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The Big Five and their role within error processing:

Evidence from event-related fMRI

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CONTENTS

1. INTRODUCTION……..1

1.1. Error processing……..…2

1.1.1. The error-related negativity (ERN)……2

1.1.2. Neural sources of error processing……6

1.1.2.1. The ACC within error processing……..9

1.1.2.2. The IFC within error processing……...14

1.1.2.3. Other brain regions within error processing……...17

1.2. Personality…….. 18

1.2.1. The Big Five: A Five-Factor Model of Personality……...19

1.2.2. Neural sources of the Big Five……22

1.3. Linking errors and the Big Five: neural findings…… 27

1.4. Current study objectives……28

2. METHODS.....30

2.1. Subjects……30

2.2. Personality measurement……...30

2.3. Activation task and measurement procedure……..32

2.4. Functional data acquisition……35

2.5. Data analyses……...35

2.5.1. Analyses of behavioral data……35

2.5.2. Analyses of functional imaging data……...36

3. RESULTS……..38

3.1. Behavioral results……..38

3.1.1. Behavioral data on the fMRI experimental task……38

3.1.2. Behavioral data on errors and their correlations with the Big Five personality traits……..41

3.2. Functional imaging results……45

3.2.1. Results from group analyses……45

3.2.2. Correlations between error activity and personality traits……47
3.2.3. Post-hoc correlation analyses with graded error types……50

4. DISCUSSION……..52
4.1. Behavioral data……52
4.1.1. Behavioral data on the fMRI experimental task……52
4.1.2. Behavioral data on errors and their correlations with the Big Five personality traits……..53
4.2. Functional imaging data on errors and the Big Five…..……..54
4.2.1. Main error effects from group analyses..……..54
4.2.2. Extraversion and error processing……..……57
4.2.2. Conscientiousness and error processing……59
4.3. Limitations and future prospects……63
4.4. Conclusion……..65

5. SUMMARY……...66

6. REFERENCES……68

Appendix……79
Acknowledgements……...85

ABBREVATIONS

A	Agreeableness
AC	Anterior Commissure
AC-PC line	Anterior Commissure – Posterior Commissure line
ACC	Anterior Cingulate Cortex
aI	anterior insula
aI/fO	anterior insula/frontal operculum
ANOVA	Analysis of Variance
BA	Brodmann Area
BW	Bandwitdth
C	Conscientiousness
CBF	Cerebral Blood Flow
CRN	Correct-Response Negativity
dACC	dorsal Anterior Cingulate Cortex
rACC	rostral Anterior Cingulate Cortex
DLPFC	Dorsolateral Prefrontal Cortex
DSM-IV	Diagnostic and Statistical Manual of Mental Disorder, 4th Edition
E	Extraversion
EEG	Electroencephalography
e.g.	exempli gratia
EPI	Echoplanar Image
ERP	Event-Related Potentials
ERN	Error-Related Negativity
ERTS©	Experimental Run Time System©
FFM	Five-Factor Model (of personality)
fMRI	functional Magnetic Resonance Imaging
FoV	Field of view
FWE	Familiy Wise Error
FWHM	Full Width at Half Maximum

GLM	General Linear Model
HRF	Hemodynamic Response Function
Hz	Hertz
i.e.	id est
IFC	Inferior Frontal Cortex
IFC/aI	Inferior Frontal Cortex / Anterior Insula
IFG	Inferior Frontal Gyrus
Inf.	Infinite
IPL	Inferior Parietal Lobule
ISI	Inter-Stimulus-Interval
L/R	Left/Right
mm	millimeter
msec	millisecond
msFC	Medial Superior Frontal Cortex
MNI	Montreal Neurology Institute
MPRAGE	Magnetization Prepared Rapid Gradient Echo
MRI	Magnetic Resonance Imaging
MR	Magnetic Resonance
N	Neuroticism
Ne	Error Negativity
NEO-PI-R	Neuroticism Extraversion Openness to Experience – Personality Inventory – Revised
O	Openness to Experience
OCD	Obsessive-Compulsive Disorder
PC	Posterior Commissure
PET	Positron Emission Tomograpy
PFC	Prefrontal Cortex
pre-SMA	pre-Supplementary Motor Area
rCBF	regional Cerebral Blood Flow
rCMRglu	regional Cerebral glucose Metabolic Rates
ROI	Region of Interest

RT	Reaction Time
SD	Standard Deviation
sec	second
SPECT	Single-Photon-Emission-Tomography
SOA	Stimulus Onset Asynchrony
SPM	statistical parametric mapping
TE	Echo Time
TR	Time of Repetition

1. INTRODUCTION

Humans inevitable make errors from time to time regardless of their general tendency to actually avoid errors. In fact, errors are considered to be crucially necessary in learning processes. Thus, error signals provide important evaluative information, since they indicate incongruence between intentions and actions and help the adjustment of behavior (Holroyd and Coles 2002). In general, humans are efficient at recognizing errors and learning from them. This ability is supported by a neural system that process errors. Studies from the field of cognitive neuroscience have suggested a neural network including the anterior cingulate cortex (ACC) and the inferior frontal cortex adjoining to the anterior insula to be responsible for error processing (Dosenbach et al. 2006; for review see: Taylor et al. 2007). Nevertheless, despite the existence of specialized neural system, it is obvious that not all individuals are equally effective in processing errors, with some committing more errors than others, some avoiding errors more than others, and some others being more bothered by the occurrence of an error than other subjects. Thus, it seems inviting to raise the question about the influence of personality when talking about errors. Do different personality traits, such as the widely accepted *Big Five* – Neuroticism, Extraversion, Openness to Experience, Agreeableness, and Conscientiousness – play a role in the way humans process errors? Further, it appears even more interesting to question whether this possible influence relates to specific neural structures or brain networks. Results from genetic studies or neurotransmitter studies suggest quite convincingly that there is a neural basis for personality. However, concrete evidence is rather small bringing together a specific function, the underlying neural circuits and how these interact with individual expressions of personality traits.

1.1. Error processing

1.1.1. The error-related negativity (ERN)

Event-related potentials (ERP) derived from electroencephalographic (EEG) recordings have been an important tool in investigating neural systems involved in different aspects of human behavior, including those related to the processing of errors. By non-invasive placing of electrodes on the scalp, voltage changes that result directly from neuronal activity can be detected and measured. This direct measure of brain activity is unique to EEG while other methods reflect brain activity indirectly, by measuring the amount of blood oxygen being expended in a particular area (functional magnetic resonance imaging, fMRI) or the amount of glucose metabolism occurring in an area (positron emission tomography, PET). In the early nineties of the last century the “error-related negativity (ERN)” (Gehring 1990) or “error negativity (Ne)” (Falkenstein et al. 1991) was observed in EEG recordings for the first time by two independent research groups. The ERN is a neural signal that can be measured in fronto-central regions of the scalp, along the midline. This electrical potential goes negative with respect to baseline (see Table 1), and occurs in response to the commission of errors or to negative feedback peaking between 100 and 150 ms thereafter (Scheffers et al. 1996). Occasionally, a relatively smaller negativity is sometimes even evident on correct trials, the so-called “correct-response negativity (CRN)”, especially when there is a high degree of uncertainty about response correctness (Pailing and Segalowitz 2004b). Following true errors or negative feedback the potential is far larger and more pronounced. Development of the ERN begins during adolescence, gradually increases during adulthood and goes hand in hand with the development of other cognitive capacities (Davies et al. 2004; Hogan et al. 2005). In general, the ERN is thought to represent a key signal of the brain during its monitoring and adjusting of flexible and goal-orientated behavior.

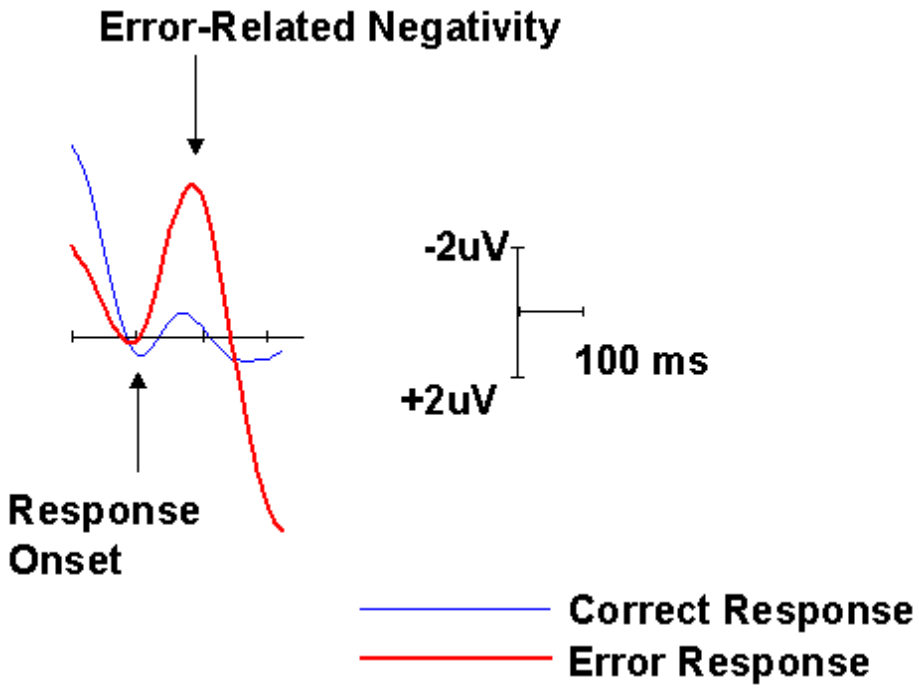


Figure 1: *Amplitude and latency of the ERN as compared to correct responses.* Blue indicates correct responses; Red indicates erroneous responses; uV indicates microvolt; ms indicates milliseconds. Figure downloaded from the world wide web on December 16th 2008: http://www.gehringlab.org/research.html

During the last years a considerable number of studies has been conducted on various conditions that might affect modulation of the ERN signal. In sum, these studies show that the ERN actually varies in its amplitude with experimental conditions, individual expressions of personality traits or psychiatric diagnoses, whereas its latency appears to be rather constant (Leuthold and Sommer 1999). A short overview is given in the following.

Variation of ERN amplitude across experimental conditions and responses: The ERN amplitude was observed to increase with increasing subjective judgment about response accuracy and certainty of error commission (Scheffers and Coles 2000). In addition, an increase of ERN amplitude was observed under conditions when

response accuracy was emphasized over speed (Falkenstein et al. 2000), whereas a decrease of ERN amplitude was observed in response to stimuli which were presented relatively infrequently. Other studies have shown the ERN to be correlated with motivational incentives, such as monetary rewards (Pailing and Segalowitz 2004a). Some findings have linked the ERN to error correction by reporting a positive association between its amplitude and the probability that an error is immediately corrected (Gehring 1993). Also, the ERN amplitude is larger after quick response corrections rather than after slow response corrections (Rodriguez-Fornells et al. 2002).

Variation of ERN amplitude according to individual differences in healthy subjects: There is increasing evidence that the ERN is substantially affected by individual differences as shown through changes in the size of signal amplitudes. For example, the personality trait *impulsiveness* seems to contribute to the variability in error signals. Within a group of healthy subjects performing a Go/Nogo task Ruchsow and colleagues (Ruchsow et al. 2005; Ruchsow et al. 2006b) found subjects with higher impulsiveness to show smaller ERN amplitudes than those with lower impulsiveness scores. Also, in a group of undergraduate students those who scored high in impulsivity displayed greater variability in ERN amplitudes across punishment versus reward conditions than those who scored low in impulsivity, supporting a relationship between impulsiveness and ERN (Potts et al. 2006). Comparable to these results, another study (Dikman and Allen 2000) found similar interaction effects between task design and the personality trait *socialization*. Subjects with lower scores in socialization displayed smaller ERN's in conditions of punishment as compared to conditions in which they were rewarded for good performance. Yet another example is the influence of the broader personality dimension *emotionality* on error processing. In a set of investigations on the influence of emotionality, individuals who were primarily characterized by negative affect and/or negative emotionality were found to display ERNs with larger amplitudes when compared to individuals without or with lesser negative affect or emotionality (Hajcak et al. 2004). Similarly, Luu et al. (2000) observed that ERN amplitude varied within individuals with high negative emotionality

as a function of task duration. In this study, ERN amplitudes decreased in a group of subjects demonstrating pronounced negative emotions as the task went on, whereas the opposite pattern was observed for the “low negative emotion” group. This result suggests that individuals with low and high grade of negative emotionality have different patterns of response-monitoring engagement. In another study, the emotional nature of the stimuli (happy or angry faces) interacted with participant’s self-reported level of task anxiety: High state anxiety individuals exhibited enhanced ERNs in response to errors on happy faces and smaller ERNs in response to errors on angry face stimuli (Compton et al. 2007). The authors of this study suggested that reactivity to the commission of errors varies not only as a function of underlying personality but also as a product of individual differences in performance expectations. Subtle differences can be found in the ERN also when assessing individuals with high grade of general anxiety and worry. For instance, undergraduates who reported high levels of obsessive-compulsive symptoms or general anxiety exhibited enhanced ERN amplitudes in response to errors, at the same time also differing in their reactivity to correct trials as compared to control subjects (Hajcak and Simons 2002; Hajcak et al. 2003). Along these lines, recent work has conceptualized the ERN as representing the activation of defensive *motivation* responses. It could be demonstrated that individuals with large ERNs display significantly larger potentiated startle responses on the trials following an error, which indicates that error reactivity may prime defensive motivation (Hajcak and Foti 2008b). Additional work examining Gray’s (1985) personality traits of *behavioral activation and behavioral inhibition*, which have been linked to approach and avoidance systems, respectively, also suggests that behaviorally inhibited individuals are more sensitive to the commission of errors due to an underlying motivation to avoid punishment (Boksem et al. 2006).

Variation of ERN amplitude across different patient populations: Several studies examined the effect of psychiatric diseases**,** such as obsessive-compulsive disorders (OCD), anxiety disorders, or depressions on error processing indexed by ERN signals. In general, these clinical populations are consistently identified by reactivity

that is specific to error trials as compared to the non-diagnosed populations which exhibit heightened reactivity to both correct and incorrect responding. For example, patients with OCD exhibited significantly larger ERN amplitudes than matched controls (Gehring et al. 2000; Ursu et al. 2003; Fitzgerald et al. 2005; Maltby et al. 2005; Ruchsow et al. 2007). The variation in amplitudes of the ERN in individuals with OCD was also associated with symptom severity, i.e. a higher levels of symptom severity was related to enhanced ERN amplitudes. Similarly, patients with anxiety disorders consistently demonstrated greater reactivity to error trials and displayed significantly larger ERN amplitudes as compared to controls. In addition, adolescents diagnosed with an anxiety disorder also demonstrated enhanced ERNs compared to age-matched controls (Ladouceur et al. 2006). Furthermore, a larger ERN amplitude (Ruchsow et al. 2006a) and feedback-ERN amplitude (Tucker et al. 2003; Ruchsow et al. 2004) were found in patients with major depression compared to controls. In contrast, patients suffering from borderline personality disorder demonstrated reduced reactivity to errors as reflected by decreased ERN amplitudes (Ruchsow et al. 2006b).

1.1.2. Neural sources of error processing

To date, a bulk of evidence has accumulated concerning the neural structures that underlie human error processing. When searching for the joint key words “error”, “processing”, and “brain” in the data base “PubMed” (provided by the U.S. National Library of Medicine and the National Institute of Health), over 1000 empirical studies can be found concerning this issue. In general, there is common agreement that the anterior cingulate cortex (ACC) acts as a pivotal player in generating error signals (for review see: Taylor et al. 2007; see also Table 1). In addition, the inferior frontal cortex with its extensions into the anterior insula (IFC/aI) is commonly reported to be activated in response to erroneous responses (Menon et al. 2001; Mathalon et al. 2003). The overall evidence suggests that these two brain structures are of outstanding relevance in human error processing, although present data indicate that

some additional brain regions accomplish important (sub-) functions related to error handling. Table 1 illustrates the most consistently identified brain regions involved in error processing as reported in previous studies.

Table 1: *Non-exhausitive listing of fMRI studies on error-related processing reporting activation in the ACC or the IFC or both*

Author/Year	Task	Comparison	ACC	IFC
Braver et al. (2001)	Go/NoGo	Errors – Corrects	+	+
Critchley et al. (2005)	Stroop	Errors – Corrects	+	+
Debener et al. (2005)	Flanker	Errors – Corrects	+	+
Dosenbach et al. (2006)	Meta-analysis	Errors - Corrects	+	+
Garavan et al. (2002)	Go/Nogo	Errors - Corrects	+	+
Hester et al. (2005)	Error Awareness	Aware vs. unaware errors - go trials	+	+
Mathalon et al. (2003)	Go/Nogo	Errors - Hits Errors - Corrects	+	+
Matthews et al. (2005)	Stop Signal	Errors (hard vs. easy) – Correct stops	+	+
Menon et al. (2001)	Go/Nogo	Errors - Correct rejections	+	+
Ramautar et al. (2006)	Stop Signal	Errors - Go trials	+	+
Ullsperger and von Cramon (2001)	Flanker	Errors - Corrects	+	+

Note. ACC = anterior cingulate cortex; IFC = inferior frontal cortex; + indicates significant activation within the corresponding brain region.

In a recent review in Neuron, Dosenbach et al. (2006) have suggested the dorsal ACC (dACC) and the inferior frontal cortex with its extensions into the anterior insula

(IFC/aI) to form the “core” of the human task set system. This task set system appears to respond highly sensitive and reliable on error signals across a lot of different tasks and studies, thus linking error processing to higher-order cognitive control systems (see Figure 2).

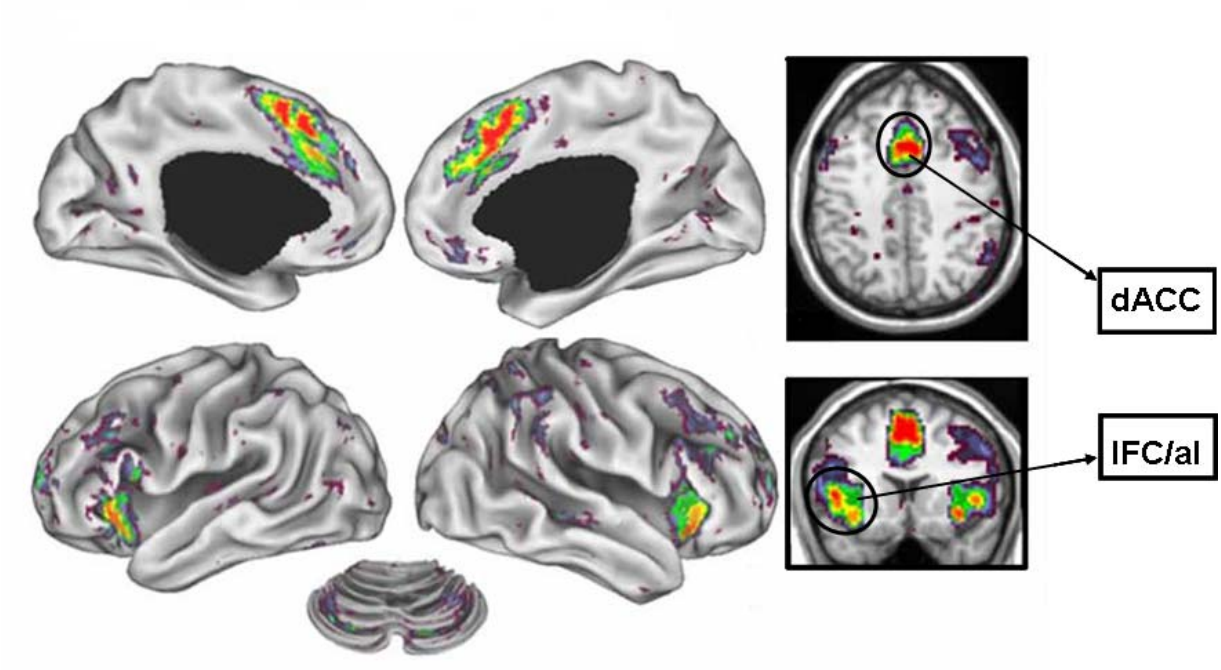


Figure 2: *Error-related signals within the “core” of the human task set system.*
Top right: Transversal view showing activation in the dorsal anterior cingulate cortex (dACC). *Bottom right:* Coronal view showing additionally the left inferior frontal cortex bordering the anterior insula (IFC/aI) as one of the major regions involved in error-related processing within the so called human task set system. Figure derived and adapted from Dosenbach et al. (2006, p. 806).

1.1.2.1. The ACC within error processing

According to initial source localizations of event-related potentials (ERP) during error processing the anterior cingulate cortex (ACC) is thought to be the major source emitting ERN signals. To date, neuroimaging studies using techniques with higher spatial resolution have supported and extended these initial estimates of source localization. These studies now conclude the medial frontal cortex, which includes the ACC, to be the most consistently activated neural region during error processing (Carter et al. 1998; Braver et al. 2001; Ullsperger and von Cramon 2001; Holroyd and Coles 2002; Garavan et al. 2003).

The ACC is typically divided into a cognitive and an affective subdivision based upon different cytoarchitectures and connectivities of these two subdivisions (see Figure 3). The cognitive subdivision incorporates the dorsal part of the ACC (dACC) and is primarily involved in the modulation of attention or executive functioning, competition monitoring, motivation processing, processing of novel stimuli, working memory, anticipation of cognitively demanding tasks, and, error processing (for review see: Bush et al. 2000). The affective subdivision corresponding to the rostral part of the ACC (rACC), shows strong connections to the amygdala, nucleus accumbens, hypothalamus, anterior insula, hippocampus and ventrolateral prefrontal cortex, and has got additionally connections to autonomic, visceromotor, and endocrine parts of the nervous system. The affective subdivision of the ACC is considered to contribute to the assessment of salience about and regulation of emotional and motivational information (Whalen et al. 1998; Mayberg et al. 1999). To date, most studies link the more dorsal part of the ACC to the processing of errors (Dosenbach et al. 2006; for review see: Taylor et al. 2007), even though several studies find error signals also in the more rostral parts of the ACC (Menon et al. 2001; Garavan et al. 2003; Hester et al. 2005).

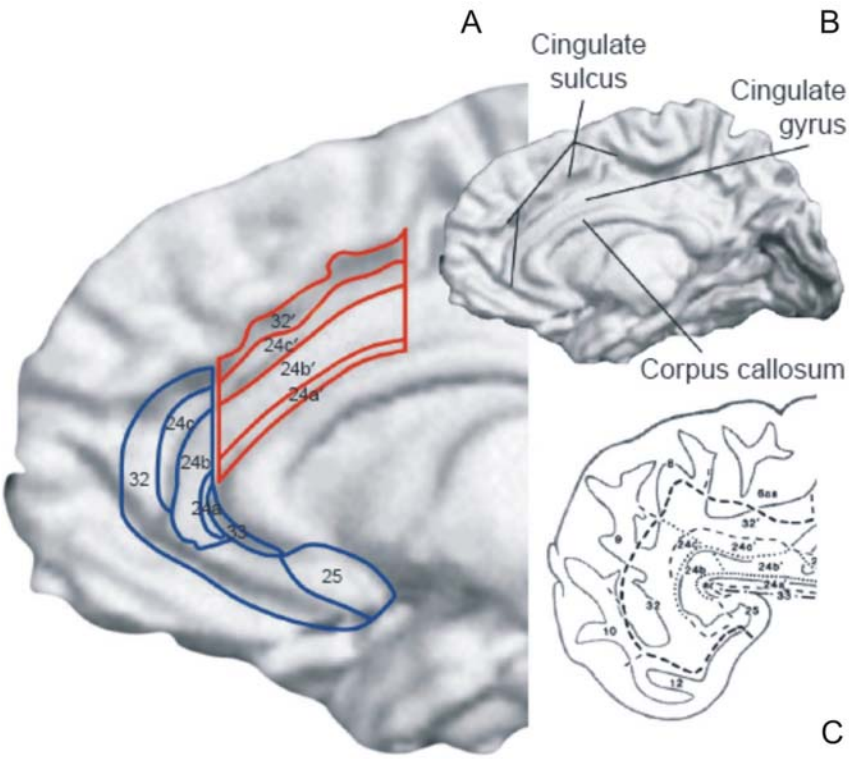


Figure 3: *Anatomy and Brodmann Areas of the anterior cingulate cortex (ACC). A.* Schematic presentation of Brodmann areas (numbers), based on the cytoarchitecture differences. Affective divisions are outlined in blue, cognitive division areas are outlined in red. *B.* Reconstructed MRI presentation of the medial surface of the right hemisphere of a single human brain (the cortical surface has been 'partially inflated'). The cingulate gyrus lies between the cingulate sulcus and the corpus callosum. *C.* Schematic flat map of anterior cingulate cortical areas. The borders of each sulcus appear as thin unbroken black lines, whereas a combination of broken and dotted lines outline cingulate areas. Figure derived and adapted from Bush et al. (2000, p. 216).

Two major competing theories of ACC function within a system for error processing are the error detection or mismatch detection theory (Falkenstein 1990; Coles et al. 2001) and the conflict monitoring theory (Botvinick et al. 2001; Yeung et al. 2004). In contrast to these more "classic" accounts of ACC functioning related to error

processing, the reinforcement learning theory proposed by Holroyd and Coles (2002) subsumes a number of the basic tenets of the previously mentioned models.

Error detection or mismatch theory. Initially in the early nineties, the ERN was conceptualized as correlating with error detection processes via response representations. In this view, the ERN is generated by the ACC due to comparison of the actual response representation and the required response. When the representation of the actual response is inconsistent with the representation of the intended response, a mismatch (error) is detected (Gehring et al. 1993; Coles et al. 2001). The elicited error signal is then conveyed to a second component of the error processing system, which is responsible for strategic and corrective adjustments. According to this theoretical framework, the process of comparison between the intended and actual outcome is caused by the response to the target stimulus itself. Error awareness is thereby not considered to be necessary to elicit neural error signals. For example, a recent fMRI study observed brain activity in response to errors regardless of error awareness (Hester et al. 2005). This theory is furthermore supported by data that show that the ERN decreases when response speed is emphasized over accuracy (Gehring 1993). Also, an enhanced ERN has been observed in association with an increase of incorrectly chosen response parameters (Bernstein et al. 1995). Despite this line of evidence, the existence of a correct-response negativity (CRN) found on accurate response trials seems to indicate that the ERN reflects more than merely an error detection process and perhaps may serve a broader function of evaluating response patterns in general, regardless of paradigm conditions or accuracy measures (Vidal et al. 2000; Vidal et al. 2003). This more expansive perspective merges well with the currently proposed model of response-monitoring and suggests that the rather narrow focus on inaccurate responding limits the applicability of the error detection theory.

Conflict monitoring theory. Similar to the error detection theory, the conflict monitoring theory also emphasizes a comparison process. However, the focus of comparison in this theory refers to the level of conflict between competing stimuli. In this sense, error

signals have been explained as a special occurrence of cognitive conflict occurring whenever a strong response tendency competes with, and must be overcome by the intended response. The conflict-monitoring theory emphases the role of the ACC in on-going performance evaluation and hypothesizes its function to detect conflict due to competing response tendencies and to relay this information to other neural regions that directly implement cognitive control such as the prefrontal cortex (PFC) (Carter et al. 1998; Botvinick et al. 2001). Support for these assumptions stem from electrophysiological and fMRI studies that revealed activation of the ACC not only on incorrect, but also on correct trials with high conflict content (Carter et al. 1998; Vidal et al. 2000; Vidal et al. 2003). It is believed that the ACC activation results from response conflict after error commission due to continued stimulus processing, whereas conflict processing on correct responses is more likely to be processed prior to subject response as reflected by other stimulus-locked ERP measures. However, this association has not been consistently supported across studies (Davies et al. 2001) and further research is needed to strengthen the results that have been found using a variety of data processing techniques. A number of other studies have tried a more integrative approach towards the debate whether ACC reflects error detection *per se* or rather conflict monitoring by suggesting a sort of 'midline brain dissociation' between both processes. They implicate that rACC might be involved in error detection (possibly linked to the emotional valence of an incorrect response), whereas dACC and pre-supplementary motor area (pre-SMA) may monitor conflict (Ullsperger and von Cramon 2001; Garavan et al. 2003). To this end a number of fMRI studies have attempted to separate error and conflict-related processes within one experimental paradigm (Braver et al. 2001).

Reinforcement-Learning Theory. Holroyd and Coles (2002) proposed a different interpretation of conflict-related and error-related ACC activation as part of their general "reinforcement learning" theory. In addition to addressing response conflict, this model focuses on the online detection of errors and gives a proposal on the progression from error detection to the production of error signals. According to the model function of the ACC is to filter sensory input and to pass the error signal. The

error signal itself is thought to be generated by the basal ganglia, which serves as an ‘adaptive critic’ by processing incoming sensory information, predicting event-related outcomes and comparing them to actual outcomes. If this comparison meets the expectation, the dopamine level increases, reinforcing the behavior. In contrast, if the expectation is violated and a negative outcome results from action, phasic shifts in the dopamine signal are produced resulting in an error signal which facilitates a change in behavior and gives humans the ability to learn from their mistakes. This error signal is distributed via the mesencephalic dopamine system in three main locations: (1) the motor controllers of the system (i.e. amygdala, PFC), (2) the control filter (the ACC), and (3) the structures being responsible for the adaptive critic (the basal ganglia). The phasic shifts of the dopamine signal among these locations disinhibit the ACC and modulate the magnitude of the error signal (Holroyd and Coles 2002; Holroyd et al. 2003). Significant support for the hypothesis that error signals in the ACC reflect a violation of expectancy comes from several studies. Holroyd and colleagues (Holroyd et al. 2004) found that subjects generated expectancies for success based on the context-specific values of stimuli, rather than their overall worth. When subjects could either win different amounts of money or win nothing at all, they produced error signals when they won nothing. By contrast, when subjects could either loose different amounts of money or loose nothing at all, they produced the strongest error signals when they lost the largest amount of money, but showed no error signals when they did not loose any money (i.e. also did not win any money). Thus, the absolute value of the outcome does not appear to matter. Rather, it is the context dependent evaluation of the outcomes and consequently the contingent expectancies generated within the actual situation that moderate error signals. Other studies showed that error signals, such as the ERN amplitude, have a direct relationship to individual expectations of success, with the largest ERNs occurring in response to errors when the probability of success is highest, and the smallest ERNs occurring in response to errors when the probability of success is lowest. Holroyd et al. (2003) tested this idea by creating conditions of frequent and infrequent rewards. In the frequent reward condition subjects had bigger ERN amplitudes in response to errors than in the infrequent condition.

However, there is also conflicting empirical evidence for the proposed expectancy violation – error signal relationship. In a recent study, subjects were rewarded randomly in 20%, 50%, or 80% of trials (Hajcak et al. 2005). According to the Reinforcement Learning theory the largest error signals should have occurred in highly probable reward conditions (80%) and the smallest error signals in low probable reward conditions (20%). Contrary to this prediction, the error signals did not differ significantly between these conditions. One critical factor, however, to be discussed here is that the rather passive receipt of rewards with random probabilities might not reflect a typical experimental context to investigate error processing. In their model of reinforcement learning error processing serves the adjustment of behavior in order to improve the outcomes of their actions. In the study by Hajack et al. (2005) subjects had no opportunity to learn from their mistakes, because of the randomly generated outcomes.

1.1.2.2. The IFC within error processing

Besides ACC activation in response to errors, the inferior frontal cortex (IFC), and in particular that part of the IFC which extends posteriorly into the anterior insular cortex (IFC/aI), has often been reported to be sensitive to errors. Several prior neuroimaging studies have even reported the dACC and the IFC/aI to be coactivated (see Table 1).

The IFC consists of three anatomical subdivisions (see Figure 4). Starting posteriorly, these are the pars opercularis roughly corresponding to BA 44, pars triangularis roughly corresponding to BA 45, and pars orbitalis roughly corresponding to BA 47. The pars opercularis borders anteriorly to the vertical ramus of the Sylvian fissure and posteriorly to the inferior part of the precentral sulcus. The pars triangularis borders posteriorly and anteroinferiorly to the vertical and horizontal rami of the Sylvian fissure, whereas the pars orbitalis borders superiorly to the horizontal ramus of the Sylvian fissure and inferiorly to the lateral orbital sulcus. Ventrally, the IFC adjoins with the anterior insular cortex.

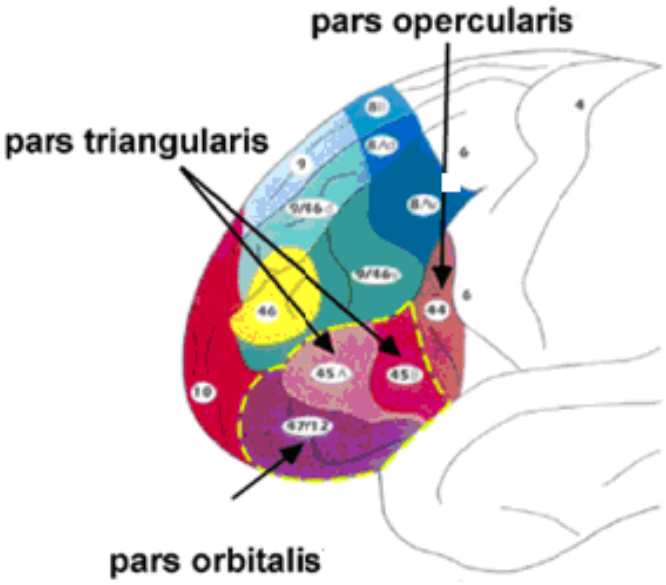


Figure 4: *Anatomical divisions within the inferior frontal cortex (IFC).* Labels highlight the opercularis (BA 44), triangularis (BA 45), and orbitalis (BA 47) subdivisions of the inferior frontal gyrus. Petrides and Pandya (2002) distinguished the portion of BA 47 as area 47/12, as it was homologous to monkey area 12 and was distinct from caudal orbital frontal cortex. Figure derived and adapted from Petrides and Pandya (2002, p. 294).

First research on functions of the human IFC dates back to Broca's work on non-fluent aphasia (Broca 1861). Nowadays, evidence has accumulated indicating a broader role of IFC beyond pure language production (Petrides 2000; Dosenbach et al. 2006), such as expressive language, working memory, and semantic generation (Broca's area) (Amunts et al. 1999; Cannestra et al. 2000; Amunts et al. 2004). In addition, evidence from fMRI studies on memory processes has suggested that the implementation of goals, i.e. intended acts to recall or to remember a specific task set, is controlled by the IFC (Henson et al. 1999; Owen 2000; for review see: Badre and Wagner 2007). Most importantly, activation of the IFC seems also involved in the processing of errors. As illustrated in Table 1, this structure is commonly found in

published results of activated regions in response to errors. Typically, studies using a Go/NoGo paradigm or an Eriksen Flanker task (Eriksen and Eriksen 1974) have observed enhanced activity following errors in clusters of activation encompassing the IFC/aI (Menon et al. 2001; Ullsperger and von Cramon 2001; Mathalon et al. 2003; Debener et al. 2005), but also studies using other experimental paradigms known to elicit errors have associated IFC activation to error signals (Critchley et al. 2005; Matthews et al. 2005; Ramautar et al. 2006). Interestingly, to date the discussion about its function within error processing has mostly been ignored.

Among the few attempts to interpret IFC activation in response to errors is the seminal review by Dosenbach et al. (2006). They conducted a methodologically sophisticated meta-analysis on studies with ten different task conditions sorted by input and output modality, such as verb generation and reading, object naming, motor timing, and analyzed them regarding task-set specific processes defined as: (a) “task-set initiation activity”, i.e. activation signals related to the beginning of a task condition, (b) “task-set maintenance activity”, i.e. activation signals which are sustained constantly during a specific task period, and (c) “error-related task-set activity”, i.e. activation signals related to erroneous responses helping the adjustment of top-down signals. The authors found that the dorsal anterior cingulate cortex bordering the medial superior frontal cortex (dACC/msFC) and the bilateral anterior insula adjoining to the frontal operculum (aI/fO) carried robust start-cue activity, sustained activity, and error-related activity. These regions were summarized to form the “core” of the human task-set system. The authors proposed that this task-set system acts in accordance to a given task instruction, and in doing so, initiates and maintains given task sets in order to configure top-down signals which aid the moment-to-moment processing. In addition, this task-set system is considered to perceive bottom-up signals about ongoing performance, indicating discrepancies about the intended and actual outcome, thus either reflecting or generating error-related signals, that in turn help adjusting ensuing top-down signals. In sum, the model proposes that not only the dACC but also the IFC bordering the bilaterial anterior insula plays an important role in error processing due to its processing of task

set representations. Still, the authors do not provide any further differentiation about possible divergent functions of these two brain structures within the human task-set system, and thus within human error processing. It remains unclear, whether the dACC and the IFC/aI are involved in error processing in similar ways, or whether the two structures hold functions within error processing which are either complementary or mutually exclusive. Nevertheless, the model contributes to a functional interpretation of IFC/aI activation in response to errors, and provides a promising direction in interpreting previous findings on error signals and IFC/aI activation.

1.1.2.3. Other brain regions within error processing

Other brain regions, such as the dorsolateral prefrontal cortex (DLPFC), the pre-supplementary motor area (pre-SMA), and the bilateral mid-insular cortex have often been reported in studies on error processing. However, most researchers agree that they do not carry a key role in error processing per se. For example, there is accumulating evidence that the DLPFC interacts extensively with the ACC to exert top-down cognitive control (Miller 2000). Specifically, Carter et al. (1998) have argued that the ACC monitors for response competition and signals to the DLPFC when cognitive control is needed. This hypothesis is supported by neuroimaging data showing ACC activation under conditions of increased monitoring of response conflict and DLPFC activations during periods of increased control in a Stroop task (MacDonald et al. 2000). Thus, DLPFC activation occurs following demands of cognitive control in consequence of an error. Activation in the pre-SMA following errors has been discussed to reflect response inhibition of motor responses under response competing conditions. Thus, its occurrence is not specific to errors per se but rather sensitive to conflict manipulation (Ullsperger and von Cramon 2001; Garavan et al. 2002; Nachev et al. 2005). Robust mid-insula activity may also accompany errors and is thought to reflect autonomic responses to the negative emotional arousal of the feedback (Garavan et al. 2003; Hester and Garavan 2004). Thus, arousal regulation related to cognitive control might be ascribed to the mid-insular cortex.

1.2. Personality

Humans differ from each other, not only concerning age, gender, and culture. Why and how they differ is less obvious and subject of research in the field of personality psychology. Contemporary research approaches to personality define personality as "…the set of psychological traits and mechanisms within the individual that are organized and relatively enduring and that influence his or her interactions with, and adaptations to, the environment (including the intraphysic, physical, and social environments)" (Larsen and Buss 2005, p. 4) As evident from this definition, some key elements are nowadays believed to be central in personality: (a) *Consistency* – It is assumed that individual subjects behave in similar ways across a variety of situations, thus personality is considered to be more or less stable over time and situations. (b) *Psychological and physiological* – Personality is most of all a psychological construct, even though empirical evidence indicates a strong relation to biological processes and needs. (c) *Impact behaviors and actions* – It is assumed that personality conditions individuals to act in a certain manner. (d) *Multiple expressions* – Personality is not only displayed in behavior but also in cognitions, emotions, and interpersonal interactions.

Over the last decades, different models have been established to describe individual differences among humans (Zuckerman and Como 1983; McCrae and Costa 1987). Their roots stem from different schools in psychology, ranging from psychodynamically influenced schools to those proposing a biological basis of individual differences. The major approaches to personality are behavioral theories, social and cognitive theories, humanist theories, and personality trait theories. Among these, trait theory has become one of the most influential approaches to personality at all. In particular, the methodological approach regarding the use of factor analysis within trait theory research has led to the establishment of quite valid, cross-cultural findings and to the acceptance of trait theory much broader than within personality research itself. According to trait theory, traits (a) are habitual patterns of thoughts, emotions, and behaviors, and (b) are considered to be relatively stable over time, to

differ among individuals, and to influence behaviour (Stagner 1977). Through the combination and interaction of various traits a personality is formed that is unique to each individual.

1.2.1. The Big Five: A Five-Factor Model of Personality

The most influential, well-established, and applicable trait theory is the Five Factor Model (FFM) of Personality (McCrae and Costa 1987). The FFM represents a hierarchical taxonomy characterizing specific personality traits through five superordinate dimensions – the so called “Big Five” - Neuroticism, Extraversion, Openness to Experience, Agreeableness, and Conscientiousness. In general, these five dimensions are meant to describe the most common and overarching individual differences in emotional, cognitive, behavioral, and motivational styles within humans (McCrae and Costa 1987). The Big Five are fairly stable across different cultures and life span (Costa and McCrae 1986; McCrae and Costa 1997; McCrae et al. 1999; McCrae et al. 2000; Egger et al. 2003; Furnham et al. 2005). To date it is believed that each of the “big” factors represents a superordinate dimension, and, in addition, summarizes a large number of distinct, more narrowly defined personality characteristics, often called “facets” (Costa and McCrae 1997).

The factor “Neuroticism” describes individuals that are prone to experience emotional instability, anxiety, moodiness, irritability, and sadness (McCrae and John 1992). Furthermore, they show the tendency to experience anger and hostility, frustration, bitterness, depression, and shyness or social anxiety. In addition, they often act on cravings rather than to abjure them and to delay gratification.

The factor “Extraversion” indicates the quantity and intensity of energy directed outwards into the social world and thus captures particularly the social dimension of personality (McCrae and John 1992). This trait characterizes people who are excitable, sociable, talkative, assertive, and emotional expressive. Highly extraverted individuals are interested in others and are friendly towards them, they prefer the

company of others, are socially ascendant, are forceful in their expression, and show a high need for environmental stimulation. In particular, they tend to experience positive emotions and seek for reward to a higher degree than less extraverted individuals (McCrae and John 1992). Furthermore, extraverted individuals show a high outside orientation, which makes them in particular sensitive to and vulnerable for negative social evaluation.

The factor “Openness to Experience” features characteristics such as imagination and insight. This trait identifies individuals who show active seeking for experiences for their own sake, who are receptible to the inner world of imagination, and who appreciate art and beauty. Furthermore, they show a high level of openness to inner feelings, openness to new experiences on a practical level, intellectual curiosity and readiness to re-examine own values and those of authority figures (McCrae and John 1992).

The factor “Agreeableness” refers to the preference to interact in a compassionate and cooperative manner. This trait includes characteristics such as trust, altruism, kindness, affection, and other prosocial behaviors (McCrae and John 1992). Highly agreeable individuals belief in the sincerity and good intentions of others, show frankness in expression and are actively concerned with the welfare of others. Furthermore, they tend to avoid interpersonal conflict, play down own achievements and show an attitude of sympathy for others.

The factor “Conscientiousness” refers to the degree of organization, persistence, control and motivation in goal directed behavior (McCrae and John 1992). In general, this trait includes characteristics such as thoughtfulness, high impulse control, and goal direction. Highly conscientious persons have prominent belief in their own self-efficacy and personal organization. Furthermore, they place their emphasis on the importance of fulfilling moral obligations, and show a high need for personal achievement and sense of direction. They show high capacity to initiate tasks and follow through to completion despite boredom or distractions, and tend to think things through before acting or speaking (McCrae and John 1992).

In general, the FFM shows a range of advantages: The predictive value of the FFM has been confirmed across a number of meta-analyses on different behavior-relevant

domains. For example, a study on the relationship between the Big Five and personality disorders according to the Diagnostic and Statistical Manual of Mental Disorders, 4th Edition, (DSM-IV) revealed that each personality disorder displays a unique and predictable five-factor profile (Saulsman and Page 2004). Another example is the predictive value of Conscientiousness in the field of job performance. A meta-analysis (Barrick 1991) revealed that Conscientiousness showed consistent relations with all kinds of performance criteria within a variety of occupational groups. In addition, they revealed that Extraversion is a valid predictor of occupations relying on social interaction skills, whereas training proficiency is predicted by the factors Openness to Experience and Extraversion.

Despite great acceptance and its wide spread, the FFM is not without its critics (Block 1995). One point of critic concerns the discussion about the exact number of factors underlying personality characterization. In contrast to the FFM, several other researchers offer a three-factor model of personality. For example, Eysenck (1981) suggests Neuroticism, Extraversion, and psychoticism to be powerful enough to describe personality. In contrast, Cloninger (1986) postulates the following three different personality dimensions: Novelty Seeking, Harm Avoidance, and Reward Dependence. Another criticism relates to the methodological approach the FFM is derived from. For example, the factor analytic method shows the disadvantage of not having a universally recognized basis for choosing among solutions with different numbers of factors. Thus, this methodological approach entails to some degree subjective judgment about the final numbers of factors. The most prominent criticism of the FFM concerns its non-theoretical approach, since to date the factor analytical finding of five dimensions of personality traits has not been explained by an underlying theory. Such a theoretical claim would require for example to determine the neural correlates of the Big Five. At present, some research is underway on determining the neural substrates of the Big Five, but since only little empirical evidence for such a neurobiological basis is present, further research in this field is necessary.

1.2.2. Neural sources of the Big Five

The interest in the neural underpinnings of personality dates back to the 19th century, when phrenology, then considered as science, became popular. In these days, phrenologists suggested that all characteristics of a person are represented in specific parts of the brain (see Figure 5). By analyzing an individuals' brain shape, phrenologists attempted to determine its personality traits.

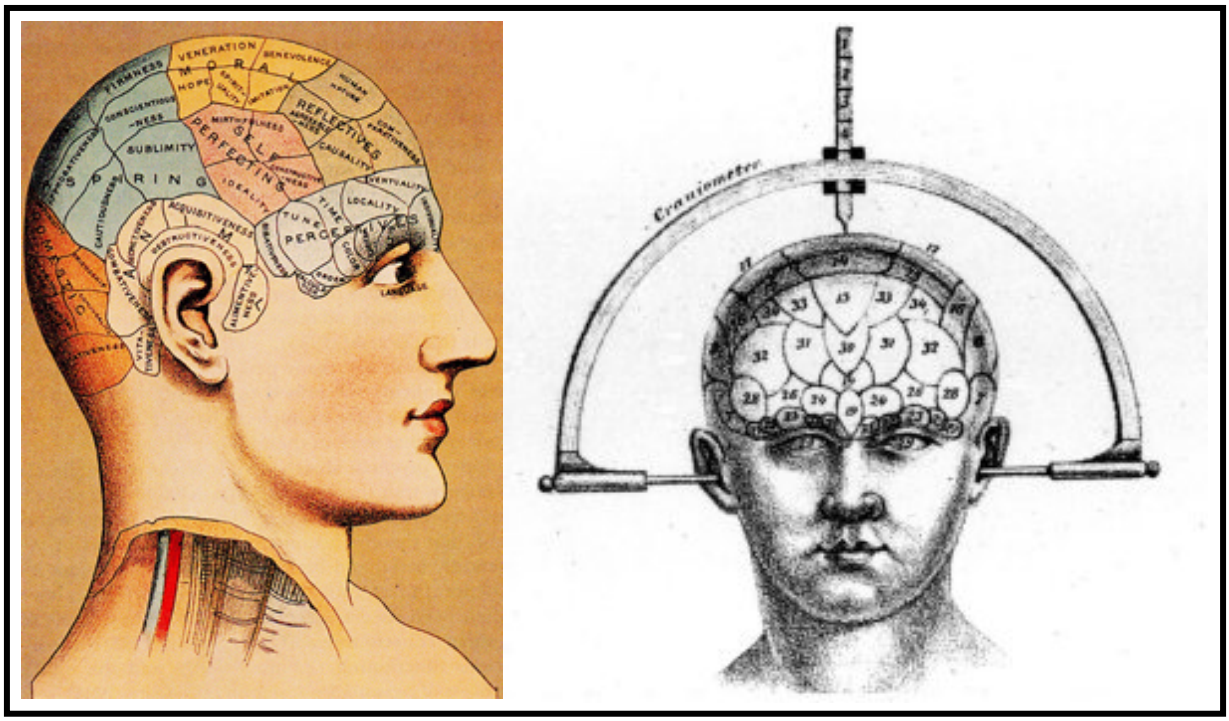


Figure 5: *Phrenology – exemplary charts and measurement instruments. Left*: Phrenological chart from the 19th century: Typical division of brain regions considered to correspond to specific personality traits and intellectual capabilities. Figure downloaded on 15th December 2008 from: http://www.artsci.wustl.edu/~mjstrube/psy315/content.html. *Right*: Illustration from the 19th century: The use of the craniometer, an instrument originally used for the determination of personality, later on for the measurement of intelligence. Figure downloaded at the world wide web on December 15th 2008 from: http://www.creationism.org/books/TaylorInMindsMen/TaylorIMMo15.htm.

Nowadays, with improving technological facilities it seems inevitable to tackle again the question about whether and where personality is encoded in the brain. In recent years, a growing amount of imaging studies has been addressed with the aim of locating brain regions associated with individual differences in personality traits, such as the Big Five. Especially the two factors Neuroticism and Extraversion have been of major interest in the attempt to linking them to neurobiological markers. One pioneer work by Mathew et al. (1984) using the xenon inhalation technique in positron-emission tomography (PET) examined the association between cerebral blood flow (CBF) and Extraversion. The authors found a negative correlation between whole brain CBF and Extraversion with reduced overall blood flow in highly extraverted individuals. The authors interpreted the results as being in line with Eysenck's (1981) claim on an inverse association of Extraversion with general cortical arousal. Stenberg et al. (1990) could replicate these findings. In addition, regional cerebral brain blood flow (rCBF) was associated with Extraversion, with lower rCBF in the temporal lobes being identified for extraverted individuals relative to introverted individuals. Unfortunately, neither of those studies worked with aligned anatomical magnetic resonance images (MRI) or standardized stereotaxic coordinate systems, thus not permitting precise neuroanatomical locations associated with Extraversion.

A first step into such a direction undertook a single photon emission tomography (SPECT) study with elderly subjects. The authors defined a number of specific regions of interest by a brain atlas and examined their association with Extraversion and Neuroticism. They only found a significant positive correlation between Extraversion and rCBF in the cingulate cortex during rest (Ebmeier et al. 1994). In contrast, a PET study conducted by Fischer et al. (1997) did not reveal any increased cerebral blood flow in cortical regions such as the cingulate region for extraverted relative to introverted individuals. Instead, Extraversion was significantly associated with increased blood flow in the caudate and putamen, both regions known to be key areas of the dopaminergic system. In another PET study by Johnson et al. (1999) Extraversion was correlated with several brain regions earlier being identified in other imaging studies, such as the anterior cingulate, the amygdala, the insula, and the temporal lobes.

As research techniques in neuroscience developed further, fMRI studies on the neural correlates of the Big Five cumulated. Interestingly, up to date hardly any attempt has been done in examining all of the five personality traits as defined through the Big Five. Instead, the major focus of interest was still on the two factors Neuroticism and Extraversion, however in the context of more constrained theoretical predictions on how these personality traits could be related to the neural system. According to Eysenck´s (1981) conception, introversion and Extraversion would reflect individual differences in a cortical arousal system modulated by reticulothalamic – cortical pathways, with extraverted individuals chronically being less cortically aroused than introverted ones. Secondly, Extraversion and Neuroticism were thought to be associated with functional and structural variability in brain regions responsible for affective processing, i.e. the ACC, the basal ganglia, orbitofrontal cortex, the amygdala, and insula (for review see: Canli and Amin 2002; Canli 2004).

Kumari et al. (2004) examined the influence of Extraversion on neural activity related to graded cognitive demands during a parametric *n*-back-Task. Extraversion was associated with increasing activity in the right DLPFC and ACC as cognitive load increased from rest to 3-back. In addition, increased activity in ACC, but not DLPFC, in response to changes from rest to 1-back and 2-back was predicted by Extraversion. Again, these results were interpreted according to Eysenck's claim on an inverse association of Extraversion with general cortical arousal.

The second direction in summarizing the neurobiological basis of both, Extraversion and Neuroticism, mainly stems from the work around the research group of Canli who argues that activation in the amygdala due to passive viewing of positive stimuli or to the experience of positive emotions per se (Canli et al. 2001; Canli et al. 2002; Canli 2004) varies as a function of individual differences in Extraversion. This claim is in line with quite consistent findings on amygdala activation as a reaction to negative stimuli independent of the influence of personality differences, and the quite inconsistent findings on amygdale activation as a reaction to positive stimuli, when not controlling for personality. In their first fMRI study, Canli et al. (2001) scanned

female subjects while they were passively viewing pictures with either positive or negative content. Extraversion was correlated with increased activity in the amygdala and ACC during the experience of positive emotions. In contrast, Neuroticism was associated with the middle temporal and frontal gyrus, but not with regions known to be related to affectivity. Similar effects were found in a further study using happy faces as positive stimuli (Canli et al. 2002). Again, Extraversion was positively associated with passive viewing of happy faces in the amygdala. This correlation was specific to Extraversion, as none of the remaining Big Five traits were acting as a modulator of increased amygdala activation to happy faces. By contrast, increased activation of amygdala in response to fearful faces was observed across all subjects independent of their personality traits. Canli (2004) has conducted a further fMRI study in order to contribute to the dissociation of mood state and moderating personality traits being evident in imaging studies on Extraversion and Neuroticism. Based on the standard definitions of Neuroticism and Extraversion, these two personality traits were a priori assigned to negative and positive mood states, respectively (McCrae and John 1992) and it was predicted that neurotic individuals should show an increased reactivity to negative emotional stimuli, while extraverted individuals were predicted to be particularly susceptible to positive emotional stimuli. The authors implemented an emotional stroop attention task and administered a self-reported personality inventory measuring Extraversion and Neuroticism, as well as a self-reported measure of mood state (Canli 2004). Analyses of the data revealed that Extraversion but not positive mood state was positively correlated with positive stimuli in the rACC. In contrast, negative mood state but not Neuroticism was associated with increased activity in the ACC. Hence, increased ACC activity in response to positive stimuli varies as a function of Extraversion, whereas increased ACC activity in response to negative stimuli varies as a function of negative mood state.

In general, Canli's proposals have found support from other studies identifying similar results on the association between Extraversion or Neuroticism and brain regions known to be responsible for affective processing. For example, using an oddball paradigm which is known to activate the ACC as a response to discrepancy detection,

Eisenberger et al. (2005) indeed found similar activation patterns as Canli (2004). Again, Extraversion was positively correlated with the rACC activation. In addition, while not controlling for negative mood state, they found Neuroticism to be positively correlated with activity of the dACC. Interestingly, both personality traits showed opposite activation patterns, with Extraversion being inversely correlated with dACC and Neuroticism being inversely correlated with rACC. Another study by Deckersbach et al. (2006) found an inverse correlation between Neuroticism and regional cerebral glucose metabolism (rCMRglu) at rest in the insular cortex and a positive correlation between Extraversion and rCMRglu in the bilateral orbitofrontal cortex. Both structures are associated with affective processing. Also in line with the previous findings is the work by Omura et al. (2005). The authors used voxel-based-morphometry (VBM) in order to examine the correlation between personality and amygdala gray matter concentration, and observed opposite correlations between the two traits of interest – Neuroticism and Extraversion – with amygdala gray matter concentration. While Neuroticism was negatively associated with gray matter concentration in the right amygdala, Extraversion was positively associated with gray matter concentration in the left amygdala. In another VBM study by Knutson et al. (2001) these results could be corroborated at the whole brain level. The authors found a negative association between Neuroticism brain size expressed as the ratio between brain tissue and the total intracranial volume. When examining the association between different subfactors of Neuroticism with the relative measure of brain size, Knutson et al. (2001) identified sub-factors that were related to the chronic experience of arousing negative emotions. These sub-factors were correlated with reduced brain sizes. The authors argue that differences between individuals concerning stress reactivity account for the reductions in brain volume.

1.3. Linking errors and the Big Five: neural findings

Another way of looking at error processes is through studies of individual differences during error processing. As outlined in previous sections, personality traits, such as the Big Five, and error processing can be seen from a neurobiological perspective, and growing research in this direction has been done.

One study tried to establish an association between error-related brain activity and personality traits according to the FFM (Pailing and Segalowitz 2004a). In this study, authors examined whether motivational states regarding one's own performance individually vary according to individual levels in Neuroticism and Conscientiousness. Subjects' correct and incorrect performance on a four-choice letter task was measured during recordings of the event-related potential ERN. The four-choice letter task had been implemented under different motivational conditions: One condition did not involve any motivation at all since no monetary reward for correct responses was given. In other conditions graded monetary incentives were offered for response accuracy under different payoff ratios for different aspects of the task (e.g. a reward ration of 3:1 choosing the correct hand versus choosing the correct finger). Additionally, subjects filled out a self-report questionnaire assessing personality traits according to the FFM. Analyses of event-related potentials revealed that both traits, i.e. Conscientiousness and Neuroticism, were correlated with the ERN amplitude on erroneous responses. As predicted by the authors, individuals high on the trait of Conscientiousness displayed less variation in ERN amplitudes across motivational manipulations of high and low reward. By contrast, individuals loading high on Neuroticism were more sensitive to motivational manipulations that alter the salience of an error event, i.e. as incentives for accurate responses increased, task engagement as reflected by increased ERN amplitudes increased, too. Thus, conscientious individuals show overall higher intentional involvement regardless of external incentives, and seem more consistently bothered by the occurrence of an error. This finding is in line with the core definition of the personality trait Conscientiousness, which is meant to describe cautiousness, discipline, and

achievement-striving behavior, and is in general thought to be an indirect measure of persistent intentionality.

Tops et al. (2006) could replicate the findings of Pailing and Segalowitz (2004a) on the relationship between Neuroticism and task engagement. They used a standard Eriksen Flanker Task (Eriksen and Eriksen 1974) and added a manipulation regarding motivation through donation of monetary incentives. Comparable to the findings described above, the ERN amplitude within highly neurotic individuals increased when rewards for correct responses were given. Furthermore, Tops et al. (2006) investigated whether task engagement, as reflected by larger ERN amplitudes, was moderated by individual concerns about social evaluation, rather than by negative emotions or personality traits associated with negative emotions, such as Neuroticism per se (Luu et al. 2000). Concerns about social evaluation were measured by assessing the personality traits Agreeableness and the disposition to experience shame. Analyses of the EEG data revealed positive correlations between Agreeableness or behavioral shame proneness, and the size of the ERN amplitude. The authors concluded that concerns about social evaluation indeed increase task engagement, as reflected by the size of the ERN amplitude, and not negative emotions per se.

1.4. Current study objectives

In sum, the preliminary work on the relation between error signals and the Big Five indicates that individual differences in personality traits are possible candidates that may moderate the way of error processing the latter being a prominent research topic in the field of cognitive neuroscience.

However, at date existing data have all been derived from electrophysiological recordings with their methodological advantage of high temporal resolution at the costs of low spatial resolution. Nevertheless, these and numerous functional neuroimaging studies convincingly suggest a quite robust neural network facilitating

the processing of errors, i.e. the ACC and the inferior frontal cortex (IFC) bordering the anterior insular cortex (Dosenbach et al. 2006; for a review see: Taylor et al. 2007). Furthermore, the way humans process errors has been examined intensively among different psychiatric populations or among sub-clinical populations differing in affective, motivational or behavioral styles. In contrast, the Big Five as trait representatives of human personality have attracted far less attention among neuroscientists. Although the interest in the neural basis of the Big Five dates back to a decade of research, to date no effort has been made in exploring how these traits may modulate neural responses on cognitive tasks though some evidence was provided to support this claim. However previous work has shortcomings in two aspects: First, none of the previous studies has ever explored the influence of all five personality traits as described by the Big Five in the same sample of subjects. Instead, each study focused on either one (e.g. Tops et al. 2006) or two (e.g. Pailing and Segalowitz 2004a) traits and their role within error processing. Second, these very few studies conducted so far have primarily focused on the use of electrophysiological event-related brain potentials.

Therefore, given the great prominence of error processing within the field of cognitive neuroscience and the astonishing lack of data on modulating effects of personality traits on the neural correlates of error processingtwo major objectives of the current study imposed: (a) Are individual differences, as reflected through individual occurrence of traits derived from the FFM, associated at all with the way errors are processed in the brain, and (b) which brain structures are involved in such a possible relationships.

To test our predictions, we used a well evaluated version of the Eriksen Flanker Task containing a Go/Nogo component in combination with event-related functional magnetic resonance imaging. We administered a self-report questionnaire known to reliably measure individual personality traits related to the Big Five.

2. METHODS

2.1. Subjects

We studied 17 healthy right-handed subjects (9 males and 8 females) recruited via advertisements. None of the subjects had any signs or history of neurological or psychiatric diseases. Handedness was assessed by the Edinburgh Handedness Inventory (Oldfield 1971). All subjects provided written informed consent and were screened to ensure that they satisfied MRI safety requirements. The use of the present paradigm within a healthy adult population had been approved by the Ethics committee of the University of Ulm previously within the context of several other studies conducted by our in-house research group. The entire group had a mean (SD) of 25.06 (4.74) years of age (range: 20 - 35) and a mean of 12.71 (1.21) years of school education, (range: 8 - 13). Males and females did not differ significantly on years of age [$F(1, 16) = .75$, $p = .40$)] or on years of school education [$F(1, 16) = 1.13$, $p = .30$)].

2.2. Personality measurement

The German version of the Neuroticism Extraversion Openness to Experience - Personality Inventory - Revised (NEO-PI-R) by Costa and McCrae (1992; German: Ostendorf 2004) was adminstered. The NEO-PI-R is based on decades of factor analytic research within clinical and healthy adult populations. In general, it is a measure of the five major domains of personality, known as the “Big Five”, as well as of six traits or facets that define each domain (see Table 2).

Table 2: *Major domains, facet scales, and exemplary items derived from the NEO-PI-R.*

Scales	Exemplary Items
Neuroticism (N)	
N1 Anxiety	"I easily get scared."
N2 Angry hostility	"I often get angry about the way people treat me."
N3 Depression	"Sometimes I feel completely worthless."
N4 Self-consciousness	"I often feel inferior to others."
N5 Impulsiveness	"Sometimes I have trouble to overcome my temptations."
N6 Vulnerability	"I often feel helpless and wish somebody to help me."
Extraversion (E)	
E1 Warmth	"I am known as an sincere and friendly person."
E2 Gregariousness	"I love to be surrounded by other people."
E3 Assertiveness	"I am dominant, self-confident, and assertive."
E4 Activity	"I often feel like exploding of energy."
E5 Excitement-seeking	"I often seek to experience more excitement."
E6 Positive emotions	"Sometimes I feel like exploding of luck."
Openness to Experience (O)	
O1 Openness to Fantasy	"I have a very vivid imagination."
O2 Aesthetics	"I feel inspired by the motives occurring in art and nature."
O3 Feelings	"Without strong sensations life would be boring."
O4 Actions	"I often try new and foreign food."
O5 Ideas	"I love to resolve problems or tricky tasks."
O6 Values	"I am open and liberal towards the habits of others."
Agreeableness (A)	
A1 Trust	"My always first reaction is to trust others."
A2 Straightforwardness	"I could never betray somebody, even if I wished."
A3 Altruism	"I try to be friendly to every person I meet."
A4 Compliance	"I prefer cooperation with others to competition with them."
A5 Modesty	"I try to be modest."
A6 Tender Mindedness	"One can never do enough for the poor and the old."
Conscientiousness (C)	
C1 Competence	"I am proud of my good judgment."
C2 Order	"I often tend to be too demanding and accurate."
C3 Dutifulness	"I always try to finish tasks precisely and conscientious."
C4 Achievement striving	"I am working hard to achieve my goals."
C5 Self-discipline	"I am a hard working person who always finishes his work."
C6 Deliberation	"I always consider possible consequences before acting."

Taken together, the five domain scales and 30 facets scales of the NEO-PI-R facilitate a comprehensive and detailed assessment of normal adult personality. There are two forms for the NEO-PI-R, one for self report and one for observer rating. Both forms consist in total of 240 items (descriptions of behavior) answered on a five point scale, ranging from “strongly disagree” to “strongly agree”. Each subscale contains 48 items (i.e. each facet of each subscale comes with 8 items). Costa and McCrae (1992) evaluated reliability and validity of the NEO-PI-R. The internal consistencies ranged from 0.75 (“Agreeableness”) to 0.83 (“Conscientiousness”), whereas the test retest reliability reported over 6 years ranged from 0.63 (“Agreeableness”) to 0.83 (“Neuroticism” and “Openness to Experience”). The convergent and divergent validity has been established against other personality inventories and projective techniques.

2.3. Activation task and measurement procedure

The paradigm used in this study was a combination of a Go/NoGo task and an Eriksen flanker paradigm (Eriksen and Eriksen 1974) which has already been used in a series of electrophysiological studies on error processing (e.g. Ruchsow et al. 2005). A classical Go/NoGo task is based on the principal to respond to a group of stimuli (Go trials) while withholding a motor response to a second group of stimuli (NoGo trials). This approach permits the determination of correct response inhibition and erroneous responses. The combination with an Eriksen Flanker task refers to the presentation of distracting and non-relevant stimuli, so called “flankers” in addition to the target stimuli that define Go and Nogo responses.

Five-letter strings were created from the letters R, U, P, V, with the action relevant targets always mid-standing. Subjects were instructed to focus on this target letter in the middle of an array (see Appendix A). During Go trials, subjects had to give a right-hand response with the index finger for the target letter R, and a right-hand response with the middle finger for the target letter U. In NoGo trials, subjects were instructed to withhold the response upon appearance of target letters P and V. Target and flanker

stimuli and were combined either congruently (RRRRR, UUUUU, PPPPP, and VVVVV) or incongruently (PPRPP, VVUVV, RRPRR, and UUVUU), with Go target stimuli flanked by visually similar NoGo target letters, and vice versa. Combination of the factors *response type* (Go/NoGo), *congruency* and *type of target letter* yielded eight different conditions with 33 trials for each condition resulting in a total of 264 trials. Occurence probability of each condition was 0.125. Presentation of each trial began with a centrally presented fixation cross for a period of 500 ms Afterwards, letter strings were centrally shown for a duration of 200 ms followed by a blank screen with a duration of 700 ms The trial ended with the presentation of three feedback stimuli. According to the subjects' performance the German expressions for either "correct", "faster", or "wrong" were presented for 500 ms (see Figure 6).

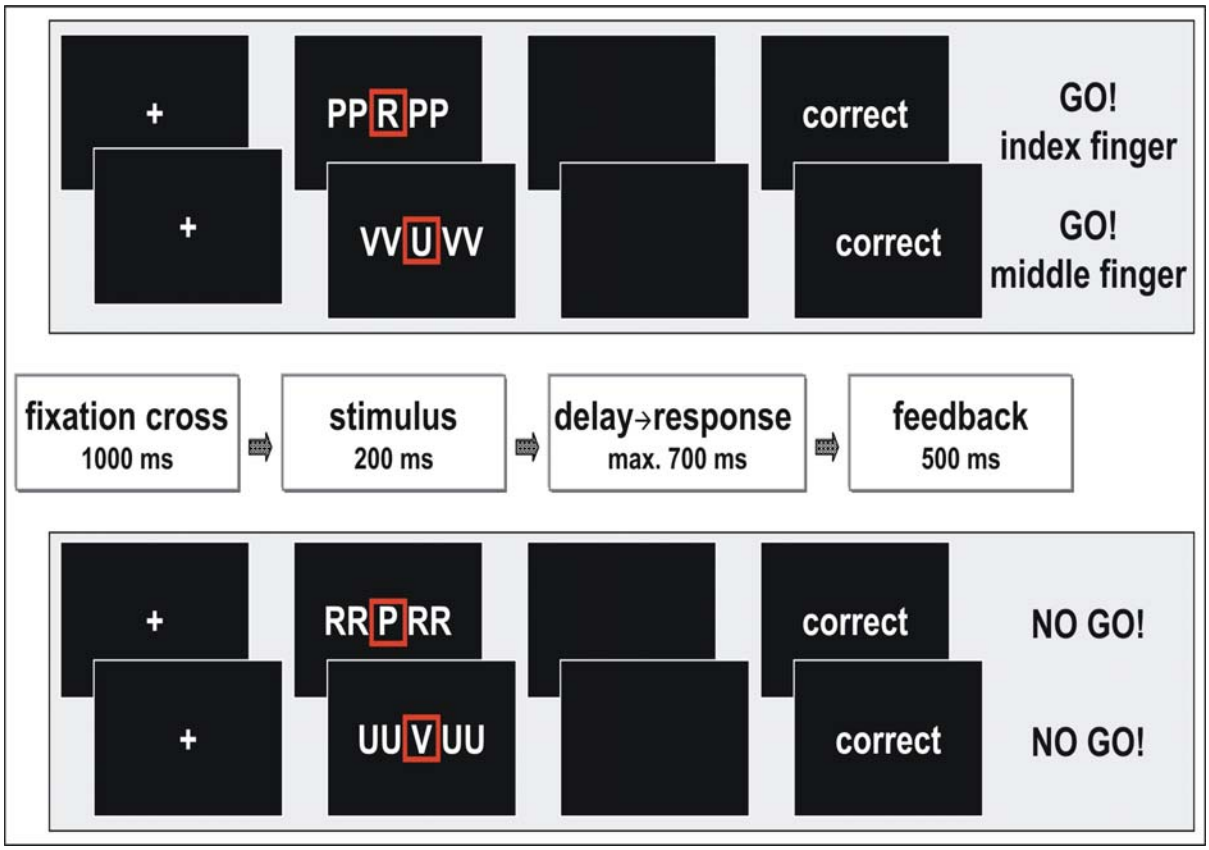


Figure 6: *Illustration of the experimental task during fMRI acquisition.*

Presentation of the experimental task was run via ERTS software (Experimental Run Time System) and was adjusted to the MRI trigger signal to ensure for synchronicity between the experiment and the fMRI recordings. Visual stimuli were centrally presented by means of MR compatible video goggles. Reaction times and correctness of subjects' responses on each trial were automatically registered by a standard personal computer that also controlled the sequence of trials. The task was implemented in a rapid event-related fMRI design with an overall averaged inter-trial interval of 4.92 seconds (sec). Ignoring the factor type of target letter (see above) averaged stimulus onset asynchrony (SOA) for congruent Go trials was 19.61 sec. For incongruent Go trials SOA was 18.95 sec. Averaged SOA for NoGo trials was 19.65 sec for congruent letter strings, and 19.60 sec for incongruent letter strings, respectively.

Subjects got acquainted to this rather challenging task during training sessions at the morning of the test day. The training version was different from the test version with respect to trial sequences and number of trials, but identical as regards the number and realizations of the eight conditions. To increase error rates in our study, the instruction emphasized speed over accuracy. Further, a reaction time (RT) deadline was individually estimated from these trainings. Mean reaction times on correct congruent and incongruent Go trials were calculated to serve as upper bounds of a time window within which the Go responses had to be executed. The rationale behind this was i) to emphasize overall speed in order to obtain sufficient frequencies of erroneous Go and NoGo responses, and ii) to exert control over the speed-accuracy trade off such that correct and false Go responses could be calculated within and above the pre-adjusted time limits (see Results section). The RT deadlines were calculated individually by averaging RTs of the training periods on correct congruent and incongruent Go trials and subtracting 15 percent afterwards. Across subjects RT deadlines ranged between 366 ms and 486 ms (mean = 430 ms, SD = 36.2 ms).

2.4. Functional data acquisition

Data were acquired using a 3.0 Tesla Magnetom ALLEGRA (Siemens AG, Erlangen, Germany) head-only MRI system using a standard transmit-receive head coil. T2*-weighted functional MR images were obtained using gradient echo-planar imaging in axial orientation along the AC-PC-line (AC = anterior commissure; PC = posterior commissure). Image size was 64x64 pixels (3.6 by 3.6 mm pixels). The volume consisted of 33 slices (Time of Repetition (TR) = 2200 ms; Echo time (TE) = 39 ms; Bandwidth (BW) = 3906 Hz/Pixel). Slice thickness was 3 mm with a gap of 0.75 mm (25%). For each session 608 volumes were acquired. The first 10 volumes of each session were discarded to avoid T1 equilibration effects. One session lasted approximately 22 minutes. At the end of an experimental session high resolution T1-weighted anatomical images were obtained using three dimensional MPRAGE sequences (Magnetization Prepared Rapid Gradient Echo): BW = 130 Hz/Px, TR = 2.3 s, TI = 1.1 s, TE = 3.93 ms, flip angle = 12°, in-planar matrix-resolution = 256×256 (1 mm x 1 mm), and at least 160 contiguous slices of 1 mm thickness in sagittal direction depending on the left-to-right extension of the subject's brain. Scan time for T1 images was about 8.5 minutes.

2.5. Data analyses

2.5.1. Analyses of behavioral data

Median reaction times (RT), expressed in milliseconds (ms), and mean error rates, expressed in percentage (%), were computed for the different conditions resulting from the combination of the factors *response type* (Go/NoGo), *congruency* (congruent/incongruent), and *response accuracy* (incorrect/correct). Within every condition, differences between incongruent and congruent trials were computed using paired *t*-tests [$P < 0.05$]. Inter-correlations among the five NEO-PI-R major domain

scores were analyzed using Pearson correlation coefficients [$P < 0.05$]. To test for relationship between individual occurrences of the five NEO-PI-R scores and performance measures in the experimental Eriksen Flanker Task (i.e. median RTs and error rates) again Pearson correlation coefficients were computed [$P < 0.05$].

2.5.2. Analyses of functional imaging data

Image pre-processing and statistical analyses were carried out using Statistical Parametric Mapping (SPM5, Wellcome Department of Cognitive Neurology, London, UK) and MATLAB 7.3 (Math-Works, Natrick, MA). This statistical approach is based on the General Linear Model (GLM) and the Gaussian Field theory.

Pre-processing. First, the functional images were corrected for slice timing differences and for motion artefacts, then spatially normalized to a standard echoplanar imaging (EPI) template in MNI standard space (standard space suggested by the Montreal Neurological Institute). Finally, all images were spatially smoothed with a 10-mm full width at half maximum (FWHM) isotropic Gaussian kernel.

Statistical first-level analyses. Individual event types (see below) were modelled as trains of delta functions at each stimulus onset convolved with a canonical hemodynamical response function (HRF). The association between each predictor and the experimental time course was calculated and served as a parameter estimate for the magnitude of neural activity for each event type. A second set of regressors was added to the design matrix using the 6 motion parameters acquired during the realignment procedures. During calculation of parameter estimates for each regressor, time series were scaled to a grand mean of 100 over all voxels and volumes within a session. Low frequency drifts were removed via a high pass filter using low-frequency cosine functions with a cut-off of 128 seconds. Model estimation was corrected for serial correlations using a first-order autoregressive model. All anatomical regions and denominations were recorded according to the atlas of Talairach and Tournoux (1988). Coordinates were peak maxima in a given cluster according to the standard MNI-template. In the 1st level analyses eight different

regressors were involved, which were defined by combination of the factors *response type* (Go/NoGo), *congruency* (incongruent/congruent), and *response accuracy* (incorrect/correct). Only errors of commission were defined as regressors of interest, i.e. missed Go events (errors of omission) were modelled but excluded from further analyses. Furthermore, differentiation between target letters was not considered at this stage of design specification. Subject specific condition effects were computed using a signed one-tailed *t*-contrasts, producing a statistical image for four contrasts: "NoGo incorrect > NoGo correct" (each for congruent and incongruent conditions) representing *NoGo errors*, and "Go incorrect > Go correct" (each for congruent and incongruent conditions) representing *Go errors*.

Second-level analyses. To account for inter-individual variance and in order to generalize from statistical inferences of condition effects and their relevant contrasts, we conducted random-effects analyses on the 2nd level making use of individual contrast images from the 1st level analyses. Since not all subjects committed erroneous responses on congruent Go and Nogo trials, analyses kept constrained to the inclusion of incongruent trials only. For identifying brain activity related to *NoGo errors* (i.e. the commission of *NoGo* errors), the individual contrast images for [NoGo incorrect > NoGo correct] were entered into a one sample *t*-test. Significance threshold was set to $P < 0.05$ with family -wise error (FWE) correction at the voxel level. The same analysis was repeated for Go errors, again for incongruent trials only.

Simple regression analyses. Correlation analyses were performed using the simple regression model in SPM5 between each of the five NEO-PI-R major domain scores and the differential neural activity on either *NoGo errors* or *Go errors*, both derived from incongruent trials only. To constrain correlation analyses to the neural circuitry associated with error processing, these analyses were inclusively masked by the network demonstrating significant effects of *NoGo* errors (see above). For correlation analyses, significance was set to a level of $P < 0.001$ uncorrected at the voxel level with an extent threshold of significant voxels at the level of $P < 0.05$ at the cluster.

3. RESULTS

3.1. Behavioral results

3.1.1. Behavioral data on the fMRI experimental task

We analyzed performance data on the combined Go/NoGo and Eriksen Flanker Task. Mean error rates (%) and mean reaction times (RT), for conditions resulting from the combination of the factors *response type* (Go/NoGo), *congruency* (congruent/incongruent), and *response accuracy* (incorrect/correct) were calculated. In addition, differences between incongruent and congruent trials within each condition were calculated. Results of mean error rates are summarized in Table 3, results of mean RT are summarized in Table 4.

As seen in Table 3, subjects showed significantly more hits (i.e. correct Go responses) within the given reaction time window on congruent (mean = 39.2 %, SD = 16.7 %) as compared to incongruent (mean = 31.3 %, SD = 12.4 %) conditions [t(16) = -4.31, p = 0.001]. In contrast, delayed hits were significantly more often observed for incongruent (mean = 48.7 %, SD = 17.0 %) than congruent (mean = 43.4 %, SD = 18.6 %) conditions [t(16) = 2.47, p = 0.025]. Incorrect responses on NoGo trials were significantly more often committed on incongruent (mean = 27.1 %, SD = 17.2 %) than congruent (mean = 9.9 %, SD = 11.2 %) conditions [t(16) = 7.10, p < 0.0001].

Table 3: *Summary statistics of the different mean error rates (%) during the fMRI combined Go/NoGo and Eriksen Flanker task*

Dependent Variable		**Error (%)**	**t(16)** ***p***
Error Rates			
Omissions on Go trials			
	Incongruent	6.6 (10.6) [5]	1.03 *(0.316)*
	Congruent	5.3 (7.6) [5]	
Commissions on Go trials (in time)			
	Incongruent	7.9 (6.2)	0.17
	Congruent	7.8 (6.8) [3]	*(0.867)*
Commissions on Go trials (delayed)			
	Incongruent	5.5 (2.9)	1.28
	Congruent	4.3 (3.3) [2]	*(0.219)*
Correct Go trials (in time)			
	Incongruent	31.3 (12.4)	-4.31
	Congruent	39.2 (16.7)	***(0.001)***
Correct Go trials (delayed)			
	Incongruent	48.7 (17.0)	2.47
	Congruent	43.4 (18.6)	***(0.025)***
Commissions on NoGo trials			
	Incongruent	27.1 (17.2)	7.10
	Congruent	9.9 (11.2) [1]	***(<0.0001)***

Note. Values are means ± SD (standard deviation) in rounded brackets; Digits in squared brackets denote numbers of subjects who did not produce any erroneous responses on the corresponding condition-by-response type-combination. Only on incongruent NoGo trials all subjects committed errors. *P*-values indicating significant effects are set in bold type and italic.

As seen in Table 4, mean RT for correct Go trials within the individually predefined reaction time window was significantly faster for congruent (mean = 367 ms, SD =

34.4 ms) as compared to incongruent (mean = 382 ms, SD = 31.2 ms) conditions [t(16) = 3.20, *p* = 0.006]. Similarly, mean RT for delayed correct Go trials was significantly faster for congruent (mean = 473 ms, SD = 42.0 ms) as compared to incongruent (mean = 483 ms, SD = 38.7 ms) trials [t(16) = 2.18, *p* = 0.044]. Also, delayed incorrect Go responses were committed significantly faster on congruent (mean = 453 ms, SD = 48.5 ms) as compared to incongruent (mean = 488 ms, SD = 59.9 ms) conditions [t(14) = 2.46, *p* = 0.027].

Table 4: *Summary statistics of mean reaction times (ms) during the fMRI Go/NoGo task*

Dependent Variable	**Median**	**t *(p)***
Reaction Times (ms)		
Correct Go Reaction (in time)		
Incongruent	382 (31.2)	t(16) = 3.20
Congruent	367 (34.4)	***(0.006)***
Correct Go trials (delayed)		
Incongruent	483 (38.7)	t(16) = 2.18
Congruent	473 (42.0)	***(0.044)***
Incorrect Go trials (in time)		
Incongruent	358 (50.3)	t(13) = 0.38
Congruent	353 (40.4)	*(0.709)*
Incorrect Go trials (delayed)		
Incongruent	488 (59.9)	t(14) = 2.46
Congruent	453 (48.5)	***(0.027)***
Commissions on NoGo Trials		
Incongruent	371 (41.6)	t(15) = -1.14
Congruent	378 (55.1)	(0.273)

Note. Values are means ± SD (standard deviation) in brackets; *P*-values indicating significant effects are set in bold type and italic; ms = milliseconds.

3.1.2. Behavioral data on errors and their correlations with the Big Five personality traits

We analyzed behavioral data on individual occurrence of Big Five traits as derived from NEO-PI-R major domain scores. Mean NEO-PI-R major domain scores and standard deviations (SD) were calculated for the entire group [Neuroticism = 85.00 (22.62); Extraversion = 116.81 (22.63); Openness to Experience = 115.31 (20.02); Agreeableness = 111.13 (13.69); Conscientiousness = 117.25 (20.13)]. No significant differences between males and females were observed [$F(5, 11) = 1.37$, $p > 0.05$]. Furthermore, within our sample of subjects, the following outliers were found, which fell just below average norm-values as derived from a representative sample (Ostendorf 2004): one female subject scored below average on Openness to Experience (Openness to Experience score of 86) and Agreeableness (Agreeableness score of 81), and, in addition, two male subjects scored below average on Conscientiousness (Conscientiousness scores of 84 and 90).

Inter-correlations between the NEO-PI-R major domain scores were calculated and are summarized in Table 5.

Table 5: *Inter-correlations among NEO-PI-R major domain scores.*

Variable	N	E	O	A	C
N	1.00	-0.53 *	-0.46	-0.51 *	-0.45
E		1.00	0.81 **	0.17	0.13
O			1.00	0.07	0.04
A				1.00	0.34
C					1.00

Note. N, E, O, A, and C are the following subscales from the NEO-PI-R: N = Neuroticism; E = Extraversion; O = Openness to Experience; A = Agreeableness; C = Conscientiousness. Values are correlation coefficients; * = significant with $P < 0.05$; ** = significant with $P < 0.001$.

Neuroticism was negatively inter-correlated with at least a minimum correlation coefficient of r = -0.45 with all other NEO-PI-R scores. Among this finding correlation with Extraversion (r = -0.53, $p < 0.05$) and Agreeableness (r = -0.51, $p < 0.05$) reached significance. Thus, Neuroticism failed to prove for orthogonality as postulated by factor analytic approaches to the Big Five and was therefore excluded from our fMRI regression analyses regarding the relationship between each of the Big Five traits and differential neural activity in response to NoGo errors of the incongruent type. Also, Extraversion was highly positively inter-correlated with Openness to Experience (r = 0.81, $p < 0.001$), but not with any other of the NEO-PI-R scores.

The major focus of the present work related to the question on the association between error processing and Big Five traits (see below). Thus, we restrained the correlation analyses between performance data derived from the experimental task and the NEO-PI-R major domain scores to erroneous responses on the experimental task (i.e. NoGo errors and Go errors). Correlation results between error rates during the fMRI experimental task and NEO-PI-R major domain scores are summarized in Table 6, correlation results between median RT on the fMRI task and NEO-PI-R major domain scores are summarized in Table 7.

Of note, we consider personality traits to be represented on a superordinate level as compared to congruency/incongruency effects of behavioral responses during the experimental task. Following this assumption, correlations were only treated as meaningful when they proved for statistical significance of at least on one of the two congruency/incongruency conditions and, in addition, proving at least for trend to significance on the other corresponding congruency/incongruency condition. Trend to significance is indicated by *P*-values below 0.100.

As seen in Table 6, Conscientiousness was significantly negativly correlated with mean percentage of incongruent Go omissions (r = -0.55, $p = 0.023$). In addition, Conscientiousness was negatively correlated with mean percentage of congruent Go

omissions with trend to significance (r = -0.45, *p* = 0.069). No other correlations reached our predefined criterion indicative for meaningful correlation (see above).

Table 6: *Correlations between error rates (%) during the fMRI Go/Nogo task and the NEO-PI-R major domain scores.*

Dependent Variable	N	E	O	A	C
Error Rates (%)					
Omissions on Go trials					
Incongruent	0.42	-0.22	-0.04	0.01	-0.55
	(0.097)	*(0.390)*	*(0.864)*	*(0.976)*	***(0.023)***
Congruent	0.46	-0.32	-0.13	0.00	-0.45
	(0.063)	*(0.217)*	*(0.608)*	*(0.995)*	*(0.069)*
Commissions on Go trials (in time)					
Incongruent	0.28	-0.49	-0.28	0.10	-0.17
	(0.284)	***(0.046)***	*(0.281)*	*(0.705)*	*(0.515)*
Congruent	0.38	-0.37	-0.25	0.04	-0.17
	(0.138)	*(0.140)*	*(0.329)*	*(0.881)*	*(0.514)*
Commissions on Go trials (delayed)					
Incongruent	0.25	-0.03	-0.17	-0.44	0.01
	(0.331)	*(0.897)*	*(0.523)*	*(0.078)*	*(0.960)*
Congruent	0.28	-0.09	-0.20	0.07	-0.38
	(0.278)	*(0.728)*	*(0.448)*	*(0.788)*	*(0.129)*
Incorrect NoGo trials					
Incongruent	0.41	-0.28	-0.04	0.08	-0.11
	(0.099)	*(0.274)*	*(0.887)*	*(0.748)*	*(0.679)*
Congruent	0.32	-0.42	-0.09	0.05	-0.35
	(0.218)	*(0.098)*	*(0.718)*	*(0.840)*	*(0.164)*

Note. N, E, O, A, and C are the following subscales from the NEO-PI-R: N = Neuroticism; E = Extraversion; O = Openness to Experience; A = Agreeableness; C = Conscientiousness. Values are correlation coefficients; *p*-values are in brackets and in italic; *P*-values indicating significant effects are set in bold type and italic; correlations of relevance are highlighted in grey.

As seen in Table 7, no correlation between erroneous reaction time data from the experimental task and the NEO-PI-R scores reached our predefined criterion for meaningful correlation (see above).

Table 7: *Correlations between median reaction times (RT) during the fMRI Go/Nogo task and the NEO-PI-R major domain scores.*

Dependent Variable		N	E	O	A	C
Reaction Times (ms)						
Commissions on Go trials (in time)						
(Congruent: N = 14)						
	Incongruent	0.01	-0.11	-0.10	-0.40	0.25
		(0.965)	*(0.673)*	*(0.704)*	*(0.108)*	*(0.338)*
	Congruent	-0.31	0.02	0.08	0.13	0.53
		(0.289)	*(0.947)*	*(0.783)*	*(0.656)*	*(0.050)*
Commissions on Go trials (delayed)						
(Congruent: N = 15)						
	Incongruent	-0.22	0.03	0.01	-0.23	0.28
		(0.391)	*(0.912)*	*(0.977)*	*(0.384)*	*(0.279)*
	Congruent	-0.20	-0.24	-0.06	-0.11	0.56
		(0.475)	*(0.392)*	*(0.818)*	*(0.718)*	***(0.029)***
Incorrect NoGo trials						
(Congruent: N = 16)						
	Incongruent	-0.17	0.23	0.27	-0.46	0.19
		(0.504)	*(0.377)*	*(0.299)*	*(0.063)*	*(0.465)*
	Congruent	-0.24	0.07	0.05	-0.37	0.25
		(0.365)	*(0.795)*	*(0.856)*	*(0.163)*	*(0.347)*

Note. N, E, O, A, and C are the following subscales from the NEO-PI-R: N = Neuroticism; E = Extraversion; O = Openness to Experience; A = Agreeableness; C = Conscientiousness. Values are correlation coefficients; *P*-values are in brackets and italic; *p*-values indicating significant effects are set in bold type and italic; ms = milliseconds.

3.2. Functional imaging results

3.2.1. Results from group analyses

The results for the contrast between incorrect and correct NoGo responses (i.e. Nogo errors) are summarized in Table 8 and, in parts, in Figure 7 (for functional imaging results on Go errors see Appendix B: Table 1, Figure 1; for functional imaging results on a conjunction analysis of NoGo errors and Go errors see Appendix C: Table 2, Figure 2; for functional imaging results on interaction effect between NoGo and Go errors see Appendix D: Table 3).

***Table 8**: Coordinates and anatomical localization of regions related to NoGo errors, estimated for trials with incongruent stimuli.*

Anatomical Region	**L/R**	**BA**	**x**	**y**	**z**	**Z**	**Number of significant voxels**
Inferior frontal gyrus/anterior insula	L	47	-36	18	-4	Inf	4036
Anterior cingulate gyrus (dorsal)	L	32	-4	24	34	7.24	2549
Inferior frontal gyrus/anterior insula	R	45	62	18	6	6.85	1771
Inferior parietal lobule	L	40	-50	-34	52	6.69	2778
Cerebellum	R		18	-60	-24	6.53	1149
Superior frontal gyrus	R	10	22	60	18	5.19	56
Inferior/superior parietal lobule	R	40/7	44	-52	54	5.08	244
Nucleus caudate	R		16	16	0	5.07	61
Postcentral gyrus	L	40/43	-64	-18	16	5.07	55
Thalamus	L		-10	-14	4	4.98	136
Superior temporal gyrus	R	22	66	-42	16	4.95	73

Note. Results of the second-level analysis: Main effects reported at a level of $P < 0.05$ family-wise (fwe) corrected at the voxel level to control for multiple comparisons. x, y and z are MNI coordinates of the peak voxel within a cluster. Z = Z-value. BA = Brodmann areas. L = left, R = right.

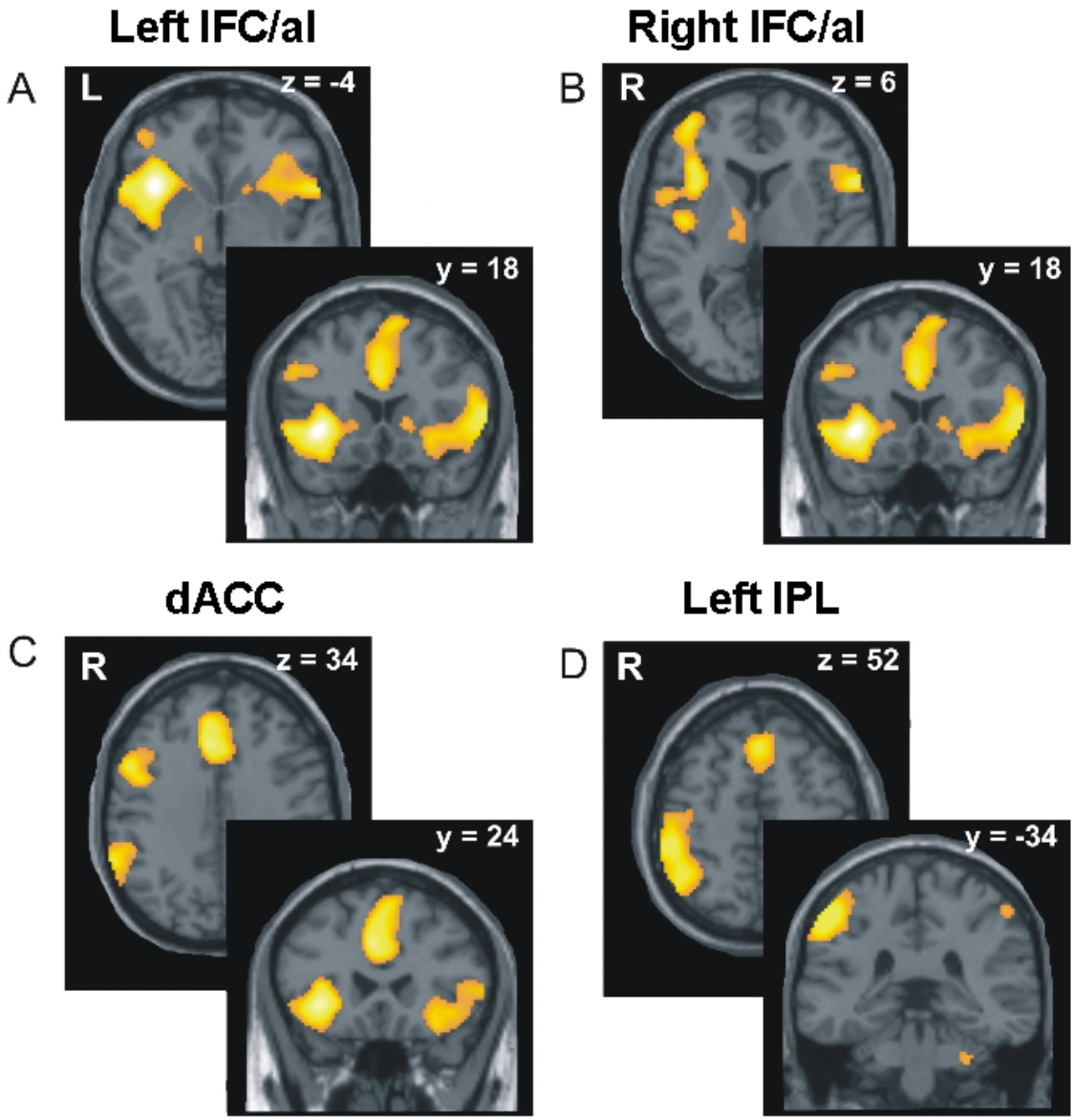


Figure 7: *Main effects of the contrast incongruent incorrect NoGo minus incongruent correct NoGo trials, derived from the second-level ANOVA.* Results are significant at *P* = 0.05 FWE corrected. Transversal and coronal slices are indicated by z and y coordinates, respectively. (A) Left lateral inferior frontal cortex adjoining the anterior insular cortex (IFC/aI, Brodmann Area [BA] 47; sliced at [-36, 18, -4]; x, y and z are MNI coordinates of the peak voxel of the corresponding cluster. (B) Right inferior frontal cortex adjoining the anterior insular cortex (IFC/aI, BA 45; sliced at [62, 18, 6]). (C) Dorsal anterior cingulate cortex (dACC, BA 32; sliced at [-4, 34, 24]). (D) Left inferior parietal lobule (IPL, BA 40; sliced at [-50, -34, 52]).

3.2.2. Correlations between error activity and personality traits

Computation of correlations between neural activities upon error processing (i.e. NoGo errors) and personality traits as measured by the NEO-PI-R was locally constrained to the network significant for the contrast reflecting incongruent *NoGo errors* (see above). Correlations were tested on significance using an *F*-test within each of the different simple regression analyses, one for each of the NEO-PI-R subscales. However, correlation analysis was not performed between Neuroticism and neural activity upon error processing, since analysis of behavioral data indicated that this trait failed to prove for orthogonality. Results from simple regression analyses are summarized in Table 9.

***Table 9**: Summary of positive and negative correlations between the differential neural activity during NoGo errors and NEO-PI-R major domain scores*

	Positive Correlation	Negative Correlation
N	n.c.	n.c.
E	x	-
O	-	(x)
A	-	-
C	x	-

Note. N, E, O, A, and C are the following subscales from the NEO-PI-R: N = Neuroticism; *E* = Extraversion; *O* = Openness to Experience; *A* = Agreeableness; *C* = Conscientiousness. *n.c.* = not calculated due to negative inter-correlations between Neuroticism and the other NEO-PI-R major domains scores. *x* indicates significant correlations between the differential neural activity from the contrast [NoGo incorrect > NoGo correct] and the NEO-PI-R major domain scores, respectively, at a significance threshold of $P < 0.001$ uncorrected at the voxel level and $P < 0.05$ corrected for spatial extent. The x in brackets indicates a trend to significance ($p = 0.065$) with Openness to Experience at -44, 16, 28 (x, y, z MNI coordinates of the peak voxel within a cluster of 81 voxels) located in the left middle frontal gyrus. – indicates non-significant correlation results at the predefined significance threshold.

Regression analysis revealed a significant positive correlation between the Extraversion score of NEO-PI-R and the magnitude of differential brain activity on NoGo errors in the right dorsal anterior cingulate gyrus (BA 32: x = 2, y = 20, z = 28; *Z* = 3.58, 383 voxels; r = 0.77; *P* = 0.001 uncorrected at the voxel level and *P* = 0.05 corrected for spatial extent; see Figure 8a). No significant negative correlation was to observe for the major domain scale Extraversion.

Also, regression analysis revealed a significant positive correlation between the Conscientiousness score of NEO-PI-R and the magnitude of differential brain activity on Nogo errors in the left inferior frontal gyrus (BA 47: x = -42, y = 24, z = -8; Z = 3.44, 273 voxels; r = 0.75; *P* = 0.001 uncorrected at the voxel level and *P* = 0.05 corrected for spatial extent; see Figure 8b). Again, no significant negative correlation was to observe for this personality trait.

No *significant* correlations at all, neither positive nor negative, were to observe for the other NEO-PI-R scores, i.e. Openness to Experience and Agreeableness. However, a negative correlation with *trend* to significance between the Openness to Experience score of the NEO-PI-R and the magnitude of differential brain activity on NoGo errors was observed in the left middle frontal gyrus (BA 9: x = -44, y = 16, z = 28, 81 voxels; *P* = 0.001 uncorrected at the voxel level and *P* = 0.065 corrected for spatial extent).

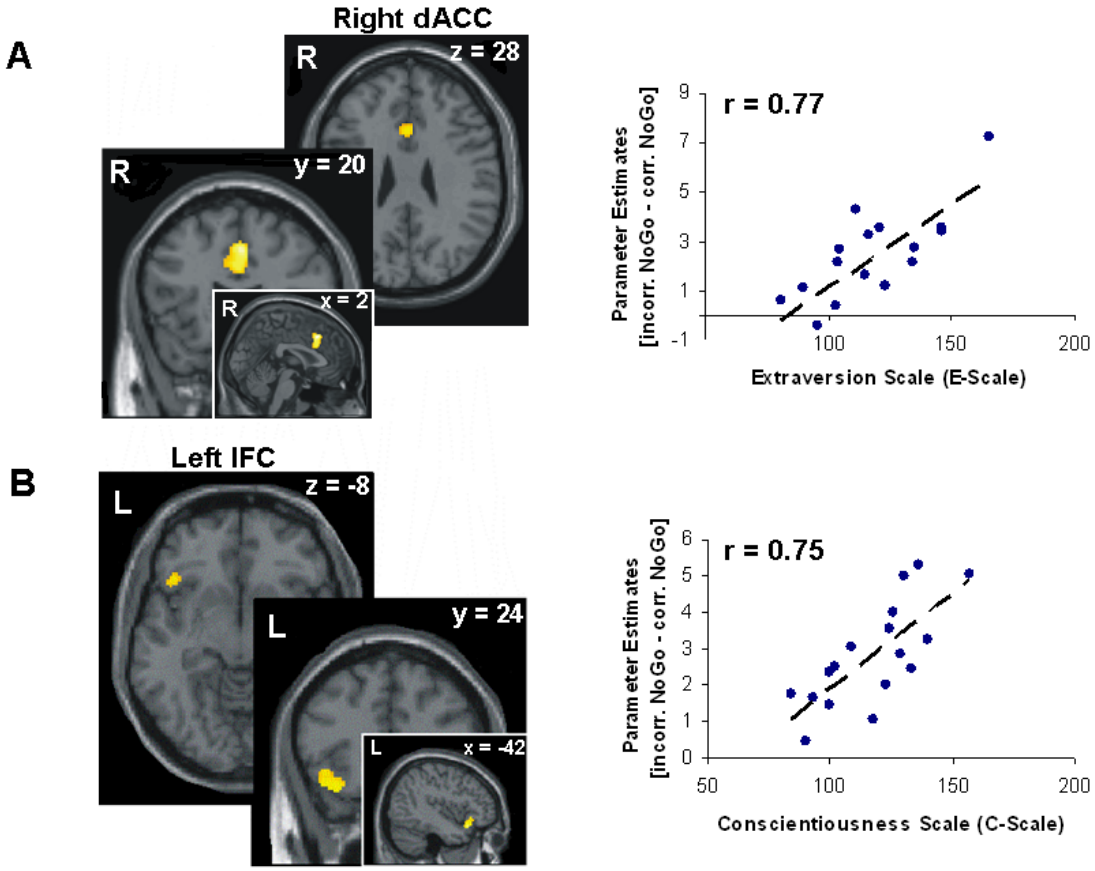


Figure 8: *Correlation between NoGo errors and Extraversion and Conscientiousness, respectively.*

Results are significant at $P < 0.001$ uncorrected at voxel level ($P < 0.05$ corrected for spatial extent). Transversal, coronal, and sagittal slices are indicated by z, y, and x coordinates, respectively. (A) *Left*: Correlation of Extraversion[1] with differential brain activity from the contrast "Incorrect NoGo > Correct NoGo" in right dACC (BA 32; sliced at MNI location 2, 20, 28; $Z = 3.58$); *Right*: Scatter plot for the corresponding coefficient at [2, 20, 28; r = 0.77]. (B) *Left*: Correlation of Conscientiousness with differential brain activity from the contrast "Incorrect NoGo > Correct NoGo" in left IFC (BA 47; -42, 24, -8; $Z = 3.44$); *Right*: Scatter plot for the corresponding coefficient at [-42, 24, -8; r = 0.75]. Note: Dashed lines represent the best linear fit; r denotes the correlation coefficient across subjects; parameter estimates stem from the contrast incorrect NoGo minus correct NoGo.

[1] To control, the above correlation was recalculated without the one subject presenting the highest value on both, parameter estimates and extraversion. The correlation remained significant [r = 0.65, t(14)3.27, $p = 0.006$].

3.2.3. Post-hoc correlation analyses with graded error types

To exert further control on present correlation of Conscientiousness with brain activity we made use of a second error type that came with our experimental paradigm containing a two-alternative forced-choice reaction component on Go trials. The rationale behind this post-hoc approach was delineated from a tentative interpretation of the above correlation between Conscientiousness and NoGo errors. If, in light of the present paradigm, one interprets individual levels of Conscientiousness as a proxy to represent different degrees to which task instructions were represented across subjects, the correlation between this trait and brain activity on errors should not be confined to the main task instruction (avoidance of NoGo errors) but also to violations of other task instructions. Compared to erroneous NoGo responses no explicit information on Go errors had been given in the task instruction (see Appendix A). The latter was only implicit in explaining subjects which buttons should be used to respond on the corresponding Go trials. Consequently, NoGo errors were seen to reflect higher-level intentional involvement, since they represent the major behavioral goal in the given task set (*high* errors), Go errors were seen to reflect lower-level intentional involvement, since they represent a subordinate goal in this given task set (*low* errors). As for the correlations above (incongruent NoGo errors) analyses were functionally constrained by an inclusive mask reflecting the neural network associated with the processing of Go errors as estimated by the contrast erroneous Go trial minus correct Go trial at a level of significance of $P < 0.05$ FWE corrected at the voxel level with an extent threshold correction of $P < 0.05$ at the cluster level (for results see Appendix B: Table 1, Figure 1). For inference of significant correlations the threshold was set at $P < 0.001$ uncorrected at the voxel level with an extent threshold correction of $P < 0.05$ at the cluster level.

We did not find significant correlations between the individual NEO-PI-R Conscientiousness scores and Go errors at the predefined statistical threshold. After lowering the significance threshold to $P < 0.05$ at the voxel level, a positive correlation was found in the left inferior frontal gyrus (x, y, z = -48, 32, -4; BA 47; Z-Value = 2.30;

40 voxels; r = 0.55; Figure 9). However, the observed activation failed significance at threshold correction of *P* < 0.05 at the cluster level (*P* = 0.818) and must be treated with caution.

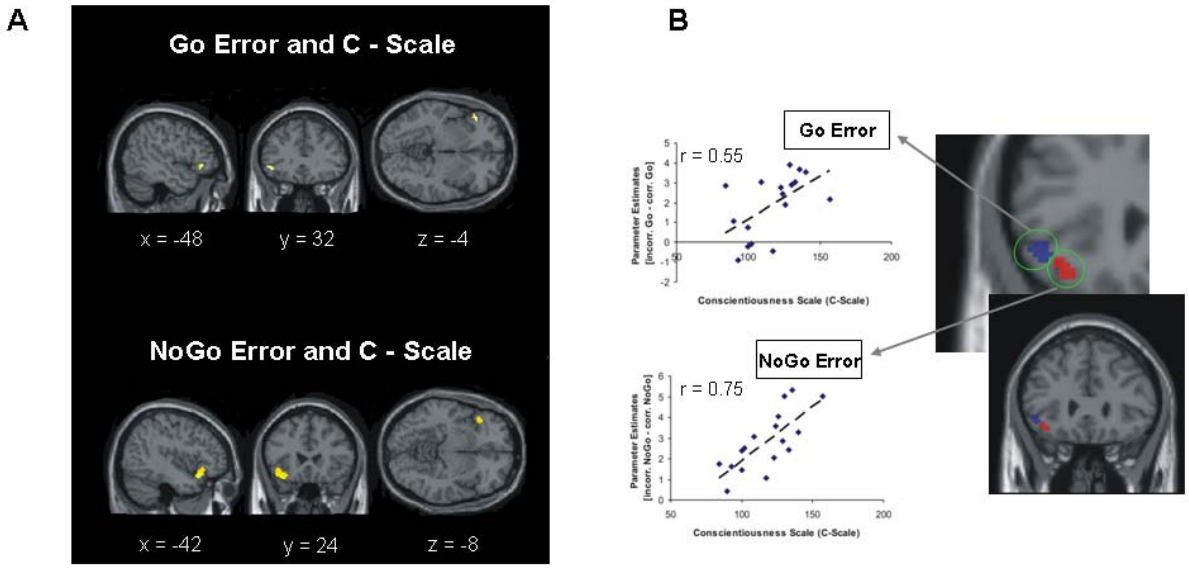


Figure 9: *Association between Conscientiousness and Go and NoGo errors.*

(A) Correlation of Conscientiousness scores with differential brain activations from the contrasts "Go incorrect > Go Correct" corresponding to Go Error (upper panel) in left IFC (*P* < 0.05 uncorrected at the voxel level, *P* > 0.05 corrected at cluster level) and "NoGo incorrect > NoGo correct" corresponding to NoGo Error (lower panel) in the left IFC (*P* < 0.001 uncorrected at voxel level, *P* < 0.05 corrected at cluster level). From left to right: Sagittal, coronal, and transverse slices. (B) Left: Scatter plots for the highest correlation coefficient for the Go Error at MNI location [-48, 32, -4; BA 47; r = 0.55; *P* = 0.021 at this voxel] and for NoGo Errors at [-42, 24, -8; BA 47; r = 0.75; *P* < 0.001 at this voxel]. Dashed lines represent the best linear fit; r denotes the correlation coefficient. Right: Two coronal slices (upper with zoom) of these regions. Voxels with correlations between Conscientiousness scores and differential brain activity on Go Error are color-coded in blue. Red color denotes significant correlation between Conscientiousness and differential brain activation during processing of NoGo errors.

4. DISCUSSION

4.1. Behavioral data

4.1.1. Behavioral data on the fMRI experimental task

Behavioral data indicated that our combined Eriksen Flanker and Go/NoGo task was effective in eliciting errors, especially for the incongruent condition, while keeping an expected ratio of more correct responses relative to incorrect responses: error rate was 27.1% for incongruent NoGo trials, and 9.9% for congruent stimuli. From prior EEG studies it is known that error signals are most likely generated under conditions when subjects perform a task relatively well (Gehring 1993). Furthermore, our task distinguished well between congruent and incongruent conditions. First, subjects committed significantly more incongruent NoGo errors relative to congruent NoGo errors. This is in line with the notion from previous studies that incongruent NoGo trials are considered to be more difficult to be inhibited than congruent NoGo trials (Dikman and Allen 2000; Vidal et al. 2000). Second, subjects showed significantly more correct hits on congruent Go trials relative to incongruent Go trials. In general, Eriksen Flanker paradigms are considered to allow for more correct responses on congruent Go trials due to weaker interference effects. This result is also in line with the finding that subjects showed significantly more hits on delayed *incongruent* trials. Delayed correct reactions on Go trials are most likely due to difficulties on discriminatory demands under interference conditions imposed by incongruent distractors. Third, subjects needed significantly more time to respond on incongruent Go trials relative to congruent Go trials, regardless of whether the response was correct within the given time window, correct but delayed, or incorrect and delayed. Again, these results fit well with the Eriksen Flanker. In contrast, we found no difference in reaction times between incongruent and congruent commissions of Nogo responses thus ruling out that different error rates are related to an unbalanced speed-accuracy-trade-off.

4.1.2. Behavioral data on errors and their correlations with the Big Five personality traits

Analysis of NEO-PI-R scores revealed that Neuroticism was negatively inter-correlated at r = -0.45 and higher with all other NEO-PI-R scores. This result indicates that within our sample Neuroticism did not show orthogonality as suggested by factor analytic approaches to the Big Five. We therefore decided to exclude Neuroticism from both behavioral and fMRI correlation analysis as regressors would be collinear, and for example a positive correlation of any variable with Openess would also negatively correlate with Neurocitism.

Furthermore, we identified a strong positive inter-correlation between Extraversion and Openness to Experience. In contrast to the findings on Neuroticism, Extraversion was not inter-correlated with any other NEO-PI-R scores. Nevertheless, we cannot exclude that Extraversion and Openness to Experience do measure at least parts of the same personality trait. However, our functional results of neural error processing suggest Extraversion to differ from Openness to Experience by observing an exclusive and significant correlation between Extraversion and NoGo errors in the dACC which was entirely absent for Openness at this location.

Following our rationale for meaningful correlations, among all Big Five traits only Conscientiousness was correlated with performance data obtained from the experimental task: The higher individual scores of Conscientiousness, the lesser omissions on Go trials were observed. This finding was significant for incongruent conditions (r = -0.55, p = 0.023), and showed trend to significance for congruent conditions (r = -0.45, p =0.069). The observed correlation can be understood to be in line with the key hallmarks of Conscientiousness defined through high concerns about adequate task accomplishment and rather planned instead of spontaneous acting (Costa and McCrae 1992). Our task instruction (see Appendix A) stressed two aspects: to respond to predefined letters, and to withhold response upon appearance of other predefined letters. Thus, conscientious individuals acted well in line with one

aspect of task instruction regarding Go responses. Interestingly, Conscientiousness was not significantly correlated with errors on NoGo responses. Regarding the given task instruction for Nogo responses, one would have expected more conscientious individuals to stronger avoid NoGo commissions. Also, one would have expected Conscientiousness to be correlated with response times on NoGo commissions, i.e. more conscientious individuals to perform in general slower. This lack of a significant association between Conscientiousness and Nogo commission on performance data, however, also indicates that our highly significant correlation between Conscientiousness and neural activity patterns associated with NoGo errors in the left inferior frontal cortex was not confounded with response time or error rate.

4.2. Functional imaging data on errors and the Big Five

4.2.1. Main error effects from group analyses

The goal of the present study was to investigate the association of Big Five personality traits as derived through the NEO-PI-R and the neural correlates of error processing. We used an event-related fMRI design in combination with a combined GoNoGo/Eriksen Flanker Task. We identified a network of brain regions involved in error processing by comparing activation during incorrect and correct NoGo events. This network contained in particular the dorsal anterior cingulate cortex (dACC; BA 32), and the left inferior frontal cortex bordering the anterior insula (IFC/aI; BA 47). Additionally, the right inferior frontal cortex (IFC; BA 45), the inferior parietal lobule (IPL; BA 40) and the cerebellum were involved in error processing. Observed areas, especially the dACC and IFC/aI regions matched well with those reported in original studies as key neural correlates of error processing (Menon et al. 2001; Garavan et al. 2003; Mathalon et al. 2003; Matthews et al. 2005) and also referred to in a unifying meta-analysis of different components of task sets (Dosenbach et al. 2006). While the

involvement of these brain structures in error processing is commonly and frequently reported, the discussion about their function within error processing is quite divergent. The dorsal anterior cingulate cortex is thought to be the major generator of error signals (Dehaene 1994; Kiehl et al. 2000; for review see: Taylor et al. 2007). Across different tasks, sample or experimental manipulations, the dACC is consistently activated in processing of errors. However, some studies also reported the rostral part of the ACC to be crucially involved in error processing (Menon et al. 2001; Garavan et al. 2003). As outlined in the introduction of our work, Holroyd and Coles (2002) have proposed a reunifying theory – the Reinforcement Learning Theory – which proposes that erroneous responses signal an outcome which is worse than expected, activating the mesencephalic dopamine system which conveys a negative reinforcement learning signal to the ACC. This generated error signal is then used to modify performance on the task at hand. Thus, signaling an error signal can be seen as a "trainer" of the ACC ensuring that future control over the motor system will be improved by adequate adjustment of neural processing.

While ACC activation on error trials is well established and well discussed, findings on increased inferior frontal cortex activation extending into insular cortex in response to errors are far less systematically discussed. The importance of this region for higher-order processes has been ignored in many cases, despite the fact that it is commonly reported in published tables of activated regions (Carter et al. 1998; Kiehl et al. 2000; Menon et al. 2001; Ullsperger and von Cramon 2001; Garavan et al. 2003). To date, most effort has been directed to discuss the insular cortex and the inferior frontal cortex as serving several other functions rather than error processing. For example, the insular cortex has been functionally interpreted to neurally represent individuals' interoceptive subjective awareness of bodily states (Craig 2002; Critchley et al. 2005), pain perception (Craig 2002), or emotional experiences such as fear, anger, sadness, and disgust (Craig 2002; Canli et al. 2001; Canli et al. 2002).

The inferior frontal cortex has mostly been functionally related to response inhibition. However, when looking on the reported data in detail, the results on the inferior frontal activation and their relation to response inhibition are far away from being definite.

Some previous studies report activation in this region due to successful inhibition (Liddle et al. 2001; Rubia et al. 2003; Picton et al. 2007), and two prior meta-analyses also indicate its involvement in successful response inhibition relative to failed trials (Wager et al. 2005; Nee et al. 2007). On the other hand, it is noteworthy that other previous imaging studies implicitly investigating response inhibition have observed increased activation in the inferior frontal cortex (bordering/overlapping with the insular cortex) in case of *failed* inhibition, i.e. errors (Carter et al. 1998; Kiehl et al. 2000; Menon et al. 2001; Ullsperger and von Cramon 2001; Garavan et al. 2002) or in case of both, i.e. response inhibition and error processing (Garavan et al. 2002; Mathalon et al. 2003; Hershey et al. 2004; Ramautar et al. 2006). In sum present data challenge the view of inferior frontal cortex and its extensions to the insular cortex as being solely involved in response inhibition per se. Instead, they suggest that this area may play a broader role in cognitive control, possibly independent of response inhibition being successful or not. Consequently, theses inconsistencies remain to be clarified.

A promising approach on a more unifying interpretation of the functional relevance of inferior frontal cortex with its extensions to the insular cortex can be seen in the model of a neural system for task sets, recently proposed by Dosenbach et al. (2006). In a cross-studies meta-analysis, the authors found the inferior frontal cortex adjoining to bilateral anterior insula to robustly present start-cue activity at the beginning of a cognitive task, sustained activity during the task, as well as error-related activity, when task execution failed. Interestingly, the second neural region emerging with the same robust result pattern of their meta-analysis was the the dorsal anterior cingulate cortex bordering the medial superior frontal cortex (dACC/msFC). The authors propose that these regions form the “core” of the human task-set system, and act in accordance with a given task instruction. By receiving additional bottom-up signals, this brain network permits for a moment-to-moment processing and hence for the control of the discrepancy between intended and actual outcomes. This model not only provides a convincing framework for the understanding of the human task-set system, but also meaningfully contributes to a broader functional understanding of the

two regions of interest. What remains open however, is the intriguing question of whether the dACC within a task-set system should play a different role compared to the IFC/aI and vice versa.

4.2.2. Extraversion and error processing

Regarding the relationships between personality traits and neural activity during error processing, one of the significant findings was the positive correlation with the personality trait Extraversion in the dorsal anterior cingulate cortex for Nogo errors. No other personality trait as derived by the NEO-PI-R modulated error processing in this specific brain region.

Several previous studies on the neural underpinnings of Extraversion have found a strong relationship with ACC activity even in the absence of any cognitive task (Ebmeier et al. 1994; Johnson et al. 1999; Canli et al. 2001; Canli 2004; Kumari et al. 2004; Eisenberger et al. 2005). This has led to the interpretation that increased ACC activation in extraverted individuals either reflects enhanced responsibility of a general cortical arousal system as suggested by Eysenck (1981), or that associated emotional processes modulate ACC activity in extraverted individuals. While noteworthy as some first attempts to give an account on this relationship these interpretations remain ambiguous to explain the correlation observed in the present study.

Even though some trait theorists consider impulsivity and Extraversion to be separate traits, there are many empirical indications that support a strong association between these traits. For example, in the first formulation of his trait theory, Eysenck (1981) has included impulsivity in his measure of Extraversion (though it was removed later on). Gray (1985) proposed impulsivity to represent the interaction of the higher-order traits of Extraversion, Neuroticism, and psychoticism, thus linking impulsivity to Extraversion. Cloninger (1986) replaced Extraversion with the higher-order trait of

novelty seeking, which itself is, according to several lines of evidence, very closely aligned with impulsivity (Zuckerman and Como 1983). Furthermore, additional evidence indicated that Eysenck's cortical arousal theory of the introversion-Extraversion dimension (Eysenck 1981) also applies to behavioral styles and biological processes which are often to be found in impulsive individuals. For example, impulsivity showed a systematic relationship to vigilance decreases (Thackray et al. 1974), caffeine-induced stress and verbal performance (Revelle et al. 1980), and driver safety (Loo 1979a). In sum, there are several hints indicating that Extraversion and impulsivity subsume similar emotional, cognitive, and behavioral styles as well as biological processes in humans.

Now regarding studies that investigated associations between impulsivity and error signals, there are findings indicating that the way humans process errors is indeed modulated by impulsivity, and that this modulation takes place in the ACC. For example, Ruchsow et al. (2005) identified at central midline electrode positions significantly smaller ERN amplitudes in high impulsive healthy individuals relative to low impulsive healthy individuals. From ERP source localizations it is most likely that midline central electrodes indicate ACC activation. Pailing et al. (2002) also found smaller ERN amplitudes and higher error rates in individuals with a tendency towards impulsive responding, i.e. with a less controlled response strategy. Similar findings were found in patients with borderline personality disorder, a psychiatric disease with impulsivity as one of its core symptoms (Ruchsow et al. 2006). There, again smaller ERN amplitudes were observed in patients with borderline personality disorders relative to healthy controls. Further insights into the relation between impulsivity and error processing could be gained by the investigation of the opposite pole of impulsivity, namely compulsivity. Gehring et al. (2000) found increased ERN amplitudes in patients with obsessive-compulsive disorder (OCD) compared to healthy controls. Within patients, the ERN amplitude was positively related with symptom severity. These findings were replicated in pediatric patients with OCD (Hajcak et al. 2008a). To summarize, impulsivity as personality trait obviously modulates human error processing in the brain. Since impulsivity and Extraversion, as outlined above, are often thought to represent one and the same personality trait

or at least are meant to share core features, our present results are in good accordance with these previous studies on impulsivity and error processing.

However, apart from reporting that there *is* a neurobiological link, to our knowledge none of the prior studies has tackled the question about *why* this relation exists and what we can learn from it.
In general, extraverted individuals are characterized by a high social outside orientation (Costa and McCrae 1992) and are highly bothered by negative social evaluation. Furthermore, they tend to seek more for positive emotions and do indeed experience positive emotions more often than introverted subjects (Costa and McCrae 1992). On a biological basis, Extraversion has been linked to higher sensitivity of the mesencephalic dopamine system to respond on potentially rewarding stimuli (Eysenck 1981), which may contribute in explaining the higher level of positive emotions observed in extraverted individuals. Theories on error processing, like Holroyd and Coles (2002), have suggested that error signals are generated when a negative reinforcement learning signal is conveyed to the ACC via the mesencephalic dopamine system. This signal is used by the ACC to modify performance on the task at hand. Hence, one possible explanation about *why* Extraversion and error signals are highly correlated in the ACC could be that extraverted individuals respond more sensitive not only to rewarding stimuli but also to the violation of expected rewarding stimuli.

4.2.3. Conscientiousness and error processing

Our second correlation finding was the highly significant positive correlation between NoGo errors and Conscientiousness in the left inferior frontal cortex (BA 47; left IFC). This region includes the pars orbitalis as a part of the inferior frontal gyrus and adjoins to the anterior insular cortex. No other NEO-PI-R personality trait modulated error processing in the IFC,. Of note, this neural activation was locally distinctive from the region (dACC) found to be significantly modulated by Extraversion.

No prior study has ever explored the neural underpinnings of Conscientiousness per se. One study has examined the association between this personality trait and error processing in the brain (Pailing and Segalowitz 2004a). The authors found that conscientious individuals were less influenced by motivational incentives such as money, and thus were more consistently bothered by the occurrence of an error as reflected by the ERN regardless of whether their performance was rewarded or not. Unfortunately, the authors did not estimate the likely local sources of this electrophysiological potential. Thus, our present study is the first to report a specific brain region being activated by errors and its activation being modulated by Conscientiousness. The left IFC (BA 47) matches very well with one of the brain regions suggested to be importantly involved in the human task-set system (Dosenbach et al. 2006).

In view of the results reported by Pailing and Segalowitz (2004a) on conscientious individuals to be more consistently and highly bothered by erroneous responses, our present results on Conscientiousness and error processing in the left IFC/aI may support this finding by taking into account some core hallmarks of this personality trait. Most importantly is the association of Conscientiousness with goal-directed behavior (Costa and McCrae 1992). High Conscientiousness relates to a desire to exert self-control and thereby to follow the dictates of one's intention. Therefore conscientious individuals focus on task accomplishment and fulfillment of obligations and are high on achievement striving, which reflects an individual's intention to accomplish given tasks expressed as a high goal orientation (Costa and McCrae 1992). Indeed, a considerable amount of data indicates that Conscientiousness is one of the best predictors of performance in the workplace (Barrick and Mount 1991). Furthermore, Conscientiousness was found to be negatively related to destructive behavioral intentions and positively related to constructive behavioral intentions as measured by responses to scenario situations (Reisert and Conti 2004). Collectively, this research suggests that the personality trait Conscientiousness reflects goal-directed behaviour. It supports that highly conscientious individuals show higher

intentional involvement when accomplishing a given task compared to less conscientious individuals, and are thus more concerned by errors since their occurrence indicates that the intended task accomplishment is not appropriate. Our observed modulating effect of Conscientiousness on error processing fits very well with these components of Conscientiousness. Most likely, the modulating effect reflects the degree to which individuals' goal direction is concerned by occurrence of errors. This assumption is in line with evidence stemming from the work on cognitive control of memory indicating convincingly that the left IFC, i.e. the same region as we found in our present study, is involved in the control of goal or task related memory representations (Wagner et al. 2001; Badre and Wagner 2007). Two dissociable processes within cognitive control processes of memory are operated by the left IFC: A controlled retrieval process that activates goal-relevant memory representations in a top-down fashion, and a post-retrieval selection process that selects among competing simultaneously active memory representations. Convergent data has emerged, supporting this proposed controlled retrieval/selection distinction (Badre and Wagner 2002; Badre et al. 2005; for review see: Badre and Wagner 2007). It has been shown that controlled retrieval is supported by the ventral and rostral portion of the left IFC, approximately corresponding to BA 47 which mostly corresponds to the region bearing the significant correlation and being activated by error signals In general. In contrast, post-retrieval selection is associated with the portion of left IFC that approximately corresponds to that part of BA 45 that includes the pars triangularis (Badre et al. 2005; Dobbins and Wagner 2005). For example, Badre et al. (2005) varied demands on controlled retrieval and on selection by manipulating judgment specificity, cue-target-associative strength, competitor dominance, and the number of competitors. Using factor analytic techniques, they obtained evidence for a meta-factor that accounted for behavioral variance across tasks evoking semantic competition and for functional variance in left IFC corresponding to BA 45, supporting a generalized control process that selects goal-relevant memory information from amongst competitors. By contrast, left anterior IFC corresponding to BA 47 was sensitive to cue-target associative strength, but not competition, consistent with a control process that retrieves knowledge that does not automatically come to mind. Of

note, the IFC has often been reported to be active under conditions of competing responses and thus been associated with response inhibition. As just outlined, since memory representations about tasks are likely to be active during competing response tendencies it seems more convincing that the IFC does not reflect response inhibition per se but rather enhanced cognitive control over task-relevant memory representations.

In summary, the left IFC enables us to strategically handle task-related memory representations in order to meet higher level goals. This is in good accordance with its role to represent the human task-set system as suggested by Dosenbach et al. (2006). In our present study, we found robust NoGo error signals being processed in exactly this brain region, together with a modulating effect of Conscientiousness. Since Conscientiousness is defined by a high striving for appropriate task accomplishment, it is plausible to assume that conscientious individuals stronger keep in mind what a given task requires for appropriate fulfillment. Therefore, we conclude that the more conscientious subjects are, the stronger are task-set related memory representations, and hence, the stronger is their neural signal when violating these representations. We found support for this interpretation by the graded effects of the two different error types thought to correspond to different levels of intentional involvement: NoGo errors representing the major response goal in our given task set, and Go errors representing the subordinate goal in our given task set. Both error types showed graded correlations with Conscientiousness in the left IFC: While NoGo errors showed a highly significant positive correlation ($r = 0.75$), the a posteriori derived positive correlation between Go errors and Conscientiousness ($r = 0.55$) showed only trend to significance.

4.3. Limitations and future prospects

Observed coefficients of correlations between neural activities upon errors and personality were comparably high when compared against those stemming from correlations of traits and performance measures. One possible explanation for this finding is that behavioral data can be seen to represent the sum of activation in all activated brain areas, whereas fMRI correlation analyses focuses on circumscribed brain regions. In this sense, it seems plausible that correlations between neural responses to errors in specific brain regions and personality traits are stronger than on the behavioral level.

It is also of note that any correlation approach only identifies relationships between variables, but not a causal association between them. Also, one can never rule out that an association between two variables may be conditioned by another not yet known or considered factor. By addressing divergent and convergent validity, a correlation approach can be further strengthened. While convergent validity applies to the fact that variables of two related concepts should be related to each other, divergent validity denotes that variables of two unrelated concepts should consequently be unrelated to each other. So, for example, a contribution to convergent validity of the correlation results with Extraversion could have been made, if we had measured additionally impulsivity measures as both traits have been shown to be closely related. Divergent validity could have been contributed if introversion as its opposite pole had been additionally taken into account. Convergent validity of the results on Conscientiousness could have been established by additionally investigating the association between neural substrates of error processing and compulsivity, a clinically relevant extreme variant of Conscientiousness. Divergent validity in this context would have to consider a construct unrelated to Conscientiousness, e.g., sensation seeking. These contributions on either convergent or divergent validities remain open issues for future studies on the same topic.

However, contributions on validity cannot not only be achieved on the level of the predictor, but also on the level of the criterion. Here, we found Conscientiousness to be correlated not only with NoGo errors, representing the violation of the major goal

of our task, but also with trend to significance with Go errors, representing the violation of a subordinate goal of our task. We strongly believe that occurrence of a significant positive correlation of Conscientiousness with one of the two criterions and a trend positive correlation with the other criterion within the left IFC is not trivial and that results therefore provide mutual support. However, as the correlation with Go errors was inferred a posteriori, replication will further determine whether or not correlations are reliable and substantial. Such a replication could strengthen our interpretation of the present relationship between Conscientiousness and the neural correlates of on error processing in the IFC.

Another limitation of the present study may concern sample characteristics. We did not formally rule out psychiatric Axis I or Axis II disorders using structured clinical interviews. Instead, we checked for extreme personality scores on the NEO-PI-R and did not find any patterns supportive of personality disorders. In addition, we asked for history of psychiatric disorders and did not obtain any indicating signs. Nevertheless, even though such approaches show face validity, they may not be adequate to fully exclude the presence of DSM-IV disorders.

Fully acknowledging these possible limitations, the present study gives directions, which we consider worthwhile for further research. For example, the rather strong associations between personality and neural error processing renders it likely, that this influence is present in virtually all such studies. Thus, measurement of personality traits by questionnaires could become routine in future functional neuroimaging exploring cognitive functions. Future research could also aim at investigating the association between Big Five personality traits and error processing within still broader samples. It also remains an open question about whether and how present correlations found in healthy adult subject would differentiate from psychiatric samples, such as borderline personality disorders or obsessive-compulsive disorders, or other age groups such as children or elderly subjects. Even more interesting, further research could also be conducted in order to investigate the association of the neural network of error processing, personality traits and their associated genotypes as derived through molecular genetic studies.

4.4. Conclusion

The present study is the first attempt to study the correlation between neural activations on error processing and all five personality traits of the Five Factor Model of personality. Our present results replicated finding from previous studies on the neural correlates of error processing and demonstrate again involvement of the dACC and the IFC/aI. Both regions have been recently linked to the human task-set system as suggested by Dosenbach et al. (2006).

The present study could further contribute to the existing knowledge about that system by identifying modulating effects of personality traits on its responsivity during error processing. We suggest that Extraversion as defined by high outside orientation and reward striving behaviour, modulates the neural signal of error processing in the dACC because the more extraverted individual's expectancy of reward is there more violated is this expectancy by the occurrence of errors. We also conclude that Conscientiousness as defined by high task accomplishment striving behavior, exerts its modulating effect on the neural signaling of errors by individually different degrees to which individuals' representations about correct task accomplishment are violated.
By this, a slightly different interpretation functional role of the IFC complex during error processing is concluded. In the framework of the human-task set system proposed by Dosenbach et al. (2006) we suggest that this complex is not merely involved in inhibitory processes per se. Rather, occurrence of predefined task stimuli elicit the corresponding task instruction (which in the context of a Go/NoGo-task is indeed inhibition of inappropriate response tendencies). The more conscientious subjects are the stronger this task instruction is represented in terms of neural activity which in turn leads to graded neural signaling of errors that represent violations of or conflict with neural representations of given task instructions.

5. SUMMARY

Errors refer to the discrepancy between intended actions and actual outcomes. Error signals provide important evaluative information and are relevant for behavior adjustment and action planning. Their processing is operated by a neural network mostly residing in the frontal parts of the brain. However, not all brain regions involved in this higher cognitive control process are yet sufficiently understood. Furthermore, investigations of possible influences of individual differences in personality traits on neural error processing are rare.

In the present study error processes were investigated in healthy adult subjects (n = 17) using functional magnetic resonance imaging. We implemented a modified version of a combined Eriksen Flanker-Go/NoGo task known from previous studies to reliably elicit errors. Our modification permitted for the distinction of two error types: so-called higher-level errors, defined as commission errors in NoGo trials considered to represent the major response goal in our task, and so-called lower-level errors, defined as commission of errors in Go trials and considered to represent the subordinate response goal in the same task. Individual differences regarding Big Five personality traits were assessed using the NEO-PI-R measure (Neuroticism Extraversion Openness to Experience - Personality Inventory - Revised). The major aim of this dissertation was to investigate the modulating effects of the Big Five personality traits on the neural signaling of erroneous responses.

Behavioral data showed that our task was again reliable in eliciting errors. Functionally, we found significant error-related neural activity in the dorsal anterior cingulate cortex and the left inferior frontal cortex bordering the anterior insula cortex. These results well align with other studies reporting on error-related neural activity. Among all personality traits only Extraversion demonstrated a significant positive correlation with NoGo-errors in the dorsal anterior cingulate cortex, and Conscientiousness with NoGo in the left inferior frontal cortex. In addition,

Conscientiousness demonstrated a positive trend correlation just above the set significance threshold with Go errors also in the left inferior frontal cortex.

Interpretations of the modulating effects of these personality traits are provided in terms of reward expectancy for Extraversion and task-set related memory representation for Conscientiousness. From the latter we conclude a slightly new interpretation of the functional role of the inferior frontal cortex complex during error processing.

Findings well align with the growing body of evidence for personality traits to modulate individual differences in neural signaling and warrants future research. We consider molecular genetic studies to be a reasonable target for future imaging studies exploring the neurobiological underpinnings of error processing and personality.

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APPENDIX

APPENDIX A: Written instruction to study subjects about the experimental task

Liebe Probandin, lieber Proband,

Im nachfolgenden Experiment wird Ihnen eine Reihe von Buchstabenketten auf dem Bildschirm präsentiert, wobei Sie auf den mittleren Buchstaben achten sollen. Diese Buchstabenketten bestehen jeweils aus 5 Buchstaben und setzten sich aus der Kombination der Buchstaben R, U, P oder V zusammen.

Ihre Aufgabe in diesem Experiment ist zweierlei:

1. Beim Erscheinen der Buchstaben R oder U in der Mitte der Buchstabenketten sollen Sie bitte so schnell wie möglich die Taste drücken. Drücken Sie dabei wie folgt: Erscheint der Buchstabe **R** in der Mitte, so drücken Sie bitte so schnell wie möglich mit dem Zeigefinger Ihrer rechten Hand die entsprechende Taste. Erscheint der Buchstaben **U** in der Mitte, so drücken Sie bitte so schnell wie möglich mit dem Mittelfinger Ihrer rechten Hand die entsprechend andere Taste.
2. Handelt es sich bei dem mittleren Buchstaben jedoch um ein **P** oder **V**, so drücken Sie die Taste bitte **nicht**. Der Druck einer Taste wäre ein Fehler.

Vom Computer werden Schnelligkeit und Korrektheit der einzelnen Antworten automatisch protokolliert.
Wenn Sie richtig reagiert haben, erscheint auf dem Bildschirm die Rückmeldung „richtig“.
Wenn Sie falsch reagiert haben, erscheint auf dem Bildschirm die Rückmeldung „falsch“.
Wenn Sie zu langsam auf die Buchstaben R und U reagiert haben, erscheint auf dem Bildschirm die Rückmeldung „schneller“.

Bitte versuchen Sie im Falle eines geforderten Tastendrucks so schnell wie möglich zu reagieren. In diesem Experiment zählt die Geschwindigkeit. Selbstverständlich sollten Sie auch versuchen, möglichst keine Fehler zu machen, und ein fehlerhaftes Drücken der Taste in den Durchgängen vermeiden, wenn KEIN Tastendruck als richtige Antwort gefordert ist!

Das Erscheinen je einer neuen Buchstabenkette wird über ein kleines Kreuz in der Mitte des Bildschirms angekündigt. Dieses soll Ihnen helfen, sich auf die Reaktion der jeweils nachfolgenden Buchstabenkette vorzubereiten.

Falls Sie Fragen zur experimentellen Aufgabe haben, wenden Sie sich bitte noch vor Beginn des Experiments an die Versuchsleiterin. Mit Beginn des Experiments sollte eine Unterbrechung zur Klärung von Verständnisfragen nicht mehr erfolgen.

APPENDIX B: Main effects for Go errors on incongruent trials [incorrect Go Minus correct Go]

***Table 1**: Coordinates and anatomical localization of regions related to Go errors estimated for trials with incongruent stimuli.*

Anatomical Region	L/R	BA	x	y	z	Z	Number of significant voxels
Superior frontal gyrus	L	6	-2	20	58	6.56	697
Inferior frontal gyrus/anterior	L	47	-48	26	-2	6.41	590
insula	L	10	-26	56	20	6.13	226
Middle frontal gyrus	L	40	-58	-50	30	5.73	305
Supramarginal gyrus	L	7	-2	-60	50	5.09	54
Precuneus	L		-36	8	40	5.01	41
Precental gyrus	R		20	18	48	4.68	10
Superior frontal gyrus	L		-48	-44	48	4.56	2
Inferior parietal lobule							

Note. Results of the second-level analysis: Main effects for Go errors reported at significance of $P < 0.05$ with family-wise (few) correction at the voxel level for multiple comparisons. x, y and z are MNI coordinates of the peak voxel within a cluster. Z = Z-value. BA = Brodmann areas. L = left, R = right.

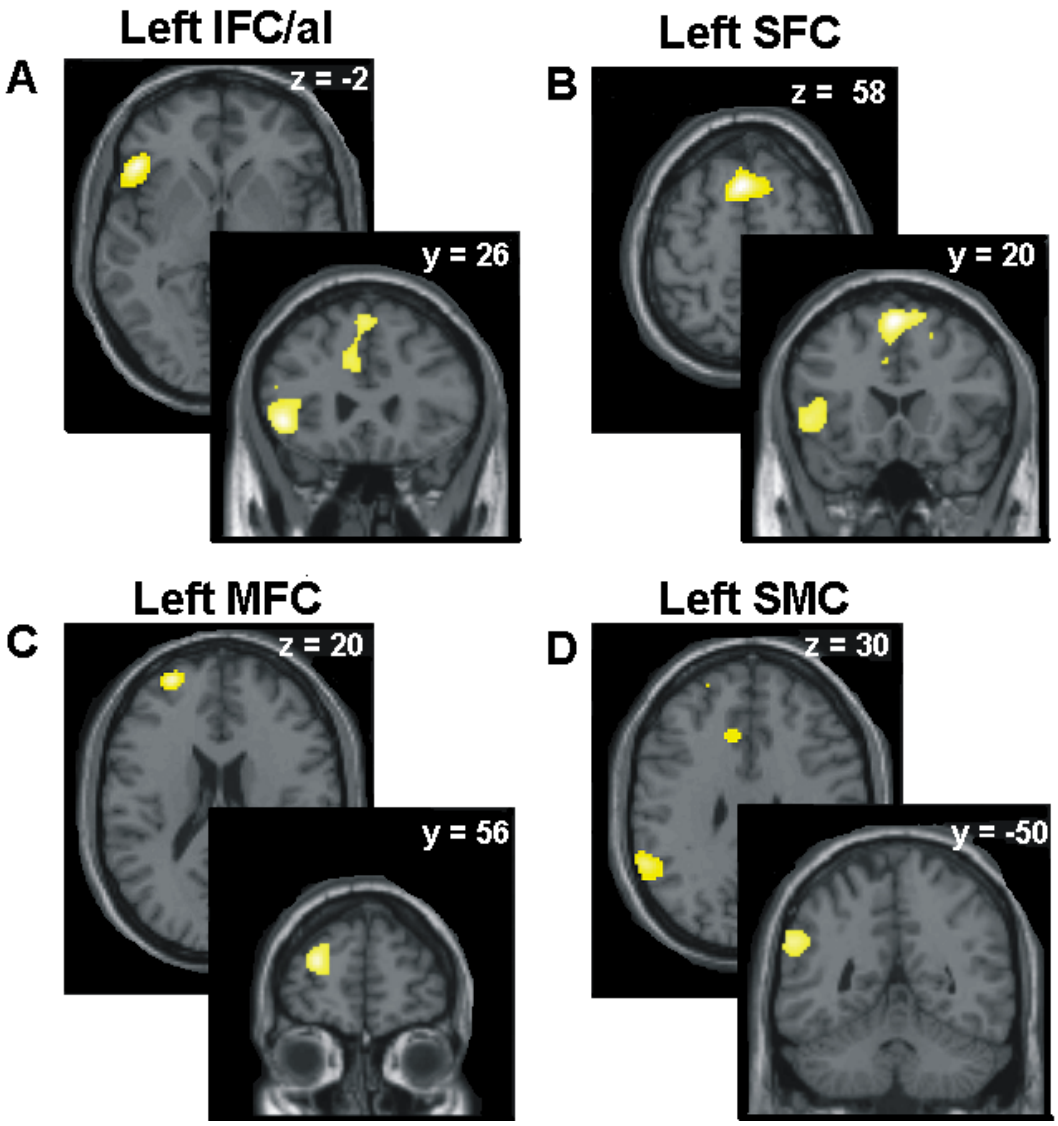


Figure 1: *Main effects of the contrast incongruent incorrect Go minus incongruent correct Go trials (i.e. Go errors), derived from the second-level ANOVA.*

Results are significant at a level of $P < 0.05$, FWE corrected. Transversal and coronal slices are indicated by z and y coordinates, respectively. (A) Left lateral inferior frontal cortex adjoining the anterior insular cortex (IFC/aI, Brodmann Area [BA] 47; sliced at [-48, 26, -2]; x, y and z are MNI coordinates of the peak voxel of the corresponding cluster. (B) Left superior frontal gyrus (BA 6; sliced at [-2, 20, 58]). (C) Left middle frontal gyrus (BA 10; sliced at [-26, 56, 20]). (D) Left supramarginal gyrus (BA 40; sliced at [-58, -50, 30]).

APPENDIX C: Conjunction analysis for both error types (NoGo errors and Go errors)

***Table 2**: Coordinates and anatomical localization of regions of voxels with significantly conjoined effects of both, NoGo and Go errors, estimated for trials with incongruent stimuli.*

Anatomical Region	L/R	BA	x	y	z	Z	Number of significant voxels
Superior frontal gyrus	R	6	2	22	56	5.84	449
Inferior frontal gyrus/anterior	L	47	-44	26	-4	5.84	266
insula	L	40	-60	-48	32	5.52	118
Supramarginal gyrus	L	10	-26	56	24	4.95	23
Superior frontal gyrus							

Note. Results of the conjunction analysis within the second-level analysis: Conjoined effects for both error types (i.e. NoGo errors and Go errors) are reported at level of $P < 0.05$ FWE corrected at the voxel level. x, y and z are MNI coordinates of the peak voxel within a cluster. Z = Z-value. BA = Brodmann areas. L = left, R = right.

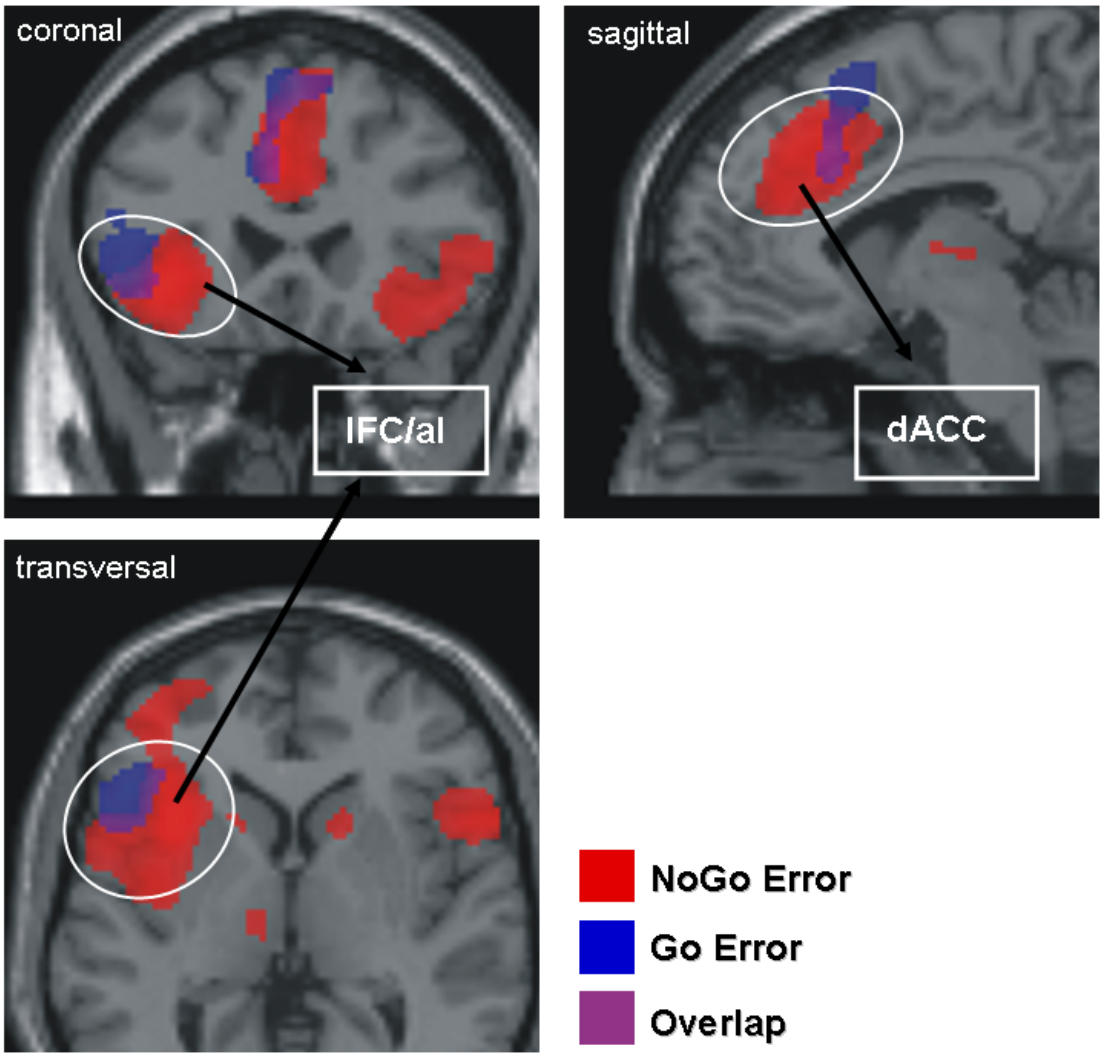


Figure 2: *Anatomical overlap of NoGo errors and Go effects, derived from the conjunction analysis within a second-level ANOVA.*

Main effects for NoGo errors, Go errors, and their significant conjunction with $P < 0.05$ FWE corrected as level of significance. Regions showing significant differential activity associated with NoGo errors [Incorrect NoGo Minus Correct NoGo] are color-coded in red. Regions showing significant differential activity associated with Go errors [Incorrect Go Minus Correct Go] are color-coded in blue. Overlapping voxels are in violet (for detailed description see table above). *Coronal and Transversal view:* left inferior frontal cortex adjoining the anterior insula (IFC/aI, BA 47) for NoGo errors (= color-coded in red), Go errors (= color-coded in blue), and their conjunction (= color-coded in violet). *Saggital view:* dorsal anterior cingulate cortex (dACC, BA 32) for NoGo errors (= color-coded in red), Go errors (= color-coded in blue), and their conjunction (= color-coded in violet).

APPENDIX D: Interaction analyses between both error types (NoGo errors and Go errors)

***Table 3**: Coordinates and anatomical localization of regions related to the interaction analyses with both error types, estimated for trials with incongruent stimuli.*

Anatomical Region	L/R	BA	x	y	z	Z	Number of significant voxels
NoGo–by-Go error interaction[A]							
[NoGo error Minus Go error]							
Inferior frontal gyrus / anterior insula	R	6	-32	18	-2	3.20	12
Go-by-NoGo error interaction[B]							
[NoGo error Minus Go error]							
Superior frontal gyrus	L	6	-6	16	60	3.87	71
Inferior frontal gyrus	L	45	-50	28	2	3.46	58

Note. Interaction effects are reported at level of significance at $P < .001$ uncorrected at the voxel level. x, y and z are MNI coordinates of the peak voxel within a cluster. Z = Z-value. BA = Brodmann area. L = left, R = right. *A.* NoGo error – by – Go error interaction analysis was performed for the contrast: [(Incorrect NoGo > Correct NoGo) > (Incorrect Go > Correct Go)]. This interaction analysis was constrained by an inclusive mask using the main effect for the [Incorrect Go > Correct Go] contrast significant at the threshold of $p < 0.001$ uncorrected at voxel level, in order to assure that only differences of "Incorrect > Correct" on Go trials were included. *B.* Go error – by – NoGo error interaction analysis was performed for the inverted contrast: [Incorrect Go > Correct Go] > [Incorrect NoGo > Correct NoGo]. This interaction analysis was constrained by an inclusive mask using the main effect for the contrast [Incorrect NoGo > Correct NoGo] significant at the threshold of $p < 0.001$ uncorrected at voxel level, in order to assure that only differences of "Incorrect > Correct" on NoGo trials were included.

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