

Brain correlates of pro-social personality traits: a voxel-based morphometry study

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Abstract Of the five personality dimensions described by the Big Five Personality Model (Costa and McCrae 1992), Extraversion and Agreeableness are the traits most commonly associated with a pro-social orientation. In this study we tested whether a pro-social orientation, as expressed in terms of Extraversion and Agreeableness, is associated with a specific grey matter phenotype. Fifty-two healthy participants underwent magnetic resonance imaging (MRI) and completed the NEO-Five Factor Inventory (NEO-FFI), a self-report measure of the Big Five personality traits. Voxel-based morphometry (VBM) was used to investigate the correlation between brain structure and the personality traits of Agreeableness and Extraversion. We found that Extraversion was negatively correlated with grey matter density in the middle frontal and orbitofrontal gyri while Agreeableness was negatively correlated with grey matter density in the inferior parietal, middle occipital and posterior cingulate gyri. No

positive correlations were found. These results suggest that pro-social personality traits seem to be associated with decreases in grey matter density in more frontal regions for Extraversion, and more posterior regions for Agreeableness.

Keywords Extraversion · Agreeableness · Structural MRI · Voxel-based morphometry

Introduction

A pro-social orientation refers to a set of dispositional attitudes, cognitions and behaviors that successfully potentiate social interactions. This orientation has traditionally been associated with several regions of the so-called “social brain,” including those associated with recognition of emotional expressions, such as the amygdala (Adolphs et al. 1994), and with theory of mind abilities, such as the medial prefrontal cortex, adjacent anterior cingulate cortex and the temporoparietal junction (Amodio and Frith 2006; Samson et al. 2004).

Two psychological dimensions seem to be present in a pro-social orientation. The first dimension includes the tendency to seek out social situations due to their reinforcing nature. In the Big Five Personality Model (Costa and McCrae 1992) this dimension corresponds to the Extraversion personality trait. Individuals scoring high in this personality trait are characterized as more sociable, behaviorally active, optimistic, and happier than low scorers (Depue and Collins 1999; McCrae and Costa 1990). A second component refers to an individual's tendency to care for others and respond empathically to their needs, a trait designated as Agreeableness in the Big Five Model. Individuals scoring high in Agreeableness are characterized as more cooperative and altruistic than low scorers.

Previous studies found some empirical evidence for different neuroanatomical correlates of Extraversion and Agreeableness. DeYoung et al. (2010) found that

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Extraversion was positively associated with the volume of the medial orbitofrontal cortex, which is known to be involved in the processing of the reward values of stimuli and approach-related behavior (Milad and Rauch 2007). Rauch et al. (2005) also found a positive association between Extraversion and orbitofrontal cortical thickness, and Cremers and colleagues (2011) found that the volumes of orbitofrontal cortex and right amygdala were positively correlated with Extraversion. Additionally, Wright et al. 2007 found positive correlations between Extraversion and the thickness of right superior frontal cortex and left middle frontal cortex. However, other studies reported negative correlations between Extraversion and cortical thickness (Wright et al. 2006) and volume (Barrós-Loscertales et al. 2006) in frontal regions.

DeYoung et al. (2010) found a positive correlation between Agreeableness and the volume of the retrosplenial region of posterior cingulate cortex, which has been implicated in the process of understanding other individuals' beliefs, a component of theory of mind (Saxe and Powell 2006); they also found a positive correlation between Agreeableness and the volume of the fusiform gyrus, a region associated with the perception of faces (Kanwisher et al. 1997). Intriguingly, the authors also found a negative correlation between Agreeableness and cortical volume in the left posterior superior temporal sulcus, which is known to be involved in mentalizing processes (Hooker et al. 2010).

The abovementioned data seem to suggest that Extraversion and Agreeableness describe distinct dimensions of pro-social behavior, likely associated with distinct brain structure phenotypes.

Thus, the objective of the present study is to explore further whether individual variation in the volume of distinct brain regions may be associated with these two dimensions of a pro-social orientation (i.e., Extraversion and Agreeableness). To study the neuroanatomical correlates of these two personality dimensions, we collected structural MRI (magnetic resonance imaging) scans of 52 healthy adults who had been assessed with the NEO-FFI personality measure, and analyzed those data using voxel-based morphometry (VBM).

We hypothesize that Extraversion is associated with prefrontal regions such as the medial prefrontal cortex and orbitofrontal cortex, because these regions are involved in the processing of social information and rewards, respectively. We additionally hypothesize that Agreeableness is associated with the medial prefrontal cortex as well as the posterior cingulate cortex and temporoparietal junction, because these regions are typically involved in understanding others' emotions and mental states, which is essential for the empathy and altruism associated with high Agreeableness.

Method

Participants

Our participants were 52 healthy volunteers (29 female and 23 male) with a mean age of 25.0 (SD=5.1) years, ranging from 19 to 52 years. Participants were recruited by informal advertising. The study was approved by the human ethics committee of the local hospital in which data were collected. Exclusion criteria for the current sample were as follows: (1) the presence of any major medical or neurological disorder; (2) dependency on or abuse in the past year of alcohol and/or drugs; (3) general MR contraindications. After signing the written informed consent form, all the participants underwent a session of personality assessment followed by an MRI scanning session.

Personality assessment

All subjects completed the Portuguese version of the NEO-Five Factor Inventory (NEO-FFI) (Costa and McCrae 1995). The NEO-FFI is the short version of the NEO-PIR. It is a psychological personality inventory that measures the five personality dimensions described by Costa and McCrae: Extraversion, Agreeableness, Conscientiousness, Neuroticism, and Openness to Experience. The instrument has 60 items (12 per domain) answered on a five-point Likert scale, ranging from "strongly disagree" to "strongly agree." The different subscales of the NEO-FFI have good internal consistency ($N=.79$, $E=.79$, $O=.80$, $A=.75$, $C=.83$), and the instrument's test-retest reliability and external validity are high. For this study, Extraversion and Agreeableness scores followed a normal distribution, assessed by Kolmogorov-Smirnov and Shapiro tests (Extraversion: $K-S(49)=.07$, $p>.05$; Agreeableness: $K-S(49)=.10$, $p>.05$).

Magnetic resonance imaging

Image acquisition

A whole-brain structural MRI acquisition sequence (MPRAGE) was conducted on a clinically approved Siemens Magnetom Avanto 1.5 T with a 12-channel head coil. One three-dimensional, high-resolution T1-weighted anatomical image volume was acquired from each subject, using the following parameters: acquisition matrix=192×192 mm; field of view=234×234 mm; repetition time=2,400 ms; echo time=3.6 ms; flip angle=8°; number of slices=160; in plane resolution=1.2×1.2 mm; and slice thickness=1.2 mm.

Voxel-based morphometry

Voxel-based morphometry (VBM) is an automated whole-brain processing method, which allows the composition of

brain tissue to be compared among (between and/or within) groups (Ashburner and Friston 2000), being an indirect measure of volume. It has been widely used in studies linking variation in personality with changes in white and gray matter (Wright et al. 2006; DeYoung et al. 2010; Omura et al. 2005; Forsman et al. 2012).

Before beginning processing, all images were visually inspected to confirm that they had not been affected by critical head motion and that participants had no brain lesions. Data were processed using the Statistical Parametric Mapping software (SPM8; Wellcome Trust Centre for Neuroimaging, University College London, UK; <http://www.fil.ion.ucl.ac.uk/spm>) executed in Matlab R2011a (MathWorks, Natick, MA). The anatomical images were first manually reoriented to the ICBM 152 average SPM template in Montreal Neurological Institute (MNI) space. Next, images were segmented into grey matter, white matter and cerebrospinal fluid using the standard unified segmentation model in SPM8. White and grey matter were co-registered across participants using the DARTEL algorithm (Diffeomorphic Anatomical Registration Through Exponentiated Lie Algebra; Ashburner 2007; Ashburner and Friston 2009) to improve registration. The resulting template was then normalized to MNI space and those deformations were applied to the grey and white matter images of the subjects. Images were then smoothed with a 10 mm FWHM Gaussian filter to reduce possible error from between-subject variability in local anatomy and to improve the normality of the data. Finally, the smoothed, modulated, and normalized grey matter maps were resampled to a $1 \times 1 \times 1$ mm voxel size and submitted to statistical analysis. Grey matter, white matter and CSF volumes were calculated with a specific Matlab script and summed to provide an estimate of total intracranial volume.

Statistical analysis

Individual grey matter maps were entered into a voxel-based multiple regression analysis to investigate linear correlations between grey matter density and the Extraversion and Agreeableness scores obtained on the NEO-FFI. Because both age and gender are important predictors of regional brain volume (Good et al. 2001) and have been shown to interact with personality (Miettunen et al. 2007), we controlled for these factors. Thus, age, total intracranial volume and gender were included in the model as covariates of no interest, and Extraversion and Agreeableness scores were included as the variables of interest. Four statistical parametric maps of regression coefficients were generated: positive and negative correlations between individual Extraversion and Agreeableness scores and grey matter volume. The results were corrected for multiple comparisons as follows. Using a Monte Carlo simulation program (Alphasim), we derived a clusterwise threshold of $p < 0.05$

by combining a $p < 0.001$ height threshold and a minimum cluster size of 430 contiguous voxels (using the global grey matter mask, FWHM=10 mm, cluster connection radius=5 mm and 1,000 iterations).

Results

The participants had mean Extraversion and Agreeableness scores and variability comparable to normative samples (Manga et al. 2004; Egan et al. 2000), with a mean extraversion score of 30.5 ± 4.94 (mean \pm SD) and a mean Agreeableness score of 29.1 ± 7.14 .

Extraversion and regional brain volume

The volumes of the bilateral middle frontal gyrus (right: peak MNI coordinates $x=32, y=9, z=57, Z=4.04$; left: $x=-27, y=25, z=37, Z=3.82$), right inferior frontal gyrus ($x=46, y=41, z=1, Z=4.02$), right superior frontal gyrus ($x=25, y=56, z=20, Z=3.74$) and bilateral orbitofrontal cortex (right: $x=49, y=57, z=-5, Z=3.75$; left: $x=-51, y=52, z=-2, Z=3.73$), were negatively correlated with Extraversion. Extraversion did not show a significant positive correlation with any brain region at the corrected level of significance. The results are shown in Fig. 1 and Table 1.

Agreeableness and regional brain volume

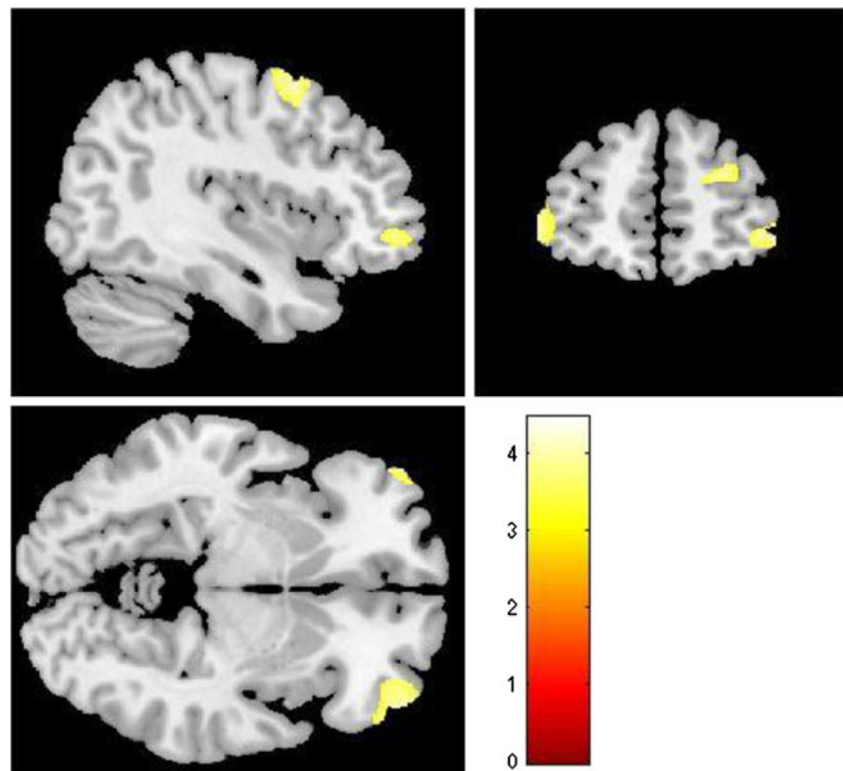
Significant negative correlations were found between Agreeableness and the volumes of the right inferior parietal gyrus (peak MNI coordinates $x=46, y=-49, z=45, Z=3.79$), left middle occipital gyrus ($x=-45, y=-84, z=5, Z=3.71$) and left posterior cingulate gyrus ($x=-11, y=-51, z=31, Z=3.66$). Smaller clusters were found at the right superior frontal gyrus, left middle frontal gyrus and left precuneus; however, these clusters are only significant at $p=0.001$, uncorrected. We found no positive correlations between agreeableness and any grey matter region (Fig. 2 and Table 2).

We did not find any significant correlations between extraversion or agreeableness and white matter volume.

Discussion

The present research examined the association between pro-social orientation as measured by Extraversion and Agreeableness and local grey matter volume throughout the brain. Both traits were negatively correlated with regional volume in a number of brain regions known to be involved in different aspects of social cognition. Extraversion was negatively correlated with the volume of prefrontal regions, whereas Agreeableness was negatively correlated with more

Fig. 1 Brain regions in which local volume was significantly related with Extraversion. Clusters, significant at $p=0.05$ (corrected), are projected on coronal, axial and sagittal sections. The *color bar* represents the t values



posterior regions such as parietal, posterior cingulate and occipital regions. Overall, these results confirmed our initial hypothesis that Extraversion would be preferentially associated with regions involved in the processing of social information and social rewards, while Agreeableness would be associated with regions more traditionally associated with components of theory of mind.

More specifically, Extraversion was found to be negatively associated with the orbitofrontal cortex and the middle prefrontal cortex. The relationship between Extraversion and the

orbitofrontal cortex has been reported in previous studies (Omura et al. 2005; Rauch et al. 2005; DeYoung et al. 2010). Extraverted individuals tend to be more sensitive to social rewards (e.g., social approval). Social rewards, like other types of rewards, are processed in dopaminergic neural circuits associated with goal-directed—in this case, social-directed—behavior (Rademacher et al. 2010), including the basal ganglia and the prefrontal and orbitofrontal regions. On the other hand, the medial prefrontal cortex is involved in social cognition and theory of mind (Gusnard et al. 2001), typical strengths of extraverted individuals.

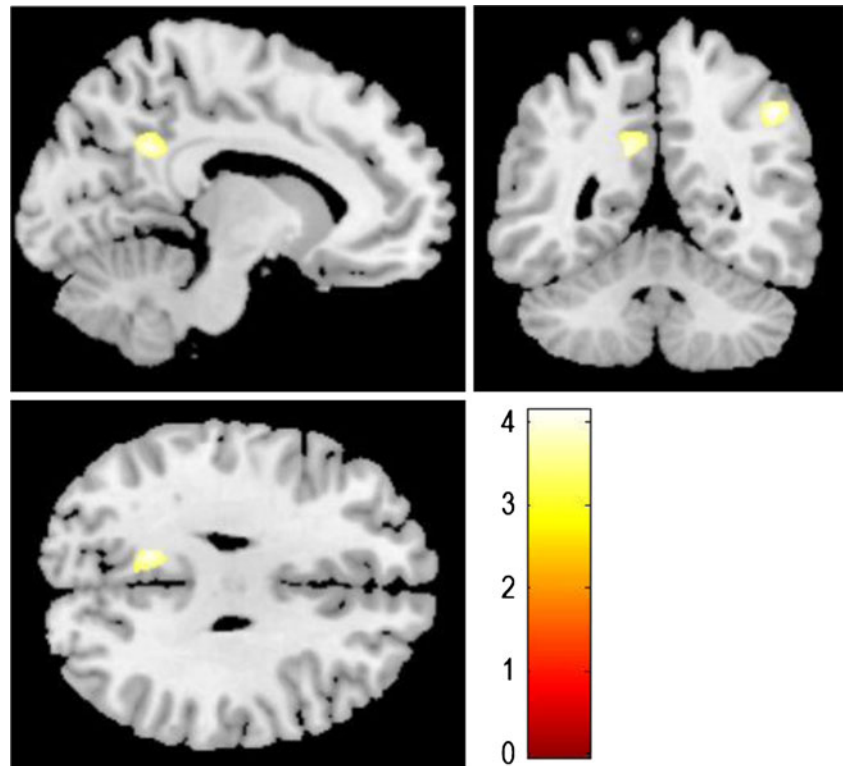
Most of the correlations between extraversion and grey matter volume found in this study were located in the right hemisphere. This is in line with previous studies that have also found negative correlations between extraversion and grey matter in several right brain areas (Forsman et al. 2012), namely in the right inferior pre-frontal cortex (Wright et al. 2006). This predominance of right areas may be explained by a hemispheric functional asymmetry namely in the pre frontal cortex, in which the right hemisphere plays an important role in dimensions of behavior inhibition such as withdrawal behavior, negative emotional valence and individual-oriented rather than affiliate behavior (for a review see Demaree et al. 2005), which are not characteristic of extroverted individuals.

Regarding Agreeableness, we found that it was negatively correlated with the inferior parietal region, a region that has been documented to play a role both in the processing of social stimuli (Johnson et al. 1999; Volkow et al. 2011) and in inhibitory control (Garavan et al. 1999).

Table 1 Grey matter regions showing a negative correlation with Extraversion. Each cluster's coordinates in Montreal Neurological Institute (MNI) space (x, y, z), maximum Z-value and size are given. All correlations were significant ($p<0.05$, corrected with Monte Carlo correction) when controlling for age, gender and total intracranial volume. Brain regions were labeled by a combination of visual inspection and the Anatomical Automatic Labeling atlas (AAL) (Tzourio-Mazoyer et al. 2002) in MRICron (Rorden and Brett 2000)

Brain area	Left/ right	Cluster size	Z value at local maximum	MNI coordinates (x,y,z)
Middle frontal gyrus	R	2704	4,04	32,9,57
Inferior frontal gyrus, pars triangularis	R	3867	4,02	46,41,1
Middle orbitofrontal gyrus	R		3,75	49,57,-5
Middle frontal gyrus	L	352	3,82	-27,25,37
Superior frontal gyrus	R	1533	3,74	25,56,20
Middle orbitofrontal gyrus	L	1009	3,73	-51,52,-2

Fig. 2 Brain regions in which local volume was significantly related with Agreeableness. Clusters, significant at 0.05 (corrected), are projected on coronal, axial and sagittal sections. The *color bar* represents the *t* values



Agreeableness was also found to be associated with the volume of the posterior cingulate cortex, an area known to be involved in understanding others' beliefs (Saxe and Powell 2006). Interestingly, individuals scoring high in Agreeableness (i.e., friendlier and more altruistic individuals) also presented a decreased volume in the left middle occipital area. This finding may suggest the role of secondary visual processing regions in the processing of complex social stimuli such as facial

Table 2 Grey matter regions showing a negative correlation with Agreeableness. Each cluster's coordinates in Montreal Neurological Institute (MNI) space (x, y, z), maximum Z-value and size are given. All correlations were significant ($p < 0.05$, corrected with Monte Carlo correction) when controlling for age, gender and total intracranial volume. Clusters marked with * survive the height threshold of $p = 0.001$ but contain fewer voxels than the 430 required by multiple comparisons correction. Brain regions were labeled by a combination of visual inspection and the Anatomical Automatic Labeling atlas (AAL) (Tzourio-Mazoyer et al. 2002) in MRICron (Rorden and Brett 2000)

Brain area	Left/ right	Cluster size	Z value at local maximum	MNI coordinates (x,y,z)
Inferior parietal gyrus	R	872	3,79	46,-49,45
Middle occipital gyrus	L	742	3,71	-45,-84,5
Posterior cingulate gyrus	L	890	3,66	-11,-51,31
Superior frontal gyrus*	R	115	3,45	23,72,6
Middle frontal gyrus*	L	22	3,31	-43,58,19
Precuneus*	L	14	3,13	-1,-64,32

expressions, eye gaze, motions and gestures. Finally, Agreeableness was also associated with cortical volume in two smaller clusters in left precuneus and left middle frontal gyrus, regions known to be involved in social-cognitive tasks although these clusters did not survive multiple comparisons correction.

It is important to note that no positive correlations were found in this study, which means that, in all the reported regions, individuals scoring higher in Extraversion and Agreeableness tended to have smaller grey matter volume.

The direction of the correlations we found is in line with previous structural studies reporting only negative correlations between Extraversion and different frontal regions (Wright et al. 2006; Barrós-Loscertales et al. 2006). However, positive relationships have also been reported (Wright et al. 2007; Rauch et al. 2005; Omura et al. 2005), which illustrates the complexity inherent in the relationship between structure and function. As suggested by DeYoung (2010), even though it is reasonable to think that a greater volume in a specific brain region will produce increased processing capacity due to a larger population of neurons, it is also possible that a smaller volume may indicate more efficiency in implementing specific functions associated with that structure.

The idea that lower grey matter density can lead to better performance is supported by several neurodevelopmental studies. Sowell and colleagues (2004) found that greater grey matter thinning in the left dorsal frontal and parietal lobes was associated with improved performance on a test of general verbal intellectual functioning. Previously, the same authors (Sowell et al. 2001) had already found negative

correlations between grey matter volume in the frontal lobes bilaterally and children's performance on a measure of verbal learning. Thus, grey matter density reduction may occur as part of normal brain maturation, which in turn may be partially attributable to increased proliferation of myelin into the periphery of the cortical neuropil (Reiss et al. 1996; Sowell et al. 1999).

The relationship between grey matter reduction and better performance in specific tasks may suggest an explanation for the exclusively negative correlations between grey matter density and Extraversion and Agreeableness found in our study.

In conclusion, our results contribute to the understanding of the neuroanatomical basis of pro-social orientation in terms of two of that orientation's dimensions: the tendencies to process cues of social reinforcement and to respond to other people's needs. More specifically, our findings seem to suggest that Extraversion is more associated with frontal regions (middle frontal and orbitofrontal gyri), including regions involved in reward processing in general, whereas Agreeableness is associated with more posterior regions (inferior parietal, middle occipital and posterior cingulate gyri) typically involved in empathy.

Limitations and future directions

Because of the inconsistency of the literature on the topic, we must be cautious when making conclusions about relations between Extraversion and Agreeableness and regional brain structure. This inconsistency is most likely due to differences in the demographic characteristics of the samples and in the specific techniques used to acquire and analyze the neuroimaging data (e.g., thresholds of significance imposed).

We must note that the present sample consisted of a cohort of young adults, with limited generalizability to populations with different demographic characteristics. In addition, personality traits were assessed with self-report measures that do not necessarily capture the complexity of the behavioral, cognitive and emotional patterns that characterize extraverted and agreeable individuals.

Future studies should thus try to replicate our findings in samples with other demographic features. In addition, future studies may also consider adopting alternative and more direct methods of volume analysis, including manual tracing of specific brain regions involved in social processing. Finally, a better understanding of the different roles of frontal and posterior regions in the distinct dimensions of pro-social orientation requires a follow-up using functional imaging methods.

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Conflict of interest The authors declare that they have no conflict of interest.

References

- Adolphs, R., Tranel, D., Damasio, H., & Damasio, A. (1994). Impaired recognition of emotion in facial expressions following bilateral damage to the human amygdala. *Nature*, *372*, 669–672.
- Amodio, D. M., & Frith, C. D. (2006). Meeting of minds: the medial frontal cortex and social cognition. *Nature Reviews Neuroscience*, *7*, 268–277.
- Ashburner, J. (2007). A fast diffeomorphic image registration algorithm. *NeuroImage*, *38*(1), 95–113.
- Ashburner, J., & Friston, K. J. (2000). Voxel-based morphometry—the methods. *NeuroImage*, *11*(6), 805–821.
- Ashburner, J., & Friston, K. J. (2009). Computing average shaped tissue probability templates. *NeuroImage*, *45*(2), 333–334.
- Barrós-Loscertales, A., Meseguer, V., Sanjuán, A., Belloch, V., Parcet, M., Torrubia, R., et al. (2006). Striatum gray matter reduction in males with an overactive behavioral activation system. *European Journal of Neuroscience*, *24*, 2071–2074.
- Costa, P. T., & McCrae, R. R. (1995). Domains and facets: hierarchical personality assessment using the Revised NEO Personality Inventory. *Journal of Personality Assessment*, *64*, 21–50.
- Costa, P. T., Jr., & McCrae, R. R. (1992). *Revised NEO Personality Inventory (NEO-PI-R) and NEO Five-Factor Inventory (NEO-FFI) professional manual*. Odessa: Psychological Assessment Resources, Inc.
- Cremers, H., van Tol, M. J., Roelofs, K., Aleman, A., Zitman, F. G., van Buchem, M. A., et al. (2011). Extraversion is linked to volume of the orbitofrontal cortex and amygdala. *PLoS One*, *6*(12), e28421. doi:10.1371/journal.pone.0028421.
- Demaree, H. A., Everhart, D. E., Youngstrom, E. A., & Harrison, D. W. (2005). Brain later-alization of emotional processing: historical roots and a future incorporating “dominance”. *Behavioral and Cognitive Neuroscience Reviews*, *4*, 3–20.
- Depue, R. A., & Collins, P. F. (1999). Neurobiology of the structure of personality: dopamine, facilitation of incentive motivation, and extraversion. *The Behavioral and Brain Sciences*, *22*, 491–569.
- DeYoung, C. G., Hirsh, J. B., Shane, M. S., Papademetris, X., Rajeevan, N., & Gray, J. R. (2010). Testing predictions from personality neuroscience. *Psychological Science*, *21*(6), 820.
- Egan, V., Deary, I., & Austin, E. (2000). The NEO-FFI: emerging british norms and an item-level analysis suggest N, A and C are more reliable than O and E. *Personality and Individual Differences*, *29*, 907–920.
- Forsman, L. J., de Manzano, O., Karabanov, A., Madison, G., & Ullén, F. (2012). Differences in regional brain volume related to the extraversion–introversion dimension—a voxel based morphometry study. *Neuroscience Research*, *72*(1), 59–67.
- Garavan, H., Ross, T. J., & Stein, E. A. (1999). Right hemispheric dominance of inhibitory control: an event-related functional MRI study. *Proceedings of the National Academy of Sciences of the United States of America*, *96*, 8301–8306.
- Good, C. D., Johnsrude, I. S., Ashburner, J., Henson, R. N. A., Friston, K. J., & Frackowiak, R. S. J. (2001). A voxel-based morphometric study of ageing in 465 normal adult human brains. *NeuroImage*, *14*, 21–36.
- Gusnard, D. A., Akbudak, E., Shulman, G. L., & Raichle, M. E. (2001). Medial prefrontal cortex and self-referential mental activity: relation to a default mode of brain functioning. *Proceedings of the National Academy of Sciences of the United States of America*, *98*(7), 4259–4264.
- Hooker, C., Verosky, S., Germine, L., Knight, R., & D'Esposito, M. (2010). Neural activity during social signal perception correlates with self-reported empathy. *Brain Research*, *1308*, 100–113.

- Johnson, D. L., Wiebe, J. S., Gold, S. M., Andreasen, N. C., Hichwa, R. D., Watkins, G. L., et al. (1999). Cerebral blood flow and personality: a positron emission tomography study. *The American Journal of Psychiatry*, *156*(2), 252–257.
- Kanwisher, N., McDermott, J., & Chun, M. (1997). The fusiform face area: a module in human extrastriate cortex specialized for face perception. *The Journal of Neuroscience*, *17*(11), 4302–4311.
- Manga, D., Ramos, F., & Mórán, C. (2004). The Spanish norms of the NEO Five-Factor Inventory: new data and analysis for its improvement. *International Journal of Psychology and Psychological Therapy*, *4*(3), 639–648.
- McCrae, R. R., & Costa, P. T. (1990). *Personality in adulthood*. New York: Guilford Press.
- Miettunen, J., Veijola, J., Lauronen, E., Kantojärvi, L., & Joukamaa, M. (2007). Sex differences in Cloninger's temperament dimensions—a meta-analysis. *Comprehensive Psychiatry*, *48*, 161–169.
- Milad, M. R., & Rauch, S. L. (2007). The role of the orbitofrontal cortex in anxiety disorders. *Annals of the New York Academy of Sciences*, *1121*, 546–561.
- Omura, K., Todd Constable, R., & Canli, T. (2005). Amygdala gray matter concentration is associated with extraversion and neuroticism. *NeuroReport*, *16*, 1905–1908.
- Rademacher, L., Krach, S., Kohls, G., Irmak, A., Gründer, G., & Spreckelmeyer, K. (2010). Dissociation of neural networks for anticipation and consumption of monetary and social rewards. *NeuroImage*, *49*, 3276–3285.
- Rauch, S. L., Milad, M. R., Orr, S. P., Quinn, B. T., Fischl, B., & Pitman, R. K. (2005). Orbitofrontal thickness, retention of fear extinction, and extraversion. *NeuroReport*, *16*, 1909–1912.
- Reiss, A. L., Abrams, M. T., Singer, H. S., Ross, J. L., & Denckla, M. B. (1996). Brain development, gender and IQ in children. A volumetric imaging study. *Brain*, *119*, 1763–1774.
- Rorden, C., & Brett, M. (2000). Stereotaxic display of brain lesions. *Behavioral Neurology*, *12*(4), 191–200.
- Samson, D., Apperly, I., & Humphreys, G. (2004). Left temporoparietal junction is necessary for representing someone else's belief. *Nature Neuroscience*, *7*, 499–500.
- Saxe, R., & Powell, L. J. (2006). It's the thought that counts: specific brain regions for one component of theory of mind. *Psychological Science*, *17*, 692–699.
- Sowell, E. R., Thompson, P. M., Holmes, C. J., Jernigan, T. L., & Toga, A. W. (1999). In vivo evidence for post-adolescent brain maturation in frontal and striatal regions. *Nature Neuroscience*, *2*, 859–861.
- Sowell, E. R., Delis, D., Stiles, J., & Jernigan, T. L. (2001). Improved memory functioning and frontal lobe maturation between childhood and adolescence: a structural MRI study. *Journal of International Neuropsychological Society*, *7*, 312–322.
- Sowell, E. R., Thompson, P. M., Leonard, C. M., Welcome, S. E., Kan, E., & Toga, A. W. (2004). Longitudinal mapping of cortical thickness and brain growth in normal children. *The Journal of Neuroscience*, *24*(38), 8223–8231.
- Tzourio-Mazoyer, N., Landeau, B., Papathanassiou, D., Crivello, F., Etard, O., Delcroix, N., et al. (2002). Automated anatomical labeling of activations in SPM using a macroscopic anatomical parcellation of the MNI MRI single-subject brain. *NeuroImage*, *15*(1), 273–289.
- Volkow, N. D., Tomasi, D., Wang, G. J., Fowler, J. S., Telang, F., Goldstein, R. Z., et al. (2011). Positive emotionality is associated with baseline metabolism in orbitofrontal cortex and in regions of the default network. *Molecular Psychiatry*, 1–8.
- Wright, C. I., Williams, D., Feczko, E., Barrett, L. F., Dickerson, B. C., Schwartz, C. E., et al. (2006). Neuroanatomical correlates of extraversion and neuroticism. *Cerebral Cortex*, *16*(12), 1809–1819.
- Wright, C. I., Feczko, E., Dickerson, B., & Williams, D. (2007). Neuroanatomical correlates of personality in the elderly. *NeuroImage*, *35*, 263–272.