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Linking trait-based phenotypes to prefrontal cortex activation during inhibitory control

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Abstract

Inhibitory control is subserved in part by discrete regions of the prefrontal cortex whose functionality may be altered according to specific trait-based phenotypes. Using a unified model of normal range personality traits, we examined activation within lateral and medial aspects of the prefrontal cortex during a manual go/no-go task. Evoked hemodynamic oxygenation within the prefrontal cortex was measured in 106 adults using a 16-channel continuous-wave functional near-infrared spectroscopy system. Within lateral regions of the prefrontal cortex, greater activation was associated with higher trait levels of extraversion, agreeableness and conscientiousness, and lower neuroticism. Higher agreeableness was also related to more activation in the medial prefrontal cortex during inhibitory control. These results suggest that personality traits reflecting greater emotional stability, extraversion, agreeableness and conscientiousness may be associated with more efficient recruitment of control processes subserved by lateral regions of the prefrontal cortex. These findings highlight key links between trait-based phenotypes and neural activation patterns in the prefrontal cortex underlying inhibitory control.

Key words: personality traits; five-factor model; inhibitory control; prefrontal cortex

Introduction

The ability to control our behaviors, thoughts and emotions is a critical capacity that allows us to successfully adapt to our physical and social surroundings. If we did not possess the ability to exert inhibitory control, even the most basic day-to-day tasks, such as reading, driving and socializing, would be difficult or perhaps even impossible. Indeed, difficulty exerting inhibitory control is associated with a reduced ability to function effectively in one's daily activities (Cahn-Weiner et al., 2000) and is implicated in most forms of psychopathology (for a review, see Verbruggen and Logan, 2008). It has even been suggested that inhibitory control provides the foundation for other subsidiary cognitive functions, such as verbal comprehension, learning and retrieval of memories (Hasher et al., 1999).

Early research exploring the neural basis of inhibitory control relied on mapping of lesions in individuals with brain pathology. These studies implicated the prefrontal cortex (PFC) and,

in particular, the functioning of the right inferior frontal gyrus (Aron et al., 2004; Chikazoe et al., 2007) as crucial for successful inhibitory control. Since that time, neuroimaging studies incorporating such technologies as functional magnetic resonance imaging (fMRI) and near-infrared spectroscopy (fNIRS) have contributed to our understanding of the neural underpinnings of inhibitory control. Using a go/no-go paradigm that requires participants to withhold a well-learned motor response to specific visual or auditory stimuli, research has shown that the right inferior frontal gyrus is reliably activated regardless of response modality (i.e. hand, eye or foot) (Van't Ent and Apkarian, 1999; Chikazoe et al., 2007). In a meta-analysis of 47 fMRI studies, Swick et al. (2011) found that inhibitory control was associated with activation within a number of cortical regions, including the right inferior frontal gyrus, middle frontal gyrus, insular cortex and inferior parietal lobule. Significant areas of activation were also identified in the left hemisphere,

specifically within the superior, middle and inferior frontal gyri. Studies using the go/no-go paradigm have also implicated the left lateral PFC and medial PFC in inhibitory control (Rodrigo et al., 2014; Tabibnia et al., 2014). The distinct functions of these subregions within the PFC, however, remain incompletely understood and may be illuminated by linking functioning within these regions to psychological phenotypes, including personality traits.

Inhibitory control and the five-factor model of personality traits

While it is recognized that inhibition-related processes are associated with a wide range of personality traits (for a review, see Nigg, 2000), it remains to be clarified how individual differences in trait-based phenotypes might be associated with activation within discrete regions of the PFC under conditions of inhibitory control. The five-factor model (FFM) is acknowledged by many researchers to provide a unified framework for conceptualizing personality traits (John et al., 2008; McCrae and Costa, 2008). Much of contemporary personality science is framed within this model, which provides a taxonomy of five personality trait domains: Neuroticism (N), Extraversion (E), Openness to Experience (O), Agreeableness (A) and Conscientiousness (C; Goldberg, 1993; John et al., 2008; McCrae and Costa, 2008). Certain FFM traits have been associated with various facets of impulsivity (Whiteside et al., 2005)—higher levels of N with negative urgency (i.e. the urge to act when experiencing a negative emotion), higher levels of E with sensation-seeking (i.e. the tendency to pursue sensory experiences that are novel, complex and intense) and lower levels of C with a lack of premeditation (i.e. minimal deliberation before acting) and less perseverance (i.e. difficulty sustaining a task). Given these associations between the FFM traits and impulsivity, these psychological phenotypes may be linked to the functioning of specific neural systems within the PFC during inhibitory control.

Only two studies, both using fMRI, have explored relationships between FFM personality trait domains and neural activation patterns underlying inhibitory control. Using an odd-ball paradigm, Eisenberger et al. (2005) found that higher N was associated with less activation in the lateral PFC, rostral anterior cingulate cortex (ACC) and posterior parietal cortex during inhibitory control, whereas lower levels of N were associated with greater activation in the dorsal ACC. With respect to E, higher levels of this trait were related to more activation in the left lateral PFC, rostral ACC and lateral parietal cortex, but with less activation in the dorsal ACC. Similarly, Sosic-Vasic et al. (2012) used a go/no-go paradigm and examined patterns of neural activation associated with commission errors (i.e. 'false alarm' responses). Consistent with the findings of Eisenberger et al. (2005), higher N was linked to less activation in the left lateral PFC, specifically within the inferior frontal gyrus. Higher C, on the other hand, was linked to more activation in this region. Additionally, higher levels of C were related to greater activation in the ACC and left medial superior frontal gyrus. Taken together, these findings are consistent with the presumed roles of N, E and C in impulsive behavior studies and specifically suggest that higher levels of N and lower levels of both E and C may be associated with less activation in neural systems underlying inhibitory control.

Present study

Although prior studies provided initial evidence that certain FFM traits may be linked to neural activation associated with inhibitory control, it remains to be clarified how distinct subregions within the PFC involved in this cognitive function might be related to key trait-based phenotypes. In this regard, two limitations of previous studies examining the potential relationships between FFM personality traits and PFC activity during inhibitory control are of note. The first limitation concerns the use of relatively small sample sizes (N = 17 in Eisenberger et al., 2005; N = 27 in Sosic-Vasic et al., 2012). This is a common limitation in personality neuroscience because of the high costs associated with individual participant runs in fMRI research (DeYoung, 2010). Findings obtained from studies employing small samples, though potentially instrumental for advancing research in novel directions, are prone to both Type I errors (false positives) and Type II errors (false negatives) because of the lower levels of statistical power that they afford (Yarkoni, 2009). The second limitation concerns the use of a single neuroimaging technology, as both previous studies used fMRI. Although fMRI is frequently used in studies of inhibitory control, other neuroimaging modalities may help to elucidate the contributions of distinct regions of the PFC during motor response inhibition (Rodrigo et al., 2014). Specifically, functional near-infrared spectroscopy (fNIRS) is an optical neuroimaging technique that provides measurements of relative changes in oxygenated hemoglobin, a parameter that may convey information distinct from the fMRI bloodoxygen level-dependent signal (Strangman et al., 2002; Steinbrink et al., 2006). Additionally, fNIRS may be advantageous for personality neuroscience research because the lower cost of individual participant runs affords greater statistical power for examining associations between personality traits and neural activity.

Building off the work of Eisenberger et al. (2005) and Sosic-Vasic et al. (2012), the present study sought to investigate relationships of FFM traits with neural activity in discrete regions of the PFC during a go/no-go paradigm using continuouswave fNIRS. On the basis of our previous research, in which we developed and validated a go/no-go paradigm for fNIRS, the present study focused on activation in three regions-ofinterest (ROIs) within the PFC that may subserve distinct inhibitory functions: (i) the left lateral PFC, which included the left inferior frontal, middle frontal and superior frontal gyri; (ii) the right lateral PFC, comprising the right inferior frontal and middle frontal gyri and (iii) the medial PFC, specifically, the right frontopolar region. Whereas higher levels of activity in the first two ROI's (bilateral PFC) have been associated with response control on the go/no-go task (Rodrigo et al., 2014), deactivations of the medial PFC may reflect the degree of performance monitoring (including task engagement), especially given the role of this region in self-referential processing (Di Domenico

On the basis of prior findings involving the FFM (Eisenberger et al., 2005; Sosic-Vasic et al., 2012), we hypothesized that higher N and lower E and C would be associated with less activation in bilateral PFC, possibly suggesting that the corresponding trait levels may be associated with less efficient recruitment of response control processes on the go/no-go task. While we had no specific hypotheses with respect to the medial PFC, given that this region is implicated in processing information relevant to the self and others (Amodio and Frith, 2006), we anticipated that functioning of the medial PFC would be associated with the more interpersonally oriented trait domains E and A. Finally, we did not have a priori hypotheses regarding activation associated with O; therefore, we conducted exploratory analyses incorporating this trait domain.

Materials and methods

Participants

In our initial validation study of the go/no-go task (Rodrigo et al., 2014), we recruited 42 right-handed healthy adults from the University of Toronto Scarborough and the surrounding community. As part of this study, 33 participants completed a self-report assessment of FFM personality traits. In addition, we recruited 73 participants who completed the same study protocol. Our final sample included 106 primarily right-handed (90.6%) healthy adults (61 women) who were on average 24.0 years old (s.d. = 8.9). The ethno-racial composition of the sample classified according to 2011 Canadian census categories was as follows: South Asian (31%), White (22%), Chinese (17%), Black (8%), West Asian (4%), Filipino (3%), Arab (2%), Korean (2%) and other (12%). All participants completed a comprehensive screen to rule out serious psychiatric or neurologic disorders (e.g. psychosis, bipolar disorder, severe head injury). No participants displayed motor difficulties that would prevent them from completing the study protocol. All participants were fluent in English and indicated that they understood all task instructions. Participants also provided written informed consent before completing study procedures. The study was approved by the Social Sciences, Humanities and Education Research Ethics Board at the University of Toronto.

Procedure

After providing written informed consent to participate in the study, participants completed a questionnaire assessing demographic information and a self-report measure of FFM personality traits. Participants were then seated in a dimly-lit room in front of a computer monitor and a keyboard. Prior to beginning the go/no-go task, written instructions were presented to the participant on the computer monitor and read aloud by the experimenter. While completing the task, participants were asked to sit comfortably and interact with the computer solely by pressing a designated button with their right index finger. While the participant completed the task, the experimenter was seated quietly behind the participant operating the fNIRS equipment. At the conclusion of the experiment, participants were compensated for their time with either course credit or compensated \$10 CAN (equivalent to approximately \$8.50 USD) per hour of participation.

fNIRS procedures and signal processing

Prior to positioning the fNIRS probe, participants' foreheads were cleaned using an alcohol swab to minimize residue such as sweat and cosmetics. The fNIRS probe was secured over the forehead, positioned in alignment with the electrode positions F7, F_{P1}, F_{P2} and F8 based on the international 10-20 EEG system (Jasper, 1958). This positioning corresponds to Brodmann areas 9, 10, 45 and 46. Neuroimaging data were acquired using the fNIR Imager 1000 (fNIR Devices, Potomac, MD), a 16-channel continuous-wave fNIRS system (see Ruocco et al., 2010; Ayaz et al., 2012). Two wavelengths of light (730 and 850 nm) were measured continuously at 500 ms intervals at a penetration of 1.25 cm.

After acquisition, recorded light intensities were visually inspected by a trained experimenter. Over- or under-saturated channels were excluded from analyses. Subsequently, signal and physiological artifacts were excluded. First, a slidingwindow motion artifact rejection algorithm (SMAR) was applied

to exclude apparent motion artifacts. SMAR uses a window size of 10 s to scan through the variation within the obtained fNIRS signal, in order to identify noise resulting from motion artifacts (Ayaz et al., 2010). This method has been shown to successfully identify and reject data segments that demonstrate unusually large signal amplitudes, which result from head motion during data collection. This was followed by the application of a lowpass filter consisting of a finite impulse response, and a linear phase filter with an order of 20 and a cut-off frequency of 0.1 Hz (Izzetoglu et al., 2005; Ayaz et al., 2012), which further excluded large fluctuations in the signal. Based on time synchronization markers received via a serial connection from a computer used to display the go/no-go task, activation segments were extracted for comparison with the processed data. Relative changes in concentrations of oxygenated hemoglobin (oxy-Hb) for each activation segment were calculated using fNIRSoft Professional Edition (Ayaz, 2010). The processed data were then aggregated to form the aforementioned ROI's, which included (i) left lateral PFC (channels 2, 4, and 5), (ii) right lateral PFC (channels 13, 14 and 16), (iii) and medial PFC (channels 9 and 10). See Figure 1 for locations of these channels on a standardized brain surface.

Personality assessment

The Big Five Inventory (BFI) (Benet-Martinez and John, 1998; John et al., 2008) is an extensively used self-report measure assessing the FFM personality trait domains. Participants were asked to indicate the extent to which they agreed that test items were personally descriptive on a scale ranging from 1 (Disagree strongly) to 5 (Agree strongly). Sample items include 'Gets nervous easily' (N), 'Is outgoing, sociable' (E), 'Values artistic, aesthetic experiences' (O), 'Is considerate and kind to almost everyone' (A) and 'Makes plans and follows through with them' (C). Descriptive statistics and correlations among the BFI scores are presented in Table 1.

Individuals differ in their tendency to consistently agree ('yea-saying') or disagree ('nay-saying') when responding to personality test items (Podsakoff et al., 2003). To control for individual differences in acquiescent and extreme responding, we ipsatized the BFI items according to the recommendations and scoring instructions provided by John et al. (2008). Specifically,

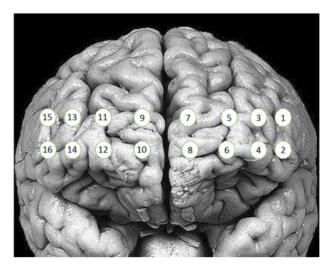


Fig. 1. A template of the prefrontal cortex depicting the location of each of the 16 fNIRS channels.

Table 1. Descriptive statistics of FFM traits

Personality trait	M	s.d.	1	2	3	4	5
1. Neuroticism	2.77	0.86	0.85				
2. Extraversion	3.22	0.88	-0.40	0.87			
3. Openness to experience	3.44	0.67	-0.04	0.23	0.76		
4. Agreeableness	3.96	0.56	-0.23	0.22	-0.03	0.70	
5. Conscientiousness	3.64	0.74	-0.25	0.12	0.07	0.29	0.83

Note: N = 106. Correlations among the ipsatized trait scores with Cronbach's alpha listed along the main diagonal. Correlations above 0.21 or below -0.22 are statistically significant (P < 0.05).

ipsatized BFI scores were computed by subtracting withinperson response means (computed across 32 semantically opposite items) from each participant's item responses and then dividing these differences by the standard deviation of the participants' item responses.

Inhibitory control task

The Scarborough Non-Affective Go/No-Go task (SNAG; Rodrigo et al., 2014) was used to measure inhibitory control using a wellestablished cognitive paradigm. On this task, participants were required to press a button with their right index finger to Go stimuli (i.e. a green circle) and withhold a response to No-Go stimuli (i.e. a red circle). Each stimulus was presented on a black screen for 500 ms. Participants were permitted 3000 ms from the onset of the stimulus to provide a response. The task consisted of 90 target stimuli and 30 non-target stimuli, arranged in six separate blocks. These six blocks were categorized into two conditions with three blocks per condition. 'Go' blocks consisted of 20 'Go' stimuli, whereas 'No-Go' blocks consisted of a pseudorandom combination of 10 'Go' and 10 'No-Go' stimuli in each block. The SNAG required participants to respond both quickly and accurately. To discourage anticipatory responding, the inter-trial interval was jittered by increments of 500 ms over a range of 4000-6000 ms, with an average of 5000 ms interstimulus interval. Each trial was separated by a white fixation cross presented on a black screen.

Data analytic approach

The fNIRS time-series data were analyzed using multilevel modeling (Snijders and Bosker, 2012). Within the context of the present study, multilevel models take into account that the experimental time-series were nested within participants and that the number of observations may be unbalanced across participants. Variance in the dependent variable is partitioned into within-person (Level 1) and between-person (Level 2) components, allowing predictor terms to be represented at both the level of the experimental observation (Level 1) and the level of the participant (Level 2). We examined the Level 1 effect at the level of inhibitory control (No-Go and cross-hair fixation), the Level 2 effect of the 'Big Five' personality trait domains, and Inhibitory Control × Personality Trait cross-level interactions on participants' relative changes in oxy-Hb across the a priori ROI's investigated in the present study. The Inhibitory Control × Personality Trait cross-level interaction terms test whether Level 1 (i.e. within-person) differences in neural activity between the No-Go and cross-hair fixation systematically depend upon Level 2 (i.e. between-person) differences in personality traits. Type I error was controlled using the False Discovery Rate approach for each set of analyses (Benjamini and Hochberg, 1995; Benjamini et al., 2001). Separate models were estimated for each personality trait domain across the ROI's.

The multilevel models were estimated in R (R Core Development Team, 2005), using the multilevel and nlme packages (Bliese, 2009). We estimated random intercept models nesting the experimentally demarcated time-series data within each participant. To account for the temporal autocorrelation in the time-series, all models were conservatively estimated using an unstructured covariance matrix and the 'between-within' method of estimating degrees of freedom (Schluchter and Elashoff, 1990).

Following the recommendations of West et al. (1996), we constructed a set of orthogonal contrast codes to examine our a priori comparison of interest, namely, the unstandardized mean differences in oxy-Hb between the No-Go condition and its local baseline (cross-hair fixation). This set of contrast codes accordingly featured a term specifying the No-Go condition as '0.5' and its local baseline as '-0.5' while the Go condition and its local baseline were both coded as '0'; independent of this comparison, this set of contrast codes featured a term specifying the Go condition as '0.5' and its local baseline as '-0.5' while the No-Go condition and its local baseline were both coded as '0'; finally, independent of both preceding comparisons, this set of contrast codes included a term specifying both the No-Go conditions and its local baseline as '-0.5', while both the Go condition and its local baseline were coded as '0.5.' Although the estimated models featured contrast code variables to comprehensively represent the experimental conditions (West et al., 1996), we strictly reported the results of the contrast variable comparing the unstandardized mean differences in oxy-Hb between the No-Go condition and its local baseline for clarity of presentation.

Results

Behavioral performances

Participants demonstrated high levels of accuracy (sum of true positives and true negatives) on the SNAG: M = 97.6%, s.d. = 2.2. Spearman correlational analyses revealed that greater levels of C were significantly related to higher accuracy (r = .28, P < 0.01), whereas the remaining trait domains demonstrated no significant associations with task performance (r's < .10, P's > 0.35. There were also no significant correlations between response times on the SNAG and any of the personality trait domains (r's < .14, P's > 0.19).

Neural activation associated with inhibitory control

As expected, significant changes in activation, between No-Go and its local baseline were observed within the three ROI's under conditions of inhibitory control (i.e. No-Go blocks). As predicted, a significant increase in activation was observed within the right lateral PFC during No-Go (b = 0.02, SE = .01, P = 0.02) and the left lateral PFC during No-Go blocks (b = 0.03, SE = 0.01, P < 0.001). Also as predicted, a decrease in activation was observed within the medial PFC during No-Go (b = -0.02, SE = 0.01, P < 0.01). These main effects are consistent with previous fMRI studies examining patterns of PFC activity during motor response inhibition (Swick et al., 2011), and with our previously reported findings using the subsample of participants reported in Rodrigo et al. (2014).

Inhibitory Control × Personality Trait interactions in the right lateral PFC

Within the right lateral PFC, significant cross-level interactions were found for N (b = -0.11, SE = 0.01, P < 0.001), E (b = 0.07, SE = 0.01, P < 0.001), A (b = 0.10, SE = 0.02, P < 0.001) and C (b = 0.07, SE = 0.01, P < 0.001).

During the local baseline period (i.e. crosshair fixation), there was no association between right lateral PFC activation and any personality trait. During inhibitory control, however, higher levels of N were associated with lower levels of activation in the right lateral PFC (b = -0.11, SE = 0.02, P < 0.0001). Specifically, participants with higher levels of N showed decreases of activation in this region during inhibitory control relative to the local baseline condition (b = -0.05, SE = 0.01, P < 0.0001), and participants with lower levels of N showed increases of activation in this region relative to the local baseline condition (b = .09, SE = 0.01, P < 0.0001). Opposite to N, higher levels of E were associated with higher levels of activation in the right lateral PFC during inhibitory control (b = .07, SE = 0.02, P < 0.01). Specifically, participants with higher levels of E showed increases of activation in this region during inhibitory control relative to the local baseline condition (b = 0.06, SE = 0.01, P < 0.0001), and participants with lower levels of E showed decreases of activation in this region during inhibitory control relative to the local baseline condition (b = -0.03, SE = 0.01, P < 0.01). Higher levels of A were also associated with significant increases in activation under conditions of inhibitory control (b = 0.10, SE = 0.04, P = 0.02). Specifically, participants with higher levels of A showed increases in activation within the right lateral PFC during inhibitory control relative to the local baseline condition (b = 0.06, SE = 0.01, P < 0.0001), whereas those who were lower in this trait showed decreases in activation during inhibitory control relative to the local baseline condition (b = -0.02, SE = .01, p < .01). Finally, higher levels of C also predicted increases in activation under inhibitory control (b = 0.07, SE = 0.03, P = 0.02). Participants who reported higher levels of C demonstrated increases in activation during inhibitory control relative to the local baseline condition (b = 0.06, SE = 0.01, P < 0.0001), whereas

those who reported lower levels of C showed decreases in activation during inhibitory control relative to the local baseline condition (b = -0.02, SE = 0.01, P = 0.01). See Figure 2 for a summary of these findings.

Inhibitory Control × Personality Trait interactions in the left lateral PFC

Mirroring the results found for the right lateral PFC, significant cross-level interactions were found for N (b = -0.12, SE = 0.01, P < 0.001, E (b = 0.08, SE = 0.01, P < 0.001), A (b = 0.08, SE = 0.02, P < 0.001) and C (b = 0.05, SE = 0.01, P < 0.001) for the left lateral

During the local baseline period, there was no association between left lateral PFC activation and any personality trait. However, during inhibitory control, higher levels of N were associated with lower levels of activation (b = -0.12, SE = 0.02, P < 0.001). Probing the cross-level interaction revealed that participants with higher levels of N displayed decreases in activation during inhibitory control relative to the local baseline period (b = -0.05, SE = 0.01, P < 0.0001), while those with lower levels of N demonstrated increases in activation during inhibitory control relative to the local baseline period (b = 0.11, SE = 0.01, P < 0.0001). Higher levels of E were associated with higher levels of activation during inhibitory control (b = 0.08, SE = 0.02, P < 0.001). Participants who reported higher levels of E demonstrated significant increases in activation during inhibitory control relative to the local baseline period (b = 0.09, SE = 0.01, P < 0.0001), whereas those who reported lower levels of E demonstrated significant decreases in activation during inhibitory control relative to the local baseline period (b = -0.03, SE = 0.01, P < 0.01). Paralleling the pattern of activation observed within the right lateral PFC, higher levels of A were associated with increased activation within the left lateral PFC during inhibitory control (b = 0.08, SE = 0.03, P = 0.02). Although participants reporting higher levels of A demonstrated significant increases in activation during inhibitory control relative to the local baseline period (b = 0.06, SE = 0.01, P < 0.0001), those

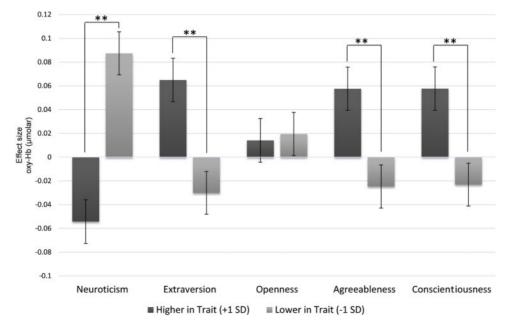


Fig. 2. Activity in the right prefrontal cortex during the No-Go condition and across the Big Five personality traits. The effect sizes correspond to the unstandardized within-person regression coefficients at high (+1 s.d.) and low (-1 s.d.) levels of the Big Five traits. (**P < 0.001)

reporting lower levels of A did not show a significant difference in activation during inhibitory control relative to the local baseline period (b = -0.01, SE = 0.01, P = 0.52). Higher levels of C were associated with only marginally increased levels of activation during inhibitory control (b = 0.05, SE = 0.02, P = 0.07). While participants who reported higher levels of C showed increases in activation during inhibitory control relative to the local baseline period (b = 0.05, SE = 0.01, P < 0.0001), those who reported lower levels of C showed no differences in activation during inhibitory control relative to the local baseline period (b = 0.00, SE = 0.01, P = 0.82). See Figure 3 for a summary of these findings.

Inhibitory Control × Personality Trait interactions in the medial PFC

Within the medial PFC, significant cross-level interactions were found for A (b = 0.09, SE = 0.02, P < 0.001) and O (b = -.04, SE = 0.02, P = 0.01). N, E and C did not demonstrate significant cross-level interactions within this ROI.

Neither A nor O were significantly associated with activation within the medial PFC during the local baseline period. However, higher levels of A were associated with increased activation during the No-Go condition (b = 0.09, SE = 0.04, P < 0.05). More specifically, those with lower levels of A showed decreases in activation during inhibitory control relative to the baseline condition period (b = -0.06, SE = 0.01, P < 0.0001), while those with higher levels of A demonstrated marginal increases in activation (b = 0.02, SE = 0.01, P = 0.07). Although O was not associated with levels of medial PFC activation during the No-Go condition (b = -0.04, SE < 0.04, P = 0.24), participants who reported higher levels of O demonstrated decreased levels of activation in this region during inhibitory control relative to the local baseline period (b = -0.04, SE = 0.01, P < 0.001). Participants who reported lower levels of O did not demonstrate any difference in medial PFC activity across inhibitory control and the local baseline period (b = 0.00, SE = 0.01, P = 1.00). See Figure 4 for a summary of these findings.

Personality and inhibitory control: results summary

To provide more easily interpretable measures of effect size between the FFM traits and neural activation during inhibitory control, we calculated semi-partial R2 values for the simple effects of personality traits on oxy-Hb levels during the No-Go condition (see Table 2). Semi-partial R² values estimate the relative variance explained by each predictor in a multilevel model (Edwards et al., 2008). As seen in Table 2, the relatively strongest effects were observed in the lateral PFC regions. Dovetailing the results of past studies (Eisenberger et al., 2005; Sosic-Vasic et al., 2012), N and E were the strongest predictors of PFC activity bilaterally during inhibitory control¹.

Discussion

The present study examined links between trait-based phenotypes and neural activation patterns during inhibitory control, while participants completed a manual go/no-go task. We first examined the relationship of FFM traits with behavioral performances on the inhibitory control task. While higher C was associated with more accurate performances, a finding consistent with prior research on this trait (Gellatly, 1996; Dudley et al., 2006; Poropat, 2009), all other personality trait domains were not significantly correlated with accuracy or response times on the task. When examining neural activation in predefined areas of the PFC that have previously been associated with reasonably distinct inhibitory control processes (Rodrigo et al., 2014), significant relations were found between neural activity and all five of the personality trait domains.

Neuroticism

Consistent with expectations, higher N was associated with less activation bilaterally in the PFC under conditions of inhibitory control. When considering that higher N reflects difficulties with regulation of both emotions and behaviors, and less activation in the lateral PFC is associated with poorer response inhibition (i.e. on a go/no-go task; Rodrigo et al., 2014), the present

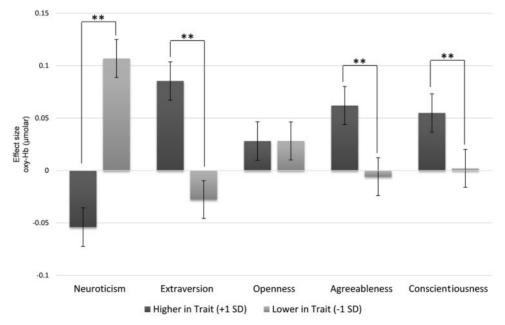


Fig. 3. Activity in the left prefrontal cortex during the No-Go condition and across the Big Five personality traits. Effect sizes correspond to the unstandardized within $person\ regression\ coefficients\ at\ high\ (+1\ s.d.)\ and\ low\ (-1\ s.d.)\ levels\ of\ the\ Big\ Five\ traits.\ (**P<0.001)$

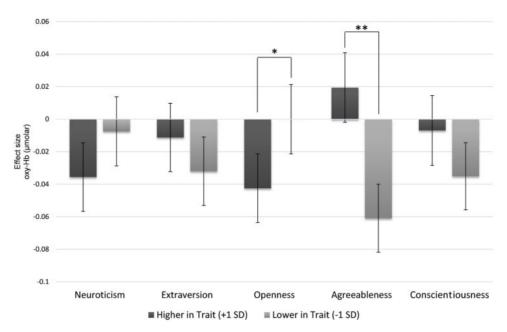


Fig. 4. Activity in the medial prefrontal cortex during the No-Go condition and across the Big Five traits. Effect sizes correspond to the unstandardized within-person regression coefficients at high (+1 s.d.) and low (-1 s.d.) levels of the Big Five traits. (*P < 0.05,**P < 0.001)

Table 2. Effect-size summary of FFM traits in the prediction of prefrontal activity during motor response inhibition

Personality trait	Semi-partial R ² values					
	Right lateral PFC	Medial PFC	Left Lateral PFC			
1. Neuroticism	0.109	0.006	0.112			
2. Extraversion	0.059	0.014	0.049			
3. Openness to Experience	0.015	4.30×10^{-5}	0.005			
4. Agreeableness	0.009	0.023	0.013			
5. Conscientiousness	0.023	0.012	0.018			

Note: Semi-partial R² values (Edwards et al., 2008) represent the portion of variance explained by FFM traits during the No-Go condition.

results may reflect a diminished recruitment of inhibitory processes within the lateral PFC for individuals higher in N. These findings converge with functional connectivity studies showing that higher N is associated with reduced connectivity in neural networks involved in cognitive and emotional control (Gao et al., 2013; Servaas et al., 2015). Diffusion tensor imaging research also indicates that individuals higher in N display poorer structural integrity within the anterior cingulum and uncinate fasciculus, white matter tracts that interconnect the lateral PFC with emotional centers such as the amygdala (Xu and Potenza, 2012). Taken together, these findings suggest that higher N may be associated with reduced activity in prefrontal systems involved in inhibitory control, and that decreased recruitment of these lateral regions of the PFC may be subserved by less efficient neural pathways that interconnect the PFC with structures involved in emotion-related processes. While most neuroimaging studies examining N used paradigms incorporating emotional stimuli and related the trait to activity in neural structures implicated in mood and emotions, such as the amygdala, insular cortex, and subgenual anterior cingulate (Paulus et al., 2003; Canli, 2004; Deckersbach et al., 2006; Haas et al., 2007a; Cremers et al., 2010), the present study provides emerging evidence that this trait may also be related to activity in neural regions involved in

control-related processes that go beyond those primarily involved in emotion.

Extraversion

In contrast with N, higher levels of E were associated with greater activity in lateral regions of the PFC under conditions of inhibitory control. Whereas it can be argued that the positive emotionality component of E shares an inverse association with N and could account for their opposing relationships with neural activation in the PFC (Canli, 2004), the two traits were not significantly correlated in the present study. Consistent with the results on the go/no-go task, research using an odd-ball paradigm has also shown that higher trait levels of E may be associated with more neural activity in the lateral PFC during inhibitory control (Eisenberger et al., 2005). As previously mentioned, functional connectivity studies examining relationships between neural structures involved in emotional and cognitive control have found reduced connectivity in individuals higher in N. Conversely, individuals higher in E show stronger functional connectivity in similar neural networks (Haas et al., 2006; Adelstein et al., 2011; Gao et al., 2013), possibly suggesting that this trait may play a role in increasing coherency in neural systems responsible for control-related processes. Given that more

narrowly delineated facets of E may be differentially associated with structural aspects of the PFC (Wright et al., 2006), the relationship between activation in the lateral PFC and other brain areas involved in inhibitory control may differ according to more specific traits associated with E (e.g. excitement-seeking, positive emotions).

Agreeableness

The interpersonal trait A showed a pattern of association with activation in the lateral PFC that was very similar to E. This trait has been linked to self-regulatory capacity (Robinson, 2007) and neurocognitive research indicates that higher standings on this trait are associated with better performances on tests of inhibitory control and cognitive flexibility (Jensen-Campbell et al., 2002). These neurocognitive findings are bolstered by research showing that higher A is associated with greater activation in the dorsolateral PFC using emotion perception paradigms (Haas et al., 2007b; Koelsch et al., 2013), as well as increased interhemispheric connectivity within the dorsolateral PFC, as measured using cortical evoked potentials following the application of transcranial magnetic stimulation (Hoppenbrouwers et al., 2010). Consistent with the notion that A may be associated with stronger engagement of neural structures involved in controlrelated processes, the trait has also been associated with greater structural integrity within neural tracts that form interconnections between the lateral PFC and posterior regions such as the caudal-inferior parietal cortex (Xu and Potenza, 2012). In conjunction with previous findings, the present study contributes further evidence to support the theory that self-regulation may be an essential component of A by demonstrating that individual differences in this trait may be reflected in differential patterns of activation within lateral aspects of the PFC involved in inhibitory control.

The medial PFC is a neural region noted for its apparent role in self-other processing, wherein simply thinking about the self or another person appears to produce an increase in activity in this region (Ellemers, 2012; Wagner et al., 2012; Di Domenico et al., 2013). In the present study, greater activation in the medial PFC was associated with higher levels of A. Individuals high in A are characterized as being more cooperative and likeable and are particularly motivated to get along with others (Costa et al., 1991; Hogan et al., 1997). Thus, the present pattern of results may suggest that higher A may reflect greater awareness of others in relation to oneself, even on a task apparently without social information processing. In this case, it is important to consider the social context of the study procedures, as participants were seated in close proximity to an experimenter who described the task and observed their performances (to ensure they followed instructions) while also operating the fNIRS equipment from behind where participants were seated. Although no interaction took place between the experimenter and the participant during the go/no-go task, the study procedures were inherently interpersonal and the observed relationship between A and medial PFC activity may have reflected greater self-monitoring of performances on the task for individuals higher in A while in the company of the experimenter. In other words, the presently observed relationship between A and medial prefrontal activity during the SNAG may be an artefact of the inherently social nature of the laboratory procedures. Research that systematically varies the social context of the study procedures may assist in disentangling the relationship between medial PFC activation and individual differences in A.

Conscientiousness

Like E and A, C was also linked to increased lateral PFC activation on the go/no-go task, a finding consistent with expectations given that higher levels of this trait typically reflect behaviors associated with stronger inhibitory control (e.g. self-discipline, deliberation). Higher C was also significantly correlated with higher accuracy on the task, paralleling neurocognitive work showing that individuals higher in C display better working memory and abstraction ability (Jensen-Campbell et al., 2002). Compared to the other FFM personality trait domains, less is understood about the relationship of C to neural activity in the PFC. Using a go/no-go task, Sosic-Vasic et al. (2012) found that individuals higher in C displayed greater activation bilaterally in the dorsolateral PFC under conditions of inhibitory control, findings that strongly converge with the present study. There is also indirect evidence showing an inverse relationship between C and metabolites in the lateral PFC reflecting cellular membrane turnover, suggesting that white matter tracts interconnecting this region with other neural centers may be less efficient in individuals higher in C. Similarly, higher levels of this trait have been associated with greater volume of the middle frontal gyrus in the left lateral PFC (DeYoung et al., 2010). Taken together, these findings provide converging evidence indicating greater white matter structural integrity and increased functional activation in lateral aspects of the PFC, in individuals higher in C, possibly indicating that the trait may alter activity in this region under conditions of inhibitory control.

Openness to experience

Unexpectedly, higher O was associated with less activation in the medial PFC. Deactivation within this region is potentially linked to increased task engagement, possibly as a result of the brain moving from a resting state to a goal-directed cognitive task (Gusnard and Raichle, 2001; Rodrigo et al., 2014). While the results are preliminary, these speculations do converge with research indicating that individuals higher in traits belonging to the broad domain of O may reach greater subjectively perceived depths of concentration during meditation (Lesh, 1970), possibly reflecting stronger task engagement. Given that this trait potentially represents a diversity of characteristics, such as aesthetic sensitivity and intellect (McCrae and Sutin, 2009), more research is needed to understand what qualities of O may be more specifically associated with the observed patterns of neural activation during inhibitory control.

Limitations

Several limitations must be noted with regard to the present study. First, whereas fNIRS provides a measure of relative change in hemodynamic oxygenation, it does not provide a measure of cortical volume. Given that specific traits have been differentially associated with volumes of the PFC (DeYoung et al., 2010), these differences could account, at least in part, for the patterns of neural activation observed in the present study. Future studies should account for cortical volume when examining task-related differences in functional neural activity associated with personality trait domains. Second, the 16-channel fNIRS system incorporated into the present study mainly provided measurements within the anterior portions of the frontal cortex; therefore, it was not possible to explore activation within deeper brain structures pertinent to inhibitory control, such as the insular cortex and ACC (Swick et al., 2011). While the cost-effectiveness of fNIRS permits recruitment of large

participant samples necessary for personality neuroscience research, it will be important for subsequent work to consider the relationship of FFM personality traits with other brain regions beyond the PFC using neuroimaging techniques capable of accessing deeper brain structures. Third, the present study solely explored the link between PFC activation during inhibitory control and higher order trait domains comprising the FFM of personality (as operationalized using the Big Five Inventory). Future research should examine the constituent facets of the FFM and interactions among these facets using participant samples large enough to provide adequate statistical power for these analyses. Finally, it is important to consider that the personality-neural activation relationships observed in the present study may be limited to conditions in which participants were required to exert inhibitory control. It is possible that FFM personality traits may show distinctive associations with neural activation depending on the cognitive paradigms employed, such as those involving working memory or problem-solving ability (Gray et al., 2005; Ruocco et al., 2014).

Summary

These findings, in conjunction with the small number of other studies on this topic, indicate patterns of neural activation during inhibitory control that appear to be associated with specific FFM personality traits. Encouragingly, many of the findings derived from this study were also observed in prior work (Eisenberger et al., 2005; Sosic-Vasic et al., 2012; Forbes et al., 2014). The present results may suggest that personality traits have the property of biasing neural activation under conditions of inhibitory control, which in turn may lead to predictable patterns of cortical engagement based on individual differences in these traits. This view of the relationship between personality traits and brain activity is consistent with that detailed in Canli (2004), which describes the neural representations of personality traits as widely distributed throughout the brain, perhaps impacting connectivity between different regions. These findings contribute to an emerging body of work showing that FFM personality traits may share unique associations with neural activity in many regions of the brain, and that these relationships may be partially dependent on the specific cognitive function under investigation.

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Conflict of interest. The fNIRS instrumentation utilized in the present study was manufactured by fNIR Devices, L.L.C. H. Ayaz contributed to the development of this technology, thus was offered a minor share in the firm fNIR Devices, L.L.C.

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