Social and Personality Psychology Compass 7/3 (2013): 158–175, 10.1111/spc3.12016

Motivation and Personality: A Neuropsychological Perspective

Philip J. Corr[1]*, Colin G. DeYoung[2] and Neil McNaughton[3]
[1]*University of East Anglia*
[2]*University of Minnesota*
[3]*University of Otago*

Abstract

Personality is strongly influenced by motivation systems that organise responses to rewards and punishments and that drive approach and avoidance behavior. Neuropsychological research has identified: (a) two avoidance systems, one related to pure active avoidance and escape, and one to passive avoidance and behavioral inhibition produced by goal-conflict; and (b) two approach systems, one related to the actions of reward seeking and one to experience and behavior related to pleasure on receiving reward. These systems mediate fluid moment-by-moment reactions to changing stimuli, with relatively stable person-specific sensitivities to these stimuli manifested in personality traits. We review what is known about these motivational traits, integrating the theory-driven approach based on animal learning paradigms with the empirical tradition of the Big Five personality model.

People differ from one another, and this fact is obvious to everyone. It is common to talk about people's personalities using lexical terms to describe their characteristic ways of thinking, feeling and behaving (e.g., 'bold', 'lazy', 'intelligent'), and we use these descriptors to infer people's intentions and likely future behavior. Personality psychologists have long analyzed the ratings of large numbers of trait descriptive adjectives to produce the most widely used taxonomy of personality: the Big Five, which includes the dimensions of Extraversion, Neuroticism, Conscientiousness, Agreeableness, and Openness to Experience/Intellect (John, Naumann, & Soto, 2008). These Big Five traits also emerge from existing personality questionnaires that were not designed specifically to measure them (e.g., Markon, Krueger, & Watson, 2005), suggesting it is a good candidate for a consensual model in personality psychology.

What the Big Five model does not immediately offer, however, is an explanation for the *causal* sources of personality traits. *Why* do people think, feel, and act in the ways that they do? People react to situations, of course; but different people react differently to the same situation, suggesting that they have different behavioral propensities. In order to answer this *why* question, we must discover what drives people's actions and reactions. Inferring motivation from observed personality has been something of a dark art in psychology. However, one promising approach to this question is based on the biology of motivational control systems, studied by psychologists for over a century in non-human animals, and for somewhat less time in humans. This approach operates on the premise that stable individual differences in behavior (personality traits) must be due to relatively stable individual differences in the operation of brain systems that produce (state) behavior from moment-to-moment. From this perspective, each of our many traits reflects the operations of a set of brain systems that has evolved to respond to a different class of functional requirements (Denissen & Penke, 2008; McNaughton, 1989; Nettle, 2006; Pickering & Gray, 1999).

In what follows, we focus on those motivational processes and personality traits most closely aligned with biological research on reactions to reward and punishment and associated approach and avoidance behavior. This focus is warranted both by the importance of these phenomena for motivation and by the existence of extensive research on them. Our aim is to offer an introduction for researchers wishing to explore the role of motivation in personality from the perspective of these underlying psychobiological systems. Only after a description of what is known about the operation of these systems do we branch out to consider the personality traits associated with them. Our major assumption is that most fundamental personality traits have a motivational core; and we aim to show that the descriptive personality research tradition, which produced the Big Five, can be integrated with the experimental research tradition that has focused on the sensitivities of basic motivation systems.

In this review, we focus on systems related to approach and avoidance primarily at the level of explanation that Gray (1975) labeled 'the conceptual nervous system', which is based on analysis of behavior as well as neurobiology and attempts to describe important psychological processes without specifying their exact instantiation in the nervous system – this approach has afforded a detailed analysis of reactions to classes of motivationally significant stimuli and can be used to derive predictions concerning the functions of the real nervous system (e.g., in fMRI studies). Rather than going into extensive detail regarding the biological basis of the systems, we focus primarily on their functions, discussing biological evidence only when it is necessary for addressing some functional question.

Approach-Avoidance Theories of Motivation and Their Relation to Personality

The most important classes of motivational stimuli can be grouped into 'rewards' and 'punishments'. Animals can be seen as cybernetic systems with attractors and repulsors (positive and negative goals) that have evolved to promote survival and reproduction (Carver & Scheier, 1998; DeYoung, 2010d). Without a tendency to approach beneficial stimuli (e.g., food, drink, and sexual mates) and to avoid aversive stimuli (e.g., predators and poisons) a species would not survive.

'Reward' and 'punishment' may seem straightforward concepts, but they hide some non-obvious complexities. For the classical behaviorist, rewards increase the frequency of the behavior leading to them, whereas punishments decrease the frequency of behavior leading to them. That is, a 'reward' is something a person will work to obtain; and a 'punishment' is something a person will work to avoid. But the behaviorist definition of 'reward' also includes a different class of stimuli, namely the termination or omission of expected punishment. The effect on behavior and emotion of the 'hope' of achieving a reward is similar to that of anticipated 'relief' through avoiding a punishment. Similarly, although a 'punishment' can be described as something people will work to avoid or escape from (or which they will attack defensively), the omission of an expected reward is experienced as punishing; an effect known as frustrative nonreward. Thus, 'fear' has important similarities with 'frustration'. (For further discussion of this literature, see Corr & McNaughton, 2012.)

These complexities can be understood straightforwardly from the cybernetic perspective, in which rewards are any stimuli that indicate progress toward or attainment of a goal, whereas punishments are any stimuli that disrupt progress toward a goal. However, in any experimental situation, it is necessary to confirm that the subject perceives stimuli as actually rewarding and punishing, as there are likely to be significant individual differences in how people react to the same stimuli (for further discussion of this point, see Corr, forthcoming).

Current approach-avoidance theories trace their origins to early researchers who posited that two motivation/emotion processes underlie behavior (e.g., Konorski, 1967; Mowrer, 1960; Schneirla, 1959), one related to reward (approach behavior and positive emotions), and the other to punishment (avoidance behavior and negative emotions). Neuroscience measures, including pharmacological manipulation, assessment of neural activity, and neuroanatomical studies, have been used to investigate the neuropsychological systems that underlie reactions to these classes of stimuli, providing confirmation of the hypothesis that distinct systems underlie reward- and punishment-related motivation (Gray & McNaughton, 2000).

This animal-based work migrated into personality psychology in the 1970s via Jeffrey A. Gray (e.g., 1970, 1972a,b, 1975, 1977), whose Reinforcement Sensitivity theory (RST) argued that the major traits of personality reflect long-term stabilities in systems that mediate reactions to different classes of reinforcing stimuli, generating emotion and shaping ('motivating') approach and avoidance behavior. The leap from understanding motivational systems to understanding personality traits requires the postulate that relatively stable individual differences exist in the operations of these brain-behavioral systems.

A personality trait can be defined as a probabilistic constant in equations that predict the frequency and intensity with which individuals exhibit various motivational states, as well as the behavioral, emotional, and cognitive states that accompany these motivational states (DeYoung, 2010c; Fleeson, 2001; Fleeson & Gallagher, 2009). Note that this assumes exposure of the population to a normal range of situations. If situations are limited to prevent exposure to some trait-relevant class of situations, then individual differences in that trait may not be manifest.

A neuropsychological approach to personality aims to understand both the biological systems that are responsible for the states associated with any given trait and the parameters of those systems that cause them to differ across individuals. The systems themselves will be present in every intact human brain, but the values of their parameters will vary from person to person. Thus, for example, all people have brain systems that respond to punishing stimuli, but in different individuals these systems respond differently to a given stimulus. It is the typical level of response of such a system in any given individual, averaged across different situations, that is associated with that individual's score on the personality trait in question. This is *not* to imply that an individual will respond the same way in all situations; rather, it implies that knowing the strength of the individual's trait predicts how he or she is likely to respond in a certain situation and, in particular, predicts variation in such responding across a set of individuals experiencing that same situation.

Many personality researchers have embraced this basic premise, and a number of personality models postulate pairs of traits reflecting sensitivity to reward and punishment (DeYoung & Gray, 2009; Elliot & Thrash, 2002; Gable, Reis, & Elliot, 2003; Zelenski & Larsen, 1999). However, a key point emphasized by Jeffrey Gray, which has not been well assimilated into this personality research, is that the approach and avoidance systems cannot be treated simply as two unitary and entirely independent entities (Corr, 2002, 2004). Before returning to the question of what personality traits are associated with sensitivity to reward and punishment, we must have a more thorough understanding of these systems.

Approach and Avoidance Systems

Multiple motivational systems control both approach and avoidance behavior. Based on his own research and that of the rest of the field, Gray identified two primary systems that control active approach and active avoidance behavior: The *behavioral approach system*

(BAS) and the *fight-flight-freeze system* (FFFS). He also, uniquely, proposed that passive avoidance behavior was controlled by the *behavioral inhibition system* (BIS) (Gray, 1982; Gray & McNaughton, 2000). The FFFS is activated by aversive stimuli, and the BIS by stimuli that indicate conflict between goals (including a specific conflict between goals with the same general motivational tendency, e.g., whether to take flight or freeze to avoid a punishing stimulus). Gray elaborated only a single system, the BAS, that controls approach, which is activated by stimuli indicating the possibility of attaining reward, but he acknowledged the existence of other reward systems dedicated to consummatory behavior. Berridge (2007, 2012) has described the two major reward systems as incentive ('wanting') and hedonic ('liking') systems. The incentive reward system is equivalent to the BAS and produces motivation to approach reward, but the hedonic reward system is responsible for the enjoyment experienced following the attainment of reward (which is, in turn, likely to produce greater motivation to approach that reward subsequently) – this is the Pleasure System (PS). The FFFS, BIS, and BAS (see Figure 1) are described in detail by Gray and McNaughton (2000) and summarized by McNaughton and Corr (2004, 2008), but the PS has been less well elaborated.

Avoidance

In personality psychology in general, and clinical psychology and psychiatry in particular, the effects of BIS and FFFS have often been conflated, leading to conceptual confusion. The action of the FFFS is evident primarily when avoidance is the only motivation—that is, when one wants nothing other than to escape the present situation. It produces active avoidance and, depending on the intensity of the perceived threat, accompanying states

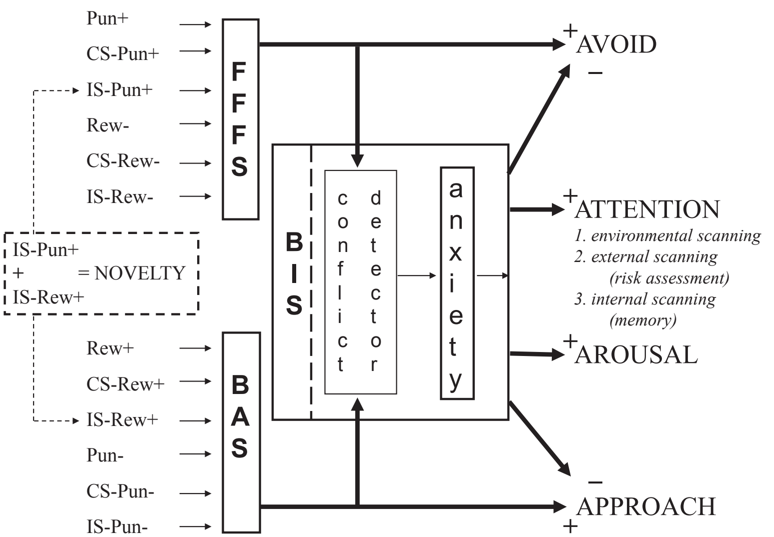

Figure 1 Relations between stimuli, the Fight-Flight-Freeze System (FFFS), the Behavioural Approach System (BAS), and the Behavioral Inhibition System (BIS). Inputs consist of rewards (Rew) or punishers (Pun) that may be presented (+) or omitted when expected (–) and of innate stimuli (IS) or conditioned stimuli (CS) that predict these events. The most common cause of BIS activation is approach-avoidance conflict (when the same stimulus activates both FFFS and BAS). However, approach-approach conflict and avoidance avoidance-conflict (as in two-way avoidance) will also activate the BIS. Figure from Gray and McNaughton (2000), and legend adapted from McNaughton and Corr (2004).

such as fear and panic. The action of the BIS is evident when there is a conflict between two general motivations or specific goals, most often seen in the form of an approach-avoidance conflict (such as desiring to talk to someone but fearing rejection). Avoidance-avoidance and approach-approach conflicts also activate the BIS, but they are less common. The BIS produces passive avoidance and risk assessment and contributes to processes that produce the state of anxiety. (To understand how an approach-approach conflict can be anxiety provoking, imagine receiving two job offers, both seeming equally good; deciding between them could be nerve-wracking – the aversive component resides in the potential of making the wrong decision and incurring a relative loss – the concept of loss aversion in economics parallels this effect; see Corr & McNaughton, 2012). Active and passive avoidance can be dissociated pharmacologically as well as behaviorally (Gray & McNaughton, 2000; Perkins et al., 2009). The BIS is generally sensitive to anxiolytic drugs, whereas the FFFS is *relatively* insensitive to anxiolytic drugs, but sensitive to panicolytic ones (for an overview, see McNaughton & Corr, 2008).

The difference between FFFS (fear) and BIS (anxiety) has been characterized by the concept of 'defensive direction': Fear operates when leaving a dangerous situation (active avoidance; 'get me out of here'), and anxiety when entering it (e.g., cautious, risk-assessment during approach behavior; 'watch out for danger') or withholding entrance entirely (complete passive avoidance; behavior inhibited to avoid encountering threat) (McNaughton & Corr, 2004). In addition, 'defensive distance' controls the type of defensive behavior observed: Different behaviors are elicited by aversive stimuli at different perceived defensive distances (Blanchard & Blanchard, 1990). In the case of defensive avoidance, the smallest distances result in explosive attack; slightly larger but still small distances result in freezing and panicked flight; and intermediate distances typically result in BIS activation and passive avoidance, as they indicate the potential for the threat to conflict with approach goals. Finally, large distances result in entirely non-defensive behavior. Defensive distance maps to different levels of the FFFS and the BIS (see Figure 2, and McNaughton & Corr, 2004, for more detail) and, therefore, determines which avoidance behavior is elicited. Physical examples of defensive distance include, in the rodent literature, distance of mouse from cat; and in the human case, distance or time from the dentist for an unpleasant procedure. In subjective terms, in humans, some threats may loom large for some people, but be relatively minor for others (e.g., sitting an important examination).

These different types of avoidance can be functionally in opposition to each other: Freezing, fighting (specifically defensive), and fleeing involve attempting to escape a threat, whereas, in contrast, behavioral inhibition can allow cautious approach to a threat. Because the active avoidance associated with the FFFS may not be adaptive in a context where conflicting goals are present (e.g., panicking too soon might draw the attention of a predator or prevent acquisition of reward), the BIS inhibits the behavioral output of the FFFS, particularly panic (see also Graeff & Del-Ben, 2008). At the same time, however, activation of the BIS increases non-specific arousal to allow a rapid switch to escape behavior if the threat becomes too great, and it also increases vigilance to scan for additional threatening information (Gray & McNaughton, 2000).

One potential point of confusion that should be clarified is that the phrase 'behavioral inhibition' might intuitively be interpreted to mean any constraint or reduction of behavior. However, not all forms of behavioral inhibition in this broad sense are dependent on the BIS, which inhibits only those actions that are specific to the conflicting goals. For example, the involuntary freezing associated with truly immediate danger is produced by the FFFS, not the BIS. Another important form of inhibition is produced by top-down

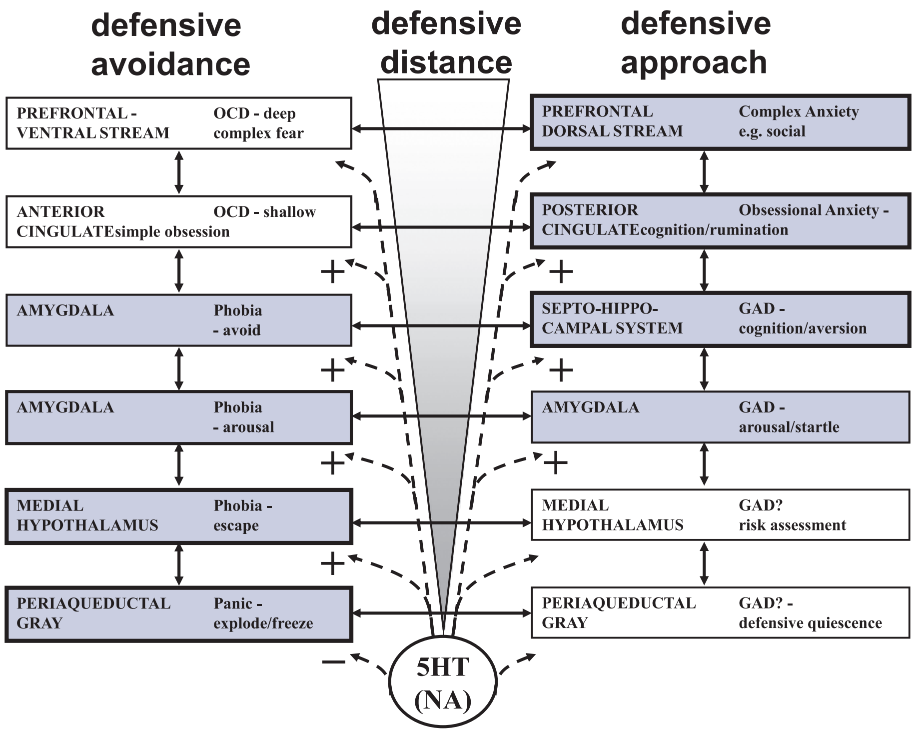

Figure 2 The two dimensional defense system. On either side are defensive avoidance (FFFS) and defensive approach (BIS), which constitute the categorical dimension of defensive direction. Each side is divided vertically into hierarchical levels, which are ordered from high to low (top to bottom) with respect both to neural level and to functional level, in the sense of the immediacy with which a response is required. Under typical ecological circumstances, the probability of engagement of the defensive avoidance system is higher at shorter defensive distances and the probability of engagement of the defensive approach system is greater at longer defensive distances, as indicated by the shading of the boxes. Each level is associated with specific classes of behavior and associated syndromes and symptoms. OCD = Obsessive Compulsive Disorder; GAD = Generalized Anxiety Disorder. Syndromes are associated with hyper-reactivity of a structure and symptoms with high activity. Given the interconnections within the system (and effects of, e.g., conditioning symptoms) will not be a good guide to syndromes. Both systems are modulated by the monoamines serotonin (5HT) and noradrenaline (NA). Figure and legend adapted from McNaughton and Corr (2004).

constraint of basic motivational systems by cortical control systems. This non-affective constraint (Depue & Lenzenweger, 2005) involves voluntary inhibition of behavioral impulses; it is not controlled by the BIS, nor is it necessarily accompanied by anxiety. Inhibition controlled by the BIS is specifically inhibition of ongoing behavior by the involuntary systems involved in the detection of conflict.

Approach

The primary function of the BAS is to move the animal up the temporo-spatial gradient (i.e., time and space axes) from its current state towards its goal state. The BAS is activated by stimuli that signal the possibility of achieving a reward, and it generates approach behavior along with the accompanying states of desire, eagerness, excitement, and hope. In contrast, the PS is less well studied than the BAS, but the two can be dissociated, for example through pharmacological manipulations involving dopamine and opiates (Berridge, 2007, 2012; Depue & Morrone-Strupinsky, 2005). The PS responds to the acquisition of reward and produces accompanying states of enjoyment, cheerfulness, and satisfaction. Activation of the PS aids in forming a representation of the reward stimulus in memory, which renders that stimulus more likely to trigger the BAS in future. Immediately following acquisition of reward, activation of PS may also be involved in shifting priorities, such that pursuit of the goal that led to PS activation is deprioritized in favor of some other goal which is farther from accomplishment (Carver, 2003).

Behavioral approach system-driven movement along the temporo-spatial goal gradient is complex and requires some form of 'sub-goal scaffolding' (Corr, 2008). The broader the goal in question, the more important is this hierarchical process, in which goals are accomplished only by pursuing a series of sub-goals (Carver & Scheier, 1998). At each stage of the temporo-spatial gradient, this process consists of (a) identifying the appropriate current goal, (b) planning behavior, and (c) executing the plan. Thus, approach behavior entails a series of sub-processes, some of which can come into conflict with each other. For example, planning is often required to achieve goals but can be disrupted by the detection of a compelling immediate goal—'…unfettered impulse can interfere with the attainment of longer term goals' (Carver, 2005, p. 312). However, at the final point of capture of the reward, fast, impulsive action may be more appropriate than planning; overcontrol of BAS-driven impulses can lead to lost opportunities (Block, 2002; DeYoung, 2010a). The systems that carry out planning are not themselves part of the BAS (or of the BIS); however, as we will discuss below, they can be driven by the BAS. Throughout the process of approach behavior, whether a distant immediate goal is pursued, it is the BAS that energizes behavior and provides the motivation to approach the goal.

Personality and Approach/Avoidance Systems

One view of personality traits is that evolutionary pressure has produced variation between individuals in the motivation systems responsible for approach and avoidance, leading to the outcome that people differ consistently in their immediate reactions to the different classes of motivational stimuli (Nettle, 2006; Penke, Denissen, & Miller, 2007). This view posits that long-term stabilities in reactions to classes of reinforcing stimuli lead to personality. Variation in these motivational reactions at the population-level has been linked to a wide range of normal and abnormal behaviors, but where should we look for motivation-related personality traits?

Two main approaches have been pursued to identify important personality traits. One, exemplified by RST, is theoretically driven and proceeds from what is known about motivational systems, attempting to deduce what traits will correspond to variation in the functioning of these systems. The other is empirically driven and looks for broad, consistent dimensions of covariation in assessments of many specific traits, only afterward attempting to identify the sources of these resulting broad trait dimensions. The latter approach is responsible for producing the Big Five model. Fortunately, with increasing interest in personality neuroscience, these two approaches are beginning to converge.

Two of the Big Five traits, Extraversion and Neuroticism, appear to reflect the primary manifestations in personality of sensitivity to reward and punishment, respectively. Evidence for this mapping has been provided in questionnaire research, in which scales measuring Extraversion are excellent indicators of a latent variable also marked by measures of positive affect and reward sensitivity, and scales measuring Neuroticism are excellent indicators of a latent variable also marked by measures of negative affect and punishment sensitivity (Clark & Watson, 2008; Elliot & Thrash, 2002, 2010; Gable et al., 2003;

Zelenski & Larsen, 1999). More recently, evidence has been accumulating that the brain systems responsible for approach/reward and avoidance/punishment are the primary neural correlates of Extraversion and Neuroticism, respectively (DeYoung, 2010c; DeYoung & Gray, 2009).

Although the links between approach/avoidance and Extraversion/Neuroticism are well established, much less research has addressed the question of differentiating among BIS, FFFS, BAS, and PS in terms of their links to personality trait questionnaires. Too little is known at this time to permit a definite mapping, but in what follows we present some recent observations that highlight the viability of a more differentiated linking of personality traits to basic motivation systems.

Avoidance Traits

Psychologists often treat rewards and punishments as objective external items. But, from the individual's perspective, they are subjective cognitive/emotional constructs. Some people will find a particular object more or less rewarding or punishing than other people. This outcome is often a result of personality and its effects on, for example, defensive distance (McNaughton & Corr, 2004) which, as we have seen above, relates to the immediacy of a threat. Thus, for one individual in a particular situation, perceived defensive distance can reflect real distance. With a greater threat, however, perceived defensive distance is shortened and so each specific behavior (e.g., freezing or avoidance) will occur at a longer objective distance. For this reason, relatively weak aversive stimuli are sufficient to trigger a strong reaction in a highly punishment-sensitive person, but, for a less sensitive person, aversive stimuli would need to be much closer to elicit a comparable reaction.

This consideration of defensive distance suggests a general tendency toward punishment sensitivity, and indeed personality theorists have often thought simply in terms of general tendencies related to reward and punishment. In the Big Five model, all traits that reflect sensitivity to punishment fall within the Neuroticism factor (DeYoung, 2010b,c; Gable et al., 2003; Markon et al., 2005). In terms of defensive distance, Neuroticism would, therefore, be associated with exaggeration of the closeness of threat.

A variety of evidence, however, suggests that personality traits associated with FFFS and BIS sensitivity may be differentiable. Measures of fear and anxiety have been distinguished through confirmatory factor analysis (CFA; Cooper, Perkins, & Corr, 2007), predictive validity studies involving selection in military training (Perkins, Kemp, & Corr, 2007), and associated facial expressions (Perkins, Inchley-Mort, Pickering, Corr, & Burgess, 2012). Other researchers have used existing scales to attempt to distinguish between fear and anxiety. In the Multidimensional Personality Questionnaire (Tellegen & Waller, 2008), for example, Depue has hypothesized that Stress Reactivity is a measure of anxiety, whereas Harm Avoidance is a measure of fear (Depue & Lenzenweger, 2005).

One of the most widely used measures in research on RST is Carver and White's (1994) BIS/BAS scales. Although this BIS scale was developed with only one avoidance system in mind, as predicted by Corr and McNaughton (2008), recent studies have used CFA to argue that this scale can be divided into separate FFFS (fear) and BIS (anxiety) components (Beck, Smits, Claes, Vandereychen, & Bijttebier, 2009; Heym, Ferguson, & Lawrence, 2008; Johnson, Turner, & Iwata, 2004; Poythress et al., 2008). However, a problem with this research is that the putative FFFS-fear subscale has only two or three items, which include the only reverse-keyed items in the scale. Their separation from the other items may, therefore, be merely a measurement artifact unrelated to substantive content. Distinguishing fear from anxiety is difficult in questionnaire measurement because, colloquially, people use these two terms interchangeably; thus, merely asking people about their fearfulness may elicit assessments of what should technically be considered anxiety (DeYoung, 2010b).

In order to address the measurement problem for BIS and FFFS sensitivity, Corr and Cooper (forthcoming) developed psychometrically separable measures of FFFS-fear and BIS-anxiety based upon a theoretical analysis of the components of the two defensive avoidance systems; that is, these were developed 'ground-up' and were not based on the modification of existing scales. The FFFS scale includes content related to flight (e.g., 'I would run fast if I knew someone was following me late at night'), freezing (e.g., 'I am the sort of person who easily freezes-up when scared'), and avoidance (e.g., 'There are some things that I simply cannot go near'), but the attempt to include items describing panic ('e.g.… 'My heart starts to pump strongly when I am getting upset) and defensive aggression (e.g., 'If I feel threatened I will fight back') in the FFFS scale proved problematic. Low base rates of panic and defensive aggression may be part of the problem here. If items describe behaviors that are manifested infrequently in normal adult human life, they may not show adequate variance to determine their association with other traits. Another source of the problem may be substantive rather than artifactual; as illustrated in Figure 2, serotonin inhibits the lowest level of FFFS response, which includes panic and defensive aggression, even while it potentiates the higher levels. This may prevent typical patterns of panic and defensive aggression from varying systematically with other manifestations of fear.

Finally, another potential source of the problem is simply uncertainty regarding how FFFS sensitivity manifests in typical patterns of human behavior. The manifestation of the 'fight' component is particularly uncertain, due, in part, to the existence of two major categories of aggression (Poulin & Boivin, 2000). Reactive or defensive aggression is aimed at eliminating a threat. Proactive or offensive aggression is aimed at acquiring resources or dominance status. Only reactive aggression is hypothesized to be controlled by the FFFS. Supporting evidence includes the finding that reactive aggression is associated with cortisol reactivity, a key biological component of the FFFS, whereas proactive aggression is not (Lopez-Duran, Olson, Hajal, Felt, & Vazquez, 2009). Individual acts of aggression may be reactive or proactive or a blend of the two, and not all questionnaire items discriminate them adequately. Reactive (but not proactive) aggression is associated with anger-proneness in children (Hubbard et al., 2002). In adults, due to the development of greater top-down control of behavior, overt reactive aggression may be a less common result of FFFS activation than anger, and anger may not be expressed in a form extreme enough to be easily assessed by questionnaire items describing aggression.

The potential importance of anger and reactive aggression as indicators of FFFS sensitivity raises another complication, which is that anger and aggression are approach-oriented, even when they serve a defensive avoidance function (Carver & Harmon-Jones, 2009; Harmon-Jones, 2003). The target of aggression must be literally approached to be attacked, even when the attack serves a purely defensive purpose. We use the traditional labels 'approach' and 'avoidance' to describe the systems related to reward and punishment, respectively, but it might be more precise to label them 'appetitive' and 'defense' systems, given the fight component of the FFFS.

As we have seen, attempts to develop questionnaire measures specifically of BIS and FFFS sensitivity have come from the theoretical approach to trait identification. Coming from the empirical direction, DeYoung (2010b) suggested that two subfactors of Neuroticism may represent distinct influences of BIS and FFFS on personality. Factor analysis of 15 different facet scales for Neuroticism produced evidence for a two factor solution

(DeYoung, Quilty, & Peterson, 2007). Correlations with over 2000 items from the International Personality Item Pool were then used to characterize the factors and develop scales to measure them (the Big Five Aspect Scales; DeYoung et al., 2007). The first Neuroticism factor, labeled Withdrawal, encompasses anxiety, depression, vulnerability, and self-consciousness; the second factor, labeled Volatility, encompasses emotional lability, irritability, and anger-proneness.

Gray and McNaughton (2000) proposed that, although neurally separable (see Figure 2), the BIS and FFFS are jointly linked to Neuroticism. Sensitivities of BIS and FFFS are likely to covary due to their mutual modulation by monoamines and also because the two systems interact biologically, such that increased BIS arousal increases FFFS arousal, and a reactive FFFS may identify more threats that serve as inputs to the BIS in its detection of approach-avoidance conflicts. Thus, the two major subfactors within Neuroticism could reflect the sensitivities of these two avoidance systems (DeYoung, 2010b). Anxiety and depression both reflect passive avoidance, making the Withdrawal factor a likely candidate for BIS sensitivity. In humans, the irritability and anger associated with Volatility may be more common manifestations of the fight component of the FFFS than any form of overt defensive aggression. Volatility also encompasses content that might be related to the tendency to panic (e.g., 'Get upset easily,' 'Rarely lose my composure'), reinforcing the possibility of its association with FFFS.

The association of Volatility with FFFS sensitivity remains speculative and additional psychometric work is necessary. However, one experimental study has supported the hypothesis that Withdrawal and Volatility reflect BIS and FFFS sensitivity, respectively, by showing that these traits differentially predict amgydala activity (Cunningham, Arbuckle, Jahn, Mowrer, & Abduljalil, 2010). The amygdala is a brain region crucially involved in the detection of motivational salience and is involved in both the BIS and FFFS (see Figure 2 and Cunningham & Brosch, 2012; Gray & McNaughton, 2000). Using fMRI, Cunningham et al. (2010) found that Volatility was associated only with valence, predicting the degree to which the amygdala was more active when perceiving negative rather than positive stimuli; whereas, in contrast, variation in Withdrawal was associated only with direction, such that it predicted the degree to which the amygdala was active when approaching either positive or negative stimuli, relative to withdrawing from them. This pattern of findings is consistent with the idea that the FFFS (governing Volatility) responds to all punishing stimuli, whereas the BIS (governing Withdrawal) responds to conflict associated with concurrent approach tendencies.

One other line of empirical research on trait structure may be relevant to the distinction between FFFS and BIS. Clinical research on comorbidity has repeatedly demonstrated distinct risk factors for anxiety and mood disorders, on the one hand, and phobias and panic disorders, on the other, and these appear to have a distinct genetic basis (Krueger & Markon, 2006; Scherrer et al., 2000). These two risk factors, labeled 'Distress' and 'Fear', may reflect BIS and FFFS sensitivities, respectively. Importantly, although Distress and Fear are distinct, they are nonetheless strongly correlated, being subfactors of a more general 'Internalizing' factor that reflects shared risk for all disorders just mentioned. Psychometric research indicates that Internalizing may be statistically indistinguishable from Neuroticism (Griffith et al., 2010). Thus, research on avoidance-related psychopathology appears to be converging with research on normal personality structure. Nonetheless, there are clearly various candidates for the traits that best represent the manifestations of BIS and FFFS sensitivity in personality, and additional research is needed to synthesize and refine our understanding of them.

Approach Traits

Gray (1982) originally speculated that the trait associated with BAS sensitivity could be characterized as 'impulsivity' because impulsive people are more likely to be sensitive to cues of the immediate possibility of reward. Although BAS sensitivity does play a role in impulsivity (e.g., Buckholtz et al., 2010), researchers have since concluded that impulsivity is not the purest manifestation of BAS sensitivity in personality because it is determined not only by individual differences in the strength of impulses to pursue immediate reward, but also by individual differences in the ability of top-down control systems to restrain and control those impulses (Depue & Collins, 1999; DeYoung, 2010a). Indeed, Extraversion rather than impulsivity appears to represent the primary manifestation of BAS sensitivity in personality (Depue & Collins, 1999; Pickering, 2004; Quilty & Oakman, 2004; Smillie, Pickering, & Jackson, 2006).

Although Extraversion has a social connotation, reward sensitivity may nonetheless be its central quality (Depue & Collins, 1999; Lucas & Baird, 2004). Many human rewards are social in nature, involving affiliation or status, and much social behavior involves approach to potential rewards. Speech, for example, can be described as approach behavior—hence the talkativeness characteristic of Extraversion. Further, Extraversion is not merely a social trait, as it also reflects drive, activity level, and the tendency to experience positive emotions regardless of social context (Lucas & Baird, 2004; Lucas, Le, & Dyrenforth, 2008).

Breaking down reward sensitivity into sub-factors has not been as systematic as the approach to identifying traits associated with BIS and FFFS, largely because Gray elaborated only a single reward system. However, the most commonly used measure of BAS sensitivity has three sub-scales in an attempt to be reasonably comprehensive in measuring traits that appear relevant: Drive, Reward Responsivity, and Fun Seeking (Carver & White, 1994). Whereas Drive and Reward Responsivity both appear to characterize sensitivity to reward primarily, Fun Seeking appears to be equally related to impulsivity and thus may not be as pure an indicator of BAS sensitivity (Wacker, Mueller, Hennig, & Stemmler, 2012).

Corr and Cooper (forthcoming) found, in replicated samples, evidence for four subfactors related to the BAS: Reward Interest (e.g., 'I regularly try new activities just to see if I enjoy them') and Goal Drive Persistence (e.g., I am very persistent in achieving my goals'), which characterize the early incentive stages of approach, and Reward Reactivity (e.g., 'I often feel that I am on an emotional high') and Impulsivity (e.g., 'If I see something I want, I act straight away'), which characterize the behavioral and emotional excitement as the final goal is reached. Emotion in the former case may be termed 'anticipatory pleasure' (or 'hope'); in the latter case it appears something akin to an 'excitement attack' of intense pleasure or joy, possibly related to the pleasure system (PS) discussed above.

In terms of the Big Five model, DeYoung (2010c) has hypothesized that the two major subfactors within Extraversion may reflect the distinction between sensitivities of the BAS and the PS. Like Neuroticism, Extraversion has two separable but correlated subfactors, which emerge from factor analysis of many Extraversion facets (DeYoung et al., 2007). On the basis of item analysis, these subfactors were labeled Assertiveness and Enthusiasm. Assertiveness encompasses traits related to drive, leadership, and dominance and, therefore, appears to reflect 'wanting' and pursuit of reward associated with BAS sensitivity. Enthusiasm encompasses both outgoing friendliness or sociability and the tendency to experience and express positive emotion and, thus, may reflect the hedonic experience of 'liking' associated with PS sensitivity. In support of the latter hypothesis, pharmacological manipulation has demonstrated that opiate response to cues of affiliation is a function of Social Closeness, a trait measure that is an excellent marker of Extraversion and reflects Enthusiasm rather than Assertiveness (Depue & Morrone-Strupinsky, 2005; DeYoung, Weisberg, Quilty, & Peterson, 2012; Markon et al., 2005). The endogenous opiate systems are involved in the positive emotions that follow attainment or consumption of reward and are important in social affiliation, making them likely candidates as part of the biological substrate of Extraversion (Berridge, 2007, 2012; Depue & Morrone-Strupinsky, 2005).

Motivation in Other Big Five Traits

One of the advantages of the Big Five model as an organizing system for personality traits is its relative comprehensiveness. Factor analysis of any sufficiently large and diverse set of trait measurements is likely to yield factors very similar to this model (Markon et al., 2005). As reviewed above, however, traits primarily related to reward and punishment sensitivity are subsumed within just two of the Big Five, namely Extraversion and Neuroticism. Given the importance of motivation for personality, this raises the question of the role of motivation in the other three Big Five traits: Conscientiousness, Agreeableness, and Openness/Intellect. Although less is known about the biological basis of these traits, what is known supports the theory that motivation is of central importance to all traits (Denissen & Penke, 2008; DeYoung, 2010c; Wilt & Revelle, 2009). We, therefore, briefly review the motivational functions associated with the other three traits of the Big Five.

Openness/Intellect

Individual differences in Openness/Intellect reflect a tendency toward cognitive exploration—that is, the tendency to seek, detect, appreciate, understand, and utilize both sensory and abstract information (DeYoung, Grazioplene, & Peterson, 2012). The compound label for this trait reflects an old debate about whether it should be labeled 'Openness to Experience' or 'Intellect', and the resolution to this debate has been that each label describes a distinct but related subfactor within the larger trait: Openness reflects engagement with sensory and perceptual information, and Intellect reflects engagement with abstract and semantic information (DeYoung, Grazioplene, et al., 2012; DeYoung et al., 2011). Importantly for the discussion of motivation, curiosity about information is at the core of Openness/Intellect; thus, the trait reflects the degree to which people find information rewarding.

An fMRI study showed that learning the answers to trivia questions about which one is curious activates the brain's reward system in much the same manner as receiving monetary, gustatory, or social rewards (Kang et al., 2009). Perhaps not surprisingly, therefore, Openness/Intellect shows a regular correlation with Extraversion, and the shared variance of the two traits constitutes a higher-order factor related to exploration and engagement in an array of approach-oriented behaviors (DeYoung, 2006; Hirsh, DeYoung, & Peterson, 2009). Whereas Openness/Intellect reflects cognitive exploration and sensitivity to the reward value of information, Extraversion reflects behavioral rather than cognitive exploration, driven by sensitivity to more tangible rewards. Both behavioral and genetic evidence suggest that Openness/Intellect is related to the dopaminergic system that is central to the BAS (DeYoung et al., 2011).

Conscientiousness

Conscientiousness, reflecting the tendency to be organized, reliable, self-disciplined, hard working, and orderly, has perhaps the most complex relation to motivation of any of the Big Five factors. Evidence suggests that Conscientiousness reflects individual differences in the top-down control systems that govern effortful control of impulses and avoidance of distraction, thereby allowing people to pursue non-immediate goals and to follow rules (DeYoung, 2010a,c). In other personality models, this trait has been described as Constraint or Effortful-Control (Clark & Watson, 2008; Evans & Rothbart, 2007). Rather than being primarily a reflection of basic motivational systems, Conscientiousness appears to reflect variation in the cortical systems that regulate motivation.

Nonetheless, although Conscientiousness involves channeling motivation toward non-immediate goals or abstract rules, the question remains: What motivates conscientious behavior itself. The possible answers provided in what follows are speculative, and we hope that they will lead to additional research. The tendency toward work and order might be motivated by a desire either to avoid punishment or to approach reward. Thus, one could expect Conscientiousness to relate in a complex manner to traits that reflect basic manifestations in approach and reward sensitivity. Not surprisingly, motivation towards achievement and success is correlated positively with Conscientiousness (Markon et al., 2005; Roberts, Chernyshenko, Stark, & Goldberg, 2005), as is the Assertiveness aspect of Extraversion that seems most likely to reflect BAS sensitivity (DeYoung et al., 2007). However, some forms of impulsivity (e.g., pursuing immediate reward without deliberation), which is a good marker of low Conscientiousness, are related positively to Extraversion and BAS (Depue & Collins, 1999; DeYoung, 2010a). This implies that reward sensitivity can drive both conscientious and impulsive behavior, despite the fact that the latter pair of traits are directly opposed. Conscientiousness, therefore, consistent with its control function, appears to reflect individual differences in the way reward motivation is channeled rather than BAS sensitivity per se.

The situation with punishment sensitivity is possibly even more complicated. The negative correlation between Conscientiousness and Neuroticism is one of the most robust correlations among the Big Five traits (Mount, Barrick, Scullen, & Rounds, 2005), which would suggest that Conscientiousness is related to low levels of avoidance. However, when Conscientiousness and Neuroticism are considered as behavioral states within individuals over time, they are positively associated (Beckman, Wood, & Minbashian, 2010)—that is, when people are behaving conscientiously they also experience more anxiety, consistent with the hypothesis that desire to avoid punishment is an important motivational component of Conscientiousness. The negative correlation between Conscientiousness and Neuroticism at the trait level may reflect the fact that successful conscientious behavior should allow people to avoid experiencing punishment, even though, while engaging in the necessary goal-directed work to do so, they are likely to experience anxiety over the possibility of punishment. These associations highlight the need to separate within-individual variance (related to dynamic processes) from between-individuals variance (related to population-level traits).

Agreeableness

The final Big Five trait we consider is Agreeableness, which represents the general tendency toward altruism, cooperation, and empathy, as opposed to aggression, callousness, and exploitation of others. Like Conscientiousness, Agreeableness is related to constraint of impulses, especially those that impinge on other people (Clark & Watson, 2008). Agreeableness has been found to predict suppression of aggressive impulses and other socially disruptive emotions (Meier, Robinson, & Wilkowski, 2006), and an fMRI study found that Agreeableness predicted activity in the left dorsolateral prefrontal cortex which is associated with emotion regulation (Haas, Omura, Constable, & Canli, 2007). Additionally, some evidence exists that brain systems involved in empathy (i.e., understanding the emotional and cognitive states of others) are involved in Agreeableness (DeYoung, 2010c). The core of Agreeableness might be described as a general motivation toward altruism. However, the nature of the underlying systems that produce this motivation are not entirely clear. Like Conscientiousness, Agreeableness may be motivated both by reward (the gratification of helping others) and by punishment (discomfort at hurting or thwarting others or anxiety about others' well-being). In future work, this trait deserves closer attention in terms of its underlying motivational features.

Conclusions

Motivation has its origins in basic systems of approach and avoidance that have been shaped by natural selection to further the pursuit of organisms' goals. Neuropsychological research points to a distinction between at least two systems of avoidance and defence (FFFS and BIS) and at least two of approach and response to reward (BAS and PS). Stabilities in the functioning of these state systems appear to be associated with persistent differences in personality traits. Future research on motivation and personality should take all of these multiple systems and their interactions into account rather than simply treating reward and punishment sensitivity as unitary entities.

An important goal for personality psychology is integrating theory-driven research on traits associated with neuropsychological systems with empirically-driven research on the structure of personality traits. Our discussion shows, in very broad outline, how this goal may be pursued. However, the neuroscience of personality has a long way to go before this integration can be fully realised. Basic motivational systems relating to reward and punishment seem well poised to provide the mechanistic basis for Extraversion and Neuroticism and their subtraits, and they may also play important roles in Conscientiousness, Agreeableness, and Openness/Intellect.

Short Biographies

Philip Corr's research focuses on individual differences in basic motivational and emotional processes, centred around the reinforcement sensitivity theory (RST) of personality. He has published three books on biological and personality psychology, and has authored numerous papers, using a wide variety of techniques, in such journals as *Journal of Personality and Social Psychology*, *Neuroscience and Biobehavioral Reviews*, and *Molecular Psychiatry*. Philip's work emphasizes the need for a unified psychology that recognises the importance of both experimental and differential approaches to understanding the structure and causation of human behaviour. Philip holds editorial posts with several journals, is a Co-Founding President of the *British Society for the Psychology of Individual Differences* (BSPID), and an elected board member of the *Society for the Study of Individual Differences* (ISSID), from where, in 2001, he won the Early Career Development Award. Philip received his BSc and PhD from the University of London and has taught previously at the Institute of Psychiatry and Goldsmiths (both University of London) and Swansea University, and is now in the School of Psychology at the University of East Anglia.

Colin DeYoung is Associate Professor in Psychology at the University of Minnesota, in the Personality, Individual Differences, and Behavior Genetics area. He received his BA from Harvard University, completed his doctorate at the University of Toronto, and worked as a postdoctoral fellow at Yale University before moving to Minnesota. In 2007, he won the J.S. Tanaka Dissertation Award for methodological and substantive contributions to the field of personality psychology, and in 2012 he won the SAGE Young Scholar Award from the Foundation for Personality and Social Psychology. His research focuses on the structure and sources of personality, combining psychometrics with the use of neuroscience methods to investigate the biological substrates of personality traits.

Neil McNaughton's research combines a range of biological manipulations with electrophysiological, behavioural and cognitive measures in animals and humans with the primary goal of understanding the relationship between the hippocampus, and particularly its theta rhythm, and the control of memory and anxiety. He has authored papers in a wide range of journals, including *Nature Neuroscience*, *Journal of Neuroscience*, and *Neuropharmacology*. He has also published two books: *Biology and Emotion* (Cambridge, 1989); and, with Jeffrey Gray, *The Neuropsychology of Anxiety: An Enquiry into the Functions of the Septo-hippocampal System* (2ed., Oxford, 2000), which provides a detailed account of brain structures involved in fear, anxiety and their disorders and their links with personality and the control of memory. He is on the editorial advisory board of *Neuroscience and Biobehavioral Reviews*. He holds an MA in Psychology and Philosophy from Oxford University and a PhD in Physiological Psychology from the University of Southampton. He held research positions at the University of Oxford and, as a Royal Society Commonwealth Bursar, at the University of British Columbia before coming to the University of Otago where he has taught for the last 30 years.

Endnote

* Correspondence address: EDU Building - 0.07, School of Psychology, Norwich Research Park, University of East Anglia, Norwich NR4 7TJ, UK. Email: p.corr@uea.ac.uk

References

Beck, I., Smits, D. J. M., Claes, L., Vandereychen, W., & Bijttebier, P. (2009). Psychometric evaluation of the behavioural inhibition/behavioural activation system scales and the sensitivity to punishment and sensitivity to reward questionnaire in a sample of eating disordered patients. *Personality and Individual Differences*, **47**, 407–412.

Beckman, N., Wood, R. E., & Minbashian, A. (2010). It depends how you look at it: On the relationship between neuroticism and conscientiousness at the within- and the between-person levels of analysis. *Journal of Research in Personality*, **44**, 593–601.

Berridge, K. C. (2007). The debate over dopamine's role in reward: The case for incentive salience. *Psychopharmacology (Berl)*, **191**, 391–431.

Berridge, K. C. (2012). From prediction error to incentive salience: Mesolimbic computation of reward motivation. *European Journal of Neuroscience*, **35**, 1124–1143.

Blanchard, R. J., & Blanchard, D. C. (1990). Anti-predator defense as models of animal fear and anxiety. In P. F. Brain, S. Parmigiani, R. J. Blanchard & D. Mainardi (Eds.), *Fear and Defence* (pp. 89–108). Chur: Harwood Academic Press.

Block, J. (2002). *Personality as an Affect-Processing System: Toward an Integrative Theory*. Mahwah, New Jersey: Lawrence Erlbaum Associates.

Buckholtz, J. W., Treadway, M. T., Cowan, R. L., Woodward, N. D., Li, R., Ansari, M. S. et al. (2010). Dopaminergic network differences in human impulsivity. *Science*, **329**, 532.

Carver, C. S. (2003). Pleasure as a sign you can attend to something else: Placing positive feelings within a general model of affect. *Cognition & Emotion*, **17**, 241–261.

Carver, C. S. (2005). Impulse and constraint: Perspectives from personality psychology, convergence with theory in other areas, and potential for integration. *Personality and Social Psychology Review*, **9**, 312–333.

Carver, C. S., & Harmon-Jones, E. (2009). Anger is an approach-related affect: Evidence and implications. *Psychological Bulletin*, **135**, 183–204.

Carver, C. S., & White, T. L. (1994). Behavioral inhibition, behavioural activation, and affective responses to impending reward and punishment: The BIS/BAS Scales. *Journal of Personality and Social Psychology*, **67**, 319–333.

Carver, C., & Scheier, M. (1998). *On the Self-regulation of Behavior*. New York: Cambridge University Press.

Clark, L. A., & Watson, D. (2008). Temperament: An organizing paradigm for trait psychology. In O. P. John, R. W. Robins & L. A. Pervin (Eds.), *Handbook of Personality: Theory and Research* (pp. 265–286). New York: Guilford Press.

Cooper, A. J., Perkins, A., & Corr, P. J. (2007). A confirmatory factor analytic study of anxiety, fear and Behavioural Inhibition System measures. *Journal of Individual Differences*, **28**, 179–187.

Corr, P. J. (2002). J. A. Gray's reinforcement sensitivity theory: Tests of the *joint subsystems hypothesis* of anxiety and impulsivity. *Personality and Individual Differences*, **53**, 511–532.

Corr, P. J. (2004). Reinforcement sensitivity theory and personality. *Neuroscience and Biobehavioural Reviews*, **28**, 317–332.

Corr, P. J. (2008). Reinforcement sensitivity theory (RST): Introduction. In P. J. Corr (Ed.), *The Reinforcement Sensitivity Theory of Personality* (pp. 1–43). Cambridge: Cambridge University Press.

Corr, P. J. (forthcoming). Approach and avoidance behavior: Multiple systems and their interactions. *Emotion Review*.

Corr, P. J., & Cooper, A. (forthcoming). *The Reinforcement Sensitivity Theory of Personality Questionnaire (RST-PQ): Development and validation*.

Corr, P. J., & McNaughton, N. (2008). Reinforcement Sensitivity Theory and personality. In P. J. Corr (Ed.), *The Reinforcement Sensitivity Theory of Personality* (pp. 155–187). Cambridge: Cambridge University Press.

Corr, P. J., & McNaughton, N. (2012). Neuroscience and approach/avoidance personality traits: A two stage (valuation-motivation) approach. *Neuroscience and Biobehavioral Reviews*, **36**, 2339–2354.

Cunningham, W. A., Arbuckle, N. L., Jahn, A., Mowrer, S. M., & Abduljalil, A. M. (2010). Aspects of neuroticism and the amygdala: Chronic tuning from motivational styles. *Neuropsychologia*, **48**, 3399–3404.

Cunningham, W. A., & Brosch, T. (2012). Motivational salience: Amygdala tuning from traits, needs, values, and goals. *Current Directions in Psychological Science*, **21**, 54–59.

Denissen, J. J. A., & Penke, L. (2008). Motivational individual reaction norms underlying the Five-Factor model of personality: First steps towards a theory-based conceptual framework. *Journal of Research in Personality*, **42**, 1285–1302.

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.

Depue, R. A., & Lenzenweger, M. F. (2005). A neurobehavioral dimensional model of personality disturbance. In M. Lenzenweger & J. Clarkin (Eds.), *Theories of Personality Disorders* (2nd edition) (pp. 391–454). New York: Guilford Press.

Depue, R. A., & Morrone-Strupinsky, J. V. (2005). A neurobehavioral model of affiliative bonding: Implications for conceptualizing a human trait of affiliation. *Behavioral and Brain Sciences*, **28**, 313–350.

DeYoung, C. G. (2006). Higher-order factors of the Big Five in a multi-informant sample. *Journal of Personality and Social Psychology*, **91**, 1138–1151.

DeYoung, C. G. (2010a). Impulsivity as a personality trait. In K. D. Vohs & R. F. Baumeister (Eds.), *Handbook of Self-Regulation: Research, Theory, and Applications* (2nd edition, pp. 485–502). New York: Guilford Press.

DeYoung, C. G. (2010b). Mapping personality traits onto brain systems: BIS, BAS, FFFS, and beyond. *European Journal of Personality*, **24**, 404–407.

DeYoung, C. G. (2010c). Personality neuroscience and the biology of traits. *Social and Personality Psychology Compass*, **4**, 1165–1180.

DeYoung, C. G. (2010d). Toward a theory of the Big Five. *Psychological Inquiry*, **21**, 26–33.

DeYoung, C. G., Cicchetti, D., Rogosch, F. A., Gray, J. R., Eastman, M., & Grigorenko, E. L. (2011). Sources of cognitive exploration: Genetic variation in the prefrontal dopamine system predicts Openness/Intellect. *Journal of Research in Personality*, **45**, 364–371.

DeYoung, C. G., & Gray, J. R. (2009). Personality neuroscience: Explaining individual differences in affect, behavior, and cognition. In P. J. Corr & G. Matthews (Eds.), *The Cambridge Handbook of Personality Psychology* (pp. 323–346). New York: Cambridge University Press.

DeYoung, C. G., Grazioplene, R. G., & Peterson, J. B. (2012). From madness to genius: The Openness/Intellect trait domain as a paradoxical simplex. *Journal of Research in Personality*, **46**, 63–78.

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**, 880–896.

DeYoung, C. G., Weisberg, Y. J., Quilty, L. C., & Peterson, J. B. (2012). *Unifying the Aspects of the Big Five, the Interpersonal Circumplex, and Trait Affiliation. Journal of Personality*. Online publication before print. doi: 10.1111/jopy.12020.

Elliot, A. J., & Thrash, T. M. (2002). Approach-avoidance motivation in personality: Approach and avoidance temperaments and goals. *Journal of Personality and Social Psychology*, **82**, 804–818.

Elliot, A. J., & Thrash, T. M. (2010). Approach and avoidance temperament as basic dimensions of personality. *Journal of Personality*, **78**, 865–906.

Evans, D. E., & Rothbart, M. K. (2007). Development of a model for adult temperament. *Journal of Research in Personality*, **41**, 868–888.

Fleeson, W. (2001). Towards a structure- and process-integrated view of personality: Traits as density distributions of states. *Journal of Personality and Social Psychology*, **80**, 1011–1027.

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**, 1097–1114.

Gable, S. L., Reis, H. T., & Elliot, A. J. (2003). Evidence for bivariate systems: An empirical test of appetition and aversion across domains. *Journal of Research in Personality*, **37**, 349–372.

Graeff, F. G., & Del-Ben, C. M. (2008). Neurobiology of panic disorder: From animal models to brain neuroimaging. *Neuroscience and Biobehavioral Reviews*, **32**, 1326–1335.

Gray, J. A. (1970). The psychophysiological basis of introversion-extraversion. *Behavior Research and Therapy*, **8**, 249–266.

Gray, J. A. (1972a). The psychophysiological nature of introversion–extraversion: A modification of Eysenck's theory. In V. D. Nebylitsyn & J. A. Gray (Eds.), *The Biological Bases of Individual Behavior* (pp. 182–205). New York: Academic Press.

Gray, J. A. (1972b). Learning theory, the conceptual nervous system and personality. In V. D. Nebylitsyn & J. A. Gray (Eds.), *The Biological Bases of Individual Behavior* (pp. 372–399). New York: Academic Press.

Gray, J. A. (1975). *Elements of a Two-Process Theory of Learning*. London: Academic Press.

Gray, J. A. (1977). Drug effects on fear and frustration: Possible limbic site of action of minor tranquilizers. In L. L. Iversen, S. D. Iversen & S. H. Snyder (Eds.), *Handbook of Psychopharmacology, vol. 8, Drugs, Neurotransmitters and Behavior* (pp. 433–529). New York: Plenum Press.

Gray, J. A. (1982). *The Neuropsychology of Anxiety: An Enquiry into the Functions of the Septo-Hippocampal System*. Oxford, England: Oxford University Press.

Gray, J. A., & McNaughton, N. (2000). *The Neuropsychology of Anxiety: An Enquiry into the Functions of the Septo-Hippocampal System*. Oxford: Oxford University Press.

Griffith, J. W., Zinbarg, R. E., Craske, M. G., Mineka, S., Rose, R. D., Waters, A. M. et al. (2010). Neuroticism as a common dimension in the internalizing disorders. *Psychological Medicine*, **40**, 1125–1136.

Haas, B. W., Omura, K., Constable, T., & Canli, T. (2007). Is automatic emotion regulation associated with Agreeableness? A perspective using a social neuroscience approach. *Psychological Science*, **18**, 130–132.

Harmon-Jones, E. (2003). Anger and the behavioural approach system. *Personality and Individual Differences*, **35**, 995–1005.

Heym, N., Ferguson, E., & Lawrence, C. (2008). An evaluation of the relationship between Gray's revised RST and Eysenck's PEN: Distinguishing BIS and FFFS in Carver and White's BIS/BAS scales. *Personality and Individual Differences*, **45**, 709–715.

Hirsh, J. B., DeYoung, C. G., & Peterson, J. B. (2009). Metatraits of the Big Five differentially predict engagement and restraint of behavior. *Journal of Personality*, **77**, 1085–1102.

Hubbard, J. A., Smithmyer, C. M., Ramsden, S. R., Parker, E. H., Flanagan, K. D., Dearing, K. F. et al. (2002). Observational, physiological, and self–report measures of children's anger: Relations to reactive versus proactive aggression. *Child Development*, **73**, 1101–1118.

John, O. P., Naumann, L. P., & Soto, C. J. (2008). Paradigm shift to the integrative Big Five trait taxonomy: History: Measurement, and conceptual issue. In O. P. John, R. W. Robins & L. A. Pervin (Eds.), *Handbook of Personality: Theory and Research* (pp. 114–158). New York: Guilford Press.

Johnson, S. L., Turner, R. J., & Iwata, N. (2004). BIS/BAS levels and psychiatric disorder: An epidemiological study. *Journal of Psychopathology and Behavioral Assessment*, **25**, 25–36.

Kang, M. J., Hsu, M., Krajbich, I. M., Loewenstein, G., McClure, S. M., Wang, J. T. et al. (2009). The wick in the candle of learning: Epistemic curiosity activates reward circuitry and enhances memory. *Psychological Science*, **20**, 963–973.

Konorski, J. (1967). *Integrative Activity of the Brain*. Chicago. IL: University of Chicago Press.

Krueger, R. F., & Markon, K. E. (2006). Reinterpreting comorbidity: A model-based approach to understanding and classifying psychopathology. *Annual Review of Clinical Psychology*, **2**, 111–133.

Lopez-Duran, N. L., Olson, S. L., Hajal, N. J., Felt, B. T., & Vazquez, D. M. (2009). Hypothalamic pituitary adrenal axis functioning in reactive and proactive aggression in children. *Journal of Abnormal Child Psychology*, **37**, 169–182.

Lucas, R. E., & Baird, B. M. (2004). Extraversion and emotional reactivity. *Journal of Personality and Social Psychology*, **86**, 473–485.

Lucas, R. E., Le, K., & Dyrenforth, P. S. (2008). Explaining the extraversion/positive affect relation: Sociability cannot account for extraverts' greater happiness. *Journal of Personality*, **76**, 385–414.

Markon, K. E., Krueger, R. F., & Watson, D. (2005). Delineating the structure of normal and abnormal personality: An integrative hierarchical approach. *Journal of Personality and Social Psychology*, **88**, 139–157.

McNaughton, N. (1989). *Biology and Emotion*. Cambridge: Cambridge University Press.
McNaughton, N., & Corr, P. J. (2004). A two-dimensional neuropsychology of defense: Fear/anxiety and defensive distance. *Neuroscience and Biobehavioral Reviews*, **28**, 285–305.
McNaughton, N., & Corr, P. J. (2008). The neuropsychology of fear and anxiety: A foundation for Reinforcement Sensitivity Theory. In P. J. Corr (Ed.), *The Reinforcement Sensitivity Theory of Personality* (pp. 44–94). Cambridge: Cambridge University Press.
Meier, B. P., Robinson, M. D., & Wilkowski, B. M. (2006). Turning the other cheek: Agreeableness and the regulation of aggression-related primes. *Psychological Science*, **17**, 136–142.
Mount, M. K., Barrick, M. R., Scullen, S. M., & Rounds, J. (2005). Higher-order dimensions of the big five personality traits and the big six vocational interest types. *Personnel Psychology*, **58**, 447–478.
Mowrer, O. H. (1960). *Learning Theory and Behavior*. New York: Wiley.
Nettle, D. (2006). The evolution of personality variation in humans and other animals. *American Psychologist*, **61**, 622–631.
Penke, L., Denissen, J. J. A., & Miller, G. F. (2007). The evolutionary genetics of personality. *European Journal of Personality*, **21**, 549–587.
Perkins, A., Kemp, S. E., & Corr, P. J. (2007). Fear and anxiety as separable emotions: An investigation of the revised reinforcement sensitivity theory of personality. *Emotion*, **7**, 252–261.
Perkins, A. M, Ettinger, U., Davis, R., Foster, R., Williams, S. C. R., & Corr, P. J. (2009). Effects of lorazepam and citalopram on human defensive reactions: Ethopharmacological differentiation of fear and anxiety. *Journal of Neuroscience*, **29**, 12617–12624.
Perkins, A. M., Inchley-Mort, S. L., Pickering, A. D., Corr, P. J., & Burgess, A. P. (2012). A facial expression for anxiety. *Journal of Personality and Social Psychology*, **102**, 910–924.
Pickering, A. D. (2004). The neuropsychology of impulsive antisocial sensation seeking personality traits: From dopamine to hippocampal function? In R. M. Stelmack (Ed.), *On the Psychobiology of Personality: Essays in Honor of Marvin Zuckerman* (pp. 453–477). New York: Elsevier.
Pickering, A. D., & Gray, J. A. (1999). The neuroscience of personality. In L. Pervin & O. John (Eds.), *Handbook of Personality*. (2nd edition, pp. 277–299). New York: Guilford Press.
Poulin, F., & Boivin, M. (2000). Reactive and proactive aggression: Evidence of a two factor model. *Psychological Assessment*, **12**, 115–122.
Poythress, N. G., Skeem, J. L., Weir, J., Lilienfeld, S. O., Douglas, K. S., Edens, J. F. et al. (2008). Psychometric properties of Carver and White's (1994) BIS/BAS scales in a large sample of offenders. *Personality and Individual Differences*, **45**, 732–737.
Quilty, L. C., & Oakman, J. M. (2004). The assessment of behavioural activation - The relationship between impulsivity and behavioural activation. *Personality and Individual Differences*, **37**, 429–442.
Roberts, B. W., Chernyshenko, O. S., Stark, S., & Goldberg, L. R. (2005). The structure of Conscientiousness: An empirical investigation based on seven major personality questionnaires. *Personnel Psychology*, **58**, 103–139.
Scherrer, J. F., True, W. R., Xian, H., Lyons, M. J., Eisen, S. A., Goldberg, J. et al. (2000). Evidence for genetic influences common and specific to symptoms of generalized anxiety and panic. *Journal of Affective Disorders*, **57**, 25–35.
Schneirla, T. C. (1959). An evolutionary and developmental theory of biphasic processes underlying approach and withdrawal. In M. R. Jones (Ed.), *Nebraska Symposium on Motivation: Vol.* 7 (pp. 1–43). Lincoln, Nebraska: University of Nebraska Press.
Smillie, L. D., Pickering, A. D., & Jackson, C. J. (2006). The new Reinforcement Sensitivity Theory: Implications for personality measurement. *Personality & Social Psychology Review*, **10**, 320–335.
Tellegen, A., & Waller, N. G. (2008). Exploring personality through test construction: Development of the Multidimensional Personality Questionnaire. In G. J. Boyle, G. Matthews & D. H. Saklofske (Eds.), *The SAGE Handbook of Personality Theory and Assessment*. London, UK: Sage.
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**, 427–444.
Wilt, J., & Revelle, W. (2009). Extraversion. In M. Leary & R. Hoyle (Eds.) *Handbook of Individual Differences in Social Behavior* (pp. 27–45). New York: Guilford.
Zelenski, J. M., & Larsen, R. J. (1999). Susceptibility to affect: A comparison of three personality taxonomies. *Journal of Personality*, **67**, 761–791.

