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Psychophysiological Measurement of Personality

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INTRODUCTION

Whereas the environment is in constant flux and causes changes in an individual's behavior over time, personality is considered the constant factor that causes stability in behavior. This constancy is likely to be hard-wired in our biology, and the brain seems the obvious place for such hard-wiring. Can we measure this hard-wiring of behavior? In this chapter we review attempts to correlate personality traits to individual differences in central nervous system functioning using psychophysiological recording techniques. This relatively small literature has been motivated by two different goals. The first has emerged from concerns about the validity of paper-and-pencil personality assessment (Eisenberger et al., 2005). Virtually all major personality inventories are based on potentially flawed subjective linguistic self-report. To further advance personality testing, it may be necessary to move to objective tests that avoid most of the motivational and response distortion associated with item transparency of self-report instruments. Psychophysiological testing seems a promising method to do so, because voluntary control over the recorded biological signals is limited

if not absent. A second motive to use psychophysiological testing in personality research is to elucidate the biological processes underlying the major dimensions of personality. Several influential models of personality, such as those by (Eysenck 1967, 1990; Eysenck and Eysenck, 1985) and (Gray 1982; Gray and McNaughton, 2000) have been strongly informed by biological theory.

The two central constructs in Eysenck's theory are neuroticism and extraversion. Neuroticism is related to activation levels in the limbic system. The limbic system includes the hippocampus, amygdala, septum, and hypothalamus and regulates emotional states such as fear and aggression. Neurotic individuals are hypothesized to have higher activation levels in the limbic system leading to lower thresholds for emotional responses. Neurotic individuals are more likely to report feelings of anxiety, guilt, and tension. Emotionally stable individuals, on the other, hand, have lower activation and higher thresholds in the limbic system, leading to attenuated responses to emotional challenges. The extraversion–introversion dimension is thought to be regulated by the ascending reticular activating system that is involved in regulating

cortical arousal. An individual's comfort level at any given time will depend on the interaction between their basal cortical arousal and the type of situation they are in; being under- or over-aroused are both less desirable than a moderate level of arousal. Introverts are prone to be overstimulated by sensory stimuli and consequently tend to withdraw from social situations, are less active, and less willing to take risks. In contrast, due to their lower base level of cortical arousal, extraverts tend to be more lively and sensation seeking and will be attracted to social situations.

In the view of Gray and colleagues, there are two basic systems that control behavior. The behavioral inhibition system (BIS) is activated by novelty and stimuli associated with punishment; that is, aversive stimuli or omission of reward. The behavioral approach system (BAS) is activated by stimuli associated with reinforcement; that is, reward or termination of punishment. Gray and colleagues located these systems in the septohippocampal system (to which the amygdala was later added) and the ventral striatum (including the nucleus accumbens). Engagement of both systems is associated with arousal as reflected in changes in autonomic nervous system activity and hormonal secretion. Gray and colleagues proposed that the most salient individual differences reflect the variation in sensitivity to stimuli associated with punishment or reinforcement and the coupled behavioral tendencies of avoidance and approach. Specifically, individual differences in the functioning of the reward system in response to appetitive stimuli are implicated in the personality traits of extraversion and novelty seeking/impulsivity. Individual differences in the punishment system in response to aversive stimuli are implicated in the personality traits of neuroticism and harm avoidance.

Psychophysiological testing

Psychophysiological testing can be used to corroborate the hypothesized biological correlates of personality, and ultimately chart the various intermediate steps in the biological pathways connecting variation in brain function to variation in behavior. In the current chapter, we will focus on the electromyographic (EMG) recording of the startle blink reflex, electroencephalographic (EEG) recording of cortical electrical activity either recorded continuously or evoked by stimulus events, and changes in brain blood flow assessed by functional magnetic resonance imaging (fMRI). These signals can, first of all, be recorded under pure resting conditions. In such a setting, subjects are typically instructed to relax, focus their attention on a fixation point and in general made to avoid engaging in any particular state of mind. In keeping with a dispositional model of personality, the idea is that this will allow their 'underlying' or 'true' level of nervous system activity to manifest. For example, if extraverted individuals are characterized by positive and neurotic individuals by negative affect as assessed by affect scales like the PANAS (Watson et al., 1988) these differences in dispositional affect should be detectable by the measurement of resting brain blood flow and electrical activity in brain regions known to be implicated in affective processing. A number of studies have indeed reported such correlations (Davidson, 1998; Ebmeier et al., 1994; Stenberg et al., 1990, 1993; Youn et al., 2002).

By contrast, Wallace (1966) conceptualized personality attributes as abilities, an approach he termed the capability model of personality. Others have proposed similar formulations of personality (Mischel and Shoda, 1995). The capability model encourages the measurement of individual differences in 'brain behavior' during controlled laboratory challenges, much as one might test intelligence or high-jumping ability. Subjects can, for instance, be made to anticipate and actually gain a reward (e.g. 5 cents per correct answer) or be punished (e.g. shock or monetary loss) during a mentally challenging task. Alternatively, they can be shown series of words with strong negative (e.g. 'sick', 'murder', 'hate', 'rape') or positive connotations (e.g. 'happy', 'wedding', 'love', 'party'). Two popular sets of affective stimuli are a series of faces compiled by Ekman and

Friesen (1978) showing primary emotions like sadness, happiness, fear or anger, and a series of images compiled by Lang et al. (1998, 2001) in the International Affective Picture System (IAPS). The IAPS stimuli are complex visual scenes that were extensively normalized for emotional valence and arousal. For instance, unpleasant images depicted snarling dogs, spiders, sharks, disgusting objects, violence, severe burns, or corpses, whereas pleasant images depicted happy babies, appetizing foods, puppies and kittens, joyful people and loving couples. Response to these emotional valenced images are usually contrasted to those seen during neutral images of, for instance, a basket, books, or fractal images.

Most of the recent work on EEG, ERP, and EMG startle blink correlates of personality and almost all of the fMRI studies, follow the capability model rather than the dispositional model. Instead of assessing differences in resting levels of the EMG startle reflex, EEG or hemodynamic brain activity, these studies have looked at the magnitude, timing, and topography of changes in these measures during experimentally induced changes in psychological state.

EMG startle reflex

The startle reflex is a defensive response elicited by intense and abrupt stimuli. In humans, the startle reflex is measured by recordings of the *orbicularis oculi* muscle around the eye (Blumenthal et al., 2005). Blinks can be reliably elicited by presenting a brief (about 50 ms) and moderately intense tone, or white noise. Typically, participants are presented with a lead stimulus that might be neutral or emotionally toned and the startle eliciting probe stimulus is presented at a certain time, termed a lead interval, following the lead stimulus onset. Startle modulation is observed when the size of the startle reflex is altered by the lead stimulus. Lead intervals less than 50 ms can produce very short lead interval facilitation (Neumann et al., 2004). Lead intervals of 50 to 500 ms produce short

lead interval inhibition, often termed pre-pulse inhibition (PPI), with maximal inhibition at lead intervals around 100 ms (Neumann et al., 2004).

EEG power and EEG asymmetry

The EEG reflects the electrical activity generated by clusters of neurons in the cortex that show synchronized changes in membrane potential due to neural activity in that brain location. EEG recordings are made from multiple electrodes affixed to the scalp (the exact number varies across studies from the standard 18 scalp electrodes up to 128 scalp electrodes). The most striking feature of the brain activity recorded by an EEG is its oscillatory character. Quantification of EEG data reflects this, in that the energy (or power) in various frequency bands is used as a main index. EEG recording has many important clinical applications because there are predictable EEG signatures associated with different behavioral states. A relaxed resting state, for instance, is characterized by high power in the alpha (8–12 Hz) frequency band, whereas under-condition of mental load power in the beta band (12–30 Hz) increases in relative strength. In addition to its sensitivity to within-subject changes in behavioral state, EEG power can also be compared across subjects, for instance as a function of personality. Because right and left hemispheres are suspected to play a differential role in emotional processing, most attention has gone to individual differences in the degree of asymmetry in left and right EEG power (Sutton and Davidson, 1997).

Event-related potentials

The event-related potential (ERP) is a stereotyped short-term change in EEG activity that is time-locked to stimulus or cognitive events. Different ERP components can be identified according to whether the voltage fluctuation is positive or negative and the time (latency) at which the peak voltage fluctuation is seen.

For instance, the P300 (or P3) reflects a positive voltage change that peaks around 300 ms following stimulus onset. These changes in amplitude and timing of the voltage can be further differentiated as a function of spatial location. Thus, it can be determined whether individuals with different personality traits show different latencies, amplitudes, or patterns in the spatial distribution of their ERPs. The ongoing nature of psychological processes means that the ERP will consist of several potentially overlapping components (Fabiani et al., 2000). The major ERP components are N1, P2, N2, and P3, followed by slow wave components that return the EEG signal to baseline. Various other components may also be identified according to specific experimental conditions, such as the error-related negativity (ERN) and the contingent-negative variation (CNV).

fMRI

In a typical fMRI experiment, a high-resolution structural scan is taken initially that allows separation of gray and white matter from each other and other tissues (cerebrospinal fluid, skull, skin, etc.). Next, the subject is exposed to repeated stimuli, for example, pictures from the IAPS. When nerve cells are activated by these stimuli they consume extra oxygen which is carried by hemoglobin in red blood cells from local capillaries. The local response to this oxygen utilization is decrease in oxygenated blood followed by an increase in blood flow, occurring after a delay of approximately 1–5 seconds. Corresponding changes in the relative concentration of oxyhemoglobin and deoxy-hemoglobin can be detected using an appropriate magnetic resonance pulse sequence that gives rise to a so-called blood oxygenation level dependent (BOLD) contrast. The average level of BOLD signal intensity can be compared in two sets of stimuli, for instance aversive pictures versus neutral pictures, to see which parts of the brain were specifically activated or deactivated by the aversive stimulus compared to the neutral stimulus. Statistical maps that take into account the multiple testing across thousands of 1–1.5 mm^3 blocks of brain tissue –voxels – show the (de)activated areas as colored blobs. These can be rendered in 3D and plotted on top of the original high-resolution structural scan for anatomical interpretation. Individual differences in the BOLD signal intensity in certain regions-of-interest (ROI) can be correlated with major personality traits like neuroticism and extraversion.

NEUROTICISM

EMG startle reflex

Response size and habituation
As a defensive response, the absolute size of the startle reflex should be larger and habituate more slowly in individuals with high neuroticism because of the association of this personality trait to hypersensitivity to aversive sensory stimuli (Eysenck et al., 1985). However, results have generally failed to support this prediction. No association has been found between startle reflex magnitude and neuroticism in a sample of male patients with schizophrenia or matched healthy controls (Akdag et al., 2003). In addition, the same study found no association between neuroticism and the rate of habituation from an early to a late block of trials. A similar failure to find any relationship between neuroticism and startle reflex magnitude has also been reported in other investigations (Hawk and Kowmas, 2003; Kumari et al., 1996).

Prepulse inhibition (PPI)
In contrast to the absolute size of the startle reflex, PPI has shown a stronger association with neuroticism. Prepulse inhibition is an index of automatic sensorimotor gating that serves to protect the processing of the prepulse from interruption from the startle stimulus

(Graham, 1979). High levels of neuroticism are associated with low levels of PPI at lead intervals of 30, 60, and 120 ms and the association may be stronger in earlier than in late trials (Swerdlow et al., 1995; Corr et al., 2002). This reduced PPI may reflect the hypersensitivity to aversive sensory stimuli thought to be present in neurotic individuals (Eysenck et al., 1985). Alternatively, neurotic individuals may allocate less attention to the processing of the prepulse and startle-eliciting stimulus, thus reducing the amount of PPI observed (Corr et al., 2002). Based on this explanation, it would be instructive to directly manipulate the participant's attention such as by using the discrimination and counting task (Filion et al., 1994). If PPI is attenuated in neurotic individuals during attended, but not ignored lead stimuli, it would suggest that the association between neuroticism and PPI is mediated by attention. A final reason for the association between neuroticism and PPI could be that it reflects the activation of emotion circuits during the task, which in turn reduces PPI due to overlapping neural systems between the circuits that govern PPI and emotion (Corr et al., 2002).

Affective modulation

According to the motivational priming interpretation of affective startle modulation (Lang et al., 1997), there will be startle potentiation when the lead stimulus induces an affective state congruent with the startle stimulus (i.e. unpleasant or aversive lead stimuli) and startle attenuation when the lead stimulus induces an incongruent affective state (i.e. pleasant or appetitive lead stimuli). Hence, affective startle modulation will be influenced by personality characteristics if these characteristics mediate responses to aversive or appetitive stimuli. In particular, individuals high in neuroticism or on the BIS scale would be expected to show enhanced startle potentiation due to their heightened sensitivity to aversive stimuli (Eysenck et al., 1985; Gray and Me Naughton., 2000). However, prior research has not always been consistent with these predictions. Startle latency potentiation during unpleasant

compared to neutral pictures has been found in participants low in neuroticism, but not in those high in neuroticism (Corr et al., 1995). High BIS participants have shown increased attenuation of startle magnitude during pleasant pictures compared to neutral pictures, which was not found in low BIS participants (Hawk et al., 2003). However, the expected startle potentiation during unpleasant compared to neutral pictures in high BIS participants was not found. Absence of a relationship between neuroticism and affective startle modulation has also been reported (Kumari et al., 1996). Various explanations have been put forward to explain why the results are inconsistent with predictions, including ceiling effects or reduced attention to unpleasant stimuli in neurotic individuals (Corr et al., 1995), or that it reflects the nature of stimuli used in terms of their arousal level (Kumari et al., 1996) or content (Kumari et al., 1996; Hawk and Kowmas., 2003).

The nature of the unpleasant stimuli may be a crucial factor in the association between neuroticism and affective startle modulation. Startle potentiation is greater when stimuli are fearful than when disgusting (Kaviani et al., 1999). Moreover, the amygdala is implicated in the fear response and it plays a central role in startle potentiation (Lang et al., 1997). The BIS is closely associated with anxiety and fear and the amygdala has been included in this formalization (Gray et al., 2000). Accordingly, a closer association between neuroticism and affective startle modulation may be found if images of fear, rather than disgust, are used. In a re-examination of the data reported by Kumari et al. (1996), it was found that low-neuroticism participants showed greater startle potentiation to low fear–high disgust film clips than high-neuroticism participants (Wilson et al., 2000). In a study that systematically manipulated the nature of unpleasant pictures, high-BIS participants, but not low-BIS participants, exhibited startle potentiation during fear pictures (Caseras et al., 2006). The high-BIS participants showed significant differences in startle modulation between pleasant and neutral, pleasant and blood-disgust, and pleasant

and fear pictures. The low BIS participants showed significant differences in startle modulation between pleasant and neutral, pleasant and blood-disgust, and blood-disgust and fear stimuli. The findings support the conclusion that individual differences in BIS functioning (and by extension, neuroticism) is associated with startle modulation during fear eliciting scenes.

EEG asymmetry

One of the most widely studied correlates of personality traits is frontal EEG alpha asymmetry; that is, asymmetry in EEG activity in the alpha frequency range (8–12 Hz) on frontal electrodes (Coan and Allen, 2004; Davidson, 2004; Davidson et al., 1985; Fox, 1991; Hewig et al., 2006). From their pioneer studies onward, Davidson and colleagues have linked frontal cortical asymmetry to an approach and a withdrawal system which bear strong resemblance to Gray's BAS and BIS system (Sutton et al., 1997). The approach system is activated by the perception of goals, elicits approach related (pre-goal-attainment) positive affect, and initiates appetitive behavior towards these goals. The neuroanatomical basis of the system is located in the left dorsolateral and medial prefrontal cortex and the basal ganglia. The withdrawal system is activated by aversive stimulation, elicits negative emotions, and leads to withdrawal behavior. The neuroanatomical basis of this system is thought to be the right dorsolateral prefrontal cortex, the right temporal polar region, the amygdala, the basal ganglia, and the hypothalamus. The amygdala may be a central structure connecting the activity of both systems (Ochsner et al., 2002).

Although EEG asymmetry seems a perfect candidate to act as a psychophysiological indicator of neuroticism, the extant literature shows large inconsistencies in statistical associations between frontal EEG asymmetry and neuroticism (and other related trait measures of personality), and it is unlikely that the methodological differences across laboratories can completely account for those

inconsistencies (Allen et al., 2004; Coan and Allen., 2004; Davidson, 2004; Hagemann, 2004; Smit et al., 2007). From a conceptual point of view, Coan and colleagues (Coan et al., 2006) question the wisdom of the widespread use of measuring frontal asymmetry in resting conditions. The use of resting conditions derives from a near axiomatically accepted dispositional model of frontal affective style in this field. In this model individuals are thought to possess a general tendency to predominantly respond with either approach-related affect (indexed by relatively greater left frontal activity) or withdrawal-related affect (indexed by relatively greater right frontal activity) across all or most situations. Instead, the capability model of frontal EEG asymmetry may be more appropriate (Coan et al., 2006). As outlined before, this model posits that meaningful individual differences in frontal EEG asymmetry exist, but that those individual differences are best thought of as interactions between the emotional demands of specific situations and the emotion-regulatory abilities individuals bring to those situations. During emotional challenges, individual differences in frontal EEG asymmetries were indeed shown to be more pronounced than during a resting condition. Moreover, they were much more reliable; that is, more resistant to measurement error induced by variation in EEG methodology, and had a more reliable relationship with criterion measures of ongoing emotional state. These findings suggest that future use of evoked changes in EEG frontal asymmetry by emotion induction rather than resting EEG may yield more robust links to personality.

ERP

Early ERP components

Early ERP components can be influenced by the sensory characteristics of stimuli, such as their intensity. Based on the hypothesized hypersensitivity to sensory stimuli, neuroticism is expected to influence these components. However, research has generally failed to find

an association between neuroticism and N1, P2, and N2 amplitude or latency (De Pascalis, 1993; De Pascalis et al., 1996; Fjell et al., 2005). The error-related negativity (ERN), however, may be influenced by neuroticism. The ERN occurs when participants make errors in a sensorimotor task (Luu et al., 2000) or when outcomes are 'worse than expected' (Holroyd and Coles, 2002) and is thought to be generated by the anterior cingulate cortex (Van Veen and Carter, 2002). The negativity peaks around 150 ms following response onset and shows a fronto-central scalp distribution (Dehaene et al., 1994). Adult participants who scored high on measures of negative affect and emotionality have shown larger ERN than participants with low scores during a visual flanker task (Luu et al., 2000). No relationship between neuroticism and ERNs at a fronto-central site during a visual flanker task has also been reported (Santesso et al., 2005), although the lack of an association may reflect the use of 10-year-old children in this study.

P3

The P3 can be elicited in an oddball task in which infrequently presented pure tones (oddballs) are randomly interspersed among frequently occurring tones of a different pitch (standards). Stelmack and Houlihan (1995) present a comprehensive review of the earlier research on P3 and personality. In one of their own studies, participants high in neuroticism had a shorter P3 latency than participants low in neuroticism (Stelmack et al., 1993). The difference may reflect that the former spend less time to evaluate a stimulus (Plooij-van Gorsel, 1981). Alternatively, the increased worrying and susceptibility to stress, which are regarded as important elements of neuroticism that adversely influence cognitive performance (Eysenck et al., 1985), may also influence P3 latency (Stelmack et al., 1993). In addition, neuroticism level produced contrasting results for P3 latency and RT in that high neuroticism was associated with faster P3 latency but slower RT. This finding was interpreted to reflect that individuals with high neuroticism have a hasty and worried

evaluation of a stimulus (short P3 latency) that requires additional processing or checking to initiate a response leading to long RT (Stelmack et al., 1993).

No relationship between P3 and neuroticism has been found in a word/non-word detection task (De Pascalis et al., 1996), an auditory oddball task (Polich and Martin, 1992; Pritchard, 1989), and auditory startle probes presented during emotionally toned slides (Bartussek et al., 1996). It is possible that some discrepant results reflect differences in the task requirements or methodological features of the experiment. For instance, using a variety of visually presented tasks, Stelmack et al. (1993) found an association between neuroticism and P3 latency with some tasks, but not others. At least in terms of amplitude, the scalp distribution may be an important variable in that high and low neuroticism participants show similarities in P3 amplitude at some electrode sites and not others. Low neuroticism participants have shown the usual scalp distribution with a clear parietal maximum, whereas high neuroticism participants show a flat scalp distribution with nearly the same level of P3 amplitude at all electrode sites with both a structural (deciding if a word was longer or shorter than six letters) and affective (rating emotional valence of pleasant, neutral, and unpleasant pictures) processing task (Bartussek et al., 1996, experiment 1). Finally, the sampling of participants may be important in that gender and age may modulate the effects of neuroticism on the P3 (Gurrera et al., 2005; Pritchard, 1989).

Several personality researchers have also examined a component of the P3 that follows a third infrequent non-target stimulus that can be embedded in an oddball task. This P3a, or novelty-P3, is an earlier, frontally distributed potential arising in part from the anterior superior temporal gyrus and anterior cingulate gyrus and may be regarded as an index of the orienting response (Soltani and Knight, 2000). The amplitude of the P3a reflects the amount of attention a participant invests in the irrelevant, unexpected, and distracter stimuli.

A negative association between neuroticism and P3a amplitude to novel environmental stimuli embedded in an auditory oddball task has been found at frontal left, frontal right, frontal centre, and parietal centre locations (Gurrera et al., 2001). A similar, though statistically non-significant, association for P3a amplitude to irrelevant auditory distracter items has also been reported (Fjell et al., 2005). In a comparison between target and novel stimuli, stronger correlations with neuroticism were generally found for the P3 amplitude during novel stimuli (Fjell et al., 2005). The authors suggested that the stronger association may reflect that individuals high in neuroticism are more susceptible to distraction and less able to inhibit responses to non-target stimuli, which accords with Eysenck's notion of hypervigilance in these individuals.

fMRI

Although emotion research has been one of the largest beneficiaries of the new brain imaging techniques (Critchley, 2003; Davidson et al., 2000; Drevets, 2001), there is a surprising paucity of studies investigating the correlation between neuroticism and fMRI responsivity. That is, there is a large literature on deviant fMRI responses in psychopathology, but most of these studies used patients with clinical anxiety disorders or depression. In these studies, it becomes hard to separate the effects of having a psychiatric disorder itself, including toxic brain effects of co-morbid hypercortisolism (Sapolsky et al., 1986), from the effects of neuroticism *per se*. Fortunately, there is an increasing number of studies that address fMRI correlates of neuroticism in samples of healthy subjects (Canli et al., 2001; Eisenberger et al., 2005; Etkin et al., 2004; Guyer et al., 2006; Most et al., 2006; Paulus et al., 2003; Schwartz et al., 2003).

Most of these fMRI studies have implied amygdala hyper-reactivity in subjects scoring high on neuroticism. Activity in the amygdala robustly increases in response to unpleasant stimuli, most prominently to fearful and angry faces, even when these stimuli are rapidly masked to prevent conscious awareness. Neuroticism was found to be associated with larger amygdala responses to unpleasant pictures from the IAPS (Canli et al., 2001). Related traits of anxiety and harm avoidance were similarly associated with a larger amygdala fMRI response to angry or fearful faces (Etkin et al., 2004; Most et al., 2006). Finally, enhanced amygdala activity was found in response to novel, neutral face stimuli in adults who had been classified as inhibited as toddlers compared with adults who were not classified as such (Schwartz et al., 2003).

Harm avoidance was also associated with larger anterior cingulate cortex (ACC) reactivity while viewing aversive pictures (Most et al., 2006). Neuroticism was similarly associated with a significant increase in the activation of the dorsal ACC in response to an oddball task (Eisenberger et al., 2005). Intriguingly, the accuracy of the detection of interoceptive signals measured as heart beat perception was much better accounted for by ACC reactivity to the odd ball stimuli ($r_2 = 0.74$) than by self-reported neuroticism ($r_2 = 0.16$) This led the authors to suggest 'that neural reactivities may provide a more direct measure of personality than self-reports do' (Eisenberger et al., 2005: 196).

Paulus et al. (2003) had subjects perform a risk-taking decision-making task in which subjects could opt to try to win a small gain at low risk or larger gains at higher risk. Harm avoidance ($r = 0.54$) and neuroticism ($r = 0.59$) significantly predicted the degree of (mostly right) anterior insula activation during a punished response. They speculate that the insular cortex may be critical for the generation of anticipatory aversive somatic markers that guide risk-taking behavior (Damasio, 1999) and for aversive outcome processing once a decision has been made. Neuroticism appears to be associated with hyper-reactivity of this structure.

There is also some evidence for an effect of neuroticism on reactivity of the frontostriatal circuitry engaged in reward processing.

Forty-four children screened for behavioral inhibition (shyness) at 4 months were retested with fMRI in adolescence (Guyer et al., 2006). This study used the cued reaction time task by Knutson and colleagues (described in more detail below) that had been found to consistently engage the caudate nucleus, putamen, and nucleus accumbens (Knutson and Bhanji, 2006; Knutson et al., 2001, 2003). In all adolescents, activation of these structures became larger as the amount of monetary reward to be gained or lost increased, but the effect was much stronger in the group that had been behaviorally inhibited at 4 months.

EXTRAVERSION

EMG startle reflex

Response size and habituation
The hypothesized lower cortical arousal in the ascending reticular activating system in extraverts suggests that extraversion will be associated with smaller startle responses and faster, more rapid rates of habituation (Blumenthal, 2001). The startle reflex is particularly relevant to test such a hypothesis as the nucleus reticularis pontis caudalis has been implicated in regulating cortical arousal (Gottesmann et al., 1995) and forms part of the acoustic startle pathway (Davis et al., 1999). In support of Eysenck's conceptualization, introverts show larger startle magnitude (Blumenthal et al. 1995; Blumenthal, 2001) than extraverts. Introversion also appears to be associated with a faster response latency to 85 dB(A) than to 60 dB(A) acoustic stimuli, whereas extraverts do not show this difference, suggesting that introverts respond more to higher intensity stimuli (Britt and Blumenthal, 1991). However, differences in response magnitude between introverts and extraverts have not always been found (Akdag et al., 2003). No relationship between BAS scores and startle magnitude was found during the intertrial intervals of an affective startle modulation experiment (Hawk et al., 2003). There is at least one report of an overall greater response probability (indicating more reactivity) in extraverts than introverts, although this was in the context of an affective startle modulation experiment (Kumari et al., 1996).

Blumenthal (2001) showed that selective attention may influence startle magnitude differently in introverts and extraverts. Introverts showed reduced startle amplitude when they directed attention towards a visual display (and away from an acoustic startle-eliciting stimulus). In contrast, startle amplitude tended to increase when extraverts direct attention towards a visual display. The difference may reflect that introverts were better able to allocate attention to the visual task, and were less distracted by the acoustic startle stimulus as less startle reactivity would be expected when attention is directed away from the modality of the eliciting stimulus (Neumann, 2002). Blumenthal (2001) also showed that the rate of startle habituation was faster in extraverts to 90 dB startle pulses than in introverts. The faster habituation in extraverts has been replicated in a study that examined habituation across individual trials during a picture slide presentation and during the intervals between the slides (LaRowe et al., 2006).

Prepulse inhibition
No association between extraversion and PPI has been found across two independent samples (Corr et al., 2002). However, a component measure of Gray's BAS activity, termed BAS-drive, is negatively correlated with PPI at lead intervals of 30, 60, and 120 ms (Corr et al., 2002). The association between BAS and PPI is further supported by an experiment that assessed PPI to an auditory stimulus during and in between picture presentations (Hawk and Kowmas, 2003). PPI assessed during a picture presentation was marginally greater among high BAS participants compared to low BAS participants. Although not statistically reliable, the same difference was found when PPI was assessed during the

intertrial intervals. However, as PPI was assessed during slides that were emotionally toned, it is not clear whether the observed effects were influenced by the affective or attentional effects of the slides. Similar to the association between neuroticism and PPI, the association between BAS and PPI may reflect that high BAS participants attend more strongly to the prepulse stimuli and that this effect may have increased PPI. Further research which systematically manipulates attention to the lead stimulus is required to test this interpretation.

Affective modulation

Predictions of the relationship between affective startle modulation and levels of extraversion are not clear. For instance, extraverts might show greater startle attenuation during pleasant lead stimuli if extraversion is associated with higher levels of positive affect. On the other hand, greater attenuation during pleasant and greater potentiation during unpleasant lead stimuli might be expected in introverts due to their higher level of arousal in the ascending reticular activating system (Kumari et al., 1996) and the observation that lead stimuli that are higher in arousal elicit more pronounced affect startle modulation effects (Lang et al., 1997). An interaction between the valence of pictures and responses latency has been reported (Corr et al., 1995). The interaction reflected that only extraverted participants showed the expected linear pattern of modulation, although the effect seemed to be strongest for fear potentiation as only the difference between unpleasant and neutral slides was statistically significant. No association between extraversion and startle modulation during emotionally toned film clips has also been reported (Kumari et al., 1996).

Gray's model would suggest enhanced affective startle modulation among high BAS and high BIS participants relative to low BAS and low BIS participants. The main difference for BIS and BAS is that the enhanced modulation for high BAS participants should reflect greater attenuation during pleasant stimuli because of the association that pleasant stimuli have

with positive reinforcement. In contrast, the enhanced modulation for high BIS participants should reflect greater potentiation during unpleasant stimuli due to the association that unpleasant stimuli have with punishment. Consistent with these predictions, robust affective startle modulation has been observed for high BAS participants, but not for low BAS participants (Hawk and Kowmans, 2003). Although no groups showed facilitation during unpleasant pictures compared to neutral pictures, only the high BAS participants showed greater startle attenuation during pleasant pictures relative to neutral pictures.

A particularly novel way to examine the relationship between extraversion and psychological processes during emotionally toned situations is to examine startle modulation during a social encounter. In such a situation, it might be hypothesized that introverts will direct their attention inwards more than extraverts (Blumenthal et al., 1995). To test this hypothesis, an experimental assistant entered the participant's room and sat behind the participant while pretending to take notes. High extraversion participants did not differ in startle amplitude between the social encounter condition and a control (no social encounter) condition (Blumenthal et al., 1995). However, in support of the predictions, low extraversion participants showed smaller startle amplitude in the social encounter condition than in the control condition (Blumenthal et al., 1995). The examination of startle modulation during a social encounter may provide a means to specifically target the modulation of startle along the extraversion/introversion dimension, in much the same way that affective startle modulation with fear-provoking stimuli, rather than disgust-provoking stimuli, may more specifically target neuroticism (Wilson et al., 2000).

ERP

Early ERP components

Early research indicated that introverts have a greater N1-P2 amplitude than extraverts when

elicited by infrequent tones (Stelmack et al., 1977), possibly reflecting that introverts attended to the tones more than extraverts. De Pascalis (De Pascalis, 1993) did not observe any direct association between N1 amplitude and extraversion, but did find a positive association between extraversion and auditory and visual N1 frontal ratios. The association reflected that extraverts showed predominantly left hemisphere engagement. These results support earlier findings in which P2 amplitude differed between extraverts and introverts when measured from the left hemisphere, but not when measured from the right hemisphere (De Pascalis and Montirosso, 1988).

Differences in attentional engagement also appear to underlie differences between introverts and extraverts in the N2. Extraverts have a shorter N2 latency than introverts to task irrelevant tone pipes that are superimposed over meaningful and meaningless speech (De Pascalis and Montirosso, 1988). In addition, the N2 amplitude is larger during meaningful speech than during meaningless speech for the extraverts, whereas the opposite difference is found for introverts (De Pascalis and Montirosso, 1988). The difference may reflect that the extraverts are more engaged or attended to the stimuli when the speech is meaningful than when it is meaningless, resulting in the greater N2 amplitude for the former condition. A more positive N2 amplitude in extraverts during a gambling task in which tones indicated a win or a loss has also been reported (Bartussek et al., 1993), although this difference was not due to a distinct effect on N2, but a consequence of a generally more positive ERP amplitude of the extraverts at the time between 250 and 400 ms after stimulus onset. The N2 amplitude of the extraverts in this study was always more positive when the tone indicated a win than a loss (Bartussek et al., 1993). Introverts, however, showed more positive N2 amplitudes to the tones indicating a loss than a win (Bartussek et al., 1993). The data appear consistent with the prediction that extraverts show larger reactivity to stimuli associated with reward than to stimuli associated with

punishment due to the activation of the BAS, whereas the opposite pattern will be found for introverts due to the activation of the BIS (Gray, 1982; Gray et al., 2000).

P3

The P3 amplitude elicited during the oddball paradigm and other similar tasks is smaller in extraverts than in introverts (Daruna et al., 1985; Polich et al., 1992; Pritchard, 1989; Wilson and Languis, 1990) and is likely to reflect the reduced attentional engagement in extraverts. Extraversion may also be related to the habituation of P3 amplitude across trials in that extraverts have displayed a greater decrease in P3 amplitude to the infrequent target stimuli across trial blocks than introverts (Ditraglia and Polich, 1991). Longer P3 latency has also been associated with higher levels of extraversion in a category matching and a same–different judgment task (Stelmack et al., 1993), a simple RT task (Doucet and Stelmack, 2000), and a reaction time task that varied stimulus and response location (Brebner, 1990). In contrast to these findings, P3 amplitude has been found to be greater in extraverts than in introverts (Cahill and Polich, 1992; Gurrera et al., 2001, 2005). Others investigations have found no relationship between extraversion and P3 (Ditraglia et al., 1991; Plooij-van Gorsel, 1981; Pritchard, 1989). One interpretation for the inconsistent pattern of results is that it reflects features of the experimental procedure. For instance, if extraverts habituate more rapidly to repetitive stimuli than introverts do (Ditraglia et al., 1991; Polich et al., 1992), different results may emerge depending on the number of trials used in the experiment (Gurrera et al., 2005). The use of community samples may also be more likely to yield a relationship than undergraduate student samples due to a greater range of extraversion scores in such samples (Gurrera et al., 2001).

The P3 elicited following the presentation of emotionally toned words may also vary as a function of extraversion for the same reasons that extraversion should be related to

affective startle modulation. Bartussek et al. (1996, experiment 1) found that a complex relationship emerged when emotionally toned and neutral words were presented during a structural processing task, requiring a decision about whether a word is longer or shorter than six letters, and an affective processing task, requiring a rating of the affective valence of emotionally toned words. In extraverts, P3 amplitudes during the structural processing task showed a maximum amplitude at parietal electrode sites and a larger amplitude for pleasant and unpleasant words than neutral words. The difference between the emotionally toned and neutral words became less pronounced at a central electrode and was not present at a frontal electrode. In contrast, introverts showed higher P3 amplitudes during the emotionally toned words than during the neutral words at a parietal site only during the affective processing task. The results seem to indicate that extraverts reacted differentially to the emotional arousal associated with the words even in a task that did not require attention to be directed towards the emotional content. For the introverts, P3 amplitude at a frontal electrode was also larger to unpleasant and neutral words than to pleasant words, a result consistent with Gray's theory of an increased sensitivity of the BIS, and thus greater reactivity to stimuli associated with punishment. In a similar vein, results from the gambling task described above found that extraverts showed larger P3 amplitudes after a loss in the preceding trial, compared to winnings (Bartussek et al., 1993). The opposite was true for the introverts as P3 amplitude was larger when having won in the preceding trial than after a loss (Bartussek et al., 1993). Signals presented after a win may have been perceived as more negative as participants were likely to expect that the next trial would be a loss because an equal number of trials resulted in a win and loss. Likewise, signals presented after a loss were interpreted as positive because participants expected that the next trial would result in a win (Bartussek et al., 1993). Based on this interpretation of

the meaning of the signals, the greater P3 amplitudes to signals presented after a loss for extraverts and greater P3 amplitudes to signals presented after a win in introverts is consistent with Gray's theory.

fMRI

The link between extraversion and functional MRI reactivity has been most systematically studied by Canli and colleagues (Canli, 2004; Canli et al., 2001, 2002, 2004). In a first study (Canli et al., 2001) they showed that the neural representation of personality traits may be widely distributed throughout the brain. In 15 different brain regions extraversion from the NEO-PI showed a significant correlation to an increase in the fMRI BOLD signal that was selective to pleasant images from the IAPS contrasted to unpleasant images. Two regions clearly stood out: the amygdala and the anterior cingulate cortex (ACC). Differential activation of these regions in extraverts has since then been replicated in different task settings (Amin et al., 2004; Canli et al., 2002). The larger response of the amygdala to pleasant IAPS pictures (Canli et al., 2001) as well as happy facial expressions (Canli et al., 2002) in extraverts is of particular interest because this structure had been primarily associated with the processing of negative affect. Indeed, as we saw, neuroticism increases the amygdala response to negatively valenced stimuli. Canli et al. (2002) clearly showed that the extraversion also influences this structure, albeit only during the processing of positive affect. Interestingly, the activation of the amygdala was left-lateralized; that is, located within the hemisphere that has been associated with positive emotions and with approach-related behavior in the EEG asymmetry literature (Davidson et al., 2000).

Because the ACC has been associated with attention to emotional stimuli (Whalen et al., 1998) the finding of larger ACC reactivity in response to pleasant stimuli would be compatible with the hypothesized attentional bias

for reward stimuli in extraverted subjects (Derryberry and Reed, 1994). However, some caution is in order with the interpretation of ACC reactivity as purely reflecting the activation of an attentional system. Critchley and colleagues have repeatedly shown that the ACC is activated by afferent and efferent activity of the autonomic nervous system (Critchley, 2003; Critchley et al., 2000, 2004, 2005). The autonomic nervous system is activated by any form of arousal, either related to fear, anger, or excitement. The larger ACC reactivity seen in extraverts may therefore also reflect a greater arousability. That this greater arousability is selective to pleasant stimuli would fit the hypothesized higher sensitivity to reward in extraverts.

In keeping, extraversion has been linked to activity in the mesolimbic dopaminergic reward processing system running from the ventral tegmental area to the lateral hypothalamus, the ventral striatum (most prominently the nucleus accumbens) and parts of the medial prefrontal cortex (Knutson and Bhanji, et al., 2006). To test reactivity of this system with fMRI recordings, Knutson et al. (2001, 2003, 2006) developed a monetary incentive-processing task in which participants see a cue indicating whether they can gain or avoid losing money and how much is at stake. After a short delay subjects must rapidly respond to a presented target. Feedback on their success (i.e. were they fast enough?) is immediate and they are presented with the amount lost or gained and their cumulative total. Functional MRI recording during this task showed that potential losses only activated the thalamus and caudate nucleus, but that the nucleus accumbens was additionally activated by the anticipation of potential gain. Large individual differences in the degree of nucleus accumbens activation were found that corresponded to the subjectively experienced cue-elicited happiness in this study and to excitement in another study (Bjork et al., 2004). Activation of the nucleus accumbens was selective to gain anticipation rather than gain outcome, since the increase in BOLD fMRI signal intensity ceased after feedback of success

(Knutson et al., 2001). In contrast, gain outcome, but not gain anticipation, did engage the medial prefrontal cortex (Knutson et al., 2003). Pooling across their studies extraversion was found to correlate with activation in the nucleus accumbens, medial caudate, and MPFC for gain versus non-gain anticipation, but not to loss versus non-loss anticipation (Knutson et al., 2006). The larger reactivity of these areas in extraversion was corroborated by another study (Cohen et al., 2005), although in this study reward evaluation rather than reward anticipation seemed to be more important.

The effects of extraversion on brain functioning are not limited to affective processing but are also evident during cognitive processing (Kumari et al., 2004; Stenberg et al., 1990). One study examined the influence of extraversion in fMRI activity during an '*n*-back' task involving memory loads (0-, 1-, 2-, and 3-back) and a rest condition in healthy men (Kumari et al., 2004). As predicted by Eysenck, maintaining adequate cognitive performance required a larger increase in cortical arousal in the extraverts as evidenced by greater changes in fMRI signal intensity from rest to the 3-back condition in the ACC and the dorsolateral prefrontal cortex. In further keeping with the neurobiological underpinnings of Eysenck's model, higher extraversion scores were negatively associated with resting fMRI signals in the bilateral thalamus, cuneus and left hemisphere language areas, suggesting lower baseline arousal in these areas, possibly due to extraverts engaging in less internal self-talk than introverts.

DISCUSSION

The above review identified a number of theoretically meaningful and reproducible correlations between psychophysiological measures and personality traits measured by some of the major questionnaires used in the field (Carver and White, 1994; Cloninger et al., 1991; Costa and McCrae, 1992; Eysenck and Eysenck, 1994). Neuroticism and related

traits have been related to larger startle modulation during fear eliciting scenes (Caseras et al., 2006; Wilson et al., 2000). These findings are in accord with Eysenck's notion of hypervigilance to threat/danger in these individuals. Such hypervigilance is also compatible with the gist of studies comparing fMRI responses in low and high neurotic subjects. These studies tended to converge on areas involved in the processing of stimuli signaling conflict threat or disgust; that is, the amygdala, the insula, and the ACC (Canli et al., 2002; Eisenberger et al., 2005; Paulus et al., 2003). Research on extraversion has shown that introverts are generally more reactive with startle amplitude than extraverts, with or without instructions to attend (Blumenthal, 2001). Furthermore, trial-by-trial habituation of the startle reflex is more rapid in extraverts. The N2 amplitude of extraverts was found to be more positive when the signal indicates a win than when the signal indicates a loss whereas the opposite pattern is found for introverts. This is consistent with the prediction that extraverts compared to introverts will show larger reactivity to stimuli associated with reward than to stimuli associated with punishment. In keeping, functional MRI studies have found extraversion to correlate with the extent of activation in the nucleus accumbens, medial caudate, and MPFC in gain versus non-gain anticipation trials (Knutson et al., 2006) and with the extent of activation in the nucleus accumbens and MPFC in response to actual reward (Cohen et al., 2005). Pleasant stimuli (e.g. happy faces) only engage the amygdala and the anterior cingulate cortex (ACC) in extraverts (Amin et al., 2004; Canli et al., 2002).

In summary, despite small sample sizes and the absence of special subject selection in most studies, significant correlations exist between psychophysiological reactivity and paper-and-pencil-based assessment of personality. These correlations are generally modest but reach into the range of large effects sizes ($r > 0.70$) where up to half of the variance in evoked EMG, EEG, or fMRI activity and self-reported personality derives from a shared underlying factor. Note, however, that

we can also turn that argument around: a large part of the variance in paper-and-pencil-based personality is not shared with psychophysiological reactivity. This raises the question of which of these types of measures best captures the theoretical construct of personality. Before we can compare their relative merit, psychophysiological indices must first be subjected to the same rigorous psychometric demands as paper-and-pencil tests. Put otherwise, they must be shown to have good test–retest reliability, validly index the brain processes they claim to index (construct validity) and to predict behavior across a wide range of situation (predictive validity). This is a huge challenge, both in terms of person-power and finance, because the complexities in the data acquisition and data analysis in psychophysiological research often reduce the sample size to very small numbers, particularly when compared with questionnaire based research.

The test–retest reliability for some psychophysiological measures has been shown to be moderate to high. For instance, good to excellent reliability has been reported for the P3 (Smit et al. in press), fMRI activation during memory encoding (Aron et al., 2006; Wagner et al., 2005), and the habituation and prepulse inhibition of the startle eye-blink reflex (Abel et al., 1998; Flaten, 2002). However, it has been disappointingly low for other measures, including affective startle modulation (Anokhin et al., 2007), EEG asymmetry (Smit et al., 2007), and fMRI activation during a working memory task (Manoach et al., 2001). This may be due to the inherent complexity of signal generation, flaws in recording techniques and strategies, or a failure to standardize testing conditions (e.g. stimuli, instructions, participant-experimenter interaction), all of which can reduce reliability.

Based on a large body of experimental studies in animals and neurological patients, the construct validity of brain activity as the basis for behavioral tendencies is very large (Kandel et al., 2000). However, there is no perfect one-to-one mapping of psychophysiological indices on brain activity. Although the temporal resolution of EEG recordings is excellent,

it is hard to estimate the exact sources in the brain generating the observed patterns of electrical activity. This so-called inverse problem arises because an infinite number of possible charge distributions in the head could lead to the same pattern on the scalp. Although clever modeling techniques have been successfully used to tackle this problem, signals that arise from more than a few dipoles remain hard to localize with precision. Localization of the source of brain activity is much better with fMRI than with EEG, but the relation between the recorded signal (blood oxygenation) and underlying neural activity remains a matter of debate. Although it is commonly assumed that it represents excitatory neural activity, there is disagreement about whether it cannot also represent inhibitory neural activity (Waldvogel et al., 2000). Second, an increase in activation during one condition is equivalent to a decrease during the other condition. What is interpreted as an increase in activation to pleasant pictures, for instance, could instead have represented a decrease in activation to unpleasant pictures. Finally, correlation does not equal causation. A brain region that is activated during a task may not play a critical role in the task's performance. The region may merely be 'listening in' to the activity in other brain areas that constitute the true sources of individual differences.

To date surprisingly little is known about the predictive validity of psychophysiological reactivity. There are a number of studies showing predictive validity of psychophysiological reactivity to the development of psychopathology; for example, in the areas of schizophrenia (Keshavan et al., 2005) and alcoholism (Hill and Shen, 2002). However, this literature is much less well developed than that for paper-and-pencil measures of personality that are known to significantly predict anxiety disorders, depression, drug abuse, and antisocial behavior (Cloninger et al., 2006; Masse and Tremblay, 1997). Also, no studies known to us have addressed the predictive validity of psychophysiology for lifestyle parameters (smoking, exercise, sexual

practices) or behavioral outcomes like career choices or job success.

In short, reliability of psychophysiological measures is currently less convincing than those for paper-and-pencil measures and validity has been far more rigorously tested for the latter. It is of note, however, that many of the studies reviewed here have silently adopted the stance that a *single* psychophysiological measure should index personality. This makes for an unfair comparison to paper-and-pencil tests that use multiple weighed items to arrive at a summary score. We believe a large increase in reliability and validity of a psychophysiological test battery could be achieved by looking at patterns of psychophysiological responding on multiple measures and to multiple types of stimuli rather than a single measure on a single class of stimuli. Ideally, multiple psychophysiological responses (ECG, SCL ERP, and fMRI) would need to be recorded consecutively, or even more ideally simultaneously, in the same subject in response to various classes of stimuli (e.g. emotional pictures, reward, and punishment). The response of each measure to each particular class of stimuli can be considered a single psychophysiological 'item'. These items would be subjected to factor analyses just as the items of personality inventories to obtain a factor structure and ultimately sum scores. Indeed 'ordinary' items for a personality inventory may be merged with psychophysiological items to obtain a hybrid 'subjective/objective' personality measure. This has the potential to anchor the new personality measure to the large existing theoretical framework based on paper-and-pencil while adding biological foundation. Therefore, rather than pitch psychophysiological recordings as more scientific alternatives to paper-and-pencil assessment, we propose to use these measurements as a way to support theory-building on the neurobiological basis of personality.

Implications for neuroscience

Although much work remains, the psychophysiological studies on personality research

reviewed in this chapter already convey a very important message to the field of neuroscience. Mainstream neuroscience is still very much focused on universal affective and cognitive brain processes at the expense of individual differences (Kosslyn et al., 2002; Plomin and Kosslyn, 2001). By not taking individual differences into account, or considering them a mere nuisance variable, many neuroscience studies may have failed to detect a link between a brain structure and the putative affective and cognitive processes in which it is involved. It had, for instance, been assumed from group fMRI recordings that the amygdala is not involved in the processing of stimuli with a positive emotional value. By bringing personality into the equation, Canli et al. (2002) have proven this wrong. The amygdala does strongly influence such processing, but its total activation is a function of the level of extraversion. In short, by not taking personality differences into account, neuroscience runs the risk of presenting us with 'universal processes' in affect and cognition that reflect the average pattern of brain activity across many individuals, but do not really occur in any single individual.

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