

Sources of Openness/Intellect: Cognitive and Neuropsychological Correlates of the Fifth Factor of Personality

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ABSTRACT We characterize Openness/Intellect as motivated cognitive flexibility, or cognitive exploration, and develop a neuropsychological model relating it to dopaminergic function and to the functions of the prefrontal cortex (PFC). Evidence is reviewed for sources of Openness/Intellect shared with Extraversion and sources unique to Openness/Intellect. The hypothesis that the cognitive functions of the dorsolateral PFC are among the latter was tested using standard measures of cognitive ability and a battery of tasks associated with dorsolateral PFC function

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($N = 175$). Dorsolateral PFC function, as well as both fluid and crystallized cognitive ability, was positively related to Openness/Intellect but no other personality trait. Additionally, facet level analysis supported the characterization of Openness/Intellect as a primarily cognitive trait.

SOURCES OF OPENNESS/INTELLECT: COGNITIVE AND NEUROPSYCHOLOGICAL CORRELATES OF THE FIFTH FACTOR OF PERSONALITY

Factor analyses of trait-descriptive adjectives and sentence-based questionnaires have indicated that the vast majority of personality descriptions can be classified using five broad domains, often called the Big Five or Five-Factor Model (Costa & McCrae, 1992a; Digman, 1990; Goldberg, 1990; John & Srivastava, 1999). Analyses of languages other than English suggest that slight variations in the content of these domains, and at least one additional domain, may be necessary to improve the cross-cultural validity of the taxonomy (Ashton et al., 2004; Saucier & Goldberg, 2001). Nonetheless, the Big Five provides a useful organizing system for personality psychology, directing inquiry and providing a common language for researchers. What this descriptive taxonomy does not provide, however, is any explanation of the sources of personality, and a biological approach, like that employed by Depue and Collins (1999) in their neuropsychological model of Extraversion, may provide deeper theoretical frameworks for the Big Five (cf. McCrae & Costa, 1999).

In what follows, we propose a neuropsychological model of Openness/Intellect, the fifth and most controversial domain, and we present a study offering support for one aspect of the model through exploration of the cognitive and neuropsychological correlates of Openness/Intellect. We are interested primarily in the immediate sources of this personality factor in the brain and its ongoing functions, rather than genetic or environmental sources. Studies revealing the heritability of the Big Five to be around 50% indicate that the more distal influences shaping personality lie both in the genes and in the environment where development occurs (Bouchard, 1994; Reimann, Angleitner, & Strelau, 1997). Genes and environment alike, however, must make their mark on the brain, if they are to affect personality.

Openness/Intellect has been the focus of considerable disagreement in debates on how best to characterize and label the Big Five domains. "Intellect" is the label for this domain most commonly used in the lexical tradition (Digman, 1990; Goldberg, 1992), while "Openness to Experience" was chosen by Costa and McCrae (1985, 1992a, 1992b), leaders in the questionnaire approach. Both of these labels are generally preferred to a third alternative, "Culture," which was used in one of the first demonstrations of the five-factor model (John & Srivastava, 1999; Tupes & Christal, 1961/1992). The current trend toward a compound label, "Openness/Intellect" (e.g., Ashton, Lee, Vernon, & Jang, 2000; Saucier, 2003), highlights the fact that these two labels complement each other by identifying different aspects of the same domain. In both lexical and questionnaire models, the fifth factor is associated with traits that might be labeled "Intellect" (e.g., intellectuality and intelligence), traits that might be labeled "Openness" (e.g., imagination, unconventionality, interest in art), and traits for which either label would be appropriate (e.g., curiosity, creativity) (John & Srivastava, 1999; McCrae & Costa, 1997; Saucier, 1992). While there is sufficient overlap between the lexical and questionnaire models to assume that Openness and Intellect refer the same domain of personality, the differences in emphasis between the lexical and questionnaire approaches have led to slightly different operationalizations of this domain in instruments used to measure the Big Five (Digman, 1990; John & Srivastava, 1999; Saucier, 1992). Of the five factors, Openness/Intellect typically shows the lowest correlations between lexical and questionnaire measures (e.g., Goldberg, 1992). One purpose of the present study was to compare the most common lexical and questionnaire measures of Openness/Intellect—Goldberg's (1992) 100 unipolar trait-descriptive adjectives (TDA) and Costa and McCrae's (1992b) Revised NEO Personality Inventory (NEO PI-R)—in terms of their cognitive and neuropsychological correlates.

McCrae and Costa's (1997; McCrae, 1993, 1994) argument that "Intellect" is too narrow a descriptor to capture the domain adequately has been helpful in drawing attention to the full range of phenomena needing explanation in any model of Openness/Intellect. Our neuropsychological model is guided, in part, by their assertion that "Openness is seen in the breadth, depth, and permeability of consciousness, and in the recurrent need to enlarge and examine experience" (McCrae and Costa, 1997, p. 826). This description

captures two key components of Openness/Intellect, which may point toward its sources: a motivational component, having to do with interest in novelty and complexity, and a cognitive component, having to do with the manner in which information is processed and organized.

Openness/Intellect in Relation to the Higher-Order Factors of the Big Five

Our understanding of both components is informed by our interpretation of the higher-order factor solution for the Big Five. While the Big Five has typically been considered the most general level of personality description and the highest level of a hierarchical model of personality, findings that the five factors are intercorrelated and group consistently into two higher-order factors suggest otherwise. The higher-order factor solution, reported by Digman (1997) and replicated by DeYoung, Peterson, and Higgins (2002), reveals that Emotional Stability (Neuroticism reversed), Agreeableness, and Conscientiousness form a first factor, while Extraversion (sometimes labeled “Surgency”) and Openness/Intellect form a second. We have offered an interpretation of these higher-order factors, or metatraits, as *Stability* and *Plasticity*, respectively (DeYoung et al., 2002). Stability and Plasticity can be considered the manifestation in personality of two overarching concerns of any organism: (1) the need to maintain a stable physical/behavioral organization to achieve various goals and (2) the need to incorporate novel information into that organization, as the state of the organism changes both internally (developmentally) and externally (environmentally). As personality traits, Stability and Plasticity reflect individual differences in the emphasis on, competence in, and capacity for meeting each of these two general needs in the ways characteristic of human beings.¹

1. Our interpretation is compatible with Digman’s (1997) suggestion that the higher-order factors might be associated with socialization and personal growth. Stability seems likely to make a child easier to socialize (and socialization may encourage Stability), while Plasticity seems likely (though not inevitably) to lead to personal growth. The labels “Stability” and “Plasticity” are intended to suggest underlying dispositions or traits rather than possible outcomes and to communicate more theoretical content than Digman’s (1997) labels, “ α ” and “ β ,” which he described as “provisional” (p. 1248). McCrae and Costa (1999) offered an alternative explanation for the higher-order factors: that they merely reflect biases in personality assessment, along two evaluative dimensions—Positive Valence (PV)

We have also proposed a provisional biological model (DeYoung et al., 2002), linking individual differences in Stability to variation in the function of the serotonergic system (governing emotional and motivational regulation; Spont, 1992), and differences in Plasticity to variation in the dopaminergic system (governing encounter with novelty and incentive reward; Depue & Collins, 1999; Panksepp, 1998). Our intention in the current article is not so much to offer new evidence for our interpretation of the higher-order factors, as to draw inferences from it in creating a more detailed model of Openness/Intellect.² For this purpose, we are interested in Plasticity, the tendency to engage actively and flexibly with novelty—in other words, to explore. We have argued that Extraversion reflects a more concrete, behavioral exploratory tendency, while Openness/Intellect reflects a more abstract, cognitive exploratory tendency (DeYoung et al., 2002). This characterization is supported by a recent study demonstrating that Extraversion scales are dominated by items reflecting behavioral traits, while Openness/Intellect scales are dominated by cognitive traits (Pytlik Zillig, Hemenover, & Dienstbier, 2002).

In both concrete and abstract domains, the exploratory tendency is likely to be regulated, at least in part, by the neuromodulator dopamine. The dopaminergic system is particularly responsive to novelty, and its activation triggers exploratory behavior (Panksepp, 1998). Depue and Collins (1999) have made a strong case for the regulation of Extraversion by dopamine, noting that both the personality factor and the neurotransmitter have been linked to incentive reward sensitivity, positive affect, and approach behavior (cf.

and Negative Valence (NV). However, in earlier work they found that PV and NV were *not* associated with biased self-reports of the Big Five (McCrae & Costa, 1995). The fact that the two evaluative factors are similar to the higher-order factors in their associations with the Big Five (McCrae & Costa, 1999), but do not appear linked to biased personality ratings, suggests instead that very general evaluations (like “superior” or “wicked”) tend to reflect the two broadest factors of personality.

2. The constructs of Stability and Plasticity are in no way intended to replace the Big Five—in a hierarchical model of personality, traits may be meaningfully distinct on one level, despite being grouped within a more general trait at a higher level. Consideration of the higher-order factor solution may aid in understanding how and why the Big Five are related to each other, without diminishing their importance.

Lucas, Diener, Grob, Suh, & Shao, 2000). A similar case can be made for Openness, based on the empirically identified relations between dopaminergic function and response to novelty, decreased latent inhibition, and cognitive function. The following review is divided in terms of dopaminergic pathways and brain structures likely to be associated with both Openness/Intellect and Extraversion, and those likely to be unique to Openness/Intellect. The Big Five are such broad personality traits that one must assume them to be multiply determined. Our model therefore proposes that Openness/Intellect depends on a number of interacting brain systems, all of which appear to be responsible for rendering the individual cognitively exploratory and flexible.

Sources of Openness/Intellect Shared with Extraversion

McCrae and Costa (1997, p. 826, quoted above) emphasize the role of novelty in their descriptions of both the cognitive and motivational components of Openness: Open people are “permeable” to new ideas and experiences; they are motivated to “enlarge” their experience into novel territory and to “examine” their experience, discovering novelty even in the previously familiar. While the dopaminergic system is often characterized as a reward system, Schultz and colleagues (Schultz, 1998; Waelti, Dickinson, & Schultz, 2001) have demonstrated that it responds not to reward as such, but to unexpected rewards or unexpected predictors of reward—that is, to positive stimuli characterized by some degree of novelty.³ Because increases in dopaminergic activity appear to be associated with greater responsiveness to the positive aspects of novelty (Panksepp, 1998), dopamine seems likely to regulate the motivational component of Openness/Intellect, in a manner similar to its regulation of Extraversion (Depue & Collins, 1999).

Dopamine may also regulate the cognitive permeability associated with Openness/Intellect. Peterson and colleagues (Peterson & Carson, 2000; Peterson, Smith, & Carson, 2002) have demonstrated that both Extraversion and Openness/Intellect are associated with

3. While “novelty” is often used to mean something totally unfamiliar, it can also be applied to a familiar stimulus that appears unpredictably or in an unfamiliar context or pattern. More generally, novelty as the totally unfamiliar may be considered a subset of the class of all things unpredicted, and it is this larger class that we mean by “novelty.”

decreased latent inhibition, and that the linear combination of the two traits (i.e., Plasticity) yields the strongest effect. Latent inhibition is a low-level cognitive phenomenon, wherein previously nonpredictive, ignored, or irrelevant stimuli are inhibited from entering awareness. It was first described in rats, which show slower learning of the predictive value of a conditioned stimulus if that stimulus has previously been shown to them repeatedly without any associated reinforcer (Lubow, 1989). Analogous paradigms reveal latent inhibition in other mammalian species, including humans (Lubow, 1989; Lubow & Gewirtz, 1995). In all species examined, latent inhibition varies in strength across individuals. In both rats and humans, dopaminergic antagonists increase latent inhibition (Shadach, Feldon, & Weiner, 1999; Weiner & Feldon, 1987), while dopaminergic agonists decrease latent inhibition (Kumari et al., 1999; Weiner, Lubow, & Feldon, 1988).

Latent inhibition appears to be an adaptation to the vast complexity of the environment relative to any organism's limited ability to attend to and model features of that environment. As a preconscious gating mechanism, latent inhibition allows phenomena already categorized as irrelevant to be ignored without further higher-level processing, thereby conserving resources. At the same time, however, latent inhibition renders the individual less permeable to previously ignored information that might become relevant and useful as his or her needs and situation change over time. The relative decrease in latent inhibition associated with Openness/Intellect and Extraversion (with its attendant increase in permeability to new information) may have adaptive consequences, leading to greater flexibility in processing information and exploring the environment. Carson, Peterson, and Higgins (2003), for example, have demonstrated that decreased latent inhibition is associated with greater real-life creative achievement, at least among high-achieving university undergraduates. (Notably, Openness/Intellect positively predicted the same measure of creative achievement; Carson, Peterson, & Higgins, *in press*). Decreased latent inhibition is not always associated with positive outcomes, however. Schizophrenia and schizotypy are both associated with decreased latent inhibition (Gray et al., 1995; Lubow, 1989). Remarkably, even this association is consistent with the involvement of dopamine in Openness/Intellect, as schizotypy is positively correlated with Openness (Ross, Lutz, & Bailey, 2002) and schizophrenia spectrum disorders are associated with abnormalities of dopaminergic function (Gray et al., 1995).

Unique Sources of Openness/Intellect

The association of both Extraversion and Openness/Intellect with positive response to novelty and decreased latent inhibition, phenomena known to be dopaminergically regulated, may help to explain why these two traits group together in a higher-order factor. Nonetheless, Extraversion and Openness/Intellect are readily differentiated at the Big Five level both conceptually and statistically (zero-order correlations between the two traits range from about .2 to .6; e.g., Digman, 1997), and one would probably be justified in considering them more different than similar. Any model of the sources of Openness/Intellect, therefore, must explain what is unique to Openness/Intellect as well as what is shared with Extraversion.

The fact that the dopaminergic systems originating in the mid-brain project to multiple brain regions may offer a clue to this distinction. We previously suggested that, while Extraversion is likely to be associated with the set of dopaminergic projections to the striatum and limbic system (cf. Depue & Collins, 1999), Openness/Intellect may be associated with the set of dopaminergic projections to prefrontal cortex (PFC) and anterior cingulate cortex (DeYoung et al., 2002). The dorsolateral region of the PFC subserves a class of cognitive functions, often designated “working memory,” which are crucial for the conscious manipulation of information. These functions are necessary for dealing with novelty, generating plans, considering possibilities, and analyzing and synthesizing abstract or complex relations (Mesulam, 2002; Miller, 2001)—activities consistent with a conceptualization of Openness/Intellect as a more cognitive or abstract exploratory tendency (as opposed to the more behavioral or concrete exploratory tendency associated with Extraversion). In their characterization of the cognitive component of Openness, McCrae, and Costa (1997) mention not only “permeability” but also “breadth” and “depth.” While permeability may stem from such low-level cognitive phenomena as decreased latent inhibition, the ability to generate the sort of cognitive complexity that could be described as “breadth” or “depth” seems likely to depend on the higher-level processes associated with dorsolateral PFC.

The functions of the dorsolateral PFC are heavily influenced by dopamine. Dopaminergic projections to the PFC are strongest in the dorsolateral region (Arnsten and Robbins, 2002), and dopamine appears to enhance dorsolateral PFC functions specifically, without

enhancing the functions of other PFC regions (Robbins, 2000). Increased dopaminergic activation in the PFC is typically associated with increased cognitive flexibility and improved performance on various tests of cognitive ability and working memory (within limits: too much dopamine impairs performance; Arnsten and Robbins, 2002). Braver and colleagues have argued that one function of the dopaminergic projections to dorsolateral PFC is to allow new information to enter working memory (Braver & Barch, 2002; Braver & Cohen, 2000). Ashby and colleagues (Ashby, Isen, & Turken, 1999; Ashby, Valentin, & Turken, 2002) have proposed that dopamine release in dorsolateral PFC (as well as in the caudate nucleus and anterior cingulate cortex) is responsible for the improvements in working memory and creative thinking that follow experimental manipulations inducing positive affect. Given that Extraversion is associated with a tendency to experience positive affect (Costa & McCrae, 1992b), Ashby and colleagues' model seems consistent with the association of Openness/Intellect and Extraversion. In light of this review, it seems reasonable to hypothesize that the dorsolateral PFC and its interaction with the dopaminergic system constitute unique sources of Openness/Intellect.

As a first step toward testing this model, we performed a study examining the relation between Openness/Intellect and various measures of cognitive function associated with dorsolateral PFC. We administered a battery of seven computerized tasks, all of which have been associated with dorsolateral PFC function through clinical studies of brain-damaged patients, animal research, and neuroimaging of intact human brain function. In addition to these tasks specifically designed to assess prefrontal function, two measures of general cognitive ability (*g*) were administered, the WAIS-III (Wechsler, 1997) and Raven's Advanced Progressive Matrices (APM), which is very highly *g*-loaded and resembles the matrices subtest of the WAIS-III (Raven, Raven, & Court, 1998). Not surprisingly, given that the domain of Openness/Intellect includes descriptors like "smart" and "intelligent," Openness/Intellect has been shown to be the only Big Five trait positively associated with IQ, a common index of *g* (McCrae, 1993; Moutafi, Furnham, & Crump, 2003).

The association with IQ provides a further reason to expect Openness/Intellect to be associated with dorsolateral PFC function: Duncan and colleagues (2000) demonstrated, using positron emission tomography, that tasks loading highly on *g* preferentially activate

dorsolateral PFC and dorsal anterior cingulate cortex, relative to tasks with low *g* loadings. Similarly, Gray, Chabris, and Braver (2003) showed with fMRI that performance on Raven's APM is correlated with lateral prefrontal activation during working memory tasks. Performance on Raven's APM has also been shown to correlate with dopaminergic function (Volkow et al., 1998).

Utilizing tests of *g* allowed us not only to replicate the association of Openness/Intellect with *g*, but also to separate fluid and crystallized *g*. Fluid *g* (*gF*) refers to raw cognitive ability, the ability to solve novel problems, applicable independently of the content of a given task. Crystallized *g* (*gC*) refers to acquired knowledge, applicable only when a task requires utilization of such knowledge, as in a vocabulary test, for example (Ackerman & Heggestad, 1997; Jensen, 1998). Because it is possible for performance on individual tasks to involve both fluid and crystallized abilities, factor analysis is an appropriate method for deriving separate scores for *gF* and *gC*. As it seems likely that both raw ability and acquired knowledge will contribute to Openness/Intellect, we hypothesized that factor scores for *gF* and *gC* would be independent predictors of Openness/Intellect. Because Duncan (1995) has argued that *gF*, rather than *gC*, is associated with the functions of dorsolateral PFC, an independent contribution of *gC* to Openness/Intellect would motivate us to specify additional brain systems as potential sources of Openness/Intellect, namely those associated with language and declarative memory. Openness/Intellect has been shown to be more strongly associated with *gC* than *gF* (Ackerman & Heggestad, 1997; Ashton et al., 2000), but whether *gF* and *gC* contribute independently to Openness/Intellect has not previously been tested.

Hypotheses

To summarize, we expected Openness/Intellect (but not Extraversion) to be associated with four cognitive variables: firstly, prefrontal function, as assessed by our battery of prefrontal tasks; secondly, *g*, as assessed by the WAIS-III and Raven's APM; and finally, *gF* and *gC*, as assessed by factor analysis of the various cognitive tests, including scores on the prefrontal battery. We assumed the latter would load primarily on *gF*, in keeping with Duncan's (1995) argument that *gF* relies strongly on dorsolateral PFC function. With all four of these variables, we were also interested in the question of

whether cognitive ability would predict variance in Openness/Intellect independently of Extraversion, which can stand as a proxy for the neuropsychological processes associated with both personality factors. Independent contributions to Openness/Intellect were tested using regression.

Using the NEO PI-R (Costa and McCrae's, 1992b), which parses each of the Big Five into six constituent traits, called *facets*, allowed us to examine the relation of Openness to the cognitive variables at the facet level as well. Based on our characterization of Openness/Intellect as a cognitive exploratory tendency and Extraversion as a behavioral exploratory tendency, we hypothesized that the "Actions" facet of Openness was likely to be more strongly related to Extraversion and less strongly related to Openness/Intellect than any other Openness facet. To put this another way, we imagined that someone who was relatively low in Extraversion but high in Openness/Intellect would be less open to novel behaviors, even though he or she should be open to ideas, values, aesthetics, etc. While many reported factor analyses have found that Actions loads more strongly on Openness than on Extraversion (e.g., Costa & McCrae, 1992b), they have usually been performed with varimax rotation, which maximizes the discrepancy between loadings on different factors. Correlations yield a less biased index of association, and we suspect they will reveal a greater strength of association between Actions and Extraversion than factor analysis will. If this proves to be the case, the Actions facet might be thought of as a function of the more general trait Plasticity. In anticipation of this result, we also hypothesized that the Actions facet would be less related to performance on the cognitive measures than the other facets of Openness.

METHOD

Participants

Participants in this study were a subset of Sample 1 in DeYoung et al. (2002). Only this subset ($N = 175$; 56 male, 119 female) completed standard measures of g and a computerized battery of cognitive tasks associated with prefrontal cortical function. All were university students, ranging in age from 18 to 38 ($M = 21.2$, $SD = 2.9$). In the larger sample from which this one was drawn, we have already demonstrated the existence of the higher-order factors of the Big Five (DeYoung et al., 2002).

Personality Measures

Personality was assessed with two common Big Five instruments, the Revised NEO Personality Inventory (NEO PI-R; Costa & McCrae, 1992a, 1992b) and Goldberg's (1992) Trait Descriptive Adjectives (TDA). The NEO PI-R consists of 240 potentially self-descriptive statements, to which participants responded using a 5-point Likert scale, and provides scores for 30 facet-level traits, 6 of which make up each of the Big Five. The TDA assesses the Big Five by means of 100 adjectives (20 for each factor) to which participants responded using a 7-point Likert scale. Additionally, composite scores for the Big Five were created by averaging standardized NEO PI-R and TDA scores for each factor.

General Cognitive Ability

General cognitive ability (*g*) was assessed by means of two measures. The first consisted of five subtests from the WAIS-III (Wechsler, 1997): Vocabulary, Similarities, Block Design, Arithmetic, and Digit-Symbol Coding. Using the previous version of the WAIS (WAIS-R) Ward and Ryan (1996) found that this shortened version affords a time savings of approximately 55% compared to the full WAIS, while maintaining a .97 correlation with full scale IQ and a reliability coefficient of .96. One participant did not complete the WAIS due to time constraints. The second measure of *g* was Raven's Advanced Progressive Matrices (APM; Raven et al., 1998), which is considered to assess mainly fluid intelligence (Jensen, 1998). Raven's APM consists of 36 increasingly difficult matrix reasoning problems, similar to those in the matrix reasoning subtest of the WAIS-III, and participants are given 40 minutes to solve as many as possible. The first unrotated factor, from principal axis factor analysis of these measures, was used as an index of *g*.

Prefrontal Measures

Similar versions of the seven computerized cognitive tasks described below have all been associated with the activity of the dorsolateral prefrontal cortex through imaging and lesion studies in humans and animals. While activation of additional brain areas has been reported for some of the measures (as described below), the dorsolateral contribution is common to all.

Self-ordered pointing. Participants were presented with 12 stimuli and instructed to click on each stimulus exactly once. After each selection, the spatial location of all stimuli changed. Four versions of the task were completed by each participant, each employing a different class of stimuli: abstract figures; pictures of easily named objects; words; nonwords (e.g.,

“xworl”). In monkeys, performance on a similar version of the task appears to be specific to midsolateral PFC (areas 9 and 46), (Petrides, 1995, 2000). Human lesion studies have confirmed the PFC as crucial for performance on this task (Petrides & Milner, 1982; Wiegersma, van der Scheer, & Human, 1990), and positron emission tomography (PET) has identified activation of areas 9 and 46 during normal human performance of this task (Petrides, Alivisatos, Evans, & Meyer, 1993).

Letter randomization. Participants were asked to randomize a four-letter span of the alphabet (e.g., “Randomize the letters from L to O”). If participants produced an acceptable sequence, they were asked to randomize a span one letter longer. If an error was made (an omission or patterned sequence, e.g., “L, M, N”), they were given another chance to randomize a span of the same length. The task terminated when participants failed two trials in a row or correctly randomized a span of 14 letters. Patients with frontal lobes lesions are impaired on this task (Wiegersma et al., 1990), and PET has revealed bilateral activation in areas 9 and 46 during normal performance (Petrides, Alivisatos, Meyer, & Evans, 1993).

Spatial and nonspatial conditional association tasks. In both of these tasks, a set of associations between pairs of stimuli must be learned by trial and error. In the spatial task, five identical circles and five identical squares were presented together in random positions on the screen. Participants were instructed that each square was associated with exactly one circle. On each trial, a circle was highlighted and participants were required to click the square they believed to be associated with that circle. Feedback was given until the correct response was made on each trial, but a trial was scored as correct only if the correct response was made on the first selection. The task was terminated after 10 consecutive correct trials, or after 100 trials. Two versions were completed, differing in the spatial arrangement of the shapes. In the non-spatial task, participants learned arbitrary associations between cue words and target words. Again, two versions were completed, one employing regular words and the other, nonwords. Monkeys with dorsolateral PFC lesions are impaired on both spatial (Petrides, 1987) and nonspatial (Petrides, 1985a) conditional association tasks. Human patients with unilateral surgical excisions (for treatment of epilepsy) of the left or right frontal lobes are similarly impaired on both spatial and nonspatial versions (Petrides, 1985b, 1990). Levine, Stuss, and Milberg (1997) found deficits specifically for patients with dorsolateral PFC lesions on a non-spatial version. PET has revealed selective activation in area 8 of the left dorsolateral PFC while performing a non-spatial version of the task (Petrides, Alivisatos, Evans, et al., 1993).

Go/No-go. Four letters flashed sequentially, repeatedly, and in random order, on the screen. Participants were required to click when two of the letters appeared (the “go” stimuli) and not to click when the other two (“no-go”) stimuli appeared. Contingencies were learned by trial and error; when a correct response was made, the word “Good” appeared and a score counter increased by 1 (the score was displayed throughout the task). The task was terminated after 200 trials or after 20 consecutive correct trials. Monkeys with dorsal prefrontal lesions show impaired performance on a simplified version of this task (Petrides, 1987). Human brain imaging studies of go/no-go performance have employed versions of the task with only one “go” and one “no-go” stimulus (Casey et al., 1997; Liddle, Kiehl, & Smith, 2001), thereby minimizing working memory demand. Dorsolateral PFC involvement seems especially likely when the working memory component is increased by the addition of more stimuli. Even in the two-stimulus version, dorsolateral activation has been detected using fMRI, especially during no-go trials, although ventrolateral and anterior cingulate activation was also present (Casey et al., 1997; Liddle et al., 2001). A dopamine agonist (d-amphetamine) has been found to improve performance on a version of this task identical to ours except for the addition of two more “go” and two more “no-go” stimuli (de Witt, Enggasser, & Richards, 2002).

Recency judgment. Participants were presented with a series of six or eight familiar nouns. Each word disappeared before the next appeared. Once the full series had been presented, the participant was shown two words from the sequence and asked to click on the word that appeared most recently. Eight trials used a six-word sequence and 14 used an eight-word sequence. Frontal lobe damage is associated with poor performance on recency judgment tasks (McDonald, Bauer, Grande, Gilmore, & Roper, 2001; Milner, Petrides, & Smith, 1985), and recency judgments have been associated with bilateral dorsolateral PFC activation in fMRI (Zorrilla, 1997).

Word fluency. Participants were given 5 minutes to enter as many words as possible beginning with the letters “st,” using an on-screen, mouse-operated keyboard. They were instructed not to use inflected forms. Both Milner and Benton have demonstrated that patients with left prefrontal damage can show impaired word fluency without presenting with a typical aphasia (reviewed in Damasio & Anderson, 1993). PET and fMRI imaging studies have demonstrated that word fluency tasks activate dorsolateral PFC areas 9 and 46 and also Broca’s area (Gaillard et al., 2000; Ravnkilde Jensen, Videbech, Gade, & Rosenberg, 2000).

Scaled PFC scores. Norms for each task were established using a sample of 444 participants, allowing for the creation of scaled scores, which were used in all analyses (Higgins, Peterson, Pihl, & Lee, submitted). The scaled scores are standardized normal scores (Anastasi & Urbina, 1997), determined by calculating a percentile rank for each participant (based on raw scores) and computing the *z*-score equivalent (based on the inverse probability function) of this percentile rank. The mean correlation between tasks in the normative sample was .27 and Cronbach's alpha was .72. A composite PFC score was calculated by averaging scaled scores from the seven tasks.

RESULTS

Lexical and Questionnaire Measures of Openness/Intellect

Table 1 shows the zero-order correlations among the Big Five as measured by the NEO PI-R and TDA. As expected, NEO PI-R Openness and TDA Intellect show the smallest correlation of any of the pairs of corresponding Big Five scales. (Neuroticism and its corresponding TDA scale, Emotional Stability, are negatively correlated because the TDA orients this scale toward the positive rather than the negative pole of the trait dimension.)

Table 1
Correlations Among NEO PI-R and TDA Big Five Scales

	1.	2.	3.	4.	5.	6.	7.	8.	9.
1. NEO-O	—								
2. TDA-I	.63**	—							
3. NEO-E	.35**	.13	—						
4. TDA-S	.24**	.13	.76**	—					
5. NEO-N	-.01	-.02	-.31**	-.36**	—				
6. TDA-ES	-.06	-.14	.13	.22**	-.82**	—			
7. NEO-A	.14	.04	.09	-.02	-.28**	.28**	—		
8. TDA-A	.16*	.18*	.36**	.21**	-.47**	.39**	.66**	—	
9. NEO-C	-.08	.18*	.13	.11	-.44**	.21**	.22**	.35**	—
10. TDA-C	-.15*	.10	.18*	.18*	-.43**	.27**	.15*	.45**	.81**

* $p < .05$, ** $p < .01$ (two-tailed)

Note. $N = 175$; NEO PI-R, Revised NEO Personality Inventory; TDA, Trait Descriptive Adjectives; O, Openness; I, Intellect; E, Extraversion; S, Surgency; N, Neuroticism; ES, Emotional Stability; A, Agreeableness; C, Conscientiousness.

Openness/Intellect and Dorsolateral PFC Function

Our approach was first to examine PFC scores and traditional measures of *g* separately before combining them in a factor analysis to separate *gF* and *gC*. Zero-order correlations showed that Openness/Intellect, but no other personality variable, is associated with PFC score (Table 2). NEO PI-R and TDA scores are similar in their association with PFC scores (as they are with all other cognitive variables as well, though correlations are generally smaller in magnitude for TDA scores).

Structural equation modeling was used to examine this association in more detail, allowing us to eliminate nonshared variance in our measures of dorsolateral PFC function and Openness/Intellect. The seven PFC tasks were used as markers for a latent variable representing dorsolateral PFC function, and a latent Openness/Intellect

Table 2
Correlations Between the Big Five and Cognitive Variables

	PFC	Voc	Sim	BD	Ar	DS	APM	<i>g</i>	<i>gF</i>	<i>gC</i>
NEO-O	.21**	.33**	.27**	.16*	.18*	-.18*	.23**	.30**	.25**	.34**
TDA-I	.18*	.24**	.20**	.16*	.11	-.15*	.19*	.24**	.22**	.26**
Comp-O/I	.22**	.32**	.26**	.18*	.16*	-.18*	.23**	.30**	.26**	.33**
NEO-E	-.10	-.04	.06	-.01	-.01	-.02	-.02	-.01	-.04	-.03
TDA-S	-.12	-.05	-.03	-.08	-.04	-.12	-.16*	-.11	-.14	-.07
Comp-E	-.11	-.05	.02	-.05	-.03	-.07	-.09	-.06	-.09	-.05
NEO-N	.05	.03	-.06	-.18*	-.07	-.01	-.02	-.11	-.09	.02
TDA-ES	-.02	.05	.09	.16*	.04	.02	.03	.12	.10	-.06
Comp-N	.04	-.01	-.08	-.18*	-.06	-.02	-.03	-.12	-.10	.02
NEO-A	-.08	.01	.02	.01	.06	.00	.04	.04	.03	.01
TDA-A	-.04	-.14	.00	.01	-.05	.12	.01	-.02	.00	-.12
Comp-A	-.07	-.07	.01	.01	.01	.07	.03	.01	.02	-.06
NEO-C	.01	-.09	.05	.09	.04	.16*	-.02	.04	.05	-.09
TDA-C	.00	-.17*	-.01	.05	.03	.19*	.00	.00	.03	-.16*
Comp-C	.01	-.14	.02	.07	.04	.18*	-.01	.02	.04	-.13

* $p < .05$, ** $p < .01$ (two-tailed)

Note. $N = 175$, except for all five WAIS variables, *gF*, and *gC*, where $N = 174$; NEO, Revised NEO Personality Inventory; TDA, Trait-descriptive Adjectives; Comp, Composite standardized scores; WAIS-III subtests: Voc, Vocabulary; Sim, Similarities; BD, Block Design; Ar, Arithmetic; DS, digit-symbol coding; APM, Raven's Advanced Progressive Matrices; PFC, composite score of seven measures of dorsolateral prefrontal cortical function; *g*, general cognitive ability; *gF*, Fluid *g*; *gC*, Crystallized *g*.

variable was created using the six NEO PI-R Openness facets plus the TDA Intellect scale. (Table 3 shows correlations among these variables.) This model, shown in Figure 1, fit the data well and indicates an association of .33 between dorsolateral PFC and Openness/Intellect. The discrepancy χ^2 for this model is not significant, $\chi^2_{(76, N=175)} = 92.65, p = .09$, indicating that the covariance matrix predicted by the model does not differ significantly from the observed matrix. Other fit indices also indicate a good fit: Root Mean Square Error of Approximation (RMSEA) = 0.035; Goodness of Fit Index (GFI) = .93; Comparative Fit Index (CFI) = .96. A CFI or GFI value above .90 (indicating that the model accounts for more than 90 percent of the observed covariance) is considered a good fit, as is a RMSEA less than 0.08 (Schumaker & Lomax, 1996), although Hu and Bentler (1999) have argued that RMSEA should be less than 0.06 to indicate close fit.

A regression using composite Big Five scores was performed to test for independent contributions of Extraversion and PFC score to Openness/Intellect. Openness/Intellect is significantly predicted by both variables ($R^2 = .13$), PFC score: $\beta = .25, t_{(172)} = 3.47, p < .002$; Extraversion: $\beta = .28, t_{(172)} = 3.92, p < .001$.

Openness/Intellect and General Cognitive Ability

Zero-order correlations (Table 2) show the expected associations between traditional measures of *g* and Openness/Intellect, with one exception. One subtest of the WAIS, Digit-Symbol Coding (DS), is significantly negatively correlated with Openness/Intellect. Among the cognitive variables, DS shows only three significant correlations out of a possible six, whereas each other cognitive variable is correlated with all the others (Table 4). These discrepancies may indicate some lack of commonality with the other cognitive measures in the underlying processes that affect performance on DS.⁴ Indeed,

4. In factor analysis of the normative sample for the WAIS-III, DS was found to have the lowest loading on *g* of the various subtests (Deary, 2001), which renders it less surprising that DS should vary more independently than the other subtests in our sample. The simplicity of the task may be responsible: DS requires a series of shapes to be copied from the top of the page, where each is paired with a digit, into a series of boxes labeled with the digit that corresponds to the shape to be entered, as fast as possible. Working memory demand is minimized by the presence of the stimulus pairings at the top of the page.

Table 3
Intercorrelation of Variables in Structural Equation Model (Figure 1)

	1	2	3	4	5	6	7	8	9	10	11	12	13
1. Intellect	—												
2. Fantasy	.41**	—											
3. Aesthetics	.50**	.43**	—										
4. Feelings	.46**	.31**	.51**	—									
5. Actions	.24**	.41**	.32**	.22**	—								
6. Ideas	.59**	.39**	.41**	.25**	.26**	—							
7. Values	.28**	.32**	.41**	.35**	.32**	.35**	—						
8. SOP	.11	.02	.15*	.06	.08	.12	.10	—					
9. LR	.11	.14	.14	.15*	.03	.11	.13	.24**	—				
10. SCA	.14	.07	.14	.05	.06	.20**	.13	.29**	.29**	—			
11. NCA	.00	-.11	-.04	.10	-.09	.05	.00	.19*	.17*	.17*	—		
12. Go/No-Go	.09	.00	.02	.01	.02	.15*	.17*	.17*	.15*	.23**	.11	—	
13. RJ	.10	.06	.09	.04	.01	.06	.09	.23**	.15*	.16*	.05	.09	—
14. WF	.14	.12	.04	.16*	.04	.20**	.07	.15*	.22**	.13	.17*	.22**	.07

* $p < .05$, ** $p < .01$ (two-tailed)

Note. $N = 175$; SOP, self-ordered pointing; LR, letter randomization; SCA, spatial conditional association; NCA, nonspatial conditional association; RJ, recency judgment; WF, word fluency.

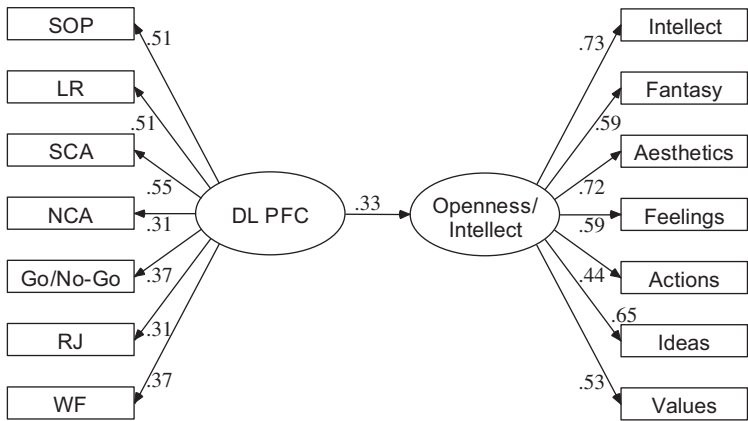


Figure 1

Structural equation model of the association between dorsolateral PFC function and Openness/Intellect. All weights are significant at $p < .01$. Discrepancy $\chi^2_{(76, N = 175)} = 92.65, p = .09$. See text for other indices of fit. SOP, self-ordered pointing; LR, letter randomization; SCA, spatial conditional association; NCA, nonspatial conditional association; RJ, recency judgment; WF, word fluency.

when the first unrotated factor, which represents g (Jensen, 1998), was extracted from the WAIS subtests and Raven's APM through principal axis factor analysis, DS showed a negligible loading compared to the other tests (Table 4). Using the factor scores from this factor analysis as our index of g ensured that only the shared variance of the various tests was included. Openness/Intellect is the only Big Five trait associated with g (Table 2), and, in regression, both g and composite Extraversion contribute to the prediction of Openness/Intellect independently ($R^2 = .17$), g : $\beta = .32, t_{(171)} = 4.54, p < .001$; Extraversion: $\beta = .27, t_{(171)} = 3.92, p < .001$.

Fluid and Crystallized Cognitive Ability

Principal axis factoring was used to determine whether fluid and crystallized g factors were evident in the cognitive measures positively associated with Openness: four WAIS subtests, Raven's APM, and PFC score. Parallel analysis was used to determine how many factors to extract (O'Connor, 2000). The eigenvalues from a principal axis factor analysis (with the number of factors extracted equal to the number of variables and the number of iterations fixed at zero)

Table 4
Correlations Among Cognitive Variables and Factor Loadings on *g*

	Voc	Sim	BD	Ar	DS	APM	<i>g</i> loading
Vocabulary	—						.56
Similarities	.64**	—					.59
Block Design	.32**	.32**	—				.74
Arithmetic	.31**	.20**	.41**	—			.51
Digit Symbol	— .11	.07	.21**	.01	—		.13
Raven's APM	.25**	.37**	.65**	.41**	.17*	—	.72
PFC Score ^a	.19*	.21**	.47**	.35**	.19*	.53**	

* $p < .05$, ** $p < .01$ (two-tailed), ^aNot included in *g* factor analysis.

Note. $N = 174$, except for correlation of PFC Score with APM (Raven's Advanced Progressive Matrices) where $N = 175$.

were compared to eigenvalues obtained from factor analysis of randomly generated datasets with the same sample size and number of variables. Factors were extracted only if their eigenvalues were greater than values that correspond to the 95th percentile of the distribution of random data eigenvalues. This ensures that the factors extracted account for more variance than factors derived from random data. As can be seen in Table 5a, parallel analysis indicated that two factors should be extracted. These were rotated using direct oblimin (Delta = 0), an oblique rotation which allowed them to remain correlated, because *gF* and *gC* are conceived as separable but related aspects of *g* (Ackerman & Heggestad, 1997; Jensen, 1998).

The first factor (*gF*) is marked primarily by Raven's APM, PFC score, and Block Design, while the second factor (*gC*) is marked by Vocabulary and Similarities, two verbal subtests of the WAIS (Table 5b). Arithmetic has its primary loading on *gF* but is the test most evenly split between the two factors. The correlation between *gF* and *gC* factor scores is .50, $p < .001$. Openness/Intellect is the only Big Five dimension positively associated with either *gF* or *gC* scores (Table 2). A regression was performed to determine whether *gF* and *gC* would predict composite Openness/Intellect independently of each other and of Extraversion. All three variables are significant or nearly significant predictors ($R^2 = .20$), *gF*: $\beta = .15$, $t_{(170)} = 1.93$, $p < .06$; *gC*: $\beta = .27$, $t_{(170)} = 3.40$, $p < .01$; Extraversion: $\beta = .28$, $t_{(170)} = 4.11$, $p < .001$.

Table 5
Parallel Analysis (5a) and Factor Loadings (5b) for Factor Analysis of
Cognitive Variables Positively Associated with Openness/Intellect

5a.	Real data Eigenvalues	Random data Eigenvalues	5b.	gF	gC
	2.33	0.42	Vocabulary	.38	.97
	0.62	0.24	Similarities	.41	.67
	0.02	0.12	Block Design	.78	.38
	− 0.09	0.03	Arithmetic	.52	.32
	− 0.13	− 0.06	Raven's APM	.84	.35
	− 0.25	− 0.14	PFC Score	.62	.24

Note. $N = 174$; gF, fluid g ; gC, crystallized g ; number of random datasets used in parallel analysis = 1000; 5b: structure matrix.

Facet-Level Analysis

Individual facets of Openness were compared in terms of their correlations with Openness/Intellect (NEO PI-R Openness and composite Openness/Intellect were both computed without the facet in question for each correlation), with Extraversion, and with the major cognitive variables (Table 6, see Table 3 for correlations with TDA Intellect). As predicted, Actions is the facet most strongly related to Extraversion and least strongly related to Openness/Intellect. A regression confirmed that composite Extraversion and Openness/Intellect contribute almost equally to variance in the Actions facet ($R^2 = .23$), Extraversion: $\beta = .31$, $t_{(172)} = 4.44$, $p < .001$; Openness/Intellect: $\beta = .30$, $t_{(172)} = 4.43$, $p < .001$.

To confirm that this pattern is obscured by the traditional use of principal components analysis with varimax rotation, we performed just such an analysis of the 30 NEO PI-R facets. After confirming that all 30 facets had their largest loading on the expected Big Five factor, we compared the loadings of the Openness facets on the Openness and Extraversion factors with those reported in the NEO PI-R manual for a large normative sample (Costa & McCrae, 1992b). Our loadings (Table 7) are largely similar to those from the NEO PI-R manual, although some caution should be used in interpreting our results simply because the discrepancy between Actions' loading on Openness versus Extraversion is less in our sample than in the normative sample; also, while Actions shows the lowest

Table 6
Correlation of Openness Facets with Openness/Intellect,
Extraversion, and Cognitive Variables

	NEO-O ^a	Comp-O/I ^a	NEO-E	TDA-S	Comp-E	PFC	<i>g</i>	<i>gF</i>	<i>gC</i>
Fantasy	.54**	.53**	.31**	.24**	.29**	.08	.18*	.13 [†]	.24**
Aesthetics	.61**	.62**	.14	.06	.11	.15*	.18*	.14 [†]	.28**
Feelings	.47**	.52**	.34**	.20**	.29**	.14 [†]	.11	.08	.18*
Actions	.44**	.37**	.40**	.30**	.37**	.04	.15*	.12	.13 [†]
Ideas	.48**	.61**	.07	.04	.06	.24**	.30**	.30**	.29**
Values	.50**	.43**	.23**	.18*	.22**	.19*	.28**	.25**	.24**

* $p < .05$, ** $p < .01$, [†] $p < .10$ (two-tailed), ^aComputed for each correlation without the facet in question.

Note. $N = 175$, except for correlations involving *g*, *gF*, and *gC* where $N = 174$.

Table 7
Openness Facet Loadings on Openness and Extraversion Compared
with Normative NEO PI-R Sample (Costa & McCrae, 1992b)

	Present sample		Normative sample	
	O	E	O	E
Fantasy	.64	.21	.58	.18
Aesthetics	.76	.06	.73	.04
Feelings	.56	.39	.50	.41
Actions	.48	.33	.57	.22
Ideas	.74	-.16	.75	-.01
Values	.68	.13	.49	.08

loading on Openness in our sample, Values does so in the normative sample. Nonetheless, our results (Table 7) make it clear that a greater difference in the association between Actions and Openness relative to that between Actions and Extraversion is found in the varimax rotated loadings than in the correlations in Table 6.

Of the six Openness facets, Actions is least strongly related to the cognitive variables, showing only one significant association (with total *g*) and a near-significant association with *gC* (Table 6). Feelings is only significantly associated with *gC*, though it also shows a near-significant association with PFC score. Fantasy is significantly associated with *g* and *gC* but is not associated with PFC score and only

Table 8
Regression of Openness Facets on Fluid and Crystallized *g*

	<i>gF</i>		<i>gC</i>		<i>R</i> ²
	β	<i>t</i> ₍₁₇₁₎	β	<i>t</i> ₍₁₇₁₎	
Fantasy	.01	0.14	.23	2.69**	.06
Aesthetics	.01	0.07	.28	3.23**	.08
Feelings	– .02	– 0.24	.19	2.21*	.03
Actions	.07	0.85	.09	1.05	.02
Ideas	.21	2.53*	.18	2.18*	.12
Values	.18	2.08*	.15	1.78 [†]	.08

p* < .05, *p* < .01, [†]*p* < .08 (two-tailed)

near-significantly associated with *gF*. Only the Ideas, Values, and Aesthetics facets are significantly associated with all four cognitive variables (and the correlation of Aesthetics with *gF* is only near-significant). The association of the facets with the cognitive variables was examined in more detail, using regression to determine independent contributions of *gF* and *gC* to each facet (Table 8). All of the facets except Actions show an independent contribution of *gC*, while only Ideas and Values show an independent contribution of *gF*.

DISCUSSION

The finding of an association between Openness/Intellect and a battery of tasks linked to dorsolateral PFC function supports the hypothesis that the cognitive functions of this brain region constitute an important source of Openness/Intellect, one not shared by Extraversion or any other of the Big Five. The association of general cognitive ability (*g*), and particularly fluid *g* (*gF*), with Openness/Intellect is also consistent with our model, given existing evidence that *gF* is associated with dorsolateral PFC (Duncan, 1995; Gray et al., 2003) and given our finding that PFC scores load primarily on the *gF* factor. The fact that fluid and crystallized cognitive ability independently predict variance in Openness/Intellect adds a further dimension to our understanding of the trait, and suggests the need to posit additional unique sources of Openness/Intellect in brain regions responsible for language and declarative memory.

Because our crystallized g (gC) factor is marked primarily by the two verbal subtests of the WAIS, both a verbal/nonverbal distinction and a crystallized/fluid distinction appear theoretically relevant. Verbal ability and crystallized knowledge both rely on cortical neural systems beyond the dorsolateral PFC. In the PFC, for example, language functions are associated with Broca's area, in the left hemisphere posterior to the dorsolateral regions associated with working memory (Deacon, 1997). For crystallized knowledge, the hippocampus and regions of the parietal and temporal cortices subserving declarative memory are likely to be important, though our focus on brain regions should not prevent us from noting that what has been learned by an individual is no doubt at least as important as where in the brain that knowledge has been stored. The fact that genetic factors appear to account for only about 50% of variance in personality (Bouchard, 1994; Reimann et al., 1997) means that the environment certainly helps to shape Openness/Intellect. Environmental influences are obviously crucial in shaping gC , and the influence of gC on Openness/Intellect, independently of gF , seems likely to reflect the contributions of education (though it may also reflect genetically determined differences in brain systems underlying crystallized or verbal ability). The importance of the environment in shaping both gC and personality may, in part, explain why gC is related to Openness/Intellect more strongly than gF is.

Measurement: Openness Versus Intellect

Our results support the position that NEO PI-R Openness and TDA Intellect are slightly different operationalizations of the same underlying construct. Despite its label, the Intellect scale incorporates descriptors that seem equally consistent with the label "Openness," such as "imaginative" and "artistic." Its correlations with the facets of NEO PI-R Openness (Table 3) are consistent with the idea that its operationalization, while not as broad as that of the NEO PI-R, still taps a variety of the facets that fall within the domain of Openness/Intellect. The strongest correlation is with the Ideas facet, but correlations with Fantasy, Aesthetics, and Feelings are all above .40—in the same range as the correlations between these facets and total NEO PI-R Openness (Table 6). Inasmuch as NEO PI-R Openness was generally more strongly related to the cognitive variables than was TDA Intellect, there is no evidence that Openness scores should

be any less indicative of traits like intellect or intelligence than Intellect scores. More important than small differences in effect sizes, furthermore, is the overall similarity in the patterns of associations with the cognitive variables. A composite of the two scales is probably equal to or better than either scale alone as an index of the total domain of Openness/Intellect.

Facets of Openness/Intellect

The ability to examine facet-level traits is certainly an advantage of the NEO PI-R, and some interesting differences in the patterns of association with cognitive variables emerged at the facet level. Fluid *g* and PFC scores were more strongly associated with two facets, Ideas and Values, than with the other four facets, and these were the only two facets to which *gF* contributed independently of *gC*. These findings suggest that dorsolateral PFC functions may contribute more to some aspects of Openness/Intellect than others (though it is important to remember that structural equation modeling showed that PFC score was related to the shared variance of all the facets).

While it is not surprising that the Ideas facet, which is most clearly related conceptually to intellect and intelligence, is more heavily associated with *gF*, one might wonder why Values should be linked to raw intelligence and the ability to solve novel problems. The Values facet includes items emphasizing moral relativism (e.g., “I believe that the different ideas of right and wrong that people in other societies have may be valid for them”; “I consider myself broad-minded and tolerant of other people’s lifestyles”) and freedom from conventional dogmatism (e.g., “I believe we should look to our religious authorities for decisions on moral issues”—reverse scored). Unconventionality has typically been located within the domain of Openness/Intellect in the lexical tradition as well (Saucier & Goldberg, 2001). But why should these attributes be associated with *gF* and PFC function? Perhaps because they require the cognitive flexibility to imagine different ways of living and to take the perspective of others. Coping with previously unfamiliar perspectives is likely to be aided by the novelty processing and abstract thinking that is controlled by dorsolateral PFC (Mesulam, 2002). We will refrain from detailing the implications of this finding for contemporary politics.

While *gF* is independently associated with only two facets of Openness, *gC* is independently associated with all facets except Ac-

tions. Fantasy, Aesthetics, and Feelings, therefore, may rely less heavily on dorsolateral PFC than on processes involved in language and memory. These three facets may also be more subject to modification by environmental factors during development. Perhaps future research will identify different developmental trajectories leading to facets of Openness associated primarily with *gC* as opposed to those associated with both *gF* and *gC*. The fact that *gC* appears to be associated with more facets of the Openness/Intellect domain may constitute another reason that total Openness/Intellect scores tend to be more strongly related to *gC* than to *gF* (Ackerman & Heggestad, 1997; Ashton et al., 2000).

Our results pertain mainly to sources of variance unique to Openness/Intellect, rather than shared with Extraversion. Our model specifies both, however, and the results of our facet-level analysis also bear on what Openness/Intellect and Extraversion share. The central dopaminergic system regulates positive motivational responses toward novelty, driving exploration (Panksepp, 1998), and we have argued that this motivation is a feature shared by Extraversion and Openness/Intellect. The hypothesis that Extraversion primarily reflects the expression of this exploratory motivation in behavior while Openness/Intellect primarily reflects its expression in cognition is supported by our finding that the Actions facet is as strongly related to Extraversion as it is to Openness/Intellect. Further, Actions is less strongly related to Openness/Intellect and cognitive abilities than are the other five Openness facets. Someone who is open without being extraverted seems more likely to explore the world cognitively than behaviorally and would therefore be less likely to score high on the Actions facet. Openness to Actions appears, in our sample at least, to stem roughly equally from Openness/Intellect and Extraversion, suggesting it might best be conceived as a function of the higher-order trait Plasticity, or at least as a relatively peripheral facet of Openness/Intellect. Attempts to replicate this finding should employ correlation and regression, rather than factor analysis with varimax rotation, to avoid artificial suppression of associations of facets with multiple Big Five domains.

Sources of Openness/Intellect

In keeping with the results described above, Openness/Intellect can be characterized broadly as motivated cognitive flexibility, or cog-

nitive exploration, emerging from multiple levels of brain function, all potentially modulated by dopamine. At the level of motivation, dopamine appears to assign positive value to novelty (Panksepp, 1998). At a preconscious level, dopaminergic activity decreases latent inhibition, rendering categories more flexible and allowing more of the complexity of the environment to become salient (Peterson et al., 2002). Finally, at a higher cognitive level, dopamine facilitates the flexible information processing accomplished by the dorsolateral PFC (Arnsten & Robbins, 2002). Dopamine may even affect the systems responsible for verbal or crystallized abilities, as memory retrieval can be facilitated by dopamine (Arnsten & Robbins, 2002).

At all three of these levels, Openness/Intellect may be attributable to the functions of specific brain systems independently of their modulation by dopamine. In its operation as a neuromodulator, dopamine is not typically *necessary* for the functions of its target neural systems, but rather increases their activation (Depue & Collins, 1999). Our model therefore specifies that individual differences in Openness/Intellect may stem, in an additive manner, from three different types of individual difference in brain function: (1) differences in the functioning of regions like the dorsolateral PFC, independent of modulation by dopamine, (2) differences in the innervation of these regions by dopaminergic neurons, and (3) differences in the sensitivity and activity of the dopaminergic system itself. This is an important caveat because the present results offer no direct evidence of dopamine's involvement in Openness/Intellect. Given what is known about the role of dopamine in dorsolateral PFC function, however, our results do fit coherently into the larger picture sketched out in our model. Further, the finding of an association between Openness/Intellect and dorsolateral PFC function is of interest in its own right, regardless of the link to dopamine.

That there appear to be multiple brain systems involved in Openness/Intellect implies that scores on the trait will not necessarily reflect all of these sources equally or in the same proportion across individuals, which may explain why the relations between performance on cognitive tasks and Openness/Intellect are not stronger. A high scorer on Openness/Intellect, for example, might be interested in novelty and very low in latent inhibition while possessing merely average cognitive abilities associated with dorsolateral PFC. Not only that, but questionnaire measures of Openness/Intellect are largely concerned with typical behavior and experience, which one

would expect to be only partly a function of the sort of maximal ability assessed by the cognitive tests (Ackerman & Heggestad, 1997). Nonetheless, we note, in accordance with Hemphill's (2003) recent meta-analysis, that effect sizes in the range of .20 to .30 constitute the middle third of effect sizes reported in psychology, when predictor and criterion variables do not share method. An effect size of .33, as found in our structural equation model of the association between latent Openness/Intellect and dorsolateral PFC variables, falls within the upper third of reported effect sizes. Using observer ratings of personality in addition to self-reports would be likely to increase effect sizes even further.

Finally, bearing in mind the degree to which the Big Five are likely to be multiply determined, we emphasize that the neuropsychological model presented here is not assumed to be exhaustive. Other brain regions helping to generate cognitive flexibility, such as the dorsal anterior cingulate cortex (dACC), may well constitute important additional sources of Openness/Intellect. The dopaminergic projections from the VTA to the frontal lobes innervate dACC as well as PFC, and, as mentioned above, the dACC is sometimes found active during tasks that also activate the dorsolateral PFC (e.g., Duncan et al., 2000; Liddle et al., 2001). The dACC has been identified as an error, anomaly, or novelty detector (Clark, Fannon, Lai, Benson, & Bauer, 2000; Holroyd & Coles, 2002). Of the neuromodulators other than dopamine, acetylcholine seems likely to be implicated in Openness/Intellect. The cholinergic system responds to novel stimuli, widely activates the cortex via the thalamus, and directly excites dopaminergic neurons (Mesulam, 1995). Recent work with genetic knockout mice has linked the cholinergic receptor M5, which is responsible for acetylcholine's direct effects on the dopaminergic system, with the modulation of latent inhibition (Yeomans, Forster, & Blaha, 2001; Wang et al., 2004).

The evidence we have provided for our model of Openness/Intellect is far from complete. However, we feel that enough evidence exists to sketch out a coherent and compelling neuropsychological model. Hopefully, our proposal will spur further research into the sources of Openness/Intellect. Pharmacological manipulations will be necessary for direct tests of the role of the dopaminergic system, and neuroimaging may offer a more definitive test of the role of dorsolateral PFC. Given the rate at which the complexities of brain function are being illuminated by neuroscience, we expect soon to see

not only neuropsychological models describing the sources of each of the Big Five, but also integrated, comprehensive models that will describe relations and interactions among personality factors. A biological approach to the Big Five affords the possibility of supplying a widely used and well-validated model of personality with new explanatory power.

REFERENCES

- Ackerman, P. L., & Heggestad, E. D. (1997). Intelligence, personality, and interests: Evidence for overlapping traits. *Psychological Bulletin*, **121**, 219–245.
- Anastasi, A., & Urbina, S. (1997). *Psychological testing* (7th ed). Upper Saddle River, NJ: Prentice Hall.
- Arnsten, A. F. T., & Robbins, T. W. (2002). Neurochemical modulation of prefrontal cortical function. In D. T. Stuss & R. T. Knight (Eds.), *Principles of frontal lobe function* (pp. 51–84). New York: Oxford University Press.
- Ashby, F. G., Isen, A. M., & Turken, A. U. (1999). A neuropsychological theory of positive affect and its influence on cognition. *Psychological Review*, **106**, 529–550.
- Ashby, F. G., Valentin, V. V., & Turken, A. U. (2002). The effects of positive affect and arousal on working memory and executive attention: Neurobiology and computational models. In S. Moore & M. Oaksford (Eds.), *Emotional cognition: From brain to behaviour* (pp. 245–287). Amsterdam: John Benjamins.
- Ashton, M. C., Lee, K., Perugini, M., Szarota, P., de Vries, R. E., Blas, L. D., et al. (2004). A six-factor structure of personality descriptive adjectives: Solutions from psycholexical studies in seven languages. *Journal of Personality and Social Psychology*, **86**, 356–366.
- Ashton, M. C., Lee, K., Vernon, P. A., & Jang, K. L. (2000). Fluid intelligence, crystallized intelligence, and the Openness/Intellect factor. *Journal of Research in Personality*, **34**, 197–207.
- Bouchard, T. J. (1994). Genes, environment, and personality. *Science*, **264**, 1700–1701.
- Braver, T. S., & Barch, D. M. (2002). A theory of cognitive control, aging cognition, and neuromodulation. *Neuroscience & Biobehavioral Reviews*, **26**, 809–817.
- Braver, T. S., & Cohen, J. D. (2000). On the control of control: The role of dopamine in regulating prefrontal function and working memory. In S. Monsell & J. Driver (Eds.), *Control of cognitive processes: Attention and performance XVIII*. Cambridge, MA: MIT Press.
- Carson, S. H., Peterson, J. B., & Higgins, D. M. (2003). Decreased latent inhibition is associated with increased creative achievement in high-functioning individuals. *Journal of Personality and Social Psychology*, **85**, 499–506.
- Carson, S. H., Peterson, J. B., & Higgins, D. M. (in press). Reliability, validity and factor structure of the creative achievement questionnaire. *Journal of Creativity Research*.

- Casey, B. J., Trainor, R. J., Orendi, J. L., Schubert, A. B., Nystrom, L. E., Giedd, J. N., et al. (1997). A developmental functional MRI study of prefrontal activation during performance of go-no-go task. *Journal of Cognitive Neuroscience*, **9**, 835–847.
- Clark, V. P., Fannon, S., Lai, S., Benson, R., & Bauer, L. (2000). Responses to rare visual target and distractor stimuli using event-related fMRI. *Journal of Neurophysiology*, **83**, 3133–3139.
- Costa, P. T., & McCrae, R. R. (1985). *The NEO Personality Inventory*. Odessa, FL: Psychological Assessment Resources.
- Costa, P. T., & McCrae, R. R. (1992a). Four ways five factors are basic. *Personality and Individual Differences*, **13**, 653–665.
- Costa, P. T., & McCrae, R. R. (1992b). *NEO PI-R Professional Manual*. Odessa, FL: Psychological Assessment Resources.
- Damasio, A. R., & Anderson, S. W. (1993). The frontal lobes. In K. M. Heilman & E. Valenstein (Eds.), *Clinical neuropsychology* (pp. 409–460). New York: Oxford University Press.
- Deary, I. J. (2001). Human intelligence differences: A recent history. *Trends in Cognitive Science*, **5**, 127–130.
- Deacon, T. W. (1997). *The symbolic species: The co-evolution of language and the brain*. New York: W. W. Norton & Company.
- Depue, R. A., & Collins, P. F. (1999). Neurobiology of the structure of personality: Dopamine, facilitation of incentive motivation, and extraversion. *Behavioral and Brain Sciences*, **22**, 491–569.
- de Witt, H., Enggasser, J. L., & Richards, J. B. (2002). Acute administration of d-amphetamine decreases impulsivity in healthy volunteers. *Neuropsychopharmacology*, **27**, 813–825.
- DeYoung, C. G., Peterson, J. B., & Higgins, D. M. (2002). Higher-order factors of the Big Five predict conformity: Are there neuroses of health? *Personality and Individual Differences*, **33**, 533–552.
- Digman, J. M. (1990). Personality structure: Emergence of the five-factor model. *Annual Review of Psychology*, **41**, 417–440.
- Digman, J. M. (1997). Higher-order factors of the Big Five. *Journal of Personality and Social Psychology*, **73**, 1246–1256.
- Duncan, J. (1995). Attention, intelligence, and the frontal lobes. In M. S. Gazzaniga (Ed.), *The cognitive neurosciences* (pp. 721–733). Cambridge, MA: MIT Press.
- Duncan, J., Seitz, R. J., Kolodny, J., Bor, D., Herzog, H., Ahmed, A., et al. (2000). A neural basis for general intelligence. *Science*, **289**, 457–460.
- Gaillard, W. D., Hertz-Pannier, L., Mott, S. H., Barnett, A. S., LeBihan, D., & Theodore, W. H. (2000). Functional anatomy of cognitive development: fMRI of verbal fluency in children and adults. *Neurology*, **54**, 180–185.
- Goldberg, L. R. (1990). An alternative “description of personality”: The Big-Five factor structure. *Journal of Personality and Social Psychology*, **59**, 1216–1229.
- Goldberg, L. R. (1992). The development of markers for the big-five factor structure. *Psychological Assessment*, **4**, 26–42.
- Gray, J. A., Joseph, M. H., Hemsley, D. R., Young, A. M. J., Warburton, E. C., & Boulenguez, P., et al. (1995). The role of mesolimbic dopaminergic and

- retrohippocampal afferents to the nucleus accumbens in latent inhibition: Implications for schizophrenia. *Behavioral Brain Research*, **71**, 19–31.
- Gray, J. R., Chabris, C. F., & Braver, T. S. (2003). Neural mechanisms of general fluid intelligence. *Nature Neuroscience*, **6**, 316–322.
- Hemphill, J. F. (2003). Interpreting the magnitudes of correlation coefficients. *American Psychologist*, **58**, 78–80.
- Higgins, D. M., Peterson, J. B., Pihl, R. O., & Lee, A. G. M. (submitted). Prefrontal cognitive ability and conscientiousness predict academic performance in high-achieving university undergraduates.
- Holroyd, C. B., & Coles, M. G. H. (2002). The neural basis of human error processing: Reinforcement learning, dopamine, and the error-related negativity. *Psychological Review*, **109**, 679–709.
- Hu, L., & Bentler, P. M. (1999). Cutoff criteria for fit indexes in covariance structure analysis: Conventional criteria versus new alternatives. *Structural Equation Modeling*, **6**, 1–55.
- Jensen, A. R. (1998). *The g factor: The science of mental ability*. Westport, CT: Praeger.
- John, O. P., & Srivastava, S. (1999). The Big Five Trait taxonomy: History, measurement, and theoretical perspectives. In L. A. Pervin & O. P. John (Eds). *Handbook of personality: Theory and research* (pp. 102–138). New York: Guilford Press.
- Kumari, V., Cotter, P. A., Mulligan, O. F., Checkley, S. A., Gray, N. S., & Hemsley, D. R., et al. (1999). Effects of d-amphetamine and haloperidol on latent inhibition in healthy male volunteers. *Journal of Psychopharmacology*, **13**, 398–405.
- Levine, B., Stuss, D. T., & Milberg, W. P. (1997). Effects of aging on conditional associative learning: Process analyses and comparison with focal frontal lesions. *Neuropsychology*, **11**, 367–381.
- Liddle, P. F., Kiehl, K. A., & Smith, A. M. (2001). Event-related fMRI study of response inhibition. *Human Brain Mapping*, **12**, 100–109.
- Lubow, R. E. (1989). *Latent inhibition and conditioned attention theory*. Cambridge, UK: Cambridge University Press.
- Lubow, R. E., & Gewirtz, J. C. (1995). Latent inhibition in humans: data, theory, and implications for schizophrenia. *Psychological Bulletin*, **117**, 87–103.
- Lucas, R. E., Diener, E., Grob, A., Suh, E. M., & Shao, L. (2000). Cross-cultural evidence for the fundamental features of extraversion. *Journal of Personality and Social Psychology*, **79**, 452–468.
- McCrae, R. R. (1993). Openness to Experience as a basic dimension of personality. *Imagination, Cognition, and Personality*, **13**, 39–55.
- McCrae, R. R. (1994). Openness to experience: Expanding the boundaries of Factor V. *European Journal of Personality*, **8**, 251–272.
- McCrae, R. R., & Costa, P. T. (1995). Positive and negative valence within the five-factor model. *Journal of Research in Personality*, **29**, 443–460.
- McCrae, R. R., & Costa, P. T. (1997). Conceptions and correlates of Openness to Experience. In R. Hogan, J. Johnson, & S. Briggs (Eds.), *Handbook of personality psychology*. Boston: Academic Press.

- McCrae, R. R., & Costa, P. T. (1999). A five factor theory of personality. In L. A. Pervin & O. P. John (Eds.), *Handbook of personality: Theory and research* (pp. 102–138). New York: Guilford Press.
- McDonald, C. R., Bauer, R. M., Grande, L., Gilmore, R., & Roper, S. (2001). The role of the frontal lobes in memory: Evidence from unilateral frontal resections for relief of intractable epilepsy. *Archives of Clinical Neuropsychology*, *16*, 571–585.
- Mesulam, M.-M. (1995). Structure and function of cholinergic pathways in the cerebral cortex, limbic system, basal ganglia, and thalamus of the human brain. In F. E. Bloom & D. J. Kupfer (Eds.), *Psychopharmacology: The fourth generation of progress* (pp. 135–146). New York: Raven Press.
- Mesulam, M.-M. (2002). The human frontal lobes: Transcending the default mode through contingent encoding. In D. T. Stuss & R. T. Knight (Eds.), *Principles of frontal lobe function* (pp. 8–30). New York: Oxford University Press.
- Miller, E. K. (2001). The prefrontal cortex. *Nature Neuroscience Reviews*, *1*, 59–65.
- Milner, B., Petrides, M., & Smith, M. L. (1985). Frontal lobes and the temporal organization of memory. *Human Neurobiology*, *4*, 137–142.
- Moutafi, J., Furnham, A., & Crump, J. (2003). Demographic and personality predictors of intelligence: A study using the NEO Personality Inventory and the Myers-Brigg Type Indicator. *European Journal of Personality*, *17*, 79–94.
- O'Connor, B. P. (2000). SPSS and SAS programs for determining the number of components using parallel analysis and Velicer's MAP test. *Behavior Research Methods, Instruments, and Computers*, *32*, 396–402. Program available online: <http://flash.lakeheadu.ca/~boconno2/nfactors.html>.
- Pandya, D. N., & Yeterian, E. H. (1984). Architecture and connection of the cortical association areas. In: A. Peters & E. G. Jones (Eds.), *Cerebral cortex*. New York: Plenum Press.
- Panksepp, J. (1998). *Affective neuroscience: The foundations of human and animal emotions*. New York: Oxford University Press.
- Peterson, J. B., & Carson, S. (2000). Latent inhibition and openness to experience in a high-achieving student population. *Personality and Individual Differences*, *28*, 323–332.
- Peterson, J. B., Smith, K. W., & Carson, S. (2002). Openness and Extraversion are associated with reduced latent inhibition: Replication and commentary. *Personality and Individual Differences*, *33*, 1137–1147.
- Petrides, M. (1985a). Deficits in non-spatial conditional associative learning after periarculate lesions in the monkey. *Behavioral Brain Research*, *16*, 95–101.
- Petrides, M. (1985b). Deficits on conditional associative-learning tasks after frontal- and temporal-lobe lesions in man. *Neuropsychologia*, *23*, 601–614.
- Petrides, M. (1987). Conditional learning and the primate frontal cortex. In E. Perelman (Ed.), *The frontal lobes revisited* (pp. 91–108). New York: The IRBN Press.
- Petrides, M. (1990). Nonspatial conditional learning impaired in patients with unilateral frontal but not unilateral temporal lobe excisions. *Neuropsychologia*, *28*, 137–149.

- Petrides, M. (1995). Impairments on nonspatial self-ordered and externally ordered working memory tasks after lesions of the mid-dorsal part of the lateral frontal cortex in the monkey. *Journal of Neuroscience*, **15**, 359–375.
- Petrides, M. (2000). Dissociable roles of mid-dorsolateral prefrontal and anterior inferotemporal cortex in visual working memory. *The Journal of Neuroscience*, **20**, 7496–7503.
- Petrides, M., Alivisatos, B., Evans, A. C., & Meyer, E. (1993). Dissociation of human mid-dorsolateral from posterior dorsolateral frontal cortex in memory processing. *Proceedings of the National Academy of Science of the U. S. A.*, **90**, 873–877.
- Petrides, M., Alivisatos, B., Meyer, E., & Evans, A. C. (1993). Functional activation of the human frontal cortex during the performance of verbal working memory tasks. *Proceedings of the National Academy of Science of the U. S. A.*, **90**, 878–882.
- Petrides, M., & Milner, B. (1982). Deficits on subject-ordered tasks after frontal- and temporal-lobe lesions in man. *Neuropsychologia*, **20**, 249–262.
- Pytlík Zillig, L. M., Hemenover, S. H., & Dienstbier, R. A. (2002). What do we assess when we assess a Big 5 trait? A content analysis of the affective, behavioral and cognitive processes represented in the Big 5 personality inventories. *Personality & Social Psychology Bulletin*, **28**, 847–858.
- Raven, J., Raven, J. C., & Court, J. H. (1998). *Manual for Raven's progressive matrices and vocabulary scales*. Oxford: Oxford Psychologists Press, Ltd.
- Ravnikilde Jensen, B., Videbech, P., Gade, A., & Rosenberg, R. (2000). Stroop's test and verbal fluency as measures of frontal lobe function: A PET study. *Journal of the International Neuropsychological Society*, **6**, 379.
- Reimann, R., Angleitner, A., & Strelau, J. (1997). Genetic and environmental influences on personality: A study of twins reared together using the self- and peer report NEO-FFI scales. *Journal of Personality*, **65**, 449–476.
- Robbins, T. W. (2000). Chemical neuromodulation of frontal-executive functions in humans and other animals. *Experimental Brain Research*, **133**, 130–138.
- Ross, S. R., Lutz, C. J., & Bailley, S. E. (2002). Positive and negative symptoms of schizotypy and the Five Factor Model: A domain and facet level analysis. *Journal of Personality Assessment*, **79**, 53–72.
- Saucier, G. (1992). Openness versus intellect: Much ado about nothing? *European Journal of Personality*, **6**, 381–386.
- Saucier, G. (2003). Factor structure of English-language personality type-nouns. *Journal of Personality and Social Psychology*, **85**, 695–708.
- Saucier, G., & Goldberg, L. R. (2001). Lexical studies of indigenous personality factors: Premises, products, and prospects. *Journal of Personality*, **69**, 847–879.
- Schultz, W. (1998). Predictive reward signal of dopamine neurons. *Journal of Neurophysiology*, **80**, 1–27.
- Schumaker, R. E., & Lomax, R. G. (1996). *A beginners guide to structural equation modeling*. Hillsdale, NJ: Erlbaum.
- Shadach, E., Feldon, J., & Weiner, I. (1999). Clozapine-induced potentiation of latent inhibition is due to its action in the conditioning stage: Implications for the mechanism of action of antipsychotic drugs. *International Journal of Neuropsychopharmacology*, **4**, 283–291.

- Spoont, M. R. (1992). Modulatory role of serotonin in neural information processing, implications for human psychopathology. *Psychological Bulletin*, **112**, 330–350.
- Tupes, E. C., & Christal, R. C. (1961/1992). Recurrent personality factors based on trait ratings. *Journal of Personality*, **60**, 225–251.
- Volkow, N. D., Gur, R. C., Wang, G.-J., Fowler, J. S., Moberg, P. J., Ding, Y.-S., et al. (1998). Association between decline in brain dopamine activity with age and cognitive and motor impairment in healthy individuals. *American Journal of Psychiatry*, **155**, 344–349.
- Waelti, P., Dickinson, A., & Schultz, W. (2001). Dopamine responses comply with basic assumptions of formal learning theory. *Nature*, **412**, 43–48.
- Wang, H., Ng, K., Hayes, D., Gao, X., Forster, G., Blaha, C. D., et al. (2004). Decreased amphetamine-induced locomotion and improved latent inhibition in mice mutant for the M5 muscarinic receptor gene found in the human 15q schizophrenia region. *Neuropsychopharmacology*, advance online publication, June 23; doi:10.1038/sj.npp.1300502.
- Ward, L. C., & Ryan, J. J. (1996). Validity and time savings in the selection of short forms of the Wechsler Adult Intelligence Scale–Revised. *Psychological Assessment*, **8**, 69–72.
- Wechsler, D. (1997). *WAIS-III administration and scoring manual*. San Antonio, TX: Harcourt Brace & Company.
- Weiner, I., & Feldon, J. (1987). Facilitation of latent inhibition by haloperidol in rats. *Psychopharmacology*, **2**, 248–253.
- Weiner, I., Lubow, R. E., & Feldon, J. (1988). Disruption of latent inhibition by acute administration of low doses of amphetamine. *Pharmacology, Biochemistry and Behavior*, **30**, 871–878.
- Wiegersma, S., van der Scheer, E., & Human, R. (1990). Subjective ordering, short-term memory, and the frontal lobes. *Neuropsychologia*, **28**, 95–98.
- Yeomans, J. S., Forster, G., & Blaha, C. D. (2001). M5 muscarinic receptors are needed for slow activation of dopamine neurons and for rewarding brain stimulation. *Life Sciences. Special Issue: Subtypes of muscarinic receptors: Proceedings of the Ninth International Symposium on Subtypes of Muscarinic Receptors*, **68**, 2449–2456.
- Zorrilla, L. T. E. (1997). Development and validation of the temporal order memory assessment for brain imaging. *Dissertation Abstracts International: Section B: The Sciences & Engineering*, **57**, 4777.