

THE PERSONALITY AND THE BRAIN: AN INEVITABLE ENCOUNTER

Eduardo J. Pedrero Pérez¹, José M. Ruiz Sánchez de León² y Marcos Llanero Luque¹

¹Ayuntamiento de Madrid. ²Universidad Complutense de Madrid

Personality is a construct that, until recent years, had not attracted much interest among neurologists and neuropsychologists. However, during the past decade, studies have proliferated that seek brain, structural and functional correlates of personality traits proposed by different theories, especially the Big Five model of personality. These studies have accumulated evidence about the fact that the five traits are related to specific brain locations, allowing us, at the present time, to be able to draw a brain map associated with each trait. More recent studies relate these features with the brain default mode network, where the compendium of implicit rules of management which we call personality resides. This will gradually take shape throughout one's lifetime through mechanisms of "experience-dependent plasticity". These proposals represent the threshold of a paradigm shift that may lead the study of "mental disorders" to the territory of alterations in brain connectivity, which is an immediate challenge for neuroscience.

Key words: Big Five Model, Brain, Default mode network, Neuroimage, Neuroplasticity, Neuroscience.

La personalidad es un constructo que, hasta los últimos años, no había suscitado demasiado interés entre los neuropsicólogos. Sin embargo, durante la década pasada han proliferado los estudios interesados en buscar correlatos cerebrales, estructurales y funcionales de rasgos de personalidad propuestos por las distintas teorías, especialmente el modelo de los cinco grandes factores de personalidad. Se ha ido acumulando evidencia sobre el hecho de que los cinco rasgos se relacionan con localizaciones cerebrales concretas pudiendo, actualmente, trazar un mapa cerebral asociado a cada rasgo. Estudios más recientes relacionan a estos rasgos con la red cerebral por defecto, donde residiría el compendio de reglas implícitas de gestión (personalidad), que se iría formando durante la vida mediante mecanismos de "plasticidad dependiente de la experiencia". Estas propuestas suponen el umbral de un cambio de paradigma que puede llevar el estudio de los "trastornos mentales" al territorio de las alteraciones en la conectividad cerebral.

Palabras clave: Modelo de los cinco grandes factores, Neurociencia, Neuroimagen, Neuroplasticidad, Red por defecto.

Personality psychology, on the one hand, and neuroscience, on the other, have at times taken routes that are far removed from mutual findings in relation to the construct that we call *personality*. The successive models proposed to explain personality, closer to the conceptual level than to the tangible nervous system, have competed with each other to accumulate empirical evidence describing its relationship with normal and pathological behaviour while neuroscience has aimed to describe the more pragmatic aspects of behaviour, with direct repercussions in pathologies or different manifestations of brain functioning. However, the encounter between the two approaches is a necessity that has long been called for:

"Psychologist and neurophysiologist thus chart the same bay –working perhaps from opposite shores, sometimes overlapping and duplicating one another, but using some of the same fixed points

and continually with the opportunity of contributing to each other's results. The problem of understanding behavior is the problem of understanding the total action of the nervous system, and vice versa. This has not always been a welcome proposition, either to psychologist or to physiologist" (Hebb, 1949; p. XIV).

The present moment represents, perhaps, the encounter between the various approaches to the study of personality in the context of a transdisciplinary understanding, characteristic of neuroscience. The latest findings indicate that the concept of personality is "*more than just a concept*" and "*personality constructs do reflect more than mere descriptive taxonomies*" (Susic-Vasic, Ulrich, Ruchow, Vasic & Grön, 2012).

Although we should refer to the typology of Pavlov as the first reference of the study of personality characteristics associated with the functioning of the central nervous system (Strelau, 1997), Eysenck was the first researcher to deal with the study of human personality from the

Correspondence: Eduardo J. Pedrero Pérez. C/ Alcalá 527. 28027 Madrid. España. E-mail: ejpedrero@yahoo.es



knowledge of the functioning of neuroendocrine structures and the application of mathematical methods, such as factor analysis, to determine the grouping of elements in higher order factors, which he called traits. His model (Eysenck, Eysenck, & Barrett, 1985) proposes the existence of three personality dimensions or traits: *neuroticism* (linked to the functioning of the autonomic nervous system), *extraversion* (linked to the ascending reticular activating system) and *psychoticism* (linked successively to the metabolism of serotonin and testosterone). Eysenck's proposal was criticised by authors such as Gray (1970) who, by performing a rotation of the dimensions proposed by Eysenck, suggested the existence of two dimensions linked to the functioning of the central nervous system: *the behavioural activation system* (BAS), related to systems of cerebral arousal, such as the frontal cortex, thalamus and striatum, and the *behavioural inhibition system* (BIS), related to the ascending reticular system and its projections to the prefrontal cortex.

Initially proposed by Digman (1989) and Goldberg (1992), *the model of the Big Five personality factors* was based on a different research strategy. The researchers found that the personality descriptors available in people's habitual language were consistently grouped, by factor analysis, into five dimensions. Further developments led McCrae and Costa (1997) to propose a personality model based on five independent factors, which was repeated in transcultural studies: *extraversion*, *neuroticism*, *conscientiousness*, *agreeableness* and *openness*. The model was a development of Gray's theory (Smits & Boeck, 2006) and, using the instrument proposed by the authors, the NEO-PI-R (Costa & McCrae, 1992), the model began to accumulate empirical evidence, becoming the predominant theory in recent decades on the structure of the human personality. The model has also been heavily criticised, among other reasons, for being a mere psychometric artefact without a theory or biological findings to sustain it, or for the lack of orthogonality of the supposedly independent factors (Block, 1995, 2001, 2010). In spite of this, researchers of the individual differences in personality see the *Big Five Factor Model* as the first explicit display of consensus on the primary dimensions of personality, upon which to investigate further.

An important development in the first decade of this century refers to a change in the focus of the research: it is possible that the neurotransmitter systems act in diverse ways (even in opposite ways) depending on the cerebral location; if the traits are behavioural programs, they

should be based on different patterns of global cerebral activity. Therefore it is not serotonin or dopamine that we should focus our interest upon, but rather which parts of the brain, which fibre bundles, and which connection patterns are related to each of the proposed traits and to the manifest behaviours that characterise them. The focus has gone from the molecule to the study of the brain as an organ in constant interaction with the environment. As some authors affirm, the route is "from genes to brain to behaviour", completed ultimately as "from the environment, to genes, to the brain, and finally to behaviour" (Raine, 2008).

The first two elements, genes and the environment have been firmly linked since epigenetic mechanisms have been known about (Petronis, 2010). Differential DNA methylation may explain differences in the traits of people with the same genetic load (Kaminsky et al., 2008). Studies on animals have shown how the manipulation of environmental epigenetic factors results in profound changes in observable behaviour (Carere, Drent, Koolhaas & Groothuis, 2010). Longitudinal studies with large samples have shown how epigenetic factors influence the genetic load, causing huge variability within its permitted margins: people who are predisposed to a certain type of behaviour will manifest it to a greater or lesser extent, or will not manifest it, depending on the environmental circumstances; but those who do not have such a genetic predisposition will not display this behaviour even in the presence of similar environmental conditions (Caspi et al., 2002). It still remained to be confirmed that personality traits, theoretically or empirically formulated, were reflected in the structure and functioning of the brain, and that they were more than merely descriptive constructs. The objective of this paper is to offer a guided tour from the formulation of the theories of personality to the latest neurological and neuropsychological findings linking the theories with the observable functioning of the central nervous system.

METHOD

The main international databases (Academic Search Premier and PubMed) were searched using the descriptors "personality" and "neuroimaging". The search was limited to studies published after the year 2000. From the two databases mentioned, 139 and 458 studies were obtained respectively. We selected studies published in prestigious journals and ones that linked structural findings in the brain with constructs (traits) previously



defined by the Big Five personality factor model, or that proposed new theoretical explanatory models to account for previous findings. Whilst not attempting to be

exhaustive, we selected studies that allowed us to establish the current state of knowledge and proposed a solid starting point for the future study of this issue.

TABLE 1
MAIN STUDIES THAT RELATE THE BIG 5 PERSONALITY FACTORS WITH NEUROIMAGING

Article	Traits studied	Technique	Main findings
Canli (2004)	N, Ex	fMRI	Finds relationship between traits and connection networks (not just isolated areas such as the amygdala).
Omura, Constable & Canli (2005).	N, Ex	fMRI and VBM	Ex positively correlated with concentration of grey matter in the left amygdala, N negative correlation with grey matter concentration in the right amygdala.
O'Gorman et al. (2006)	All 5 trait	Combination of different methods	The traits were strongly associated with cerebral perfusion at rest in a variety of cortical and sub-cortical regions, providing further evidence of the hypothesis on the neurobiological basis of personality
Kalbitzer <i>et al.</i> (2009)	Op	PET	Op is related to cerebral markers of serotonergic activity.
DeYoung et al. (2010)	All 5 traits	fMRI	Finds a relationship between traits and different volumes in brain areas, proposing a biological model of personality.
Wei et al. (2011)	N, Ex	rsfMRI	N showed negative correlation with homogeneity in the left middle frontal gyrus and Ex with homogeneity in the medial PFC, an important part of the DMN, suggesting the relationship between the DMN and personality. Additionally, Ex correlated positively with homogeneity in the insula, cerebellum and cingulate cortex, suggesting associations between individual differences in Ex and brain regions involved in emotional processing.
Adelstein et al. (2011)	All 5 traits	fMRI-sr	Proposes a mapping of brain areas related to the 5 traits, finding individual differences in the general distribution, in resting states (DMN).
Xu & Potenza (2012)	All 5 traits	DTI	N was associated with worse white matter integrity in extensive cortical and subcortical structures, contrary to Op.
Sosic-Vasic et al. (2012)	All 5 traits	fMRI	Co correlated positively with activity in the left inferior frontal gyrus, the adjacent anterior insula and the anterior cingulate gyrus. N correlated negatively with activity in the inferior frontal cortex, reflecting the negative inter-correlation between the two scales observed at the behavioural level.
Servaas et al. (2013)	N	Meta-analysis	Differences found in brain activation associated with N during fear learning, the anticipation of aversive stimuli and the treatment and regulation of emotions.
Bjørnebekk et al. (2013)	All 5 traits	DTI	Associations between N, Ex and Co with structures in various brain areas, but not for Op and Ag.
van Tol <i>et al.</i> (2013)	N, Ex	fMRI	Decreased functional connectivity of medial PFC, ventrolateral PFC and ventral striatum with fronto-opercular network prominence in MDD patients compared to controls, related to extraversion, but not to neuroticism.
Sampaio et al. (2014)	All 5 traits	rsfMRI	The 5 personality traits were consistently related to different areas of DMN.
Passamonti et al. (2015)	Op	fMRI in tasks and states of rest	Openness was positively associated with functional connectivity between the ventral tegmental right substantia nigra, the main source of dopaminergic inputs to the brain, and the ipsilateral dorsolateral PFC, key coding region, maintenance and updating of information relevant to adaptive behaviours.
Kong et al. (2015)	All 5 traits	VBM	Traits such as N, Ex and Co contributed to social wellbeing, but only Ex acted as a mediation mechanism underlying the relationship between the volume of the medial prefrontal dorsolateral cortex and social wellbeing, suggesting that this trait could play an important role in the acquisition and processing of social wellbeing.

N= Neuroticism, Ex= Extraversion, Op= Openness, Co= Conscientiousness, Ag= Agreeableness. fMRI = Functional magnetic resonance imaging, VBM= Voxel based morphometry, DTI= Diffusion tensor imaging, PET= Positron emission tomography, CVM= cerebral volume, rsfMRI = resting state functional magnetic resonance; PFC= prefrontal cortex; DMN= Default mode network.



RESULTS

Many researchers have addressed this issue since the turn of this century (Table 1): the initial studies by Canli (2004) began to search for the cerebral correlates of the traits of the five-factor model. Using high resolution magnetic resonance and voxel-based morphometry, Canli found that *extraversion* was positively correlated with the concentration of grey matter in the left amygdala, whereas *neuroticism* was negatively correlated with the concentration of grey matter in the right amygdala (Omura, Constable & Canli, 2005). Other studies have been progressively completing the mapping of areas related to these two traits and their relation to negative emotionality (van Tol et al., 2013). Although most of the studies focused on grey matter and its connections with subcortical structures, Xu and Potenza (2012) studied white matter using diffusion tensor imaging, finding that *neuroticism* was associated with poor integrity of the white matter, involving extensive cortical interconnections between cortical structures (e.g., the prefrontal cortex) and subcortical structures (e.g., the amygdala), whereas *openness* displayed the opposite relations. Bjørnebekk et al. (2013) also found that *neuroticism* was the trait most related to the brain structure, being related to a lower total brain volume, a widespread decrease in white matter microstructure and a lower surface area of the frontotemporal zone; high scores on *extraversion* were associated with a lower thickness in the inferior frontal gyrus and *conscientiousness* was negatively associated with the arealisation of the temporoparietal junction.

The relationships between *neuroticism* and certain brain structures have been solidly verified by meta-analytical studies (Servaas et al., 2013), while the other traits have not yet been consistently linked to specific brain structures, although several studies are increasingly approaching each trait with different brain structures, locations and functions (DeYoung et al., 2010; Kalbitzer et al., 2009; O'Gorman et al., 2006). For example, *openness* seems to be linked to the connectivity between the right substantia nigra of the ventral tegmental area and the ipsilateral dorsolateral prefrontal cortex, a region responsible for encoding, maintaining and updating the relevant information for adaptive behaviour (Passamonti et al., 2015), whereas *extraversion* is the trait that is most consistently linked with social wellbeing, which correlates with the thickness of the grey matter in the medial prefrontal dorsolateral cortex (Kong, Hub, Xue, Song & Liu, 2015). There are few data on the relationship between

conscientiousness and *agreeableness* and the markers of brain functioning.

There appears to be evidence that the volume of different brain areas is related, at least in part, to the personality traits, and this has some genetic basis (Lewis et al., 2014). However, as will be seen later, the epigenetic factors seem to be more related to the variability observed in functional studies, especially in traits such as *agreeableness* (Van der Cruyssen, Heleven, Ma, Vandekerckhove & Van Overwalle, 2015).

In short, there seems to be enough evidence to support the aforementioned assertion, according to which the personality traits of the *Big Five factor model* reflect more than merely descriptive taxonomies to the extent that the traits have solid evidence of external validity that links them to the structural and functional variables of the brain (Sosic-Vasic et al., 2012). However, these studies still left many questions unanswered: how is personality “formed” in the brain? Do the neuroimaging studies –usually based on the performance of specific tasks– reflect the true sense of something as static and persistent as personality? Through what mechanisms are genetic substrates linked to learning history and experience in order to configure the structural and functional changes that lie beneath the individual personality? Where –in what part of the brain– is the personality, if it can be located?

At the beginning of the last decade, a number of researchers observed that when the individual is not performing any task, or is in a period of rest between tasks, the brain is not really at rest (Raichle, MacLeod, Snyder, Powers, Gusnard & Shulman, 2000). There is a neural network that remains active, which is known as the *default mode network* (DMN), when the neural *task oriented network* (TON) is not active in the pursuit of a specific objective (Figure 1). Later studies confirmed the existence of the DMN (Greicius, Krasnow, Reiss & Menon, 2003; Raichle & Snyder, 2007; Raichle & Snyder, 2007) and associated errors in its functioning with different pathologies such as schizophrenia (Jafri, Pearlson, Stevens & Calhoun, 2008) or Alzheimer's disease (Sperling et al., 2009), among others.

However, the study of the default network has focused increasingly closely on its relationship with personality. Indeed, the DMN appears to be closely linked to both normal personality traits –i.e., positive emotionality (Volkow et al., 2011)– and personality disorders –e.g., borderline (Krause-Utz et al., 2014; Wolf et al., 2011) or antisocial (Tang, Liao, Wang & Luo, 2013). As expected, the *Big Five*



Factor Model has attracted the most interest, with strong relationships being found between the DMN and isolated traits, such as *extraversion* (Lei, Zhao & Chen, 2013), *extraversion* and *neuroticism* (Wei et al., 2011) or all five together and their relationships with different sections of the default network (Sampaio, Soares, Coutinho, Sousa & Gonçalves, 2013), it being possible, at this time, to have a proposed brain mapping in relation to the traits of the model (Adelstein et al. 2011).

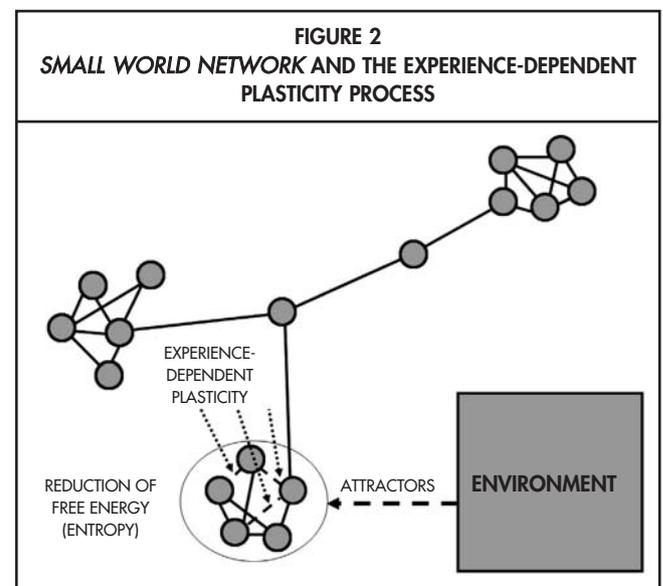
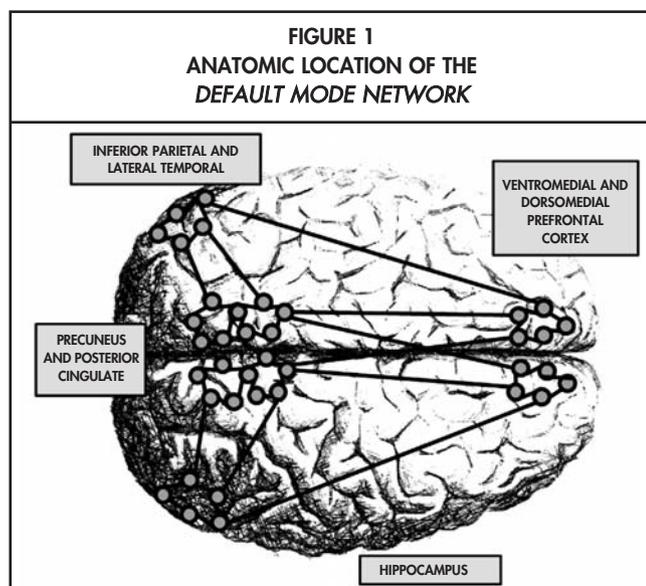
Thus it appears that the DMN would represent the neurological substrate where the product of the interaction between the genetic load and experiences in the individual's relationship with its environment is deposited, representing, ultimately, an *instruction manual* which directs, in a stable and persistent manner, the way in which the subject manages its relationship with the world, its quest for reinforcement, its coping with conflicts, its personal goals and values: in short, where its personality resides. But these merely correlative findings require assumptions about the way in which this depositing of rules occurs over time, a hypothesis that should be tested in future studies. Peled (2012) has suggested that there are three elements to consider: *connectivity*, *entropy reduction* and *experience-dependent plasticity* (Figure 2).

As for the first element, the DMN –but not only this network– would be mainly organised based on what are known as the “*small world networks*” that would allow the concentration of information in limited groups of neurons and could send the processed information to remote control centres which would produce the multimodal integration. Secondly, learning is a process that involves the formation

and strengthening of interneuronal connections, so that together they tend to be activated in stimulus situations and similar patterns of activation or “*attractors*”, tending to reduce free energy or entropy; which we would call, in psychological terms, *the reduction of uncertainty*. Finally, the experience of interaction with the environment, aimed at reducing uncertainty, modifies neuronal connectivity through mechanisms of *experience-dependent plasticity*, which, ultimately, is the step in which the experience is deposited in the brain, modulating what we call personality. The author has come to suppose that the whole of psychopathology could be explained through these mechanisms and alterations –*globalopathies*. Thus, errors in the mechanisms of free energy reduction would explain anxiety and mood disorders (*entropathies*), errors in connectivity mechanisms would explain psychotic disorders (*connectopathies*) and errors in the default network would explain personality disorders (known in English as “*resting-state networkopathies*” or *pathologies of the default network*; Peled, 2013). The confirmation of these hypotheses would imply major changes, not only in understanding the etiology and the pathophysiological mechanisms of behavioural disorders –as suggested years ago (Buckner, Andrews-Hanna & Schacter, 2008)– but also in clinical practice and the psychotherapeutic and pharmacological approach (Peled, 2012; Fox & Greicius, 2010).

DISCUSSION

Although it would have seemed improbable decades ago, the encounter between the personality and the brain was inevitable. Where else would the personality be





located? Advances in neuroimaging techniques have enabled us to seek the cerebral substrates of merely theoretical or empirically derived constructs, such as personality traits. At present, we can say that there are reasonable grounds to believe that individual experience interacts with genetic endowment to modify the brain architecture, through neuronal plasticity mechanisms, and to enable the development of behavioural rules in some way: a kind of idiosyncratic *instructions manual* that enables the subject to anticipate the consequences of its behaviour and reduce uncertainty.

Fortunately, these findings provide us with more questions than answers. Among them it is still unclear how the DMN interacts with the networks that are activated depending on each specific task; for example, how it affects attentional mechanisms during driving, in memory storage and subsequent recall of information, or if the individual responds angrily to the subtle offence of a person with whom he is conversing. Indeed, if the DMN is the substrate of this general *instructions manual* that we call personality, it could be hypothesised that, in situations where there is an *objective*—which implies the implementation of the executive functions—the DMN would move to a secondary level (or a de-activated state, as suggested by the available studies), prioritising the decisions generated in the prefrontal circuits. In fact, what is suggested is that beyond the *executive brain* there would be a *directing brain*, which would establish the general strategies or trans-situational rules of functioning. So how does the DMN influence the decision-making of the prefrontal cortex in the different situations (e.g., opportunities, threats and challenges) that the environment proposes at each moment? Does some form of active connection persist when the central role is assumed by the task-oriented network? Is there some form of modulation or influence of management style in the response to specific situations? In short, how does personality influence decision-making?

The question has more implications. If what is measured by the personality test is the individual's consciousness regarding his or her instructions manual, is it possible that these principles have little to do with what the subject does when faced with a particular task? Within this question lies one of the unresolved debates in the field of psychology: the effect of the environment on behaviour. The personalist theories have opposed, for decades, those who advocate from situationist perspectives that it is the situation that determines the behaviour. It is possible that while the DMN is more linked to traits, what are known as

the *cognitive styles* are closer to the execution of tasks related to the prefrontal cortex, more related to the situation in which a response is required. Or perhaps some of these cognitive styles that are studied as components of personality—such as *field articulation* (the degree to which the individual is dependent on or independent of the structure of the visual field around him), *conceptual differentiation* (the degree to which more differences or similarities are perceived between objects), *conceptual style* (the degree to which one analyses or syncretises as the preferred strategy for categorising concepts) or the *impulsivity-reflectivity* dimension—are artefacts of the DMN active on the secondary level.

There is no doubt that a stream of hypotheses are currently being generated that must be proven in the coming years. Far from the temptation of reductionism (“*everything is in the brain*”) we now know that this organ cannot be studied without including the concept of *interaction*. It may indeed be that *everything is in the brain*, but the brain is constantly changing due to the interaction with the environment. Each new learning, each new experience is transformed immediately into structural changes in the brain that experiences it. Locating the concept of personality as a stable element in an organ which is in perpetual change is an exciting task to which we must pay attention. If over the next decades some of the hypotheses discussed in this paper were proven to be true or false this would inevitably lead to a paradigm shift in the study of personality, but also in the study of psychopathology and psychotherapy; to take one simple example, the effectiveness of some of the therapies known as third generation therapies, such as those based on *mindfulness* or meditation techniques, may be justified by their effect on the areas of the brain, such as the DMN, which are only accessible in states of inactive wakefulness or functional rest of the brain (Brewer, Worhunsky, Gray, Tang, Weber & Kober, 2011).

This article has been limited to the studies that link a model of personality traits, the most accepted one currently by the scientific community, and studies that find a relationship with brain structures and circuits, using various neuroimaging techniques. Of course, there are other models and, moreover, the technical means are continuously improving, which will allow further progress to be made in the near future. As we have seen, the interest in this issue is barely a decade old, the most important studies being concentrated in the last five years. This means that many studies have not yet been replicated and the knowledge is rather dispersed. However, we can



already confirm one important thing; the study of personality has left the territory of theoretical formulations to link itself definitively to brain functioning. This is the main conclusion that we can draw at present.

REFERENCES

- Adelstein, J. S., Shehzad, Z., Mennes, M., DeYoung, C. G., Zuo, X. N., Kelly, C. *et al.* (2011). Personality is reflected in the brain's intrinsic functional architecture. *PLoS ONE*, *6*, e27633.
- Bjørnebekk, A., Fjell, A. M., Walhovd, K. B., Grydeland, H., Torgersen, S. & Westlye, L. T. (2013). Neuronal correlates of the five factor model (FFM) of human personality: Multimodal imaging in a large healthy sample. *Neuroimage*, *65*, 194-208.
- Block, J. A contrarian view of the five-factor approach to personality description. (1995). *Psychological Bulletin*, *117*, 187-215.
- Block, J. (2001). Millennial contrarianism. *Journal of Research in Personality*, *35*, 98-107.
- Block, J. (2010). The Five-Factor framing of personality and beyond: some ruminations. *Psychological Inquiry*, *21*, 2-25.
- Brewer, J. A., Worhunsky, P. D., Gray, J. R., Tang, Y. Y., Weber, J. & Kober, H. (2011). Meditation experience is associated with differences in default mode network activity and connectivity. *Proceedings of the National Academy of Sciences USA*, *108*, 1-6.
- Buckner, R. L., Andrews-Hanna, J. R. & Schacter, D. L. (2008). The brain's default network anatomy, function, and relevance to disease. *Annals of the New York Academy of Sciences*, *1124*, 1-38.
- Canli, T. (2004). Functional brain mapping of extraversion and neuroticism: learning from individual differences in emotion processing. *Journal of Personality*, *72*, 1105-1132.
- Carere, C., Drent, P. J., Koolhaas, J. M. & Groothuis, T. G. G. (2010). Epigenetic effects on personality traits: early food provisioning and sibling competition. *Behaviour*, *142*, 1329-1355.
- Caspi, A., McClay, J., Moffitt, T., Mill, J., Martin, J., Craig, I. W. *et al.* (2002). Role of genotype in the cycle of violence in maltreated children. *Science*, *297*, 851-854.
- Costa, P. T. & McCrae, R. R. (1992). *Revised NEO personality inventory (NEO-PI-R) and the five factor inventory (NEO-FFI): Professional manual*. Odessa, Florida: Psychological Assessment Resources Inc.
- DeYoung, C. G., Hirsh, J. B., Shane, M. S., Papademetris, X., Rajeevan, N. & Gray, J. R. (2010). Testing predictions from personality neuroscience: brain structure and the Big Five. *Psychological Science*, *21*, 820-828.
- Digman, J. M. (1989). Five robust trait dimensions: Development, stability, and utility. *Journal of Personality*, *57*, 195-214.
- Eysenck, S. B. G., Eysenck, H. J. & Barrett, P. (1985). A revised version of the psychoticism scale. *Personality and Individual Differences*, *6*, 21-29.
- Fox, M. D. & Greicius, M. (2010). Clinical applications of resting state functional connectivity. *Frontiers in Systems Neuroscience*, *4*, 19.
- Goldberg, L. R. (1992). The development of markers or the big five factor structure. *Psychological Assessment*, *4*, 26-42.
- Gray, J. A. (1970). The psychophysiological basis of introversion-extraversion. *Behaviour Research and Therapy*, *8*, 249-266.
- Greicius, M. D., Krasnow, B., Reiss, A. L. & Menon V. (2003). Functional connectivity in the resting brain: A network analysis of the default mode hypothesis. *Proceedings of the National Academy of Sciences USA*, *100*, 253-258.
- Hebb, D. O. (1949). *The organization of behavior: a neuropsychological theory*. New York: Wiley & Sons Inc. Reedición por Taylor & Francis e-Library, 2009.
- Jafri, M. J., Pearlson, G. D., Stevens, M. & Calhoun, V. (2008). A method for functional network connectivity among spatially independent resting-state components in schizophrenia. *Neuroimage*, *39*, 1666-1681.
- Kong, F., Hu, S., Xue, S., Song, Y., & Liu, J. (2015). Extraversion mediates the relationship between structural variations in the dorsolateral prefrontal cortex and social well-being. *Neuroimage*, *105*, 269-275.
- Kalbitzer, J., Frokjaer, V. G., Erritzoe, D., Svarer, C., Cumming, P., Nielsen, F. A. *et al.* (2009). The personality trait openness is related to cerebral 5-HTT levels. *Neuroimage*, *45*, 280-285.
- Kaminsky, Z., Petronisa, A., Wang, S. C., Levine, B., Ghaffara, O., Floden, D. *et al.* (2008). Epigenetics of personality traits: an illustrative study of identical twins discordant for risk-taking behavior. *Twin Research and Human Genetics*, *11*, 1-11.
- Krause-Utz, A., Veer, I. M., Rombouts, S. A., Bohus, M., Schmahl, C. & Elzinga, B. M. (2014). Amygdala and anterior cingulate resting-state functional connectivity in borderline personality disorder patients with a



- history of interpersonal trauma. *Psychological Medicine*, 44, 2889-2901.
- Lei, X., Zhao, Z. & Chen, H. (2013). Extraversion is encoded by scale-free dynamics of default mode network. *Neuroimage*, 74, 52-57.
- Lewis, G. J., Panizzon, M. S., Eyer, L., Fennema-Notestine, C., Chen, C. H., Neale, M. C. *et al.* (2014). Heritable influences on amygdala and orbitofrontal cortex contribute to genetic variation in core dimensions of personality. *Neuroimage*, 103, 309-315.
- McCrae, R. R. & Costa, T. P. (1997). Personality trait structure as a human universal. *American Psychologist*, 52, 509-516.
- O'Gorman, R. L., Kumari, V., Williams, S. C., Zelaya, F. O., Connor, S. E., Alsop, D. C. *et al.* (2006). Personality factors correlate with regional cerebral perfusion. *Neuroimage*, 31, 489-95.
- Omura, K., Constable, R. T. & Canli, T. (2005). Amygdala gray matter concentration is associated with extraversion and neuroticism. *Cognitive Neuroscience and Neuropsychology*, 16, 1905-1908.
- Passamonti, L., Terracciano, A., Riccelli, R., Donzuso, G., Cerasa, A., Vaccaro, M. *et al.* (2015). Increased functional connectivity within mesocortical networks in open people. *Neuroimage*, 104, 301-309.
- Peled, A. (2012). Personality disorders disturbances of the physical brain. *Medical Hypotheses*, 79, 487-492.
- Peled, A. (2013). Brain "Globalopathies" cause mental disorders. *Medical Hypotheses*, 81, 1046-1055.
- Petronis, A. (2010). Epigenetics as a unifying principle in the aetiology of complex traits and diseases. *Nature*, 465, 721-727.
- Raichle, M. E., MacLeod, A. M., Snyder, A. Z., Powers, W. J., Gusnard, D. A. & Shulman, G. L. (2000). A default mode of brain function. *Proceedings of the National Academy of Sciences USA*, 98, 676-682.
- Raichle, M. E. & Snyder, A. Z. (2007). A default mode of brain function: A brief history of an evolving idea. *Neuroimage*, 37, 1083-1090.
- Raine, A. (2008). From genes to brain to antisocial behavior. *Current Directions in Psychological Science*, 17, 323-328.
- Sampaio, A., Soares, J. M., Coutinho, J., Sousa, N., Gonçalves, O. F. (2014). The Big Five default brain: functional evidence. *Brain Structure and Function*, 219, 1913-1922.
- Servaas, M. N., van der Velde, J., Costafreda, S. G., Horton, P., Ormel, J., Riese, H. *et al.* (2013). Neuroticism and the brain: A quantitative meta-analysis of neuroimaging studies investigating emotion processing. *Neuroscience & Biobehavioral Reviews*, 37, 1518-1529.
- Smits, D. J. M. & Boeck, P. D. (2006). From BIS/BAS to the Big Five. *European Journal of Personality*, 20, 255-270.
- Sosic-Vasic, Z., Ulrich, M., Ruchow, M., Vasic, N. & Grön, G. (2012). The modulating effect of personality traits on neural error monitoring: evidence from event-related fMRI. *PLoS ONE*, 7, e42930.
- Sperling, R. A., LaViolette, P. S., O'Keefe, K., O'Brien, J., Rentz, D. M., Pihlajamaki, M. *et al.* (2009). Amyloid deposition is associated with impaired default network function in older persons without dementia. *Neuron*, 63, 178-188.
- Strelau, J. (1997). The contribution of Pavlov's typology of CNS properties to personality research. *European Psychologist*, 2, 125-138.
- Tang, Y., Liao, J., Wang, W. & Luo, A. (2013). Identifying individuals with antisocial personality disorder using resting-state fMRI. *PLoS ONE*, 8, e60652.
- Van der Cruyssen, L., Heleven, E., Ma, N., Vandekerckhove, M., Van Overwalle, F. (2015). Distinct neural correlates of social categories and personality traits. *Neuroimage*, 104, 336-346.
- van Tol, M. J., Veer, I. M., van der Wee, N. J., Aleman, A., van Buchem, M. A., Rombouts, S. A. *et al.* (2013). Whole-brain functional connectivity during emotional word classification in medication-free Major Depressive Disorder: Abnormal salience circuitry and relations to positive emotionality. *NeuroImage: Clinical*, 2, 790-796.
- 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*, 16, 818-825.
- Wei, L., Duan, X., Yang, Y., Liao, W., Gao, Q., Ding, J. R. *et al.* (2011). The synchronization of spontaneous BOLD activity predicts extraversion and neuroticism. *Brain Research*, 1419, 68-75.
- Wolf, R. C., Sambataro, F., Vasic, N., Schmid, M., Thomann, P. A., Bientreux, S. D. *et al.* (2011). Aberrant connectivity of resting-state networks in borderline personality disorder. *Journal of Psychiatry & Neuroscience*, 36, 402-411.
- Xu, J. & Potenza, M. N. (2012). White matter integrity and Five-Factor personality measures in healthy adults. *Neuroimage*, 59, 800-807.

