PART I

Explanatory Models For Personality

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Psychophysiological and Biochemical Correlates of Personality

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> The degree of activation, as shown by the writer in various publications (Duffy, 1962), appears to affect both sensory sensitivity and motor response, and is involved in those consistencies of behavior that we call personality characteristics. (Duffy, 1966: 281)

INTRODUCTION

Considering that these quoted words were written by Elizabeth Duffy 40 years ago, the view expressed was prescient indeed. There is considerable evidence today, from psychophysical, psychophysiological and biochemical procedures (formerly considered measures of activation), establishing that the personality dimension of extraversion (E) is characterized by individual differences in sensitivity to simple physical stimulation and in the expression of motor responses. At the time when Duffy expressed her views, however, the association of personality with sensory sensitivity and motor processes was far from clear. In fact, in an assessment of the personality literature, Duffy (1962: 273) concluded that 'Any survey of physiological studies of personality must recognize the surprising fact that relatively few investigators have reported relationships of any magnitude between physiological measures and measures of behavior within the normal population.' Since that time, however, there was considerable progress in delineating reliable relations between personality traits and physiological processes. This progress was abetted by the development of rigorous personality typologies; by compelling, large-scale projects determining the heritability of personality traits; by refinement and development of physiological measurement procedures; and by exploiting new paradigms for probing psychological processes such as sensation, attention, learning and memory that are manifest in individual differences in personality. In this chapter, we mark this progress by assessing the current status of the psychophysiological and biochemical correlates of personality traits.

The nomenclatural framework for the present review consists of the three major personality dimensions of E, emotional stability–instability/neuroticism (N), and psychoticism (P)/impulsive sensation-seeking (ImpSS). These personality traits emerge as fundamental factors in most major personality typologies (e.g. Costa and McCrae, 1992; Eysenck and Eysenck, 1991; Zuckerman, 2002) and they capture the bulk of psychophysiological and biochemical research on individual differences in personality. An emphasis in this review is placed on electrocortical procedures (i.e. electroencephalography (EEG) and event-related potentials (ERPs)), and biochemical analyses (i.e. dopamine, serotonin, and cortisol), because these measurement procedures predominate in current research on personality. Conclusions drawn from earlier reviews of research on the biological bases of personality are briefly stated. An attempt is made to focus the functional significance of the biological procedures and paradigms on the social and behavioural expressions that characterize the personality dimensions, but the theoretical frameworks that inspired much of this research are left to other authors in this volume.

PSYCHOPHYSIOLOGICAL AND BIOCHEMICAL CORRELATES OF EXTRAVERSION

In previous reviews, it was concluded that there were fundamental differences between introverts and extraverts in their reaction to sensory stimulation and in their expression of motor activity (Matthews and Gilliland, 1999; Stelmack, 1997). There is compelling evidence from a range of measurement procedures indicating that introverts are more reactive or sensitive to simple sensory stimulation than are extraverts. Introverts display lower absolute auditory sensitivity (e.g. Stelmack and Campbell, 1974), lower pain thresholds (e.g. Barnes, 1975), lower noise thresholds (e.g. Dornic and Ekehammer, 1990), larger skin conductance responses to moderate intensity tones (e.g. Smith, 1983), and larger ERP amplitude to simple physical stimulation (e.g. Stelmack and Michaud-Achorn, 1985). Moreover, there was evidence from brainstem auditory evoked potentials indicating that these intensity effects are evident at the level of the auditory nerve (e.g. Stelmack and Wilson, 1982). These effects meld with the preference of introverts for quiet and solitude (Campbell and Hawley, 1982) and with their tendency toward withdrawal as a coping strategy in stressful social situations (Endler and Parker, 1990).

Introverts and extraverts differ in their expression of motor behaviour on a variety of tasks that require a simple motor response, with extraverts initiating faster and more frequent responses than introverts (e.g. Brebner and Flavell, 1978). These effects appear relevant to the disposition of extraverts to liveliness, activity, and talkativeness (Eysenck and Eysenck, 1975), involvement in athletic activities (Eysenck et al., 1982), restlessness in restricted environments (Gale, 1969), and preference for physical activity (Furnham, 1981). Moreover, there was evidence employing psychophysiological procedures that differences in motor activity between introverts and extraverts can be referred to peripheral nervous system processes (Stelmack and Pivik, 1996). There is good evidence that variation in dopaminergic activity (DA) is an important determinant of differences in E (e.g. Rammsayer et al., 1993). In general, more recent research on E and differences in sensory sensitivity and motor expression, using electrocortical and biochemical measurement procedures, endorse these findings.

Extraversion and the electroencephalograph

The electroencephalograph (EEG), recording electrical activity of the brain from small electrodes affixed to the scalp, was an important

method for assessing cortical activity of the brain in the early study of the ascending reticular activating system (ARAS; Lindsley, 1951) and in exploring the role of the ARAS in attention, memory and learning. The hypothesis that differences in E were determined by differences in cortical excitation and inhibition (Eysenck, 1957) and cortical arousal (Eysenck, 1967) fostered extensive analysis of E and the EEG. In early reviews (Gale, 1973; O'Gorman, 1977), support for the notion that introverts are characterized by higher levels of cortical arousal (indexed by lower EEG alpha wave activity) than extraverts was equivocal. These reviews did prompt improvements in design and recording techniques in subsequent research. Later reviews conceded that the direction of the results of these inquiries is towards higher levels of cortical activity for introverts (Matthews and Gilliland, 1999; Stelmack and Geen, 1992).

In more recent research, the ambiguous history of research on E using EEG recording is continued rather than clarified. The specific conditions under which reliable effects are replicated remain indeterminate. Tran et al. (2001) observed greater EEG activity in the 8–13 Hz (alpha) frequency range for extraverts than introverts but only at frontal electrode sites. This contrasts with other positive reports (e.g. O'Gorman and Lloyd, 1987) showing greater EEG activity at posterior electrode sites where alpha activity is maximal. In a project similar to Tran et al. (2001), higher E was associated with greater activity in low-frequency EEG bands (delta and theta) at temporal and parietal sites, and lower alpha activity at temporal and frontal sites (Knyazev et al., 2002). In another well-executed project, no EEG effects for E were observed (Schmidtke and Heller, 2004). Notably, the functional significance of the EEG effects in the studies cited here, when they are observed, is opaque. Typically, the EEG recordings were obtained while participants opened and closed their eyes. Without some experimental manipulation, few inferences of the functional significance of the EEG can be made. An exception here is the work by Knyazev et al. (2002), where participants performed mental arithmetic during the EEG recording in an attempt to manipulate arousal level. Even in this case, however, the behavioural effect of this manipulation was not measured.

There was considerable interest in the claim that activation of right anterior cortical areas is associated with the expression of negative affect, whereas activation of left anterior cortical areas is associated with the expression of positive affect (Davidson and Fox, 1982). Investigation of these effects was drawn into the personality domain by Hagemann et al. (1999) who exploited the association of E with positive affect and N with negative affect (Tellegen, 1985). Contrary to expectations, higher negative affect scores were associated with greater activation at left anterior temporal cortical areas. As Hagemann et al. (1999) note, this result is typical of the mixed outcomes that plague EEG research on emotion and mood. No differences in EEG activity between introverts and extraverts were observed.

The line of inquiry initiated by Hagemann et al. (1999) was pursued by Gale et al. (2001). During EEG recording, participants were asked to empathise and rate photographs expressing positive and negative affect. Negative valence photographs elicited greater activation at left frontal cortical sites, an effect that endorses the sensitivity of the EEG measures to the affect manipulation. Robust effects were reported with extraverts exhibiting greater alpha activity at frontal, temporal and occipital sites.

Gale et al. (2001) state that their data accord with the view that extraverts are characterized by lower levels of tonic arousal as proposed by Eysenck (1967). Alternatively, one could argue that introverts were more reactive to the photographic stimuli than extraverts, a view concordant with an extensive literature showing the greater sensitivity of introverts to sensory stimulation in general (Stelmack, 1990). The positive and negative valence photographs did not exercise

interactive effects on E; that is, one would suppose that the positive affect induction would favour the extraverts, resulting in greater frontal left hemisphere cortical areas. Overall, when EEG is recorded under resting conditions or with minimal or uncontrolled stimulation, the studies cited provide little consistent evidence associating E with greater alpha activation.

Extraversion and event-related potentials

Event-related potentials (ERPs) are records of the electrocortical activity in the brain that is evoked by physical stimuli and modulated by psychological processes such as attention, memory and cognition. ERPs are derived by averaging ongoing EEG activity that is time-locked to specific stimulus events. It is assumed that random EEG activity emanating from neural sites that are not engaged in the repeated presentation of the stimulus is cancelled out in the averaging. What remains is a signature of the neural activity that occurred during the processing of the stimulus. This signature is a result of the initial activation of peripheral nerves and nuclei in the brainstem and of the subsequent sequence of neural activity along cortical projection pathways.

Extraversion and sensory ERPs

Early research on E and ERPs examined waveforms that were elicited by simple sensory stimuli such as brief light flashes or simple tones. Initially, inconsistent effects were reported that yielded to replicable results as the conditions for favourable findings became apparent. In ERP waveforms to tones, larger amplitude for introverts than extraverts is observed with some consistency for ERP waves that develop 100–200 ms following stimulation, notably when stimuli are (1) moderately intense, (2) lower frequency, and (3) presented in mixed serial order (Bruneau et al., 1984; Stelmack and Michaud-Achorn, 1985). These effects, which account for about 10% of the variation in E, are congruent with the greater response to stimulation in introverts than in extraverts observed with psychophysical and autonomic system measures. Subsequently, there were few attempts to examine E and ERP using systematic changes in stimulus intensity or frequency. Occasionally, however, the enhanced response to auditory stimulation is observed incidentally (e.g. Doucet and Stelmack, 2000).

Extraversion and brainstem auditory evoked responses

A number of authors explored differences between introverts and extraverts by recording brainstem auditory evoked responses (BAER). BAER waveforms capture electrical activity along the auditory pathway that develops within the first 10 ms of acoustic stimulation. The neural generators of these waves, the auditory nerve (wave I), cochlear nucleus (wave II), lateral lemniscus and inferior colliculus (wave V), are well documented. The shorter BAER wave V latency for introverts than extraverts is the effect more consistently observed (Bullock and Gilliland, 1993; Stelmack and Wilson, 1982; Swickert and Gilliland, 1998). A recent report from Gilliland and colleagues is perhaps the most definitive (Cox-Fuenzalida and Gilliland, 2001). Introverts exhibited shorter wave V latency than extraverts, with correlations in several analyses ranging from $r = 0.23$ to 0.28. Gender effects, which are known to influence BAER latency, were not accounted for in these analyses. On the whole, the effect sizes were comparable to the marginally significant effects with smaller sample size reported by Stelmack et al. (1993a).

Although effect sizes tend to be modest, accounting for less than 10% of variation in E, the shorter wave V latency for introverts than extraverts is a reliable effect that is consistent with the greater reactivity to physical stimuli of introverts observed with other measures. The BAEP is exquisitely sensitive to changes in stimulus intensity with higher intensity stimulation evoking shorter latency

and larger amplitude BAEP waves. Because collaterals from the auditory tracts ascending through the brainstem innervate the ARAS, the amygdala and the cortical centres, the BAEP effects do endorse the arousal hypothesis as noted by Matthews and Gilliland (1999), and also the view espoused by Woodward et al. (2001) concerning the role of the amygdala for highly reactive children. From a neurophysiological perspective, however, the inhibitory influence of the olivocochlear nucleus on brainstem nuclei is reduced or absent for intensities above 75 dB and these inhibitory effects are independent of the reticular system (Desmedt, 1975). Thus, the BAEP effects cannot be understood in terms of a corticoreticular loop as adopted by Eysenck as the basis for individual differences in E. The independence of BAEP waves from descending inhibitory effects is underscored functionally by the remarkable invariance of BAEP waves during different stages of sleep and arousal (Campbell and Bartoli, 1986) and even during metabolic coma (Chiappa, 1990). Similarly, the weight of the evidence indicates that BAEP waves are not influenced by directed attention (Connolly et al., 1989; Picton et al., 1981).

Extraversion and P3

The P3 wave is a positive ERP wave that develops maximum amplitude at about 300 ms in simple decision tasks. This wave is usefully exploited in cognitive psychology, to study attention, memory and decision making. In general, the latency of the P3 is widely accepted as a measure of stimulus evaluation time that is independent of response selection and execution processes (Kutas et al., 1977). The P3 wave decreases in amplitude with increases in task difficulty and can be parsimoniously understood as an index of processing capacity (Kok, 2001). Several investigators examined individual differences in E during an auditory oddball task where a P3 wave develops to deviant stimuli presented among a series of standard stimuli. The most consistent effect is larger P3 amplitude for introverts than extraverts (Brocke et al., 1996; Daruna et al., 1985; Ortiz and Maojo, 1993; Polich and Martin, 1992; Wilson and Languis, 1990). Similarly, smaller decrements in P3 amplitude across trial blocks for introverts were reported (Ditraglia and Polich, 1991), although opposite effects were subsequently observed (Cahill and Polich, 1992). Null effects were reported by Pritchard (1989). In early work, the larger P3 amplitude for introverts would be attributed to differences in the amount of resources allocated to the processing of the deviant stimuli. Other interpretations of the effects are possible, for example differences in processing capacity, or even differences in sensitivity to stimuli. There is some evidence that P3 is larger to more intense stimuli (e.g. Gonsalvez et al., 2007). The understanding of these P3 differences is hampered because the effects have not been put to the test of direct manipulation or concomitant behavioural evaluations.

Individual differences in E and P3 amplitude and latency were also explored in several decision-making paradigms. The outcomes of this work were equally varied. Introverts displayed larger P3 amplitude than extraverts during a difficult visual vigilance oddball task (Brocke et al., 1996). Brocke et al. (1997) subsequently observed this effect under quiet conditions, but extraverts exhibited larger amplitude than introverts when the task was performed during noisy conditions. A larger P3 amplitude for extraverts was also observed in a visual classification task (Stenberg, 1994). More recently, larger P3 amplitude for extraverts was observed to high intensity target tones in an auditory oddball task (Guerrera et al. 2001). No differences in P3 amplitude between introverts and extraverts were reported in several studies using a series of elementary cognitive tasks (Stelmack et al., 1993b), simple response and stimulus-response compatibility tasks (Doucet and Stelmack, 2000), or difficult target recognition tasks (De Pascalis, 1993).

The larger P3 amplitude for introverts than extraverts to moderate intensity target tones during an auditory oddball task was observed

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with sufficient consistency to regard it as a valid effect that accounts for about 10% of variation in E. How the effect is interpreted and what it contributes to our understanding of E is not yet decided. In general, the effect is congruent with the greater electrodermal response amplitude for introverts observed in orienting response paradigms. These effects are regarded as intensity effects reflecting the greater sensitivity to stimulation of introverts. A systematic investigation of the effects of intensity on P3 is clearly desirable to assess that hypothesis. The larger P3 amplitude for extraverts observed in some studies is a puzzling effect that also requires more intensive investigation to disentangle sensory and motor contributions. There is little evidence linking E to differences in P3 amplitude on elementary cognitive tasks. Moreover, there is scant evidence of differences in P3 latency that would link E to differences in cognitive processing speed.

Extraversion and lateralized readiness potentials

There is a copious literature that implicates differences in the expression of motor behaviour as a fundamental determinant of differences in E (e.g. Doucet and Stelmack, 2000). These differences in motor expression were examined using simple response time (SRT) measures. Although faster and more frequent responding for extraverts was frequently observed, null effects were also reported often. Some progress in clarifying the disparities in this SRT work involved distinguishing between response decision time (DT), the time from stimulus onset to the release of the home button; and movement time (MT), the time from the release of a home button to the subsequent press of a target button.

In early research using response time measures with elementary cognitive tasks (Stelmack et al., 1993), an association between E and individual differences in MT was observed, but not in DT. In subsequent work, MT was manipulated directly by varying the response button distance and by examining the interactive effects of stimulus and response compatibility (Doucet and Stelmack, 2000). Extraverts displayed faster MT than introverts under all conditions. The pattern of results also suggested that the effect reflected differences in the initiation of movement rather than in the acceleration of movement from the home button to the target response button. Because there were no individual differences in DT or P3 latency and amplitude, these effects implicate peripheral motor processes as determinants of E rather than central cortical mechanisms mediating sensory discrimination or stimulus evaluation. This question was explored in studies that employed an ERP measure termed the lateralized readiness potential (LRP).

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The LRP is an ERP measure that permits direct assessment of movement initiation processes following stimulus-related processing. The LRP is derived by recording ERPs from electrodes placed over the motor areas of the left and right cortical hemispheres. Responses initiated by the left and right hand elicit greater electrical activity in the contralateral hemisphere. ERPs derived from the same side as the overt motor response are subtracted from the ERP of the contralateral hemisphere. When these difference waves are averaged across hands, they yield the LRP, reflecting pure hand-related ERP asymmetry. Analysis of the interval between the onset of the stimulus and the onset of the LRP (stimulus-linked LRP) is a measure for the duration of pre-motor activity, including stimulus analysis, response preparation and some aspects of response selection. In contrast, analysis of the interval between the onset of the LRP and the onset of the behavioural motor response (response-linked LRP) is a measure of the duration of motor activity independent of stimulus processing. There is a consensus that the LRP is generated in the primary motor cortex (Coles, 1989). A pattern of greater activity in the response-linked LRP for extraverts than introverts and no differences in stimulus-linked LRP or P300 latency and amplitude would confirm the involvement of primary cortical motor processes as relevant determinants of individual differences

in E rather than central cortical mechanisms that are involved in sensory discrimination or stimulus evaluation.

Rammsayer and Stahl (2004) obtained LRPs in an auditory two-choice go/no-go task. With this task, longer response-linked LRP latencies were found for introverts than extraverts indicating faster speed of motor processing in extraverts than in introverts. There were no E differences, however, for stimulus-linked LRP latencies. The failure to demonstrate a difference in stimulus-linked LRP latencies was attributed to the low task demands induced by the auditory task. In a second study (Stahl and Rammsayer, 2004), a complex discrimination task was applied to increase pre-motor, cognitive task demands. With this condition, stimulus-linked LRP latencies were shorter for introverts than extraverts, indicating faster pre-motor information processing for introverts. However, there were no differences in response-linked LRP latencies, a failure attributed to the absence of a no-go condition (Stahl and Rammsayer, 2004).

Extraversion and dopamine

Dopaminergic (DA) projections from mesencephalic cell groups are divided into two functionally distinct systems, the mesostriatal and the mesolimbocortical (e.g. Robbins and Everitt, 1995). Mesolimbcortical DA is important in locomotor activity, active avoidance, incentive/reward motivation, associative learning and working memory (Kimberg et al. 1997; Müller et al., 1998; Robinson and Berridge, 2000; Salamone, 1994; Sokolowski et al., 1994; Tzschentke, 2001). Mesostriatal DA neurons serve to inhibit and modulate the striatum (Björklund and Lindvall, 1986), which in turn exerts a powerful inhibitory effect on the thalamus and the reticular formation (Carlsson and Carlsson, 1990). Any increase in mesostriatal DA activity counteracts the inhibitory effect of the striatum, resulting in increased reticular arousal and, for example, enhanced sensory sensitivity. From this perspective, differences in DA brain mechanisms between introverts and extraverts may mediate the greater sensory sensitivity in introverts compared to extraverts (Rammsayer, 2004).

Rammsayer et al. (1993) addressed the question, 'Does pharmacologically induced decrease in brain DA activity differentially affect the transmission of sensory input into motor output in introverts and extraverts?' After pharmacological blockade of DA synthesis by means of alpha-methyl-para-tyrosine (AMPT), both DT and MT were markedly impaired in introverts but not in extraverts on a choice reaction time task. While DT indexes cognitive processes such as stimulus evaluation and response selection that are mediated by the mesolimbocortical DA system (Cohen and Servan-Schreiber, 1992; Rammsayer and Stahl, 2006), MT is a valid indicator of motor execution that is primarily mediated by mesostriatal DA activity (Amalric et al., 1993; Dunnett and Robbins, 1992; Salamone et al., 1993).

Because AMPT produced a non-specific decrease in DA activity, the D2 receptor blocker remoxipride was chosen in a subsequent study to selectively affect homeostasis of dopaminergic transmission (Rammsayer, 1998). Remoxipride primarily inhibits neurons of the mesolimbocortical DA system. In introverts, remoxipride caused a reliable increase in DT compared to extraverts, while MT was not affected in either group. Taken together, these findings indicate that introverts are more responsive to pharmacologically induced changes in D2 receptor activity than extraverts, irrespective of the specific DA system involved.

Although there are interactions between neurotransmitter systems, the observed differences between introverts and extraverts in the transmission of sensory input into motor output seem to be a clear function of DA modulation (Rammsayer, 2003). Depue and Collins (1999) argued that the mesolimbocortical DA system is the neurobiological substrate that mediates E and resulting in differences in incentive-facilitated behaviour.

Although their model is based on an integration of behaviour, affect and both cortical and subcortical neural mechanisms, it still lacks direct corroborative evidence from human pharmacopsychological studies (cf. Lawrence et al., 1999).

Following the model of Depue and Collins (1999), Wacker et al. (2006) combined behavioural and EEG measures with pharmacological treatment. As predicted, they found that the agency facet of E modulated the effect of 200 mg of sulpiride, a D2 receptor blocker, on behavioural and EEG measures. However, because dose-dependent pharmacological effects of sulpiride are unclear, (cf. Rammsayer, 1997), that effect is not definitive.

AU: Rammsayer, 1997; not in ref list. Please provide details.

Using single photon emission tomography (SPECT), Gray et al. (1994) found no association between D2 receptor binding and E. In two subsequent PET studies (Breier et al., 1998a; Farde et al., 1997), a positive correlation was reported between D2 receptor density and E. Similar studies (Breier et al., 1998b; Kestler et al., 2000), however, failed to observe this relation. These inconclusive findings appear indicative of a complex relation between D2 receptor density and E.

In these PET studies, participants remained passive during the recording. Fischer et al. (1997), however, presented their subjects with videotaped scenes of individuals walking in a park during the PET recordings. Enhanced activity for introverts compared to extraverts in brain areas associated with the mesostriatal DA system was observed. This finding endorses DA as a basis for differences in E and accords with greater DA responsiveness for introverts than extraverts proposed by Rammsayer (1998, 2003; Rammsayer et al., 1993). For Fischer et al. (1997), the visual stimulation may have been the critical condition for eliciting increased mesostriatal DA activity for introverts. In the absence of experimental or pharmacological manipulation, mesostriatal DA activity for introverts and extraverts are within a similar range (Rammsayer et al., 1993) and thus no differences in E are expected under passive conditions.

Genetic factors that may influence E and cause variations in DA were also explored. Benjamin et al. (1996) and Ebstein et al. (1996) reported differences in E and the type-4 dopamine receptor (DRD4) gene. Numerous subsequent studies both supported (Benjamin et al., 2000; Ekelund et al., 1999; Noble et al., 1998; Okuyama et al., 2000; Ono et al., 1997; Strobel et al., 1999; Tomitaka et al., 1999) and failed (Burt et al., 2002; Ekelund et al., 2001; Gebhardt et al., 2000; Jönsson et al., 1997, 1998, 2002; Kuhn et al., 1999; Mitsuyasu et al., 2001; Persson et al., 2000; Pogue-Geile et al., 1998; Soyka et al., 2002; Strobel et al., 2002, 2003b; Vandenbergh et al., 1997) to support these findings.

The failures to replicate an association between DRD4 polymorphism and E was attributed to the use of different questionnaires for personality assessment, methods that inflate the potential for false positive results, lack of statistical power, lack of control for ethnic variability, or demographic differences among the studies participants (cf. Burt et al., 2002; Malhotra and Goldman, 2000; Strobel et al., 1999). None of these factors convincingly justify the failures to replicate the positive findings. Overall, the large number of null results challenges the significance of DRD4 polymorphism as a biological basis of E.

Although Noble et al. (1998) reported a positive association between the D2 dopamine receptor gene (DRD2) and high novelty seeking, other studies failed to show such an association (Burt et al., 2002; Cruz et al., 1995; de Brettes et al., 1998; Gebhardt et al., 2000).

Extraversion and cortisol

Cortisol is a corticosteroid hormone produced by the adrenal cortex with widespread actions that help to restore homeostasis after stress. Cortisol levels show a circadian rhythmicity, with peak values found in early morning and lower levels in the evening. Unlike N, E does not appear to be associated with

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variability in early morning salivary cortisol levels (Munafò et al., 2006). There is also no evidence for a relationship between E and circadian cortisol rhythm or basal and stimulated free cortisol concentrations (Roy, 1996; Schommer et al., 1999; Zobel et al., 2004). However, a significant correlation between E and plasma levels of cortisol in the early afternoon was recently reported (LeBlanc and Ducharme, 2005).

PSYCHOPHYSIOLOGICAL AND BIOCHEMICAL CORRELATES OF NEUROTICISM

In personality classification schemas, such as the Eysenck Personality Questionnaire (Eysenck and Eysenck, 1991) or the NEO-PI (Costa and McCrae, 1992), N is an emotional stability–instability dimension that assesses differences in mood swings, negative affect, worry and tension. N is an important predictor of stress management, interpersonal effectiveness, and the development of clinical disorders involving anxiety, depression and hostility (Zuckerman, 2005). Accordingly, N was the focus of intensive investigation with psychophysiological procedures and biochemical assays.

Many of the early psychophysiological studies that examined differences in E also examined differences in N. However, significant effects for N were seldom reported in studies where simple physical stimulation was the principal variable manipulated (Fahrenberg, 1987). Psychophysiological methods that record electrodermal, cardiac and electrocortical activity are especially sensitive to changes in stimulus intensity. The dearth of psychophysiological effects of physical stimulation for N suggests that sensitivity to stimulation is not a determinant of differences in N. This view is endorsed by the paucity of evidence linking N to differences in sensory thresholds, pain thresholds or noise thresholds, and the psychological reports of those processes. The vulnerability of N to negative valence stimulation and to stress (notably social stress such as ego threat) that was frequently demonstrated was confirmed with both psychophysiological methods and with biochemical assays.

Neuroticism and the EEG

In a 1981 review that spanned 45 years of research, Gale cited 29 EEG investigations of personality that assessed the relation of EEG indices to E. Overall, the conditions under which the recordings were made were benign. They were better suited to examine the psychophysiological bases of differences in attention and arousal that characterise E than hypotheses linking N to differences emanating from limbic activity. None of the studies cited in that review reported significant associations with N. Subsequent studies using improved technology to derive absolute indices of EEG power reported the same null effects for N (Matthews and Amelang, 1993; O'Gorman and Lloyd, 1987). However, Ivashenko et al. (1999) did associate higher N with greater beta activity in right temporal areas.

Stenberg (1992) manipulated affective demands with conditions involving neutral, pleasant and unpleasant imagery and examined absolute indices of EEG activity for individuals differing in N. Higher anxiety scorers (i.e. high N and low E) exhibited greater theta activity at right frontal sites than lower anxiety scorers across all conditions, an effect indicative of higher overall emotionality. The high anxiety group also exhibited greater beta activity in the temporal region during the unpleasant imagery condition. Similar effects were observed in a study that manipulated arousal level by engaging participants in a mental arithmetic task that is known to pose an ego threat (Knyazev, 2002). Higher N was characterized by higher beta and gamma activity in frontal regions, and lower delta and theta activity in temporal, parietal and left frontal areas.

Several authors explored the relationship between EEG asymmetry measures and N scales. Asymmetry measures are obtained by subtracting left hemisphere EEG power from right hemisphere EEG power. In the main, this work stemmed from research on emotion by Davidson (1993) and colleagues. In their schema, greater left frontal EEG asymmetry is implicated in the experience of positive affect and right frontal EEG asymmetry is implicated in the experience of negative affect. Given the association of N with negative affect, higher N may be characterized by greater right frontal asymmetry. Some support for this hypothesis was reported by Schmidt (1999) who observed greater relative right frontal EEG activity for individuals who scored higher on a shyness scale. EEG activity recorded under resting conditions observed that higher N was also associated with greater relative right posterior activity (Schmidtke and Heller, 2004) and with greater mid-frontal asymmetry variability (Minnix and Kline, 2004).

Neuroticism and dopamine

Because high N scores are indicative of emotional liability, vulnerability to stress, or proneness to anxiety (e.g. Bolger and Schilling, 1991), N can be viewed as a security measurement of potentially threatening environmental stimuli (Lee et al., 2005). Brain DA is involved in monitoring activities and also in cognitive and attentional processes (e.g. Saint-Cyr, 2003). From this perspective, high N may be characterized by higher levels of brain DA activity that enable more sensitive or intense reactions to perceived stressors.

Preliminary evidence does suggest a functional relationship between the DA neurotransmitter system and N-related personality traits (i.e., detached or avoidant behaviour). For example, subjects with the D2 receptor gene haplotype 1 exhibit a more neurotic and immature defence style compared with those without haplotype 1 (Comings et al., 1995). Two PET studies (Breier et al., 1998; Farde et al., 1997) revealed a negative association between D2 receptor density and individual detachment scores. Another study, using SPECT, yielded a positive correlation between striatal D2 receptor density and N (Lee et al., 2005). Similarly, Kestler et al. (2000) reported that the depression facet of NEO-PI N was associated with striatal DA receptor density measured by PET. However, Gray et al. (1994) failed to observe an association between N and D2 receptor binding in the basal ganglia. Additional support for the involvement of D2 receptor mechanisms in N is provided by a molecular genetic study where an association between a DRD2 promoter variant and measures of detachment and lack of assertiveness was reported (Jönsson et al., 2003).

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Neuroticism and serotonin

N is an important liability factor for the development of anxiety and depressive disorders (e.g. Kendler et al., 1993). Because serotonin specific reuptake inhibitors are effective in the treatment of depression, neuronal mechanisms involved in pre-synaptic serotonin reuptake may be implicated in N. Serotonergic activity in the brain, which is involved in many affective disorders (Graeff et al., 1996), is mediated by the serotonin transporter gene (5-HTT). The principal function of 5-HTT is to remove serotonin from the synaptic cleft by returning it to the pre-synaptic neuron where the neurotransmitter can be stored for later re-release. 5-HTT expression is particularly abundant in cortical and limbic areas engaged in modulation of emotional aspects of behaviour (Westenberger et al., 1996). In humans, two common alleles, the short and long alleles, in a variable repeat sequence of the promoter region of 5-HTT were linked to N (e.g. Lesch et al., 1996; Sen et al., 2004b). N also mediated the association between 5-HTT polymorphism and lifetime major depression (Munafò et al., 2006). Analysis of genotype–phenotype

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relations in healthy volunteers by means of imaging-genomics studies (Hariri and Weinberger, 2003) endorse an association between 5-HTT polymorphism and N; that is, increased responses of the amygdala as a function of the short allele in the linked promoter region of the 5-HTT (Hariri et al., 2005).

Numerous studies failed to confirm an association between 5-HTT polymorphism and N (e.g. Ball et al., 1997; Deary et al., 1999; Ebstein et al., 1997; Flory et al., 1999; Jorm et al., 1998; Mazzanti et al., 1998; Willis-Owen et al., 2005). Several possible explanations for these inconsistent results were proposed, namely a small sample size, different methods of personality assessment and phenotype ascertainment, or population stratification. Attempts to circumvent these methodological constraints, however, also failed to form a consensus. Five meta-analyses were also inconclusive (Munafò et al., 2005; Munafò et al., 2004; Munafò et al., 2003; Schinka et al., 2004; Sen et al., 2004a)

Animal research on the serotonin receptor subtype 5-HT_{1A} provides converging evidence for serotonin as a biochemical correlate of N. Anxiety is more pronounced in mice lacking 5-HT_{1A} receptors than controls (Parks et al., 1998; Ramboz et al., 1998). Further, 5-HT_{1A} receptor agonists were effective in the treatment of anxiety (e.g. Sramek et al., 1997). A negative correlation between the anxiety facet of the NEO PI-N scale and cortical 5-HT_{1A} receptor binding potential was also observed in a PET study of healthy volunteers (Tauscher et al., 2001); that is, high N is characterized by lower 5-HT_{1A} receptor density. An association between HTR1A-1019 polymorphism and the NEO-PI-R N (Strobel et al., 2003a) also endorses a relation between allelic variation in the 5-HT_{1A} receptor and the expression of the anxiety and depression aspects of N.

Neuroticism and cortisol

The hypothalamic–pituitary–adrenal (HPA) axis is a major part of the neuroendocrine system that controls reactions to stress and regulates mood. HPA dysregulation, as indicated by excess cortisol response after HPA stimulation, was identified as an indicator of depression (Pariante and Miller, 2001; Plotsky et al., 1998). Given that N is a powerful predictor of depression, an association between N and HPA dysregulation is plausible. Both N and HPA dysregulation operate as risk and vulnerability factors for depression (Holsboer, 2000). High N and HPA dysregulation are indicative of less effective coping with stress, critical life events, and psychological challenges. Several studies explored the relationship between these N and HPA.

McCleery and Goodwin (2001) were the first to demonstrate differences in HPA regulation as a function of N. Specifically, low N exhibited a stronger cortisol response than high N. This effect may be indicative of a down-regulated HPA axis for high N to prevent harmful over-activation. Subsequently, Zobel et al. (2004) observed the reverse pattern of cortisol response; that is, stronger cortisol responses were positively associated with N. Zobel et al. (2004) suggested that HPA dysregulation may provide a biochemical basis for N and depressive temperament. Higher cortisol levels for high N individuals without a previous history of depression (e.g. Bridges and Jones, 1968; Portella et al., 2005) provides additional evidence that high N is associated with altered HPA regulation. Overall, however, the relationship between N and HPA is not resolved.

PSYCHOPHYSIOLOGICAL AND BIOCHEMICAL CORRELATES OF IMPULSIVE SENSATION SEEKING

Research on impulsiveness is a challenge because it is a complex construct with multiple meanings. In the Eysenck three factor model, all three factors, E, N and P, relate to some aspects of impulsiveness: venturesomeness is a feature of E, while narrow impulsiveness is a feature of P and N (Eysenck, 2004).

P also features prominently on an SS factor that is appropriately termed impulsive unsocialized sensation seeking (ImpSS) (Zuckerman et al., 1988). There is a substantial psychophysiological literature that explores individual differences in SS and the biochemical analysis of individual differences in ImpSS has flourished in recent years.

Psychophysiology of sensation seeking

From the psychophysiological literature, three conclusions can be drawn. First, there is little evidence of individual differences in base level of arousal between high and low scorers in SS using measures of skin conductance level, EEG desynchronization, or resting heart rate (Stelmack and Geen, 1992). These null effects negate the proposal that high SS is characterized by low tonic arousal (Zuckerman, 1979).

Second, there is good evidence that high SS scorers react more intensely to stimulation than low SS scorers under some conditions. High SS scorers exhibit larger skin conductance responses than low SS scorers to novel stimulus items that are relevant to the SS scale (SSS; Zuckerman, 1979), for example pictures of hang-gliding, marijuana smoking, mountain climbing, and sexual and violent stimuli (e.g. Smith et al., 1986). In general, these effects provide good support for the construct validity of the SSS, but provide little insight into the biological bases of SS.

Third, there are reliable individual differences in SS, accounting for about 10% of variation, that are observed in an augmenting-reducing paradigm with visual ERP changes to increases in the intensity of light flashes. Individuals with high scores on the disinhibition subscale of the SSS exhibit an increase in amplitude of an ERP wave (P1, N1) that develops at about 100 ms following stimulation. Low sensation seekers exhibit a decrease in amplitude with an increase in intensity of the light flashes whereas high sensation seekers exhibit an increase in response amplitude (Buchsbaum, 1971; Lukas, 1987). More recent evidence from carefully executed studies endorses this view (e.g. Brocke et al., 1999).

The augmenting-reducing effect was considered as evidence supporting the view that high SS is characterized by lower tonic arousal, and that stimulation is amplified, or simple physical stimulation is experienced more intensely than in low SS scorers, in order to raise arousal to an optimal level (Zuckerman, 1979). Alternatively, in the absence of evidence indicative of differences in base levels of arousal, it can be argued that augmenting-reducing is an intensity effect in which high SS scorers are less sensitive to stimulation than low SS scorers and that low SS scorers initiate inhibitory, protective mechanisms in response to high intensity stimulation that result in smaller responses, (Smith et al, 1989). Coincidentally, it has been shown that a high ImpSS is characterized by greater pain tolerance, greater E, less hypochondriasis, higher absolute sensory thresholds (Goldman et al., 1983; Kohn et al., 1982) and smaller P3 amplitude to negative valence emotional stimuli (De Pascalis et al., 2004). This suggests that high SS scorers may engage in intense stimulating activities, not to achieve an optimum level of arousal, but because they can endure intense stimulation.

Impulsive sensation seeking and dopamine

Zuckerman (1994) proposed the construct of impulsive unsocialized sensation seeking (ImpSS) as an independent trait of personality, with Eysenck's P scale as its strongest marker (Zuckerman et al., 1988). According to Eysenck and Eysenck (1976), a continuum can be drawn from normal through psychopathic behaviour to psychotic states. In this view, the biological basis of P is continuous for healthy individuals and psychotic patients. Increased DA activity is a prominent hypothesis in neurochemical theories of schizophrenia (cf. Davis et al., 1991).

DA activity can also be expected to vary with P or ImpSS (Pickering and Gray, 2001; Zuckerman, 2005). Overall, there is good evidence associating DA activity and P

Although it is premature to determine whether E is more strongly related to brain DA than P/ImpSS, there are a number of DA mediated effects related to P or psychosis proneness rather than to E, e.g. latent inhibition (e.g. Gibbon and Rammsayer, 1999; Lubow and Gewirtz, 1995), negative priming (e.g. Beech and Claridge, 1987; Swerdlow et al., 1995), and pre-pulse inhibition (e.g. Kumari et al. 1997; Simons and Giardina, 1992).

Netter and Rammsayer (1991) administered the DA antagonist haloperidol and the DA precursor L-dopa to normal subjects and tested them on a reaction time task. While high SS scorers tended to feel more relaxed and perform better after haloperidol, low SS scorers performed better after L-dopa, effects indicative of more responsive DA activity in high ImpSS scorers (Zuckerman, 1993). A negative relationship between P and D2 receptor binding in the basal ganglia was reported in a PET study by Gray et al. (1994). Because an increase in DA activity results in down-regulation of post-synaptic receptors, as indicated by a decrease in number of receptors or post-synaptic receptor sensitivity (Creese et al., 1977), the association between P and D2 binding is indicative of increased DA activity for P. Initially, this conclusion appears congruent with the hypothesis of increased brain DA in schizophrenia. However, DA hypothesis of schizophrenia predicts enhanced activity in the mesolimbocortical DA, whereas the Gray et al. (1994) finding referred to the functionally independent mesostriatal DA.

Impulsive sensation seeking and cortisol

An early study by Ballenger et al. (1983) reported that SS was characterized by low levels of free cortisol. Subsequent studies measuring cortisol baseline levels (Gerra et al., 1999) and cortisol response values (Gerra et al., 1998) failed to observe that negative relationship to ImpSS. More recently, a reliable inverse relation between cortisol and SS was reported for male, but not for female college students (Rosenblitt et al., 2001).

SUMMARY AND CONCLUSIONS

Overall, there was good progress in focusing the fundamental facts of the psychophysiological and biochemical correlates of personality. The greater sensory reactivity of introverts than extraverts to simple sensory stimulation observed with a wide range of psychophysical and psychophysiological procedures is well established. There is also good progress in demonstrating differences in motor expression between introverts and extraverts with psychophysiological procedures. The faster movement time for extraverts on simple response time tasks, and the absence of P3 latency effects (an index of stimulus processing speed) does point to the involvement of peripheral and or/cortical motor processes as relevant determinants of individual differences in E rather than central cortical mechanisms that are involved in sensory discrimination or stimulus evaluation. The application of lateralized readiness potentials is a promising procedure for articulating the sensory and motor effects.

Biochemical analysis of the DA system, which is involved in the neuroregulation of sensory input and motor output, is proposed as a biochemical determinant of individual differences in E (Rammsayer, 2004). Although biochemical analyses revealed that DA turnover is the same in introverts and extraverts (Rammsayer et al., 1993), there is good evidence from different procedures for E differences in responsiveness to deviations from the physiological level of DA activity in the brain, with introverts more susceptible to changes in D2 receptor activity than extraverts.

The disappointing outcome of early psychophysiological research on N, using simple physical stimulation, has yielded more promising results with some EEG procedures. Although the effect is not conclusively established, the association of higher N with greater right frontal EEG activity was observed in several reports, notably under negative affect conditions.

Biochemical analyses of individual differences in N are equivocal. There is some evidence linking N and D2 receptor mechanisms, but this evidence is piecemeal. Analyses of the serotonergic system are inconclusive. Although there is good evidence relating depression to HPA dysfunction (as indexed by excess cortisol response following HPA stimulation) and although N is an important predictor of depression, no firm association betweeen N and HPA dysfunction is established.

With respect to ImpSS, psychophysiological research indicates: (1) no reliable individual differences in tonic levels of physiological activity, (2) greater response to highly novel, exciting, or disturbing stimuli for higher SS, and (3) larger response (greater tolerance?) to higher intensity physical stimulation for higher SS. Although far from conclusive, there is increasing evidence relating P/ImpSS to increased or more reactive DA activity.

The review of psychophysiological and neurochemical research presented in this chapter aimed to focus the biological basis of personality and individual differences. The arousal construct was central to the early examination of personality from a physiological perspective. A distillation of that work is incorporated in this review. Over the past four decades, the neurosciences provided new findings, constructs, and models in an attempt to improve our understanding of the biological determinants of behaviour and individual differences, often without integration of previous effects that were reported. As Matthews and Gilliland (1999) suggested, this scenario may have lead, unintentionally, to an oversimplification of a number of neurophysiological processes. Both these considerations could contribute to the inconsistency of effects noted in this review. Clearly, future research must make an effort to exploit reliable effects and to incorporate them in a paradigm of personality that leads to a meaningful appreciation of how neural processes, neurotransmitters, and hormones contribute to individual differences in personality.

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