Neurophysiological Underpinnings of Personality:

Extraversion and Neuroticism

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Personality neuroscience is an emerging field which aims to account for the biological mechanisms informing personality. In this literature review, I assess the biological underpinnings of two personality traits, Extraversion and Neuroticism. Extraversion is conceived of as the positive emotionality dimension of personality and is associated with sensitivity to rewards and approach behaviour. As such, Extraversion is hypothesized to be a dopaminergically modulated system that converges with the so-called behavioural approach system. In contrast, Neuroticism is conceptualized the personality dimension of negative emotionality and is associated with sensitivity to punishment. As such, Neuroticism is hypothesized to be serotonergically modulated and converges with the joint sensitivity of two systems, the fight-flight-freeze-system and behavioural inhibition system.

Personality psychology rests on the presupposition that all meaningful individual differences are nested in the lexicon of the world's languages (cf. the lexical hypothesis; Goldberg, 1999). Personality is conceptualized as probabilistic descriptions of the intensity and regularity individuals display disparate and divergent affective, behavioural, cognitive, and motivational states (DeYoung, 2010; Fleeson & Gallagher, 2009). Trait-nouns and type-adjectives, subjected to factor analyses, converge into five broad dimensions of personality ('Big Five'): Openness/Intellect, Conscientiousness, Extraversion, Agreeableness, and Neuroticism (Costa & McCrae, 2008). The 'Big Five' traits reliably emerge across cultures (McCrae et al., 1998; Park et al., 2022) and are highly heritable; genetic influences are suggested to account for 40-55% in trait variability (Bouchard & McGue, 2002). Consequently, personality psychology directly implicates neuroscience and physiology so as to synthetically and mechanically account for biological mechanisms informing personality.

From this, Collin DeYoung's (2015) Cybernetic Big Five Theory (CB5T) departs. CB5T asserts that any adequate and comprehensive theory of personality must be nested in cybernetics: the study of goal-oriented, self-directed systems (DeYoung, 2015). Cybernetic systems can set and attain goals by referencing and comparing their current state to a desired set-goal, receive continuous feedback about progress, and in turn adopt their behaviour so as to align their current trajectory with one that culminates in set-goal fulfilment (DeYoung, 2015). For example, individuals that desire social stimulation can arrange to meet up with friends but can likewise leave if they feel overly socially stimulated. Cybernetic systems are thus both adaptable systems informing behaviour in relation to desired goals. Each individual is engaged in a plethora of goals simultaneously, and thus CB5T's conceptualization of personality is necessarily broad, defining personality as (a) each individual's unique evolutionary variation, detectable in complex patterns of (b) dispositional traits, (c) characteristic adaptations, and (d) self-defining life narratives, which are (e) differentially situated in culture and society (McAdams & Pals, 2006, p. 204).

This literature review will focus on the biological and neurochemical components of a subset of the personality dimensions as defined in the CB5T framework (DeYoung, 2015). More specifically, the biological constituents of traits Extraversion and Neuroticism will be discussed in detail and current state of knowledge assessed. The reason for this narrowing is twofold: First, neuroscientific research covering Extraversion and Neuroticism has accumulated the most reliable data; second, Extraversion and Neuroticism map differentially onto Jeffery Gray's Reinforcement Sensitivity Theory (RST; DeYoung, 2015; Gray & McNaughton, 2000). DeYoung has argued that subcomponents of Gray's RST and the 'Big Five' are conceptually equivalent (e.g., see Allen & DeYoung, 2017; DeYoung, 2015) and in this review, the evidence for that assertion will be assessed. Note that results measuring personality with measures purported to assess Gray's RST will be described using CB5T terminology, where appropriate.

Extraversion

Extraversion is the personality dimension of sociability and positive emotions. Individuals with high levels of trait Extraversion exhibit a greater sensitivity to rewards and arousability, are more exploratory, and display more approach behaviour (Allen & DeYoung, 2017; DeYoung, 2013; Gray & McNaughton, 2000). In the CB5T framework, Extraversion is broken down into the aspects *Assertiveness* and *Enthusiasm* (DeYoung et al., 2007), which reflect goal-drive and goal-enjoyment, respectively (DeYoung, 2015). Both aspects of Extraversion implicate the reward system but do so differentially as a function of the nature of a given reward. For our purposes, it is necessary to distinguish between incentive and consummatory rewards: incentive rewards reflect cues that signal movement towards a goal and are associated with Assertiveness; consummatory rewards reflect actual goal attainment and are associated with Enthusiasm (DeYoung, 2013, 2015). Sensitivity to rewards is thus considered the cardinal feature of Extraversion, in turn implicating the dopaminergic system as reward sensitivity is dopaminergically modulated (Depue & Collins, 1999). For example, dopamine agonists and antagonists increase and decrease reward-seeking behaviour, respectively (DeYoung, 2013; Gray & McNaughton, 2000; Wilt & Revelle, 2017).

According to Gray's RST, the dopaminergic system is purported to be the biological substrate of the behavioural approach system (BAS). BAS mediates reactions to appetitive stimuli, activates approach behaviour when faced with a discriminant stimulus signalling reward and non-punishment, and generates anticipatory pleasure (Depue & Collins, 1999; Gray & McNaughton, 2000). As such, BAS is a reward-orienting system which corresponds well with the functions associated with Extraversion (DeYoung, 2013). For example, both Extraversion and BAS are associated with left-dominant hemispheric asymmetry (Vecchio & De Pascalis, 2020), which is associated with both positive affectivity and information processing related to approach behaviour (Harmon-Jones, 2004), in turn implicating consummatory and incentive reward sensitivity, respectively (Allen & DeYoung, 2017). Moreover, questionnaires designed to assess BAS show high convergent validity with self-reported Extraversion levels (Keiser & Ross, 2011; Quilty et al., 2013; Smits & Boeck, 2006). Thus, as Extraversion and BAS are both hypothesized to be dopaminergically modulated approach and reward-orienting traits which converge into a single factor when measured with self-reports, DeYoung (2013, 2015) argues that the two are conceptually equivalent. Contributorily, the cortical structures associated with BAS; including the dorsal striatum, nucleus accumbens, and orbitofrontal cortex (Depue & Collins, 1999; Gray & McNaughton, 2000); are also associated with Extraversion. For example, a reasonably large structural MRI study (N = 116) found a positive association between Extraversion and volume of medial orbitofrontal cortex (DeYoung et al., 2010).

The orbitofrontal cortex (OFC) is hypothesized to code the value of rewarding stimuli and track performance (Bromberg-Martin et al., 2010; Depue & Collins, 1999). DeYoung et al.'s (2010) study, cited above, corroborate previous studies with analogous results; Omura et al. (2005) found a positive correlation between Extraversion and gray matter concentration in the bilateral OFC, albeit post-hoc; Rauch et al. (2005) found a positive correlation between Extraversion and cortical thickness of the medial OFC. Taken together, Extraversion and BAS both implicate the OFC, all link to the dopaminergic system (Bromberg-Martin et al., 2010; Depue & Collins, 1999), which in turn further substantiates the claim for conceptual equivalence. That said, Kapogiannis et al. (2012) failed to replicate the association between Extraversion and OFC, albeit in a cohort of older adults (mean age = 72). This replication failure can partly be explained by the tendency for levels of Extraversion to decline over life-span development, and specifically to decline rapidly from the age of 50 (Terracciano et al., 2005). Future studies should thus aim to disentangle whether a positive association between Extraversion and OFC volume is moderated by age, especially in older adults.

Electroencephalography (EEG) studies provide further evidence for the hypothesized role of dopamine and reward sensitivity in Extraversion (Cooper et al., 2014; Koehler et al., 2011; Mueller et al., 2013; Proudfit, 2015; Smillie et al., 2010; Vecchio & De Pascalis, 2020; Wacker et al., 2010). Extraversion is robustly associated with more posterior versus anterior delta/theta resting state brain oscillations, as measured with an EEG at the centerline electrode sites (Koehler et al., 2011; Vecchio & De Pascalis, 2020; Wacker et al., 2010). Further, posterior versus anterior slow wave brain oscillations have been implicated with the dopaminergic system; in Wacker et al. (2010), the correlation between posterior versus frontal slow-wave oscillations and *Agentic Extraversion* was strongly modulated by pharmacologically induced changes in dopamine activity. Agentic Extraversion corresponds to the Assertiveness aspect (cf. "jangle fallacy": same trait different name; DeYoung, 2013) and is thought to be directly implicated dopaminergic functioning (Depue & Collins, 1999).

It should be noted that both Assertiveness and Enthusiasm aspects of Extraversion predict similar levels of evocable positive affectivity (Smillie et al., 2013), and both aspects are nested in the dopaminergic system (DeYoung, 2013); albeit variation in Assertiveness, compared with Enthusiasm, is hypothesized to be more strongly associated with dopamine (cf. Wacker et al., 2012). In Koehler et al. (2011), polymorphisms of the dopamine D2 receptor (DRD2) gene and Extraversion were independently associated with slow-wave posterior versus anterior oscillations, but not associated with each other. That implies that (a) Assertiveness and Enthusiasm are differentially modulated by dopamine (cf. Depue & Collins, 1999; DeYoung, 2013; Wacker et al., 2012), and (b) slow-wave posterior versus frontal oscillations predict trait Extraversion better than polymorphisms in dopaminergic receptor genes. Taken together, slow-wave posterior versus frontal oscillations have been suggested to constitute a trait marker of Extraversion (Allen & DeYoung, 2017).

Implicating reward sensitivity directly, Extraversion is associated with an event-related-potential (ERP) known as feedback-related negativity (FRN; DeYoung et al., 2021)[1], thought to reflect dopamine-mediated valuation of reward prediction error outcomes (Smillie et al., 2013, p. 228), characterizing outcomes as either better-than-predicted or worse-than-predicted (Proudfit, 2015; Sambrook & Goslin, 2015). Dopaminergic projections from the ventral tegmental area (VTA) to the nucleus accumbens and anterior cingulate cortex (ACC) appear central in valuation of reward prediction error outcomes (Bromberg-Martin et al., 2010; Schultz, 2007)[2]. The FRN is modulated by phasic dopaminergic responses[3] to unpredicted rewards and unpredicted non-rewards, which in turn inform the ACC (Holroyd & Coles, 2002). A more negative FRN is the result of phasic decreases in dopaminergic activity following unpredicted non-rewards (i.e., predicted reward not delivered, indicating ongoing events to be worse than expected), while a less negative FRN is the result of increases in phasic dopaminergic activity following unpredicted rewards (i.e., unexpected delivery of reward, indicating ongoing events to be better than expected; Holroyd & Coles, 2002).

From the preceding paragraph, we can derive that individuals high in Extraversion should exhibit a more negative FRN when the system detects that ongoing events are worse

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[1] Confusingly, feedback-related negativity is also known as *reward positivity* (RewP); subtracting losses from gains (i.e., worse-than expected from better-than-expected) results in a gain-related positivity waveform. Proudfit argues that naming the difference waveform reward positivity "more closely reflects the functional significance of variability in the ERP following gain versus loss feedback" (Proudfit, 2015, p. 450).

[2] $Dopamine\ response = reward\ predicted - reward\ predicted$ (Schultz, 2007).

[3] Phasic dopamine responses are spike-dependent dopamine releases into the synaptic cleft, usually following rewarding stimuli, which in turn is rapidly removed through re-uptake mechanisms before it can diffuse into the extracellular space. In contrast, tonic dopamine release refers to a slow and steady secretion of dopamine in small concentrations into the synaptic cleft which, in turn, allows it to escape the synaptic cleft and enter the extracellular space. In short, phasic dopamine responses reflect quick bursts of dopamine active for a short amount of time and tonic dopamine responses reflect slower but longer lasting dopamine releases (Grace, 2000).

than expected and a less negative FRN when ongoing events are better than expected. Cooper et al. (2014) and Smillie et al. (2010)**,** comparing high-Extraverts with low-Extraverts, found that FRN was more negative following unpredicted non-rewards and less negative following unpredicted rewards. In Mueller et al.'s (2013) study, an association between Extraversion and negative FRN amplitude following failure was detected *only* when participants were incentivized to win, with a non-significant ($p = 0.061$) association without incentivization. Moreover, and implicating dopamine directly, the association disappeared following administration of a dopamine antagonist. Taken together, quicker-than-expected progress towards a goal (cf. unpredicted reward) appears to elicit a greater dopaminergic response in individuals high in Extraversion, consistent with the hypothesized associations between Extraversion, reward sensitivity, and dopamine (Depue & Collins, 1999; DeYoung, 2013).

In conclusion, reward sensitivity is the cardinal feature of Extraversion, which in turn implicates the dopaminergic system (Depue & Collins, 1999). Individuals high in Assertiveness are more likely to approach novel environments if they perceive them to indicate a movement towards rewarding stimuli (cf. incentive rewards) and individuals high in Enthusiasm derive more enjoyment from rewarding stimuli (cf. consummatory rewards; DeYoung, 2013). Like Extraversion, BAS is a dopaminergically driven approach system that is sensitive to rewards (Gray & McNaughton, 2000), and measures of BAS highly converge with measures of Extraversion (Quilty et al., 2013). This has lead DeYoung (2013, 2015) to question whether it is reasonable to separate the two constructs. The evidence reviewed above suggests Extraversion and BAS to be conceptually equivalent, which is advantageous as it allows for a larger amount of evidence to be critically reviewed in accordance with the aim to account for the biological mechanisms informing personality synthetically and mechanically.

Neuroticism

Neuroticism is the personality dimension of negative emotions. Individuals with high levels of Neuroticism are more sensitive to threats, punishments, uncertainty, and errors, which manifests as a greater inclination to experience fear, anxiety, depression (DeYoung, 2015; Gray & McNaughton, 2000). In the CB5T framework, Neuroticism is broken down into *Volatility* and *Withdrawal* (DeYoung et al., 2007), reflecting active defence from fear-evoking stimuli and passive avoidance of conflicting goals so as to facilitate goal-conflict reconciliation, respectively (Allen & DeYoung, 2017). Neuroticism is the personality dimension that has been subjected to the greatest amount of neuroscientific research (cf. DeYoung et al., 2021) as it emerges as a robust predictor for psychopathology and mental disorder comorbidity (e.g., depression, anxiety, personality disorders; Lahey, 2009). The CB5T framework builds on Gray's RST, conceptualizing Neuroticism as a joint sensitivity of a fight-flight-freeze-system (FFFS) and a behavioural inhibition system (BIS; DeYoung, 2015; Gray & McNaughton, 2000).

The FFFS is conceptualized as a system that actively eliminates threats and fear-evoking stimuli (e.g., by employing active avoidance or escape behaviours; Gray & McNaughton, 2000). Traits related to anger, irritability, hypervigilance, and emotional lability are associated with FFFS, implicating active defence responses, and in turn converge with the Volatility aspect (DeYoung et al., 2021). In contrast, BIS is conceived of as a system that reconciles conflicting goals (e.g., approach-avoidance) by recursively looping anxiety provoking content so as to increase its negative perceptual valence, which in turn facilitates behavioural resolution in favour of either approach or avoidance (Gray & McNaughton, 2000). Traits related to anxiety and depression are associated with BIS, which in turn implicates a disposition for passive avoidance (i.e., a tendency to avoid potential punishment and/or error by slowing or inhibiting behaviour), and thus converge with the Withdrawal aspect (DeYoung et al., 2021; see also Pickering & Corr, 2008).

The neurotransmitters serotonin and norepinephrine modulate FFFS and BIS (Gray & McNaughton, 2000), and are thus both likely implicated in Neuroticism. However, more evidence has accumulated for the role of serotonin. For example, Quilty et al. (2008) showed that selective serotonin reuptake inhibitors (SSRIs) lead to a greater reduction in Neuroticism levels compared with reuptake inhibitors targeting norepinephrine and dopamine. Quilty et al. also found reductions in Neuroticism levels to moderate subsequent declines in depression, wherein greater declines in Neuroticism were associated with lower levels of depression. This implies that SSRIs are effective for combatting depression insofar as they concurrently decrease Neuroticism levels. Relatedly, Tang et al. (2009) conducted a randomized placebo-control trial and found SSRIs to decrease Neuroticism levels by half a standard deviation during an 8-week intervention. Moreover, Neuroticism levels among participants receiving SSRIs were 6.8-times lower compared with a placebo group at the end of the trial. Lastly, in a positron emission tomography (PET) study (N = 83), Neuroticism predicted frontolimbic serotonin 2A receptor binding potential (Frokjaer et al., 2008) which indicates upregulated serotonin receptor sites in response to presynaptic serotonin-release impairments, in turn resulting in decreased levels of available serotonin (cf. Bhagwagar et al., 2006; Duman, 2004)[4]. Taken together, the studies just reviewed dovetail with the hypothesized role of serotonin in Neuroticism and suggest Neuroticism and depression to be intertwined.

As previously mentioned, Neuroticism has been researched the most in personality neuroscience (cf. DeYoung et al., 2021). As such, a few convincing findings warrant mentioning. First, a study with over 1000 participants found a correlation between amygdala volume and Neuroticism (left amygdala: r = 0.14; right amygdala: r = 0.09; Holmes et al., 2012). It has long been established that the amygdala and negative affectivity are related (cf. Allen & DeYoung, 2017), but studies prior to Holmes et al. (2012) had been inconsistent. However, as the average correlation in personality psychology is 0.21 (Hemphill, 2003), and detecting an effect of 0.1 with 80% power at $p < .05$ necessitates a sample size of 783, inconsistent findings are to be expected in small samples. Second, Neuroticism is associated with smaller total brain volume (Bjørnebekk et al., 2013; Knutson et al., 2001), a finding suggested to be the result of elevated levels of cortisol (cf. hypercortisolemia), which in turn potentiates excitotoxic processes in neurons (Knutson et al., 2001, p. 689). Lastly, Neuroticism is in general associated with right-dominant hemispheric asymmetry (Saffiera et al., 2020; Vecchio & De Pascalis, 2020; Wacker et al., 2010), and in turn negative affectivity. More specifically however, Withdrawal is associated with right-dominant asymmetry but Volatility appears to be associated with left-dominant asymmetry (Harmon-Jones, 2004). Recall that Extraversion is also associated with left-dominant and approach behaviour. However, unlike Extraversion, approach motivation evoked by Volatility arises from fear and anger and is thus phenomenologically different from the reward-orienting approach associated with Extraversion. In sum, evidence suggests Withdrawal to be more associated with feelings of negative emotions (cf. depression), and Volatility with anger and hypervigilance (Harmon-Jones, 2004; Vecchio & De Pascalis, 2020).

In conclusion, Neuroticism appears to be serotonergically modulated; increased levels of serotonin lead to a reduction in levels of Neuroticism, which in turn moderates the treatment efficacy of SSRIs for depression (Quilty et al., 2008; Tang et al., 2009). Neuroticism is biologically underpinned by markers known to be associated with increased negative affectivity (i.e., amygdala volume and right-hemispheric asymmetry; Holmes et al., 2012; Wacker et al., 2010) and frequent experiences of stress (i.e., smaller total brain volume

[4] In other words, increased serotonin 2A binding potential indicates greater receptor density due to impaired serotonin release (Duman, 2004), and can be understood as greater sensitivity (cf. opposite of dependence). Moreover, the impairment can be treated with serotonin *antagonists* among individuals unresponsive to SSRIs, which substantiates concurrent serotonin receptor insensitivity and low availability (Duman, 2004, p. 423-424).

and hypercortisolemia; Bjørnebekk et al., 2013). Individuals high on Volatility are more likely to approach the source of their negative emotions as a result of greater feelings of fear, while individuals high on Withdrawal are more likely to ruminate over their perceived negative experience and in turn are more prone to depression (DeYoung et al., 2021; Harmon-Jones, 2004). Notably, questionnaires designed to measure FFFS and BIS show high convergent validity with, and map differentially onto, self-reported level of Neuroticism (cf. Volatility and Withdrawal; Keiser & Ross, 2011; Smits & Boeck, 2006). That said, no study has to my knowledge assessed how BIS and FFFS scales map onto the aspects of Neuroticism directly using the CB5T framework and its associated measures (cf. DeYoung et al., 2007). Given the robust predictive power of Neuroticism for psychopathology (Lahey, 2009), disentangling how the different aspects differentially predict mental disorders such as depression, anxiety, and personality disorders such as psychopathy is vital in future research.

Summary and Future Directions

In this literature review, I have assessed the biological underpinnings of Extraversion and Neuroticism (DeYoung, 2015; Gray & McNaughton, 2000). As outlined above, Extraversion is a dopaminergically modulated reward-orienting system, while Neuroticism is a serotonergically modulated negative emotionality system (Quilty et al., 2008, 2013). Extraversion is associated with an increased volume of the orbitofrontal cortex (OFC) volume (DeYoung et al., 2010) but this finding has failed to be replicated in older adults (Kapogiannis et al., 2012). Although Extraversion declines over life-span development (cf. Terracciano et al., 2005), future research should aim to disentangle the association between OFC volume and Extraversion. Further, given that both Extraversion and the Volatility aspect of Neuroticism predict left-dominant hemispheric asymmetry (Harmon-Jones, 2004), research encapsulating personality at the aspect level ought to be conducted so as to partial out the association. Relatedly, future research should aim to assess whether total brain volume, cortisol levels, and amygdala volume are differentially predicted by the two aspects of Neuroticism (Bjørnebekk et al., 2013; Holmes et al., 2012; Knutson et al., 2001).

The aspects of personality as defined in the CB5T framework were empirically derived as opposed to clinically interpreted (DeYoung et al., 2007). As such, they should be brought to bear on the biological mechanisms underpinning personality with greater frequency than they have been to date. Current trends in personality neuroscience suggest such efforts to be under way (DeYoung et al., 2022). As previously mentioned, Extraversion can be equated with the behavioural approach system (BAS), while Neuroticism represents the joint sensitivity of a fight-flight-freeze-system (FFFS) and behavioural inhibition system (BIS) in Gray's reinforcement sensitivity theory (Allen & DeYoung, 2017; Gray & McNaughton, 2000). However, while the claim of Extraversion being conceptually equivalent to BAS is well substantiated (see DeYoung et al., 2021), more research is needed to assert the FFFS and BIS to be conceptually equivalent to Volatility and Withdrawal, respectively. To attain conceptual equivalence, researchers should continue their efforts to compartmentalize the 'Big Five' into aspects according to the CB5T framework. That said, the current state of knowledge dovetails with the conceptualization of Neuroticism comprising of the joint sensitivity of FFFS and BIS (DeYoung et al., 2021). To conclude, personality neuroscience is a relatively young field with many interesting avenues not detailed in this review. By my estimation, the neurochemical evidence is by far the most exciting. To take but one example, psychophysiological explanations for differential treatment efficacy of pharmacological agents targeting depression (e.g., Quilty et al., 2008) further our ability to alleviate psychological pain and suffering. As such, there is every reason to be optimistic about the future of personality research and what it will bring to bear on the human condition (DeYoung et al., 2022).

References

Allen, T. A., & DeYoung, C. G. (2017). Personality neuroscience and the five factor model. In T. A. Widiger (Ed.), *The oxford handbook of the five factor model* (pp. 319–349). Oxford University Press.

Bhagwagar, Z., Hinz, R., Taylor, M., Fancy, S., Cowen, P., & Grasby, P. (2006). Increased 5-HT(2A) receptor binding in euthymic, medication-free patients recovered from depression: A positron emission study with [(11)C]MDL 100,907. *The American Journal of Psychiatry*, *163*(9), 1580–1587. https://doi.org/10.1176/ajp.2006.163.9.1580

Bjørnebekk, A., Fjell, A. M., Walhovd, K. B., Grydeland, H., Torgersen, S., & Westlye, L. T. (2013). Neuronal correlates of the five factor model (FFM) of human personality: Multimodal imaging in a large healthy sample. *NeuroImage*, *65*, 194–208. https://doi.org/10.1016/j.neuroimage.2012.10.009

Bouchard, T. J., & McGue, M. (2002). Genetic and environmental influences on human psychological differences. *Journal of Neurobiology*, *54*(1), 4–45. https://doi.org/10.1002/neu.10160

Bromberg-Martin, E. S., Matsumoto, M., & Hikosaka, O. (2010). Dopamine in motivational control: Rewarding, aversive, and alerting. *Neuron*, *68*(5), 815–834. https://doi.org/10.1016/j.neuron.2010.11.022

Cooper, A. J., Duke, Ã., Pickering, A. D., & Smillie, L. D. (2014). Individual differences in reward prediction error: Contrasting relations between feedback-related negativity and trait measures of reward sensitivity, impulsivity and extraversion. *Frontiers in Human Neuroscience*, *8*. https://doi.org/10.3389/fnhum.2014.00248

Costa, P. T., & McCrae, R. R. (2008). The revised NEO personality inventory (NEO-PI-R. In G. J. Boyle, G. Matthews, & D. H. Saklofske (Eds.), *The SAGE handbook of personality theory and assessment* (Vol. 2, pp. 179–198). Sage Publications, Inc. https://doi.org/10.4135/9781849200479.n9

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*(3), 491–517. https://doi.org/10.1017/s0140525x99002046

DeYoung, C. G. (2010). Personality neuroscience and the biology of traits. *Social and Personality Psychology Compass*, *4*(12), 1165–1180. https://doi.org/10.1111/j.1751-9004.2010.00327.x

DeYoung, C. G. (2013). The neuromodulator of exploration: A unifying theory of the role of dopamine in personality. *Frontiers in Human Neuroscience*, *7*. https://doi.org/10.3389/fnhum.2013.00762

DeYoung, C. G. (2015). Cybernetic big five theory. *Journal of Research in Personality*, *56*, 33–58. https://doi.org/10.1016/j.jrp.2014.07.004

DeYoung, C. G., Beaty, R. E., Genç, E., Latzman, R. D., Passamonti, L., Servaas, M. N., Shackman, A. J., Smillie, L. D., Spreng, R. N., Viding, E., & Wacker, J. (2022). Personality neuroscience: An emerging field with bright prospects. *Personality Science*, *3*, e7269. https://doi.org/10.5964/ps.7269

DeYoung, C. G., Grazioplene, R. G., & Allen, T. A. (2021). The neurobiology of personality. In O. P. John & R. W. Robins (Eds.), *Handbook of personality: Theory and research* (pp. 193–216). The Guilford Press.

DeYoung, C. G., Hirsh, J. B., Shane, M. S., Papademetris, X., Rajeevan, N., & Gray, J. R. (2010). Testing predictions from personality neuroscience. *Psychological Science*, *21*(6), 820–828. https://doi.org/10.1177/0956797610370159

DeYoung, C. G., Quilty, L. C., & Peterson, J. B. (2007). Between facets and domains: 10 aspects of the Big Five. *Journal of Personality and Social Psychology*, *93*(5), 880–896. https://doi.org/10.1037/0022-3514.93.5.880

Duman, R. S. (2004). The neurochemistry of depressive disorders: Preclinical studies. In D. S. Charney & E. J. Nestler (Eds.), *Neurobiology of mental illness* (2nd ed., pp. 421–439). Oxford University Press.

Fleeson, W., & Gallagher, P. (2009). The implications of Big Five standing for the distribution of trait manifestation in behavior: Fifteen experience-sampling studies and a meta-analysis. *Journal of Personality and Social Psychology*, *97*(6), 1097–1114. https://doi.org/10.1037/a0016786

Frokjaer, V. G., Mortensen, E. L., Nielsen, F. Å., Haugbol, S., Pinborg, L. H., Adams, K. H., Svarer, C., Hasselbalch, S. G., Holm, S., Paulson, O. B., & Knudsen, G. M. (2008). Frontolimbic serotonin 2A receptor binding in healthy subjects is associated with personality risk factors for affective disorder. *Biological Psychiatry*, *63*(6), 569–576. https://doi.org/10.1016/j.biopsych.2007.07.009

Goldberg, L. R. (1999). A broad-bandwidth, public domain, personality inventory measuring the lower-level facets of several five-factor models. *Personality Psychology in Europe*, *7*(1), 7–28.

Grace, A. A. (2000). The tonic/phasic model of dopamine system regulation and its implications for understanding alcohol and psychostimulant craving. *Addiction*, *95*(8s2), 119–128. https://doi.org/10.1046/j.1360-0443.95.8s2.1.x

Gray, J. A., & McNaughton, N. (2000). *The neuropsychology of anxiety: An enquiry into the functions of the septo-hippocampal system*. Oxford University Press.

Harmon-Jones, E. (2004). Contributions from research on anger and cognitive dissonance to understanding the motivational functions of asymmetrical frontal brain activity. *Biological Psychology*, *67*(1), 51–76. https://doi.org/10.1016/j.biopsycho.2004.03.003

Hemphill, J. F. (2003). Interpreting the magnitudes of correlation coefficients. *The American Psychologist*, *58*(1), 78–79. https://doi.org/10.1037/0003-066x.58.1.78

Holmes, A. J., Lee, P. H., Hollinshead, M. O., Bakst, L., Roffman, J. L., Smoller, J. W., & Buckner, R. L. (2012). Individual differences in amygdala-medial prefrontal anatomy link negative affect, impaired social functioning, and polygenic depression risk. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, *32*(50), 18087–18100. https://doi.org/10.1523/JNEUROSCI.2531-12.2012

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*(4), 679–709. https://doi.org/10.1037/0033-295x.109.4.679

Kapogiannis, D., Sutin, A., Davatzikos, C., Costa, P., & Resnick, S. (2012). The five factors of personality and regional cortical variability in the baltimore longitudinal study of aging. *Human Brain Mapping*, *34*(11), 2829–2840. https://doi.org/10.1002/hbm.22108

Keiser, H. N., & Ross, S. R. (2011). Carver and Whites' BIS/FFFS/BAS scales and domains and facets of the Five Factor Model of personality. *Personality and Individual Differences*, *51*(1), 39–44. https://doi.org/10.1016/j.paid.2011.03.007

Knutson, B., Momenan, R., Rawlings, R. R., Fong, G. W., & Hommer, D. (2001). Negative association of neuroticism with brain volume ratio in healthy humans. *Biological Psychiatry*, *50*(9), 685–690. https://doi.org/10.1016/S0006-3223(01)01220-3

Koehler, S., Wacker, J., Odorfer, T., Reif, A., Gallinat, J., Fallgatter, A. J., & Herrmann, M. J. (2011). Resting posterior minus frontal EEG slow oscillations is associated with

extraversion and DRD2 genotype. *Biological Psychology*, *87*(3), 407–413. https://doi.org/10.1016/j.biopsycho.2011.05.006

Lahey, B. B. (2009). Public health significance of neuroticism. *American Psychologist*, *64*(4), 241–256. https://doi.org/10.1037/a0015309

McAdams, D. P., & Pals, J. L. (2006). A new Big Five: Fundamental principles for an integrative science of personality. *American Psychologist*, *61*(3), 204–217. https://doi.org/10.1037/0003-066X.61.3.204

McCrae, R. R., Costa, P. T., Del Pilar, G. H., Rolland, J.-P., & Parker, W. D. (1998). Cross-cultural assessment of the five-factor model. *The Revised NEO Personality Inventory. Journal of Cross-Cultural Psychology*, *29*(1), 171–188. https://doi.org/10.1177/0022022198291009

Mueller, E. M., Burgdorf, C., Chavanon, M.-L., Schweiger, D., Wacker, J., & Stemmler, G. (2013). Dopamine modulates frontomedial failure processing of agentic introverts versus extraverts in incentive contexts. *Cognitive, Affective, & Behavioral Neuroscience*, *14*(2), 756–768. https://doi.org/10.3758/s13415-013-0228-9

Omura, K., Todd Constable, R., & Canli, T. (2005). Amygdala gray matter concentration is associated with extraversion and neuroticism. *NeuroReport*, *16*(17), 1905–1908. https://doi.org/10.1097/01.wnr.0000186596.64458.76

Park, J., Broek, K. L., Bhullar, N., Ogunbode, C. A., Schermer, J. A., Doran, R., Ardi, R., Hanss, D., Maran, D. A., Albzour, M., Aquino, S. D., Ayanian, A. H., Chegeni, R., Chukwuorji, J. C., Enea, V., Ghanbarian, E., Ghorayeb, J., Jiang, F., Kehinde, O. A., & Lins, S. (2022). Comparison of the inter-item correlations of the Big Five Inventory-10 (BFI-10) between Western and non-Western contexts. *Personality and Individual Differences*, *196*, 111751. https://doi.org/10.1016/j.paid.2022.111751

Pickering, A. D., & Corr, P. J. (2008). J.A. gray's reinforcement sensitivity theory (RST) of personality. In G. J. Boyle, G. Matthews, & D. H. Saklofske (Eds.), *The SAGE handbook of personality theory and assessment* (Vol. 1, pp. 239–256). Sage Publications, Inc. https://doi.org/10.4135/9781849200462.n11

Proudfit, G. H. (2015). The reward positivity: From basic research on reward to a biomarker for depression. *Psychophysiology*, *52*(4), 449–459. https://doi.org/10.1111/psyp.12370

Quilty, L. C., DeYoung, C. G., Oakman, J. M., & Bagby, R. M. (2013). Extraversion and behavioral activation: Integrating the components of approach. *Journal of Personality Assessment*, *96*(1), 87–94. https://doi.org/10.1080/00223891.2013.834440

Quilty, L. C., Meusel, L.-A. C., & Bagby, R. M. (2008). Neuroticism as a mediator of treatment response to SSRIs in major depressive disorder. *Journal of Affective Disorders*, *111*(1), 67–73. https://doi.org/10.1016/j.jad.2008.02.006

Rauch, S. L., Milad, M. R., Orr, S. P., Quinn, B. T., Fischl, B., & Pitman, R. K. (2005). Orbitofrontal thickness, retention of fear extinction, and extraversion. *NeuroReport*, *16*(17), 1909–1912. https://doi.org/10.1097/01.wnr.0000186599.66243.50

Saffiera, C. A., Hassan, R., & Ismail, A. R. (2020). Preventive and curative personality profiling based on EEG, ERP, and big five personality traits: A literature review. *Journal of Computational and Theoretical Nanoscience*, *17*(2/3), Article 2/3.

Sambrook, T. D., & Goslin, J. (2015). A neural reward prediction error revealed by a meta-analysis of ERPs using great grand averages. *Psychological Bulletin*, *141*(1), 213–235. https://doi.org/10.1037/bul0000006

Schultz, W. (2007). Behavioral dopamine signals. *Trends in Neurosciences*, *30*(5), 203–210. https://doi.org/10.1016/j.tins.2007.03.007

Smillie, L. D., Cooper, A. J., & Pickering, A. D. (2010). Individual differences in reward–prediction–error: Extraversion and feedback-related negativity. *Social Cognitive and Affective Neuroscience*, *6*(5), 646–652. https://doi.org/10.1093/scan/nsq078

Smillie, L. D., Geaney, J. T., Wilt, J., Cooper, A. J., & Revelle, W. (2013). Aspects of extraversion are unrelated to pleasant affective-reactivity: Further examination of the affective-reactivity hypothesis. *Journal of Research in Personality*, *47*(5), 580–587. https://doi.org/10.1016/j.jrp.2013.04.008

Smits, D. J. M., & Boeck, P. D. (2006). From BIS/BAS to the big five. *European Journal of Personality*, *20*(4), 255–270. https://doi.org/10.1002/per.583

Tang, T. Z., DeRubeis, R. J., Hollon, S. D., Amsterdam, J., Shelton, R., & Schalet, B. (2009). Personality change during depression treatment. *Archives of General Psychiatry*, *66*(12), 1322. https://doi.org/10.1001/archgenpsychiatry.2009.166

Terracciano, A., McCrae, R. R., Brant, L. J., & Costa, P. T. (2005). Hierarchical linear modeling analyses of the NEO-PI-R scales in the baltimore longitudinal study of aging. *Psychology and Aging*, *20*(3), 493–506. https://doi.org/10.1037/0882-7974.20.3.493

Vecchio, A., & De Pascalis, V. (2020). EEG Resting Asymmetries and Frequency Oscillations in Approach/Avoidance Personality Traits: A Systematic Review. *Symmetry*, *12*(10), Article 10. https://doi.org/10.3390/sym12101712

Wacker, J., Chavanon, M.-L., & Stemmler, G. (2010). Resting EEG signatures of agentic extraversion: New results and meta-analytic integration. *Journal of Research in Personality*, *44*(2), 167–179. https://doi.org/10.1016/j.jrp.2009.12.004

Wacker, J., Mueller, E. M., Hennig, J., & Stemmler, G. (2012). How to consistently link extraversion and intelligence to the catechol-O-methyltransferase (COMT) gene: On defining and measuring psychological phenotypes in neurogenetic research. *Journal of Personality and Social Psychology*, *102*(2), 427–444. https://doi.org/10.1037/a0026544

Wilt, J., & Revelle, W. (2017). Extraversion. In T. A. Widiger (Ed.), *The oxford handbook of the five factor model* (pp. 57–81). Oxford University Press.