableness and social information processing. In these studies, empathy was positively associated with activity in the mirror neuron system, medial prefrontal cortex, and/or superior temporal sulcus during observation and imitation of others' actions (Gazzola, Azev-Zadeh, & Keysers, 2006; Kaplan & Iacobono, 2006) or during perception of others' emotional expressions (Chakrabarti, Bullmore, & Baron-Cohen, 2007; Schulte-Rüther, Markowitsch, Fink, & Piefke, 2007). Another study (Tankersley, Stowe, & Huettel, 2007) found that a self-report measure of altruism was positively associated with individual differences in activity in posterior superior temporal sulcus, while observing another agent perform a task, in contrast to performing the task oneself.

Other brain regions, beyond those typically identified as involved in social information processing, have also been associated with trait measures of empathy. One study (Chakrabarti et al., 2007) demonstrated that viewing different emotional expressions led to correlations of empathy with activity in brain regions functionally relevant to the specific emotion in question (e.g., observing happiness activated the ventral striatal reward system more strongly for participants high in empathy). Another study (Singer et al., 2004) found that empathy was associated with brain activity in the insula and anterior cingulate (regions involved in the affective component of pain), while watching a loved one experience pain. These findings suggest the degree to which empathy may involve recruiting brain regions involved in relevant emotions while observing others, a process potentially coordinated by the brain regions described above as subserving social information processing.

Agreeableness, like Neuroticism, has been associated with variation of the serotonin transporter gene (Canli & Lesch, 2007; Jang et al., 2001; Wand et al., 2002), but there are other

endogenous psychoactive substances in addition to serotonin that may contribute to Agreeableness, including the sociosexual neuropeptides oxytocin and vasopressin and the sex hormones testosterone and estrogen. Oxytocin is involved in social bonding (Depue & Morrone-Strupinsky, 2005), and acute administration of oxytocin in human males has been found to improve their ability to identify others' emotional states from facial expressions (Domes, Heinrichs, Michel, Berger, & Herpertz, 2007). Testosterone is linked to aggression, and evidence exists to suggest that higher exposure to testosterone is linked to reduced Agreeableness. The ratio of the length of the fourth finger to the second (4D:2D) is an index of prenatal exposure to testosterone (Manning, 2002; McIntyre, 2006). Not only has 4D:2D been linked to aggression (McIntyre et al., 2007), it has also been shown to correlate negatively with Agreeableness (Luxen & Buunke, 2005).

Conscientiousness

Whereas Agreeableness is associated with the maintenance of social stability between individuals, Conscientiousness appears to reflect the tendency to maintain motivational stability within the individual, to make plans and carry them out in an organized and industrious manner. Such top-down control of motivation should be necessary only in species capable of formulating long term goals that might conflict with more immediate urges. In personality studies of other species, only the chimpanzee, our nearest evolutionary neighbor, has yet been found to possess a trait directly analogous to Conscientiousness (Gosling & John, 1999).

Conscientiousness may represent the purest manifestation in personality of the ability and tendency to constrain immediate impulses in favor of longer-term goals. Many traits that are theoretically and statistically related to Conscientiousness, such as Cloninger's Novelty Seeking or Zuckerman's Impulsive Sensation Seeking, appear to be less specific than Conscientiousness,

in that they load heavily on other Big Five factors in addition to Conscientiousness. This non-specificity may reflect the fact that problems of impulse control could be exacerbated both by weakness of whatever systems override impulses (the presumed substrate of Conscientiousness) or by potentiation of the impulses themselves. A factor analysis of many questionnaire measures of impulsivity (Whiteside & Lynam, 2004) found four factors, only two of which (labeled *lack of perseverance* and *lack of premeditation*) mapped onto Conscientiousness. The other two, labeled *urgency* and *sensation seeking*, mapped onto Neuroticism and Extraversion, respectively, and appeared to describe strong impulses related to punishment and reward. In a similar vein, Depue and Collins (1999) argued that, although theorists have often associated impulsivity with Extraversion, impulsivity might be better conceived as a compound trait emerging from the combination of high Extraversion and low Constraint or Conscientiousness. High Neuroticism may also play a role in this compound (Whiteside & Lynam, 2004).

When considering research on the biological basis of the various impulsivity-related traits, one must bear in mind that most are related to multiple Big Five dimensions. Zuckerman (2005) noted that many studies have found Impulsive Sensation Seeking and similar traits to be associated with high levels of dopaminergic function and low levels of serotonergic function. However, he argued that dopamine is associated with the approach tendencies reflected in these traits, whereas low serotonin is related to the absence of control or restraint. Involvement of serotonin in control and restraint is consistent with findings that serotonin is associated with Conscientiousness (Manuck et al., 1998, Rosenberg et al., 2006).

Another biological factor that may be related to Conscientiousness is glucose metabolism. Glucose represents the basic energy source for the brain, and a number of studies indicate that blood-glucose is depleted by acts of self-control and that the extent of this depletion

predicts failures of self-control (Gailliot et al., 2007; Gailliot & Baumeister, 2007). Further, a self-report measure of trait self-control, which correlates highly with Conscientiousness, similarly predicts failures of self-control (Gailliot, Schmeichel, & Baumeister, 2006; Tangney, Baumeister, & Boone, 2004). Perhaps individuals whose metabolism provides their brains with an ample and steady supply of glucose are likely to be higher in Conscientiousness. If individual differences in glucose metabolism prove to be involved in Conscientiousness, one will also want to know what brain systems are consuming glucose to fuel acts of self-control. The prefrontal cortex seems likely to be involved, given its central role in planning and voluntary control of behavior, and given that its consumption of glucose appears relatively high (Gailliot & Baumeister, 2007). An fMRI study (Brown, Manuck, Flory, & Hariri, 2006) showed that brain activity in ventral prefrontal cortex during a response inhibition task was negatively associated with a questionnaire measure of impulsivity that is strongly negatively correlated with Conscientiousness (Whiteside & Lynam, 2001).

Openness/Intellect

Openness/Intellect is perhaps the least studied of the Big Five from a psychobiological perspective. However, Openness/Intellect is the only Big Five trait consistently positively associated with intelligence, and one study found it to be the only Big Five trait associated with performance on a battery of working memory and cognitive control tests (DeYoung, Peterson, & Higgins, 2005), all of which had been validated through neuroimaging and brain lesion studies as indices of dorsolateral prefrontal cortical function. The attentional network in which the dorsolateral prefrontal cortex plays a key role has been consistently linked to fluid intelligence, the ability to solve novel problems (Gray & Thompson, 2004). Work on the neurobiology of intelligence, working memory, and attention may, therefore, aid in identifying the neural

substrates of Openness/Intellect. As mentioned above, dopamine may be involved in Openness/Intellect (DeYoung et al., 2005; Harris et al., 2005); dopamine strongly modulates the function of lateral prefrontal cortex (Arnsten & Robbins, 2002) and has been linked to individual differences in fluid intelligence and working memory through genomics, pharmacological manipulation, and neuroimaging (e.g., Volkow, 1998; Mattay et al., 2003).

Though some have argued that intelligence and personality are categorically distinct (e.g., Eysenck, 1994), such an approach is not consistent with the rationale behind the development of the Big Five personality model as a comprehensive classification of trait descriptors – as such, it cannot arbitrarily exclude descriptors related to intelligence. Some of the debate on this subject has stemmed from the fact that the label “Openness to Experience” is not very similar to “intelligence,” conceptually (McCrae, 1994; McCrae & Costa, 1997). However, other researchers have used the label “Intellect” for this trait, and use of the compound label Openness/Intellect reflects the conclusion that Openness and Intellect simply reflect different aspects of one larger domain of personality (DeYoung et al., 2005; Johnson, 1994; Saucier, 1992). These two aspects are related but separable and appear to have partially distinct genetic bases (DeYoung et al., 2007). Fluid intelligence and working memory seem to be related primarily to the aspect of Openness/Intellect that can be described as Intellect, whereas crystallized or verbal intelligence is associated not only with Intellect but also with the artistic and contemplative traits that characterize the Openness aspect of the domain (DeYoung et al., 2005, 2007). Together Openness and Intellect appear to describe a range of traits related to cognitive and perceptual flexibility and exploration and to the various brain processes that support these cognitive functions (DeYoung et al., 2005).

Conclusion

A neuroscience approach to personality research has the potential to provide personality psychology with explanatory models. The Big Five appears to be a promising broad framework for conceptualizing individual differences in phenotypic traits in terms of basic psychobiological functions. The Five Factor Theory of McCrae and Costa (1999) makes a similar claim but does not go on to elaborate specific hypotheses about the biological sources of individual traits. As the above review demonstrates, however, neuroscientific research on personality has advanced to the point where some hypotheses can be made.

The youth of the field of personality neuroscience necessitates that many of these hypotheses currently exist at a fairly low level of resolution. Both traits and the brain systems that underlie them will need to be more specifically defined as the field progresses. Each of the Big Five covers a broad domain of psychological functioning. Although the biological mechanisms discussed above may be at least partially responsible for the coherence of these domains (i.e., the covariance of the lower-level traits within them), specific biological mechanisms must also differentiate their lower-level traits. For example, each of the Big Five appears to be divisible into two distinct phenotypic aspects with partially distinct genetic bases (DeYoung et al., 2007; Jang et al., 2002). At an even lower level of the hierarchy, the many facet-level traits within each domain similarly show unique genetic contributions (Jang et al., 2002; Jang, McCrae, Angleitner, Riemann, & Livesley, 1998). Eventually, personality neuroscience may explain the covariation of traits at many levels of the personality hierarchy.

Traits are probabilistic constructs representing the frequencies and intensities of particular classes of affect, behavior, and cognition across situations (Fleeson, 2001; Mischel & Shoda, 1998). Standard personality measures provide little information about the situations that

elicit these processes for any given individual, but methods exist to make such assessments (Fleeson, 2007; Roberts, 2007; Wood & Roberts, 2006). Exploring the neural mechanisms involved in linking basic tendencies to specific eliciting situations may become the ultimate in fine-grained analysis, as the field of personality neuroscience progresses. Such investigations, however, must be integrated with knowledge of how personality is organized at the broadest levels, where large neural networks and broadly acting neuromodulators are likely to be important across situations that share only some broad features. Psychobiological models of the Big Five and their metatraits are a promising place to begin.

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