Affective personality differences in neural processing efficiency confirmed using fMRI

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Abstract

To test for a relation between individual differences in personality and neural processing efficiency, we used fMRI to assess brain activity within regions associated with cognitive control during a demanding working memory task. Fifty-three participants completed both the self-report BIS-BAS personality scales and a standard measure of fluid intelligence (Raven's Advanced Progressive Matrices). They were then scanned as they performed a 3-back working memory task. A mixed blocked / event-related fMRI design enabled us to identify both sustained and transient neural activity. Higher BAS was negatively related to event-related activity in dorsal anterior cingulate, lateral prefrontal cortex, and parietal areas in regions of interest identified in previous work. These relationships were not explained by differences in either behavioral performance or fluid intelligence, consistent with greater neural efficiency. The results reveal high specificity of the relationships among personality, cognition, and brain activity. The data confirm that affective dimensions of personality are independent of intelligence, yet also suggest that they might be inter-related in subtle ways, because they modulate activity in overlapping brain regions that appear critical for task performance.

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Some important aspects of the human psyche are consistently revealed in brain function but not in overt behavior (Wilkinson & Halligan, 2004). The central focus of this article is one such endophenotype, namely *neural processing efficiency,* or the relative ease with which someone performs a given information processing task. Individuals who need to exert greater mental effort to perform a task or compensate for stressful circumstances (Hockey, 1997) can be said to have lower efficiency. The key individual differences may not be revealed in overt behavior (performance) despite real and important differences in the facility with which that performance level is achieved (i.e., efficiency). Relatedly, one function of the prefrontal cortex may be to exert compensatory control over behavior when additional demands are imposed (Braver *et al.*, 1997; Bunge *et al.*, 2000). In this article, we use fMRI to study individual differences in personality, compensatory control, and neural efficiency during a cognitive load.

Eysenck and Calvo (1992) elaborated the idea of cognitive processing efficiency, doing so to account for exceptions in the literature on the effects of trait anxiety on performance. Anxious individuals often have lower performance (especially on difficult tasks), but not always. Why should there be exceptions? Eysenck and Calvo drew a key distinction between *performance effectiveness* and *processing efficiency*. Effectiveness refers to an objectively measurable level of performance, such as the percentage of questions answered correctly on a test. Efficiency refers to the ratio between effectiveness and the amount of effort needed to attain the criterion level of performance. According to Eysenck and Calvo, anxiety impairs processing efficiency more than it impairs performance effectiveness, thereby leaving open whether performance is actually impaired or not on a given occasion. High-anxious individuals are hypothesized to be less efficient but can compensate by expending additional effort on the task. This hypothesis holds considerable explanatory potential. A practical difficulty with testing the cognitive processing efficiency model, however, is that one of its central constructs, mental effort, cannot be measured directly in behavioral performance. To overcome the difficulty, one possibility is to use physiological indicators of effort (M. W. Eysenck & Calvo, 1992; Fairclough & Houston, 2004; J. R. Gray & Braver, 2002).

A potentially useful physiological index of mental effort is task-related activity within working memory networks, including dorsal anterior cingulate cortex (ACC) and the lateral prefrontal cortex (PFC) (J. R. Gray & Braver, 2002). Dorsal ACC is part of the network of brain areas that support cognitive control (e.g., Bush *et al.*, 2000; Devinsky *et al.*, 1995; MacDonald *et al.*, 2000; Paus, 2001; Paus *et al.*, 1998). Activation in the dorsal ACC has been reported for complex or difficult cognitive tasks (Bush et al., 2000; Devinsky et al., 1995; Paus, 2001; Paus et al., 1998), and for this reason appears related to mental effort. Interestingly, activity in the ACC has been linked to peripheral psychophysiological responses (Critchley *et al.*, 2001), and such peripheral measures are also used to index mental effort (e.g., Fairclough & Houston, 2004). The lateral PFC is also part of a wider network subserving cognitive control. The magnitude of dorsolateral PFC activity varies parametrically with working memory load at a group level (Braver et al., 1997), and activity in ventrolateral and dorsolateral PFC increase with performance differences, as tested at an individual level (Rypma & D'Esposito, 1999). Finally, individual differences in fluid intelligence predict brain activity in the lateral PFC during a working memory task (J. R. Gray *et al.*, 2003).

While recent investigations of personality have often focused on individual differences in affective processes (Canli *et al.*, 2002; Costa & McCrae, 1980; Larsen & Ketelaar, 1991), there is also theoretical and empirical work focusing on differences in information processing, including working memory (Humphreys & Revelle, 1984). Several recent studies illustrate this emphasis. For example, extraversion correlated positively with performance on a verbal n-back task (Lieberman & Rosenthal, 2001), which is known to recruit the PFC and central executive component of working memory (Braver et al., 1997). Of note, extraverts performed better only under conditions that imposed a high cognitive load (e.g., multi-tasking but not single tasks), consistent with a processing efficiency explanation. Under conditions of low cognitive load, introverts may be able to compensate for lower processing efficiency by increased exertion of mental effort, but as task difficulty increases, such compensation reaches its limits. Extraverts also had better performance in a Sternberg task (Lieberman, 2000) and a prospective memory task (Heffernan & Ling, 2001), both of which recruit the prefrontal cortex.

Our focus is on two personality traits that we refer to as *behavioral approach sensitivity* (BAS) and *behavioral inhibition sensitivity* (BIS) (Carver *et al.*, 2000; Carver & White, 1994; J. A. Gray, 1994; Sutton & Davidson, 1997). In theory, BIS represents individual differences in sensitivity to cues of threat (threats induce behavioral inhibition and withdrawal), and BAS represents individual differences in sensitivity to cues of reward (rewards induce behavioral approach). Personality theorists are essentially unanimous that two major personality dimensions are associated with differences in emotional processing (Costa & McCrae, 1980; J. A. Gray, 1994; Larsen & Ketelaar, 1991; Zelenski & Larsen, 1999). These are typically called extraversion and neuroticism, although some theorists call them BAS and BIS, or positive affect and negative affect. Certainly, BAS and BIS are related to extraversion and neuroticism, although the exact relation is debated. Although perhaps not the dominant view, Carver, Sutton, and Scheier (2000) argued that BIS and BAS may represent what is most fundamental about neuroticism and extraversion. We are interested in possible relations between individual differences in sensitivity to cues of reward (BAS) and cognitive control processes, with the guiding intuition that individual differences in goal-directed (reward seeking) processes might relate to differences in the cognitive and neural mechanisms support goal-directed behavior (i.e., cognitive control, including working memory).

Several theories of extraversion use the concept of arousal to explain the personality – cognition relationships. This account is based on two assumptions: Eysenck suggested that extraverts and introverts were mainly differentiated by their basal arousal level, extraverts having a lower arousal level than introverts (H. J. Eysenck, 1967). And it is posited that the effects of arousal on cognitive performance conform to an inverted-U function (Yerkes & Dodson, 1908), in which moderate levels of arousal have a beneficial effect on performance, whereas low or high levels have a detrimental effect, especially in complex cognitive tasks (Humphreys & Revelle, 1984). The consequence is that introverts are expected to perform better than extraverts in low-arousal tasks, but to be outperformed by extraverts in high-arousal tasks. A more contemporary version of the arousal account is provided by Lieberman and Rosenthal (2001), who proposed to link the concept of arousal with catecholamine activity, more particularly to dopamine and norepinephrine. Norepinephrine is more related to wakefulness and anxiety, and dopamine to positive affect and novelty detection. Intriguingly, dopamine is released during demanding tasks (Aalto *et al.*, 2005).

There are few neuroimaging studies of personality and processing efficiency, although several imaging studies have examined personality and activity during cognitive tasks (e.g., Ebmeier *et al.*, 1994; Kumari *et al.*, 2004). We recently investigated the effects of personality on working-memory related activity using a block-design fMRI study (J. R. Gray & Braver, 2002).

In 14 participants, we found a negative correlation between activity in dorsal ACC (also called caudal ACC) and BAS. In addition, we found marginal relations between ACC activity and BIS. Behaviorally, in 129 participants, we found a weak, positive relationship between BAS and n-back performance ($r = .18$, $p < .05$), with a larger effect size in the 14 participants who were scanned ($r = .27$). Despite significant results, a limitation of the fMRI study was the small sample size.

Individual differences in neural processing efficiency have also been related to cognitive variation, and in particular have been hypothesized to help explain the relation between intelligence and brain activity (Haier *et al.*, 1992). On the basis of a negative correlation between psychometric intelligence and cerebral glucose metabolic rate, Haier and colleagues suggested that greater neural efficiency should help individuals achieve higher scores on intelligence tests. Other work suggests that whether high IQ individuals show a pattern of greater neural efficiency depends upon participant sex and task content (Neubauer *et al.*, 2002), and positive correlations are also found (J. R. Gray et al., 2003; Haier *et al.*, 2003). Negative relations could reflect behavioral differences (working longer on a task should lead to greater activity), and so by themselves do not unambiguously imply differences in neural efficiency specifically. Importantly, psychometric intelligence has been consistently related to the speed of information processing, e.g., as assessed by inspection time (for reviews see Deary, 2000; J. R. Gray & Thompson, 2004). Moreover, inspection time is supported by brain activity in two networks (Deary et al., 2004), one apparently related to cognitive control (based on localization to regions associated with cognitive control). Thus prior work suggests that, at a minimum, it may be important to assess and control for psychometric intelligence when investigating personality differences in neural processing efficiency. A third dimension of personality (as assessed using the NEO-PI), Openness to Experience, has been consistently related to intelligence and cognitive function, so much that it is increasingly referred to as Openess / Intellect (DeYoung *et al.*, in press).

The aim of this paper is to extend empirical work on personality, mental effort, and processing efficiency at a neural level. To do so, we follow-up and extend a conceptually similar investigation in our previous study (J. R. Gray & Braver, 2002). The current report replicates this study closely, but goes beyond it by: a) considering affective and cognitive variables simultaneously, controlling for individual differences in fluid intelligence and behavioral performance when assessing personality effects, b) using a mixed state-item design, to assess both transient and sustained neural activity, c) examining regions outside of the ACC that also support cognitive control and working memory, and d) doing so in a large fMRI sample (n=53). The two key empirical questions we address are: Does the negative correlation between BAS and working-memory-related activity hold in areas known to be critical for working memory and cognitive control? And is this relationship not explained by differences in behavioral performance or fluid intelligence? We sought and found clear evidence for both questions, strongly suggesting that higher BAS is related to less mental effort and greater neural processing efficiency. Psychometrically, our overall approach is very strong: an initial exploratory investigation in a first dataset (J. R. Gray & Braver, 2002) followed by a confirmatory investigation in an independent dataset (here).

Method

Participants

Participants were healthy, right-handed, native English speakers (n=60, 29 male; age 18–37 years) from Washington University and the surrounding community, screened to exclude a history of neurological disorder, current psychoactive medication, or factors contra-indicating fMRI. All participants gave written informed consent. None participated in our previous report (J. R. Gray & Braver, 2002); that is, the samples are completely independent. The experiment was approved by the Washington University Medical Center Human Subjects Committee. Of the 60 participants who completed the protocol, some had fMRI datasets that were compromised by excessive head movement, technical problems, unacceptably low behavioral performance, or too few correct trials for estimating event-related responses. This left n=53 for one set of analyses (sustained state-related activity and transient item-related activity) and n=48 for a second set of analyses (in which item-related activity was further classified into trial types with varying degrees of difficulty).

Procedure and Design

To assess variation in personality, we used the 20-item self-report BIS-BAS scales (Carver & White, 1994) and EPQ-R (S. B. G. Eysenck *et al.*, 1985), administered prior to the fMRI session.

To assess variation in cognitive ability, we used the Raven's Advanced Progressive Matrices (APM) (Raven *et al.*, 1998), a standard test of fluid intelligence, also administered prior to the fMRI session. Fluid intelligence was taken to be the number of correct responses on APM set II (36 questions) made in 40 minutes, after practice on three items from APM set I.

To assess variation in neural activity, we used fMRI to assess activity as participants performed a 3-back working memory task that was administered using PsyScope (Cohen *et al.*, 1993) on a Macintosh G3 (Apple Computer, Cupertino, CA, USA). The 3-back task consisted of viewing a series of stimuli. The instructions were to indicate for each stimulus whether it matched or did not match the stimulus seen exactly three previously ("3 back"). Responses were made using fiber-optic response keys. To respond with high accuracy, participants must keep track of several stimuli at once, every few seconds updating which stimuli are relevant. Most participants found this challenging but not overly so. For a given scanning run, stimuli were either all words (concrete English nouns) or all faces (unfamiliar, male and female intermixed) (J. R. Gray *et al.*, 2002). Stimuli were shown one per trial for 2.0 s, with a fixation point (cross-hair) shown between stimuli (for 0.36 s). Each scanning run had 4 unanalyzed trials, followed by four blocks of 21 task trials (16 task stimuli with 5 crosshair fixation trials, 2.36s each, randomly interspersed to introduce temporal jitter) and 23.6s (10 trials) of resting fixation (a dash), for a total of 128 trials per scanning run (2.36s per trial).

MR image acquisition and analysis

Localizer images, a high-resolution structural image (MPRAGE), and a series of functional images were collected on a Siemens 1.5T Vision system. Functional (echo planar) images consisted of 16 axial slices, each 8mm thick with 3.75 x 3.75 mm in-plane resolution.

Data from two scanning runs per participant are reported here (one run with words, one run with faces, order counterbalanced), although additional runs were also obtained. Just prior to each scanning run, participants watched one of six 7 min videos, two of which were emotionally neutral and four of which were emotionally evocative (order counterbalanced). The videos were included as part of another investigation focusing on the emotional conditions. All imaging data reported here are from the two neutral conditions.

Based on our prior work, we had specific functional-anatomic predictions, including both the direction of correlations as well as which brain regions should show them. We therefore opted to conduct region-of-interest (ROI) analyses exclusively, using ROIs from published work. This strategy allows a direct and conservative replication, while also remaining sensitive to potentially weak effects (controlling for false positive results by having specific predictions, rather than by correcting for multiple comparisons across the whole brain). Because we were also interested in the potential relation with intelligence, we also examined activity within four ROIs that had been defined previously within the current dataset (n=48) on the basis of their relation to fluid intelligence (J. R. Gray et al., 2003), Figure 1a: bilateral lateral PFC (BA 44/45/46: left 21 voxels at –46 18 24 and right 65 voxels at 44 9 21) and bilateral parietal cortex (BA 40: left 8 voxels at –56 –42 33, right 12 voxels at 46 –33 45). These were the only regions that plausibly mediated the relation between fluid intelligence and working memory performance, and thus are especially interesting to examine in regard to mental effort, processing efficiency, and compensatory control. We also examined four subregions in ACC, using the same regions as defined previously in a fully independent sample (n=14) (J. R. Gray & Braver, 2002). The four ACC regions, Figure 1b, were defined on the basis of comparing 3-back task activity against a resting fixation, as showing either predicted activation (caudal / dorsal ACC: 110 voxels centered on Talairach coordinate 22 9 45) or predicted deactivation (posterior-rostral ACC: 47 voxels at 22 24 12; rostral ACC: 83 voxels at 2 42 9; subgenual ACC: 26 voxels at 2 36 26).

Specifically, we predicted to replicate our previously observed negative correlation between BAS and working memory related activity in dorsal ACC and the four ROIs related to fluid intelligence, but not in the three other ACC subregions. We were agnostic whether the relation should hold in item-related activity, state-related activity, or both.

The data were preprocessed and analyzed in several stages prior to the extraction of activation values from the ROIs. After movement and artifact correction, functional images were normalized within each scanning run and temporally aligned within each brain volume.

Functional images were resampled into 3 mm isotropic voxels, transformed into atlas space (Talairach & Tournoux, 1988), and smoothed with a Gaussian filter (9mm FWHM). We then constructed two general linear models (GLM) for each subject, each estimating activity at each voxel. The first GLM was created which included state and item regressors for face and word conditions separately, allowing us to statistically separate neural signals that were sustained across the task block ("state") from those that were transient ("item") (Braver *et al.*, 2003; Donaldson *et al.*, 2001).

To permit a more detailed analysis in terms of trial types that varied in the demand for cognitive control, the second GLM was similar but had three types of items rather than one generic item type. In a previous study involving the n-back task and RAPM scores (J. R. Gray et al., 2003), strong differences in behavioral performance demonstrated that different n-back trials vary considerably in difficulty. This effect suggested a differential relation to the demand for cognitive control: higher demand on "lure" trials (nontarget trials with a 2- 4- or 5-back match, in which a strong spurious sense of familiarity led to high interference), low demand on "nonlure trials" (low interference nontarget trials with no previous match, or with a match that was not temporally proximal to the 3-back item), and intermediate demand on target trials (3-back match).

Both GLMs gave estimates of the magnitudes of the state and item activity, indexed in terms of the percentage of change in the MR signal. The magnitude estimates were then averaged over all voxels within a given ROI, and then over stimulus type. The resulting average values were then correlated with individual difference variables.

Results

Behavioral data

The distributions of BIS and BAS scores were consistent with other samples (Carver & White, 1994; J. R. Gray & Braver, 2002), with good variability: BIS scores (mean 20.4, SD 3.99, range 10 to 27) and BAS scores (mean 40.7, SD 5.8, range 26 to 52). APM scores were above the general population average (mean 26.0, SD 4.27, range 11 to 34), also with a good range. As expected, participants' BIS, BAS, and APM scores were uncorrelated, $r = -.06$ for APM with BAS, $r = -.04$ for APM with BIS.

There was no correlation between BAS and mean accuracy in the working memory task (assessed in terms of the signal detection measure, d'), $r = -.03$, nor between BAS and mean response time (RT), $r = -.19$, p's > .10.

The intercorrelations among personality variables were as expected, with positive relations between BAS and E, $r = .56$, $p < .001$, and BIS and N, $r = .59$, $p < .001$, a marginal correlation between BIS and E, $r = -.24$, $p = .087$; all other p's > .15.

Neuroimaging data

State- and item-related activity. As predicted, BAS was negatively correlated with item-related activity in the five *a priori* ROIs related to cognitive control (dorsal ACC, bilateral PFC, and bilateral Brodmann Area [BA] 40; see Table 1). The negative correlation indicates lower item-related activation for participants with higher BAS scores. There were negative correlations between BAS and activity in left lateral PFC, left parietal lobe, and right parietal lobe, and right lateral PFC. Confirming our previous findings, BAS correlated negatively with activity in dorsal ACC. When formally testing for differences in the strength of correlations (adjusting for the fact that these correlation coefficients are not statistically independent; see Meng *et al.*, 1992), the BAS - activity relation was more strongly negative in dorsal ACC than in the other three ACC subregions, all p's < .05. Although BAS correlated positively with item-related activity in subgenual ACC (representing less item-related deactivation for higher BAS), this correlation was not predicted *a priori*, and did not survive a Bonferroni correction for the 6 comparisons (3 ACC subregions x 2 activity types). On the other hand, some correlations that were not predicted *a priori* nonetheless survived correction for multiple comparisons. Specifically, BIS correlated positively with state-related activity in rostral ACC (less sustained deactivation for higher BIS), and BAS was positively correlated with state activity in right BA 40.

Critically, the above relationships between BAS and item activity (in dorsal ACC, bilateral PFC, and bilateral parietal lobe, and between BIS and state activity in rostral ACC) were not explained by behavioral performance or fluid intelligence. Specifically, the partial correlations between personality (BAS, BIS) and task-related activity, when controlling for APM scores (fluid intelligence), accuracy, or RT, were either the same or larger than the zero-order correlations.

<u>Activity on specific trial types.</u> As shown previously, behavioral performance on the n-back task demonstrated that some of the trials were more difficult than other trials, with lure trials imposing a markedly higher demand on cognitive control than target or nonlure trials. Therefore, we investigated whether the relationship between BAS and transient (item) activity would also be specific to one trial type, or whether it would hold generally across all trial types.

The correlation with BAS did not hold selectively to the lure trials, the condition with the highest demand for cognitive control (see Table 2). BAS was related to lure trial activity, but was also related to activity on other trial types. BAS predicted transient neural activity (at significant or marginally significant levels) in 8 of 12 tests (4 regions x 3 activity type combinations). These relationships persisted, even after controlling for APM scores, for accuracy, or for RT. BIS had no relation to activity on specific trial types.

Activity estimates from a block-design analysis. To facilitate comparison to our prior report (J. R. Gray & Braver, 2002), we also analyzed the current data in a block-design rather than state-item analysis. The dorsal ACC – BAS correlation held slightly more strongly, $r = -.37$, $p = .006$, whereas none of the other ACC regions correlated significantly with BAS, all r's $< .16$, p's $> .25$.

Correlation with extraversion. Given the strong correlation between BAS and Extraversion, it is not surprising that Extraversion was related to brain activity in much the same way as BAS.

Discussion

The results provide clear answers to the two empirical questions we started with. First, BAS was indeed associated with greater task-related activity in all five theoretically relevant brain regions, namely bilateral lateral PFC, bilateral parietal cortex, and dorsal ACC. Moreover, these results also held when controlling statistically for individual differences in behavioral performance and fluid intelligence. The specificity of these effects directly implies that the results are not simply an artifact of high BAS individuals being less willing to work at the task (and so engaged these neural networks less strongly, which would also be revealed in behavioral differences), nor that high BAS individuals are simply more intelligent and so did not need to recruit these networks as strongly to achieve the same level of behavioral performance. Thus, the overall pattern of results strongly indicates BAS-related individual differences in neural processing efficiency, and argue against a differential recruitment of mechanisms that are otherwise equivalently efficient (e.g., due to motivation, intelligence, and other nonspecific factors).

The data also bear on relationship between two major dimensions of human individual differences: affective aspects of personality and intelligence (cf. Bates & Rock, 2004). On the one hand they confirm that personality and intelligence are independent, because they had no correlation and made independent contributions to lateral PFC and parietal activity. Yet by the same token, the two constructs might be inter-related, because they modulate activity in overlapping brain regions that appear critical for task performance.

The observed correlation with BAS in dorsal ACC (-.28, item-related activity) was in the same direction albeit weaker than the correlation we observed previously (-.63 in the neutral conditions, block design). Although the previous 95% confidence interval (r = -.87 to -.18) includes the current value, the weaker effect here could also reflect increased susceptibility to noise in the state-item design. The dorsal ACC-BAS correlation was indeed stronger when conducting a block-design analysis (r = -.37) instead of the state-item analysis, yet still weaker than our previous report. This underscores the value of conducting confirmatory (replication) studies, and of using large samples.

The BAS effect did not hold exclusively on trials imposing the strongest demand on cognitive control, namely the lure trials. Instead, the neural processing efficiency associated with high BAS individuals effectively held across all trial types—not uniformly, but clearly lacking the strong specificity to the lure trials that we observed for fluid intelligence in these same participants (J. R. Gray et al., 2003). One possibility is that even the nonlure and target trials impose some demand on cognitive control, but just less than the lure trials. Indeed, behaviorally, accuracy on target and nonlure trials was also significantly correlated with fluid intelligence (*r*'s = .29 to .36) while brain activity on those trials was not.

To speculate, a possible mechanistic explanation of the BAS – activity relationship derives from a recent theoretical account of extraversion, based on the neurotransmitter dopamine. Depue and Collins (1999) argued that individual differences in extraversion are due to variation in a network of dopaminergic neurons involving the ventral tegmental area, the nucleus accumbens and projections to cortex. Dopamine function may modulate executive control by protecting or updating representations of goal states that lead to reward (Ashby *et al*., 1999; Braver & Cohen, 2000). Therefore, higher extraversion may relate to more efficient executive control abilities, resulting from their common relationship with midbrain DA function. Brain areas belonging to the dopaminergic circuit are more activated in extraverts than in introverts during positive emotions (Canli et al., 2002). In addition, reward significantly increased working-memory related activation in the dorsal lateral prefrontal cortex during an n-back task (Pochon et al., 2002) and was related to dorsal ACC activity during a decision-making task (Bush et al., 2002). Thus dopaminergic systems are a more specific candidate for further investigation of personality – neural processing efficiency relations.

Our results may also have implications for Eysenck's theory of extraversion (H. J. Eysenck, 1967). Although BAS and extraverion are different constructs in theory, in practice, their measures are highly redundant (Rusting & Larsen, 1999; Zelenski & Larsen, 1999). Contrary to Eysenck’s original hypothesis, that extraverts have lower resting arousal levels, EEG studies suggest extraverts do not show a reduced level of cortical arousal at rest (Gale, 1986). However, in studies that examine nervous system responsiveness to moderate levels of stimulation, extraverts do consistently show smaller or slower responses than introverts (Bullock & Gilliland, 1993; Gale, 1983). Consequently, extraversion appears to be related primarily to differences in nervous system *reactivity* rather than tonic level of arousal (Green, 1984;

Stelmack, 1990). Our results are consistent with this hypothesis, because high-BAS individuals showed a smaller magnitude of hemodynamic response than low-BIS individuals to the n-back working memory task. While it remains an open question to what extent this relationship between cerebral blood flow and extraversion holds true for other cortical regions and other forms of stimulation, that we observed this relation in our paradigm is consistent with the proposal that extraversion effects are strongest during goal-directed behavior.

Our results are opposite in direction from those reported by Kumari and colleagues (2004), in which higher Extraversion scores (as assessed by a slightly difference measure than we used: H. J. Eysenck & Eysenck, 1991) predicted greater activity during a n-back task in 11 subjects. Kumari and colleagues interpreted this result as consistent with Eysenck's theory, as representing a lower baseline level in high E subjects from which they can become more strongly activated (i.e., a greater difference between baseline and task). Although this interpretation is possible, it goes against considerable evidence suggesting that higher extraversion is associated with lower arousability (a smaller movement from baseline), rather than a lower arousal level (a lower baseline) (Green, 1984; Stelmack, 1990). We cannot be entirely sure of the reason for the apparent discrepancy between the results, yet it is unlikely that the slightly different personality scales used to assess extraversion could be responsible for a reversal of the effect. A replication in a large sample in *a priori* ROIs while controlling for behavioral variables (including intelligence) could go a long way toward reconciling the apparently conflicting results.

We also found evidence that a second dimension of personality, BIS, is related to sustained activity within rostral (and perhaps posterior-rostral) ACC. Although not predicted *a priori*, this result survived correction for multiple comparisons, and accords well with previous work, including PET studies of resting brain activity and individual differences in trait negative affect (Zald *et al.*, 2002) and explicit manipulations of anxiety (Simpson *et al.*, 2001). The same result held for Neuroticism.

In sum, for BAS (and Extraversion), the data provide strong support for the hypothesis of personality differences in neural processing efficiency. The data confirm and extend our previous findings (J. R. Gray & Braver, 2002) for having a large sample, more nuanced measures, and for including other relevant brain regions. More broadly, the data have implications for biological theories of personality, and suggest that understanding the function of the prefrontal, anterior cingulate, and parietal cortex will require understanding individual differences in both affective and cognitive variables.

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Table 1: Personality predicts working-memory-related activity

		BAS		BIS		E		N	
ROI	Center	State	Item	State	Item	State	Item	State	Item
Lateral prefrontal									
L BA 46/45	-46,18,24	-.01	**-.42** * **(-.41** *)	.19	.02	-.12	**-.38** *	.02	-.09
R BA 44/45	44, 9, 21	.09	**-.27** * **(-.26** *)	.11	-.21	-.10	-.18	.10	-.26
Parietal									
L BA 40	-56,-42, 33	.07	**-.42** * **(-.42*)**	.11	.14	-.04	**-.39** *	.27	-.11
R BA 40	46, -33, 45	**.38** * (**.38***)	**-.31** * **(-.31*)**	.09	-.05	.14	**-.35** *	.26	-.03
Anterior cingulate									
Dorsal BA 24	-2, 9, 45	.06	**-.28** * **(-.27*)**	.20	.07	.01	**-.30** *	.22	.02
Posterior rostral	-2, 24, 12	.08	.04	.30 +	-.08	-.09	.01	**.32** *	-.05
Rostral	2, 42, 9	.08	.07	**.41** * (**.41** *)	-.16	-.20	.04	**.35** *	-.10
Subgenual	2, 36, -6	.10	.28 + (.28 +)	.16	-.14	.04	.14	.28 +	-.19

Notes. N=53. Values are zero-order correlations (*df* = 51) between individual-difference variables (BIS, BAS, E, N) and brain activity (state, item). Values in parentheses are the weakest of three partial correlations (*df* = 50) after controlling for fluid intelligence (APM), accuracy on the 3-back task (*d*'), and average RT for correct trials on the 3-back task. Center = center of ROI mass in Talairach coordinates (Talairach & Tournoux, 1988), see Figure 1. BAS = Behavioral Approach Sensitivity, BIS = Behavioral Inhibition Sensitivity, E = extraversion, N = Neuroticism, L = left, R = right. LPFC = lateral prefrontal cortex. ROI = region of interest.

* $p < .05$, corrected for multiple comparisons

+ $p < .05$, not corrected for multiple comparisons

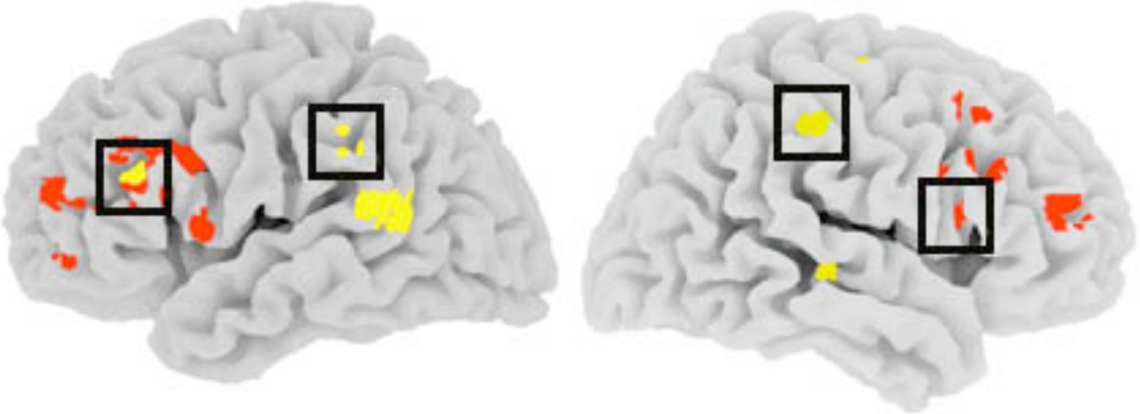
Table 2: Personality and specific trial types

	BAS			BIS		
	Lure	Target	Nonlure	Lure	Target	Nonlure
Lateral prefrontal						
L BA 46/45	-.29	-.20	-.38	-.09	-.06	.02
R BA 44/45	-.37	-.30	-.35	-.01	.01	.18
Parietal						
L BA 40	-.29	.02	-.16	-.10	-.20	-.14
R BA 40	-.16	-.28	-.29	-.03	-.02	.07

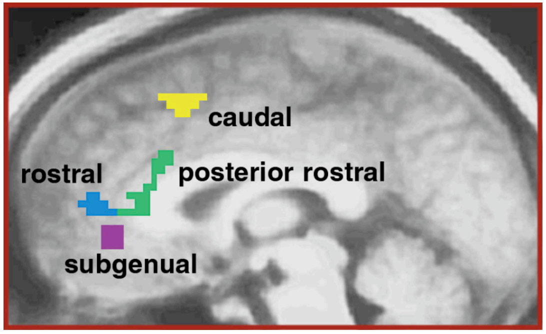
Notes. N=48 (see text). Regions and abbreviations are the same as in Table 2. Lure trials = high demand for cognitive control, Target = intermediate demand, Nonlure = lower demand (see text). *df* = 46 for zero-order correlations, 45 for partial correlations. Correlations of brain activity with fluid intelligence (APM) are reported in Gray et al. (2003).

Figure 1. Regions of interest, in **a)** lateral prefrontal and parietal cortex (adapted from Gray et al., 2003, with permission), shown on lateral views of the left and right hemispheres (left on the left); and **b)** anterior cingulate cortex (from Gray & Braver, 2002, with permission), shown in a sagittal view, anterior to the left; here, caudal is synonymous with dorsal.

a)



b)



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