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2. Psychobiological accounts of personality traits: On the shoulders of giants

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British psychologists such as Hans Eysenck and Jeffrey Gray have been giants in the field of individual differences, offering psychobiological accounts of major personality traits such as extraversion (E) and neuroticism (N), as well as the cluster of impulsive antisocial sensation seeking (ImpASS) personality facets, marked by Eysenck's psychoticism (P) scale. These theories have stimulated vibrant research programmes worldwide, including several within British psychology departments. This article provides a snapshot of classic and contemporary British research into the affective, behavioural and cognitive processes which characterise personality.

2.1. The personality theories of Eysenck and Gray

Individual differences research can justifiably claim to have played a central role in the history of British psychology, as the first article, by Matthews and Petrides, in this issue illustrates. Especially in Britain, the area of personality has been dominated by the contributions of two of the most prolific and well-cited psychologists in the world, Hans Eysenck and Jeffrey Gray. These giants in the field approached personality from distinct starting points but left a related legacy with their coherent and testable frameworks for understanding the biological bases of major personality dimensions (see Nyborg, 1997, and Corr, 2008, for perspectives on their work). In this article we take a look at contemporary British research that builds upon their legacy. We shall adopt Eysenck's tripartite division of personality (the 'giant three' model) as our launching point: extraversion (E), neuroticism (N) and psychoticism (P). We list the facets contributing to each of these dimensions in Box 1. It should be noted that this choice does not reflect some Anglocentric bias against the Big Five model (McCrae & Costa, 2003) that originated in the US. It simply reflects our view, and that of Eysenck (1992) and Gray, that there is much in common between the two frameworks. Specifically, high P scores equate to a combination of low conscientiousness and low agreeableness.

1.2. Extraversion (E)

In contrast to European and American traditions, the work of Eysenck and Gray was notable for providing a framework that went beyond mere description, towards an explanation of the causal bases of personality and individual differences. Eysenck (1967) proposed that E was related to differences in thresholds for arousal in the ascending reticular activating system. This led to testable predictions about the behaviour and cognition of introverts and extraverts under differing levels of arousal. These predictions have met with mixed experimental success (Matthews & Gilliland, 1999), but still provide a framework for current findings. For example, Smillie and Gökçen (2010) recently examined whether the effects of caffeine on

working memory performance, as assessed with the widely-used n-back task, differed between those who self-reported their E as high and those who reported it as low. They found that caffeine facilitated performance under high, but not low, working memory load conditions, and only for participants who were highly extraverted. This followed an earlier fMRI study, also using the n-back task, which found that higher scores on a self-report measure of E, but not N and P, were associated with increasing levels of activation in the dorsolateral prefrontal cortex and anterior cingulate as working memory load increased (Kumari, Ffytche, Williams & Gray, 2004). Findings such as these highlight both the role that E plays in modulating basic cognitive processes, and the general robustness of Eysenck's causal approach.

Gray developed a related framework (involving the Behavioural Approach System; Pickering & Gray, 1999), which suggests that variation in dopamine (DA) pathway functioning underpins a major dimension of personality. A widespread view is that this dimension may be E (e.g. Depue & Collins, 1999). Indeed, recent British work supports this idea. One of the roles DA plays in reward-mediated behaviour is signalling that a reward is better or worse than expected (via a reward prediction error; RPE). RPE has been shown to modulate an event-related potential (ERP) occurring 200-300 msecs after motivationally salient stimuli. A negative deflection in this time frame has been referred to as feedback-related negativity (FRN). Smillie, Cooper and Pickering (2011) found, using an associative learning task, that the FRN in response to an unpredicted reward and to an unexpected non-reward differed between high and low extraverts; specifically, the FRN was more negative after an unpredicted non-reward, and less negative following an unpredicted reward, for the high extraverts when compared with the low extraverts. An earlier study by the same group (Smillie, Cooper, Proitsi, Powell & Pickering, 2010) had also found that those with at least one copy of the A1 allele on the DRD2 gene (a gene influencing the functioning of DA receptors) had significantly higher self-reported E scores than those without a copy of this allele. These findings highlight the substantive and on-going role that Gray's work has played in our understanding of the biological bases of E.

2.3 Neuroticism (N)

Neuroticism, or low emotional stability, is one of the most robust personality factors seen in all virtually descriptive models of personality (Zuckerman, 2005). This is not surprising because, following Eysenck's lead, most personality models adopt the personality-psychopathology continuity model of mental illness. This assumption motivated Eysenck's (1944) factor analysis of a medical checklist given to neurotic military draftees during World War 2. The soldiers had not experienced the trauma of battle; instead, their 'breakdowns' were in response to being away from home and undergoing basic military training. In addition to a bipolar hysteria (extraversion) and dysthymia (introversion) factor, Eysenck discerned a second dimension that reflected the degree of disturbance, namely, N. For the rest of his life, Eysenck worked on statistically refining his measure of neuroticism, seeking to explain it in terms of neurophysiological processes, initially (1957) in terms of Pavlovian excitatory and inhibitory processes and later (1967) in terms of limbic activation. Eysenck's neurophysiological speculations were never entirely satisfactory, but at the very least stimulated work towards clarification.

It fell to Eysenck's student, Jeffrey Gray, to propose a more viable model of Neuroticism. Gray (1981) was able to point to fundamental flaws in Eysenck's theory; his alternative account today forms the highly influential reinforcement sensitivity theory (RST) of personality. In its original form, Gray (1970) proposed that a major dimension of personality (anxiety) reflected an individual's sensitivity to punishment. Gray argued that this dimension comprised approximately two parts N plus one part introversion. This original suggestion spawned a plethora of research, starting with a trickle of studies in the 1970s, leading to a flood in the 2000s (for a summary, see Corr, 2008).

The most recent version of RST (Corr & McNaughton, 2008) proposes that one's level of N reflects sensitivity to punishment and threat in general. However, within N, there are two traits/emotions, each of which maps on to one of the two major systems for defensive behaviour. *Fear* and *trait fearfulness* arise from the functioning of the *fight-flight-freeze system* (FFFS), which is responsible for mediating reactions to all aversive stimuli (e.g. punishment, nonreward and frustration), and is involved in active avoidance and escape behaviour. At the extreme end of the continuum, this system (and personality trait) maps onto clinical conditions such as phobia, panic, and OCD. *Anxiety* arises from variations in the sensitivity of the *behavioural inhibition system* (BIS), which is responsible for detecting and resolving goal conflict, especially between FFFS-related aversive motivation and approach-related appetitive motivation. The BIS is involved in cautious behaviours in potentially dangerous situations (i.e. passive avoidance) and, once activated, it generates risk assessment behaviour, rumination and increased arousal. These aspects, in their more extreme form, map onto anxiety disorders and explain many of their salient features (worry, rumination, anticipation of negative events).

Recent research supports Gray's model. For example, there is psychometric support for the separation of fear and anxiety, as revised RST demands (Cooper, Perkins & Corr, 2007). Perkins, Ettinger, Davis, Foster, Williams & Corr (2009) showed that an anti-anxiety drug (lorazepam), given to healthy volunteers, reduced a human behavioural analogue of rodent risk assessment behaviour, whereas a drug used to treat panic disorders (citalopram) had no effect on this behaviour. These results are in line with the revised RST as risk assessment is a product of the anxiety system (the BIS) specifically, rather than the fear system (the FFFS). In a subsequent study (Perkins, Ettinger, Williams, Reuter, Hennig & Corr, 2011), the same laboratory measure of flight intensity, in 200 healthy participants, was significantly correlated with a standard questionnaire measuring fear of tissue damage to one's body; and Spielberger's state anxiety measure was unrelated to flight intensity, as predicted by RST. DNA was taken from these participants and genotyped for a single nucleotide polymorphism (SNP) within the serotonin 2a receptor gene (HTR2A) on chromosome 13. This candidate gene was selected because the C allele in this SNP is known to be associated with increased susceptibility to pure (but not co-morbid) panic disorder (see Perkins et al., 2009). Carriers of the C allele (vs. non carriers) showed significantly higher levels of flight intensity. Once again, revised RST, which associates panic disorder with extreme sensitivity of the FFFS, is supported by these data.

2.4. Psychoticism (P)

First, we must deal with Eysenck's unfortunate choice of name for this scale, reflecting his belief that psychoticism reflected a disposition towards psychotic illness ("psychosis-proneness"; Eysenck, 1992). High scorers on the P scale, however, do not have a significantly elevated risk of schizophrenia (Chapman, Chapman & Kwapil, 1994) nor do schizophrenic

patients score highly on scales containing many P items (Cochrane, Petch & Pickering, 2010). We prefer, along with the likes of Zuckerman (1993), to view P as a marker of a cluster of traits we call Impulsive Antisocial Sensation Seeking (ImpASS; Pickering, 2004). The clinical analogue of those who score highly on the P scale is not schizophrenia/psychosis, but rather psychopathy (Corr, 2010) or, more broadly, cluster B personality disorders (i.e. antisocial, borderline, narcissistic). Gray also said relatively little about the P scale, although he did publish papers in which P was used as a marker of psychosis-proneness (e.g. Baruch, Hemsley & Gray, 1988). Perhaps because of the lack of a sound theoretical steer from Eysenck and Gray, there has been a relative dearth of work attempting to pin down the psychobiological features of healthy people with high ImpASS (high P) scores (especially in the cognitive domain).

However, Corr (2010) has recently reviewed the small body of work on P and cognition and concluded that the studies point to specific attentional control problems in those with high P scores, emphasizing their difficulties with tasks requiring attentional flexibility. Recent studies have extended this idea by showing that individuals with high P scores were inflexible in adjusting their focus of attention during an experiment investigating "task-switching" in which the instructions about which stimulus to attend to were suddenly changed (Tharp & Pickering, 2011). High P participants were, however, impaired only after one kind of attentional cue shift condition (called "perseveration"). After the switch in the perseveration condition, the previous attentional targets (e.g. green stimuli) had to be ignored while the new targets of attention (e.g. blue stimuli) were the focus of attention. High P participants were unimpaired by attentional switches in the so-called "learned irrelevance" condition: here, a previously ignored stimulus type (e.g. white stimuli) became the new attentional target after the switch, and the stimulus type (e.g. red stimuli) to be ignored was novel thereby removing any perseveration effects. The effect of P was dissociated from the effects of other variables in the study, including working memory (WM) capacity; those with high WM capacity were better able to cope with task switches in both switch conditions, relative to those with low WM capacity.

Problems with cognitive flexibility in high P individuals may extend outside the strictly attentional domain: Smillie, Cooper, Tharp and Pelling (2009) found that high P individuals were inflexible when learning from feedback during a category learning task in which the rules concerning which stimulus was the correct choice were changed without warning (e.g. from blue stimuli to stimuli on the left of the display, etc.). Once again, in this study, the effects of P were found to be statistically independent of WM; individuals with high WM capacity were better able to cope with category rule switches than individuals with low WM capacity. The category learning task used in the study was modelled closely on the Wisconsin card-sorting task (WCST), which has for many years been widely used in neuropsychological research and practice to measure perseverative (i.e. inflexible) tendencies in patients with frontal lobe damage. As the WCST shows activation of the dorsolateral prefrontal cortex in neuroimaging studies (see Cabeza & Nyberg, 2000), these findings may suggest that the cognitive inflexibility of high P individuals could derive from the operating characteristics of their prefrontal brain regions.

2.5. Summary

This brief overview shows that research into the psychobiological substrates of basic personality dimensions is currently flourishing in Britain and elsewhere. Moreover, the theoretical frameworks of the two giants who kick-started this area of inquiry are still

strongly shaping much of the research agenda, albeit that modern technologies (such as neuroimaging and DNA genotyping) are now being recruited to help with the quest.

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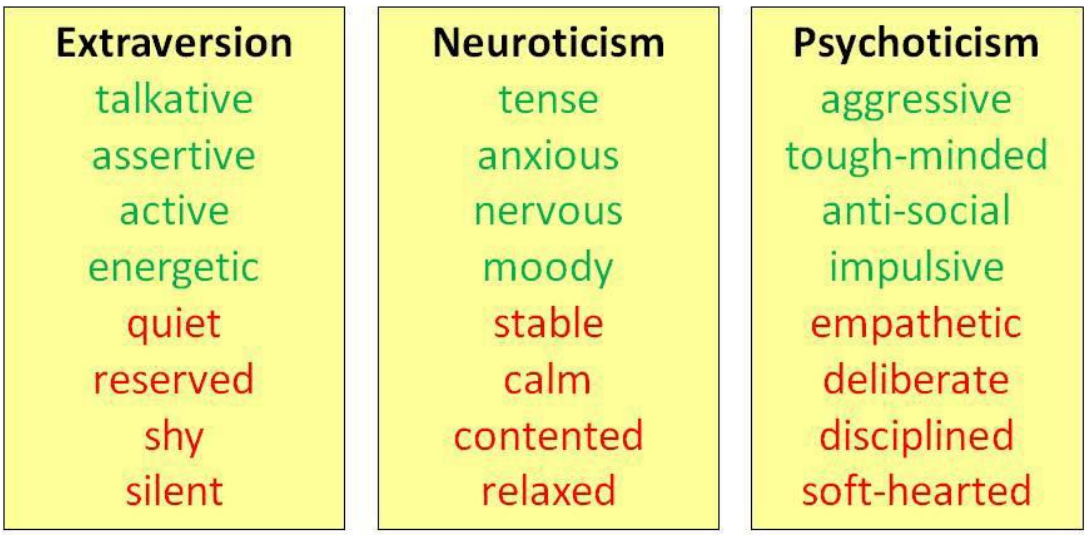
2.7. Figures



Box 1: A partial list of subtraits (or facets) of Eysenck's Giant Three personality dimensions. The facets listed in green are characteristics of the high pole of the dimension; those listed in red characterise the low pole.